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Anne-Laure Fragnière

Luring *Drosophila suzukii* with its host plants to mitigate infestation in vineyards

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Anne-Laure Fragnière https://orcid.org/0000-0002-8060-7288

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Department of Biology

University of Fribourg (Switzerland)

Luring *Drosophila suzukii* with its host plants to mitigate infestation in vineyards

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Anne-Laure Fragnière

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Thesis supervisor(s)		Dean
Prof.tit. Sven Bacher	Dr. Patrik Kehrli	Prof. Ulrich Ultes-Nitsche

Summary

The polyphagous invasive spotted wing drosophila (SWD), *Drosophila suzukii* Matsurama (Diptera: Drosophilidae), has rapidly spread worldwide within the last decade, affecting stone fruit, berry and grape production. The European CORE Organic project Biovine (www.biovine.eu) aimed to develop natural solutions based on plant diversity to control pests and reduce pesticide dependence in vineyards. As part of this global project, our research explored the potential application of trap crops for protecting grapes from SWD damage. To limit SWD egg-laying in vineyards, trap cropping, i.e. luring a pest away from a crop with attractive host plants in its vicinity, might be an interesting but so far neglected control approach. A potential trap crop should be more attractive but also ideally restrict pest development. In the first year, we screened a large range of host plants to assess SWD preference for oviposition and developmental performance in their fruits in no-choice and multiple-choice experiments. In the second year, we selected plant species and evaluated SWD preference for them compared to grapes and their protection potential against SWD infestation in two-choice experiments under laboratory and semi-field conditions. We assessed the efficacy of one candidate trap crop in a small-scale field experiment and the effect of trap crop abundance on grape infestation under semi-field conditions in the third year. We identified 16 plant species with potential for trap cropping from the first year of experiments. Subsequently, we choose to evaluate 11 candidate trap crops in the two-choice experiments in the second year. We identified one plant species, *Ampelopsis glandulosa* var. *brevipedunculata*, as promising trap crop. This species was strongly preferred for oviposition and SWD developmental performances were weak in its fruits. In addition, it reduced the infestation of adjacent grapes. We could also eliminate from the trap crop selection process three candidate plant species as the infestation of adjacent grapes increased in their presence. In the third year, we tested one candidate trap crop, *Lonicera xylosteum*, in a small-scale field experiment. We demonstrated no protective effect of *L. xylosteum* on grapes in this experiment. Nevertheless, we have evidence from the semi-field experiments that the abundance of the trap crop has a critical influence as a too low abundance might increase damage instead of providing crop protection. Our study demonstrates the challenges of trap cropping development and sets the basis for future development of trap cropping in vineyards.

Résumé

La mouche du cerisier, *Drosophila suzukii* Matsurama (Diptera: Drosophilidae), s'est rapidement répandue dans le monde entier au cours de la dernière décennie, affectant la production de fruits à noyau, de baies et de raisins. Le projet européen CORE Organic Biovine (www.biovine.eu) vise à développer des solutions utilisant la diversité végétale pour lutter contre les ravageurs et réduire la dépendance aux pesticides dans les vignobles. Dans le cadre de ce projet, notre étude s'est intéressée à l'utilisation de plantes-pièges pour protéger le raisin des dommages causés par *D.suzukii*. Pour limiter la ponte de ce ravageur dans les vignobles, le développement de plantes-pièges, consistant à éloigner un ravageur d'une culture en disposant des plantes hôtes attractives à proximité, pourrait être une approche de contrôle intéressante. Cependant, cette méthode de lutte a été jusqu'à présent négligée. Idéalement, une plante-piège devrait également limiter le développement du ravageur. Durant la première année, nous avons évalué une large gamme de plantes hôtes pour déterminer la préférence de *D. suzukii* pour la ponte et son niveau de développement dans les fruits grâce à des expériences sans choix et à choix multiples. Au cours de la deuxième année, nous avons sélectionné certains candidats et évalué la préférence des SWD pour ceux-ci par rapport au raisin, ainsi que leur potentiel de protection dans des expériences à deux choix en laboratoire et en conditions semi-naturelles. Enfin, au cours de la troisième année, nous avons évalué l'efficacité d'une plante-piège, *Lonicera xylosteum,* dans une expérience en champ à petite échelle ainsi que l'effet de l'abondance des plantes-piège sur l'infestation du raisin dans des conditions de semi-naturelles. La première année d'expérimentation a permis d'identifier 16 espèces de plantes présentant un potentiel pour être utiliser comme plantes-piège. Par la suite, nous avons choisi d'évaluer 11 candidates dans les expériences à deux choix au cours de la deuxième année. Nous avons identifié une espèce végétale, *Ampelopsis glandulosa* var. *brevipedunculata*, comme plante-piège prometteuse. Cette espèce était fortement préférée pour la ponte et le développement de *D. suzukii* était faible dans ses fruits. En outre, elle a réduit l'infestation sur du raisin attenant. A ce stade, nous avons également pu éliminer du processus de sélection des plantes-piège trois espèces végétales, car l'infestation sur du raisin attenant augmentait avec leur présence. Enfin, nous n'avons démontré aucun effet protecteur de *L. xylosteum* sur la vigne dans l'expérience de terrain. Néanmoins, nous avons démontré que l'abondance de plantes-piège est critique, car une abondance trop faible pourrait augmenter les dommages au lieu de protéger la culture. Notre étude illustre les défis du développement de plantes-piège et jette les bases pour un futur développement de cette méthode de contrôle contre *D. suzukii* dans les vignobles.

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General introduction

Current challenges in agriculture

The latest IPBES report again warned about the threats posed by the dramatic decline of biodiversity and its primary drivers, such as land use change and the introduction of invasive alien species (Diaz et al., 2019). Twenty years ago, the Millennium Ecosystem Assessment (2005) reported that between 20% to 50% of land in half of the biomes had been converted for human use, especially intensive food production, leading to the drastic reduction of native biodiversity. This decline is particularly impressive in insects. Hallmann (2017) reported a reduction of more than 75% of insect biomass over 30 years in German protected areas. At the current rate, we might lose about 40% of the insect species in the short term, and land use change, including intensive agriculture and urbanisation, has been identified as the main driver of insect losses (Sánchez-Bayo & Wyckhuys, 2019). Ecosystem functions and services for which we rely primarily on insects and arthropods, such as natural pest control or crop pollination, are therefore threatened (Balvanera et al., 2006; Cardinale et al., 2012; Hooper et al., 2005).

Concurrently, global changes increase the pressure to intensify agriculture (Bommarco et al., 2013). Crop losses due to insect pests are likely to rise by 10 to 25% in grain crops because temperature increases will likely increase insect metabolic rate and population growth, especially in temperate climates (Deutsch et al., 2018; Oerke, 2006). Further losses are also likely as a consequence of the increasing introduction rate of alien species (Seebens et al., 2021), some of which may establish as serious crop pests (Mack et al., 2000; Paini et al., 2016; Sileshi et al., 2019, see for example Cini et al., 2012; Desneux et al., 2011; Early et al., 2018; Gilligan et al., 2011). Therefore, it is crucial to develop efficient pest control methods that support food production and at the same time promote local biodiversity and ecosystem resilience (Oliver et al., 2015).

Perennial crops, such as perennial grain crops, orchards or vineyards, present advantages over annual crops for preserving biodiversity, ecosystem functions and services in agricultural landscapes as they mimic natural vegetation (Pimentel et al., 2012; Vico & Brunsell, 2018; Werling et al., 2014). Yet, vineyards are often grown as intensively managed monocultures among perennial crops. Consequently, vineyard-dominated landscapes usually harbour more pest outbreaks than more diversified landscapes (Altieri & Nicholls, 2002; Paredes et al., 2021)

and use large amounts of pesticides (Altieri, Nicholls, et al., 2005; Lucas et al., 2011; von Glasenapp & Bosshard, 2013).

The systematic application of pesticides has become a contentious topic that is increasingly being politicised because of the long-term adverse side effects it might have on human health and the environment (Barzman & Dachbrodt-Saaydeh, 2011). Negative environmental impacts of pesticide use, such as toxic effects on non-target organisms or the selection of resistant pests, can hinder the development of sustainable food production (Biondi et al., 2012). To preserve vineyard ecosystem functions and services while maintaining productivity in rapidly evolving conditions, winegrowers, although cultivating a perennial crop, should be provided with as many alternative pest control methods as possible to avoid being left with only pesticide use as a solution.

Diversification strategy

To protect crops from pest damage while minimising impacts on the environment, reviews and meta-analyses suggest that promoting plant diversity (crop and non-crop) at different spatial scales, often referred to as "a diversification strategy", might enhance biodiversity and many ecosystems services, including natural pest control (Isbell et al., 2017; Letourneau et al., 2011; Tamburini, Bommarco, et al., 2020). Larsen (2017) showed that insecticide use in the vineyard could be drastically reduced in highly diverse landscapes for table grapes and to a lesser extent for wine grapes. Management solutions should thus contribute to restoring ecological heterogeneity within agroecosystems (Benton et al., 2003).

Diversifying agricultural landscapes to increase pest control relies on the targeted manipulation of biotic interactions between plants, pests and predators (Gaba et al., 2014; Gurr et al., 2017). Usually, manipulating plant species diversity is intended to indirectly enhance natural biological control services by favouring pest predator populations and thus top-down control (Albrecht et al., 2020; Tschumi et al., 2016). Yet, plant diversity can also affect pest species directly. This strategy has received little attention so far compared to top-down pest control.

In agricultural landscapes, diversification has often been encouraged by supporting semi-natural habitats around crops (Holland et al., 2017). The proportion of semi-natural habitats is for instance essential for vineyards' potential to conserve dry grassland plant species (Nascimbene et al., 2016). In perennial crops, plant diversity can be promoted at field scale via the use of cover crops. In Swiss vineyards, vegetation cover between grapevine rows have first

been introduced to reduce soil erosion (Schütte & Bergmann, 2019). However, the current selection of plant species for understory vegetation focuses on increasing the grapevine's vigour through competition for water and nitrogen (Dittrich et al., 2021; Novara et al., 2021). The diversity of plant species in cover crops also yields governmental subsidies for winegrowers in Switzerland, as it might benefit the diversity of other organisms (OFAG, 2021). In general, cover crops benefit the arthropod community (Geldenhuys et al., 2021; Shapira et al., 2018), although the direction of the response can vary between trophic levels according to the disturbance level created by the cover crop management (Bruggisser et al., 2010).

Still, there is little evidence that cover crops sufficiently reduce specific pest species (Daane & Costello, 1998; Reiff et al., 2021), supporting both pests and predators (Danne et al., 2010). In addition, the response of crop pests and predators to landscape composition, i.e. the proportion of semi-natural habitats and crops, is often inconsistent (Karp et al., 2018) and changes according to pest origin, with more complex landscapes increasing the abundance of invasive crop pests whilst decreasing native ones (Tamburini, Santoiemma, et al., 2020). It is therefore difficult to control specific pest species when plant diversity is managed in such a generalised way (Tscharntke et al., 2016). A better understanding of particular functional links between plants and pests species and pests and predators may improve pest control in perennial crops (Jacquot et al., 2019; Rasche et al., 2017; Simon et al., 2011).

Pest control method

The selection of attractive but low-quality host plants, defined as "attractive sinks" (Battin, 2004), has been demonstrated to impact organism populations negatively, thereby resulting in ecological traps (Delibes et al., 2001; Schlaepfer et al., 2002). Although the concept of ecological traps was first described in the context of habitat quality and its implication for the conservation of endangered species (Schlaepfer et al., 2002), it can nowadays be extended also to be applied to develop environmental friendly agricultural pest management strategies (Gardner et al., 2018). To reduce crop damage, increasing the proportion of ecological traps in the crop's vicinity could promote bottom-up pest control (Center & Dray, 2010; Daugherty et al., 2007; Gratton & Denno, 2003; Wan et al., 2019).

Management strategies altering crop-pest interactions by modifying the availability of alternative host plants within the agricultural system already exist (González-Chang et al., 2019). One such strategy is trap cropping, a traditional pest control approach based on the plant species' capability to attract pest species. As the pest has a strong egg-laying or foraging

preference for an alternative host plant, the pest is lured away from the crop towards the so-called "trap crop", preventing damage to the crop (Hokkanen, 1991; Shelton & Badenes-Perez, 2006). In addition to the preference of the pest for the trap crop, the trap crop should also retain the pest to limit pest spillover back into the crop (Blaauw et al., 2017; Boucher et al., 2003; Holden et al., 2012; Ludwig & Kok, 1998; Shelton & Badenes-Perez, 2006). More generally, trap crops can also be seen as the "pull" component in "push-pull" pest control strategies (Cook et al., 2007).

At field scale, the area where the trap crop is planted might also support local biodiversity, e.g. if the trap crop is a shrub, flowering plant species may grow in its vicinity and provide a nectar source or shelter to other organisms (Shapira et al., 2018). Offering attractive host plants for egg-laying but in which the pest is retained, either through low developmental performances in the trap crop (dead-end trap cropping) or through the implementation of additional measures reducing the spill-over of the pest from the trap crop (traditional trap cropping), creates attractive but low-quality habitat patches corresponding to "ecological traps" or "attractive sink" (Battin, 2004; Delibes et al., 2001).

Although it is implemented at the field scale, the interest in trap cropping goes beyond field limits. (Hendrichs et al., 2007; Schellhorn et al., 2008). Manipulating the proportion of sink and source (i.e. high attractiveness and quality) habitat patches at a regional scale might in turn affect pest population dynamics (Donovan & Thompson, 2001; Frouz & Kindlmann, 2015; Togni et al., 2021). Recognising pest sources in agricultural landscapes can also help adjust crop surroundings locally and are essential to plan area-wide management. For instance, the diversification on a larger scale critically influenced the success of the biological control of the Western grape leafhopper, *Erythroneura elegantula* Osborn, in Californian vineyards (Wilson 2016). Trap cropping acting at both field (local) and landscape scales can be of interest to control mobile polyphagous pest species, requiring generally area-wide management strategies (Klinken et al., 2019; Vreysen et al., 2007, 2019)

Drosophila suzukii

The fruit fly pest *Drosophila suzukii* (SWD) Matsumura (Diptera: Drosophilidae), native to Southeast Asia, is among the most challenging invasive polyphagous pest species to control (Asplen et al., 2015; Walsh et al., 2011). Within the last decade, SWD has invaded most continents (Bieńkowski & Orlova-Bienkowskaja, 2020; Cini et al., 2012; Deprá et al., 2014; Kwadha et al., 2021; Walsh et al., 201. Although not considered a severe pest in its native range,

SWD has emerged as a serious threat to fruit production on other continents (De Ros et al., 2013; Farnsworth et al., 2017; Goodhue et al., 2011; Mazzi et al., 2017) and could possibly impact berry plant species in natural habitats (Bühlmann et al., 2021).

Berry crops mostly affected by SWD include soft-skinned fruit such as cherries, blueberries, raspberries, blackberries and grapes or stone fruits, including plums and apricots (Abraham et al., 2015; Bellamy et al., 2013; Burrack et al., 2013; Harris et al., 2014; Ioriatti et al., 2015; Lee et al., 2011, 2015; Walsh et al., 2011). In Californian raspberry production between 2009 and 2014, SWD has caused revenue losses of about 2% in conventional farms and up to almost 6% in organic farms (Farnsworth et al., 2017). De Ros et al. (2013) estimated a total revenue loss of over €3.3 million in Italy, accounting for SWD damage in cherry, blackberry, blueberry, raspberry and strawberry crops combined.

Beyond rapid fruit decay caused by SWD larvae development, the wound in the fruit skin caused during egg-laying attracts SWD and other Drosophilidae. This can further facilitate secondary infection via the microbial community, thus causing greater damage to the fruit (Lewis et al., 2019; Rombaut et al., 2017). In grapes, infection of wounds due to yeast and bacterial associations can cause outbreaks of sour rot disease (Barata et al., 2012). When a grape is affected, various yeast species transform grape sugars into ethanol, whilst some bacteria subsequently transform ethanol into acetic acid (Hall et al., 2018). The presence of an elevated level of acetic acid is detrimental to vinification, seriously impacting wine production and table grape sales (Barata et al., 2011; Rombaut et al., 2017). If sour rot is observed during the harvest, the entire grape bunch must be discarded, leading to significant losses (Barata et al., 2012; Shrader et al., 2019). However, the role of SWD in the development of this disease is still debated (Entling & Hoffmann, 2020; Ioriatti et al., 2018) as sour rot outbreaks are multifactorial, and it is thus difficult to quantify the share of responsibility of SWD or other Drosophilids (Rombaut et al., 2017). Nevertheless, Swiss winegrowers consider SWD a severe threat, and the magnitude of the impact depends on the location and grape variety (Ioriatti et al., 2015; Knapp et al., 2019).

After winter diapause (Dalton et al., 2011; Shearer et al., 2016; Tochen et al., 2014; Zerulla et al., 2015), SWD populations build up from wild hosts scattered within semi-natural habitats (Tonina et al., 2018) and early available crops (Cahenzli, Bühlmann, et al., 2018). Due to its short life cycle — ranging approximately from 10 to 17 days depending on the hosts and temperature — and high reproductive potential (Emiljanowicz et al., 2014; Hamby et al., 2016;

Tochen et al., 2014, 2016), SWD may reach large populations at the end of the summer (Panel et al., 2018; Wiman et al., 2014), increasing the risk of infestation in vineyards (Ioriatti et al., 2015).

Worldwide, management practices to control SWD infestations primarily rely on frequent insecticide application for most crops (Haye et al., 2016). Gress et al. (2019) have reported in the US the emergence of SWD resistance to the insecticide Spinosad, which is also usually accepted in organic production. Nevertheless, cultural management practices, including sanitation measures, such as the use of nets, mineral powders (lime, Kaolin) or mass trapping, were first implemented in many countries (Haye et al., 2016; Walsh et al., 2011) in line with integrated pest management guidelines emphasising first the use of preventive tactics (Kogan, 1998; Vreysen et al., 2007). Yet, current lure and baited traps against SWD lack species specificity (Cloonan et al., 2018).

In Swiss vineyards, the preventive measures applied to avoid cool and humid microhabitats favouring SWD include leaf removal around grape bunches and low vegetation in the inter-rows (Linder et al., 2017, 2020). Using nets around vineyards has been shown to reduce infestation but is an expensive and labour-intensive measure. In addition, nets can impair plant protection product application on grapes, mainly against fungal diseases (Linder et al., 2017). Currently, in Switzerland, the application of clay-based powder Kaolin has shown good efficacy as a preventive method against SWD infestation (Cahenzli, Strack, et al., 2018; Linder et al., 2020) and is well adopted by Swiss winegrowers (Knapp et al., 2019).

Biological control options such as introducing natural SWD predators, parasitoid wasps, nematodes or pathogens are currently under investigation and have previously been reviewed in Lee et al. (2019). However, thus far, no singular option has been found to reduce the infestation rate sufficiently on its own under field conditions. It is therefore crucial to develop more alternative control methods so that preventive and curative strategies work in synergy to improve SWD control whilst simultaneously preserving environmental functions and avoiding the use of insecticides.

The thesis

Various national and European projects have sought to limit the impact of pesticide use on the environment (Barzman et al., 2015; CORE Organic, 2018; European commission, 2009). In this context, CORE organic (Coordination of European Transnational Research in Organic Food and Farming Systems) funded the project "BIOVINE", which aimed at lowering arthropod pests, soil-born pests and foliage disease pressure in organic vineyards by selectively increasing plant diversity within or around vineyards (www.biovine.eu). The present work is part of the work package addressing the control of arthropod pests in viticulture. It aims at selecting the most suitable host plants to develop a trap cropping strategy to control SWD damage in grape production. Over two consecutive growing seasons, we conducted nested experiments, aiming to shortlist potential candidate trap crop species that could be tested under field conditions during the third year. This thesis is divided into three standalone chapters intended for publication (Figure 1). The numbering of the tables and figures will be specific for each section of this thesis. Each chapter will be immediately followed by the corresponding supplementary material section.

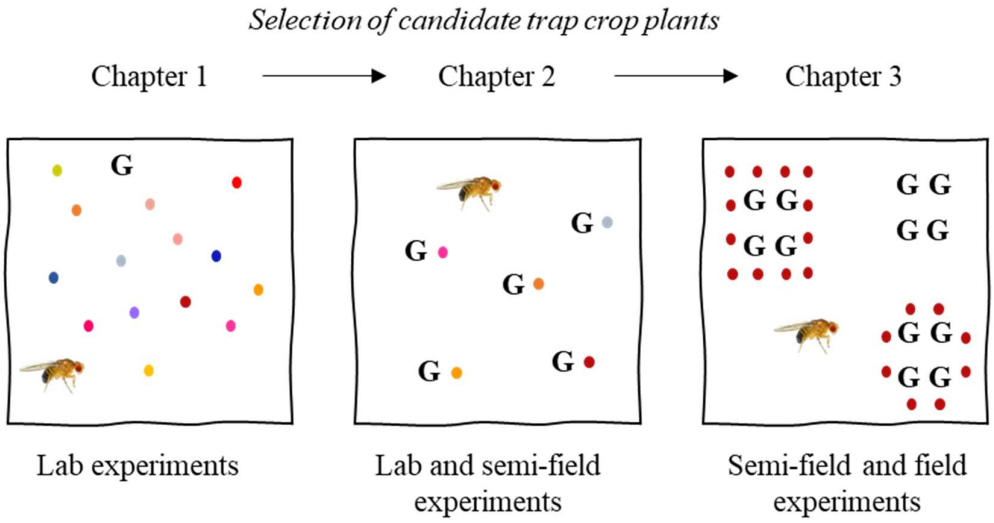

Figure 1: Graphical summary of the thesis. G stands for grapevines and coloured dots for different candidate trap crop plants.

Chapter 1

SWD is a highly polyphagous fly and shows preference patterns for egg-laying among fruit species (Bellamy et al., 2013; Kenis et al., 2016; Lee et al., 2015; Poyet et al., 2014). To identify host plants that could be of interest as a trap crop for SWD management, we initially screened a large range of potential host plant species under laboratory conditions by testing SWD preference for egg-laying among a set of fruit species. To avoid creating a trap crop that aided SWD larval development that would promote nearby crop infestations, we also measured the development performance of SWD in those fruits: the ideal trap crop candidate would be highly preferred for egg-laying but would also not be suitable for SWD development. As SWD considers various cues to make a choice for preferential oviposition, we subsequently characterised each fruit species to investigate whether selected fruit species presented common characteristics. This was intended to help focus the search for a good trap crop against SWD.

Chapter 2

To select candidate trap crops specifically to protect vineyards, we used the plant species identified as candidate trap crops in Chapter 1 to test SWD preference alongside grapevines in two-choice preference experiments. With this, we could measure if the preference for the candidate trap crop was maintained under semi-field conditions. In addition, we could evaluate the protection potential of the candidates comparing the infestation level of all grapevines next to the candidate trap crop species.

Chapter 3

Based on the results of Chapter 2, we selected one plant species, *Lonicera xylosteum*, that best fitted our criteria for trap cropping. We created small-sized experimental vineyards and tested the potential of this candidate trap crop as a perimeter trap cropping strategy under field conditions. In addition, we evaluated under semi-field conditions, the impact of trap crop abundance on grape infestation.

Chapter1 - Identifying candidate host plants for trap cropping against *Drosophila suzukii* in vineyards

Abstract

The egg puncture of the spotted wing drosophila (SWD), *Drosophila suzukii* Matsurama (Diptera: Drosophilidae), provide entrance points for sour rot disease in grape berries, thereby affecting wine quality. To limit SWD egg-laying in vineyards, trap cropping, i.e. manipulating host plant composition in the crop vicinity to lure the pest away from grapes to more attractive host plant fruits, might be an interesting but so far neglected control approach. A potential trap crop should be more attractive to the pest for oviposition than the crops and ideally restrict pest development. We studied the fruits of 60 plant species. We determined their attractiveness as oviposition sites (preference) and their impact on SWD developmental performance (emergence success, development duration in adults, and wing length as a proxy for body size) in laboratory assays. Our work identified 16 host plants for which SWD showed a strong preference for egg-laying compared to grapes and in which SWD developmental performance was weak. Host preference was strongly limited by fruit skin hardness, but SWD performance was only marginally affected by fruit acidity and sugar content. However, none of these traits affected emergence success. These findings provide valuable insights into identifying candidate trap crop plants that could be further tested in field studies to reduce the impact of SWD on grapes.

Introduction

Soft fruit 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 (Goodhue *et al.* 2011; Farnsworth *et al.* 2017). In grape production, oviposition punctures during grape maturation provide an entrance for yeasts and bacteria associated with sour rot disease, which impacts wine quality (Rombaut *et al.* 2017; Ioriatti *et al.* 2018) and can lead to significant economic loss (Knapp *et al.* 2021).

SWD is ubiquitous across agricultural landscapes subsisting throughout the year in semi-natural habitats (Cahenzli *et al.* 2018b; Tonina *et al.* 2018), making it difficult to control. Thus, effective pest management should be considered beyond the field scale (Kenis *et al.* 2016), integrating multiple control methods (Haye *et al.* 2016; Fan *et al.* 2020). In vineyards, pest management strategies recommend first the use of preventive and sanitation measures to avoid favouring the presence of SWD within the crop (Knapp *et al.* 2019). For example, nets or cultural techniques, such as leaf removal or mowing, are often used to reduce SWD populations in vineyards (Linder *et al.* 2017, 2020). However, when pest densities are too high and preventive methods fail, farmers primarily rely on applying biological insecticides (Walsh *et al.* 2011; Knapp *et al.* 2019). Currently, no commercially viable biological control option against SWD is available (Lee *et al.* 2019); therefore, alternative control methods are still needed to enhance the integrated pest management (IPM) strategy against SWD (Vreysen *et al.* 2007; Zhou *et al.* 2011; Tait *et al.* 2021).

Non-crop plant species can be exploited to modify crop-pest interactions within the agricultural system (González-Chang *et al.* 2019). Still, such bottom-up pest control against SWD in vineyards has not received much attention so far. Many polyphagous insect species, including agricultural pests such as SWD, show oviposition preference patterns among their host plants (West & Cunningham 2002; Bellamy *et al.* 2013; Sarwar *et al.* 2013). Understanding such preference patterns for SWD could help develop trap cropping management strategies, providing a sustainable and low-maintenance management option.

Trap cropping consists of planting preferred host plants in the proximity of the primary crop to lure the pest away, thus preventing pest damage to crops (Hokkanen 1991; Shelton & Badenes-

Perez 2006). Trap crops should also minimise pest spill-over back to the crop, i.e. retain the pest within the trap crop (Ludwig & Kok 1998; Boucher *et al.* 2003; Shelton & Badenes-Perez 2006; Holden *et al.* 2012; Blaauw *et al.* 2017). To achieve this, areas containing trap crops are commonly sprayed with insecticide, thus reducing both spill-over and the total amount of insecticide used on the crop (Ellsworth *et al.* 1992; Mitchell *et al.* 2000; Cavanagh *et al.* 2009; Lin *et al.* 2015; Tomaseto *et al.* 2019). Additional measures can be adopted to limit spill-overs. Examples include the release or support of natural predators (Rust 1977; Virk *et al.* 2004; Rhino *et al.* 2016; Gordon *et al.* 2017), the mechanical removal of the pest and/or the mechanical destruction of the trap crop decreasing subsequent pest generations (Rust 1977; Swezey *et al.* 2007; Cotes *et al.* 2018). Trap crops can also be combined with repellents to enhance diversion from the crop plant (Krause Pham & Ray 2015). Repulsive plant species, or plant extracts, and cultivation techniques that create unfavourable conditions for the pest can be implemented within the crop to divert the pest towards the trap crop (Cook *et al.* 2007; Khan *et al.* 2007; Lamy *et al.* 2018).

An alternative approach to traditional trap cropping is to utilise trap crops that are preferred as oviposition sites but do not allow for larval development. This trap cropping strategy is called dead-end trap cropping and constitutes a so-called "ecological trap" (Battin 2004). Such suboptimal host choices occur for many herbivorous insect species as pest preference and performance are not always correlated (Mayhew 2001; Gripenberg *et al.* 2010). Dead-end trap cropping has been successfully implemented to control the spotted borer, *Chilo sacchariphagus* (Bojer, 1856) (Lepidoptera: Crambidae), in sugarcane crops on Reunion Island (Nibouche *et al.* 2012, 2019; Jacob *et al.* 2021) and has recently gained interest for controlling other pest species (Grundy *et al.* 2004; Badenes-Perez *et al.* 2014; Rhino *et al.* 2014, 2016; Mhatre *et al.* 2021; Sacchi *et al.* 2021). Attentions for dead-end trap cropping to control SWD has recently emerged with the detection of discrepancies between SWD preference and SWD developmental performance in host plants (Poyet *et al.* 2015; Diepenbrock *et al.* 2016). It has for example been investigated to protect strawberries in small-scale glasshouse experiments (Ulmer *et al.* 2020).

Fruit traits can affect the preference and performance of SWD and are thus crucial in developing effective tap cropping strategies. The influence of fruit traits has first been assessed in studying the susceptibility of different crop varieties to SWD (Lee *et al.* 2015; Cloonan *et al.* 2018). It has been shown that fruit skin hardness of different grape varieties was correlated with SWD's host preference for egg-laying (Ioriatti *et al.* 2015; Kehrli *et al.* 2017a; Tonina *et al.* 2018;

Shrader *et al.* 2019; Entling & Hoffmann 2020; Mazzetto *et al.* 2020). Several studies investigated the role of shape and colour in trap design to enhance mass trapping (Rice *et al.* 2016; Kirkpatrick *et al.* 2018a), suggesting that colour might also affect host choice (Little *et al.* 2018, 2020). To quickly assess the potential susceptibility of a crop or the potential value of a plant for trap cropping, it is, therefore, relevant to investigate how easily measurable fruit traits, such as skin hardness or colour, might be associated with plant preferences of the pest across a broader host range. Moreover, traits related to fruit composition, such as pH and sugar content, can affect multiple physiological processes in insects (Harrison 2001; Frago & Bauce 2014) and thus might be valuable parameters to differentiate host suitability variations in SWD development (Kamiyama & Guédot 2019; Young & Long 2020). Fruits traits could thus help characterise promising traditional trap cropping and dead-end trap cropping candidates against SWD.

In this study, we compare the relative preference of SWD for fruits of a range of potential host plant species as oviposition sites and its subsequent developmental performance to identify plant species with the highest potential as trap crops for protecting vineyards. To find fruits that are both preferred for oviposition but unsuitable for SWD development, we evaluated 60 host plants native or introduced in Switzerland 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) the SWD preference for fruits of various plant species as oviposition sites in no-choice and multiple-choice experiments and 2) the SWD developmental performance in these plant species (emergence success, development time, and offspring size) within developmental assays. Based on our results, we 3) investigated the impact of fruit traits on pest preference and performance. We expected that skin hardness and fruit colour would affect SWD preference for egg-laying while 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 berry plant host species and narrowed down host plants that have a fruiting period matching the grape maturation period in western Switzerland (Table S1) (Mitsui *et al.* 2010; Baroffio *et al.* 2014; Lee *et al.* 2015; Poyet *et al.* 2015; Kenis *et al.* 2016). Between the 31st of July and the 1st of October 2018, we conducted weekly fruit sampling in several locations, including botanical gardens, parks, natural hedges and garden centres, enabling us to gather 60 fruit 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 from a supermarket. 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 detaching easily from the petiole. All fruits were collected with the petiole intact to avoid damage, then stored in a cooler for transportation and kept at 4 °C until experiments started within the same week of the collection. Before experiments, fruits were rinsed with tap water and individually checked for the presence of injuries or eggs; only undamaged berries without eggs were used in the experiments.

To assess SWD preference among hosts for egg-laying, we performed no-choice preference tests for each plant species and multiple-choice preference tests with the entire set of species collected that specific week (Table S2).

No-choice preference test

According to the quantity of ripe fruit available and the number of times a species was sampled, the number of replicates for the no-choice tests varied between 4 and 21 for each species. Approximately 1.5 g of intact fruit were placed into a cylindrical plastic jar (3 cm diameter x 6 cm height) covered with a fine mesh lid for each replicate. We exposed the fruits to three females and one male SWD. All flies used in the experiments were at least five days old and had been reared on a homemade growing media in a common rearing with contact with many other flies (i.e. females were assumed to have been mated before the experiment). After 24h in a growing chamber (22°C, 75% RH, 16/8 day/night), flies were removed and we recorded under a stereo microscope the relative number of eggs laid in each jar (egg number per gram of fruit) to evaluate the SWD preference for each fruit species as an oviposition site.

Multiple-choice preference test

We placed an equivalent quantity of the different fruit species on petri dish lids (3.5 cm diameter) inside rectangular boxes (25 x 15 x 8 cm; 6 replicates each week). As the number of fruit species, and thus the quantity of fruit per box, was not constant over the weeks, we adapted the number of flies within the boxes, ensuring 0.8 female flies per gram of fruit. We always added half as many males than females to ensure mating while saving time when preparing the experiments. After introducing the flies, we closed the boxes with a mesh lid to allow air exchange. The position of Petri dishes within the box and of the boxes in the growing chamber

(22°C, 75% RH, 16/8 day/night) were randomly assigned. After 24 h of exposure, we counted the number of eggs on each fruit species in a box and calculated the relative proportion.

Developmental assays

To determine the suitability of the host species for SWD development, we allowed the eggs on fruits from the previous tests to develop in individual jars (3 cm diameter x 6 cm height) for three weeks in a growing chamber (22°C, 75% RH, 16/8 day/night), which is sufficient time to allow for regular SWD development (Tochen *et al.* 2014). The fruit weight (before SWD exposure) and the number of eggs were known for each replicate from the previous experiments. We monitored the jars daily, recording the time, the number and the sex of flies emerging. We calculated the emergence rate as the number of emerged flies divided by the number of eggs for each replicate. Emerged flies were preserved in 70% ethanol. We chose to measure the wing length of each individual under a stereo microscope as the distance from the anterior crossvein to the end of the second longitudinal vein of the right wing.

Fruit characteristics

To examine fruit characteristics that may be linked to pest preference, we measured skin hardness and elasticity for five individual fruits of each species using a texture analyser (TAxT2i Texture Analyzer, Stable MicroSystem, Needle probe P/2N 2mm). The impact of colour on preference for egg-laying was assessed only on a subset of the 60 plant species in laboratory two-choice preference tests running from August to September 2019 and 2020 (i.e. *Ampelopsis glandulosa var. brevipedunculatata* (=*Ampelopsis brevipedunculatata*), *Cestrum fasciculatum*, *Cornus amomum*, *Phytolacca americana, Lycium barbarum*, *Lonicera xylosteum, Prunus lusitanica*, *Rhamnus cathartica*, *Rubus fruticosus var. lockness*, *Sambucus ebulus*, *Sambucus nigra*). To do so, we placed an equivalent quantity of a fruit of the species mentioned above and a Mara grape berry (n=22-68 for each fruit species) on opposite ends inside a rectangular plastic box (5 x 7 x 2cm) covered with a mesh-lid in a growing chamber (22°C, 75% RH, 16/8 day/night). Before SWD exposure (one female SWD per gram of fruits arranged inside the box), each box was photographed (FinePix ISpro, Fujifilm ©, UV-Nikkor 105mm lens, focal 6) under a constant light source (Polilight PL500, Rofin ©). The number of eggs laid on each fruit species was recorded after 24h. We characterised the luminance and hue of fruit colour on pictures using the CIE 1976 L*a*b colour space, a method commonly employed in quantitative, comparative colour comparison studies (Weatherall & Coombs 1992;

Weller 2021). This colour space is based on the colour opponent theory, which describes the colour vision in humans and many insects, including *Drosophila melanogaster* (Song & Lee 2018; Schnaitmann *et al.* 2020). Three parameters describe it: the parameter L expresses the colour luminance, varying 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). Parameter *b* describes the colour hue on an axis from blue to yellow ($b<0$ toward blue, $b>0$ towards yellow). The *L*a*b* parameter values from each picture were extracted using Photoshop (2020, version 21). As the colour of individual fruits was not always consistent on the whole fruit surface, we extracted L*a*b parameter values from an averaged surface area of the fruit. We used a white standard in each picture to correct the difference in light between the replicates.

To explore the drivers of fruit suitability, we measured the acidity and sugar content of each of the 60 species. We crushed intact fruits that were surplus at the end of the experiments to extract and filter their juice. We then determined the sugar content of the juice with a numerical refractometer (Brix unit) and measured the acidity of the juice using a Mettler-Toledo pH meter.

Statistical analyses

All statistical analyses were conducted in R (version 4.1.2, R Core Team, 2021). To assess the difference in SWD preference and performance between plant species in the no-choice test, we used linear mixed-effects models (LMMs) (library *lmerTest* version 3.1.3, Kuznetsova, Brockhoff, and Christensen, 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 and the emergence success (number of emerged adults/number of eggs laid) as response variables (Box-Cox transformed) and included plant species as fixed factor and the experimental date as a random factor. We fitted two other models with the development time and the wing length as response variables, with a Box-Cox transformation only on the wing length variable. 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 to complete the linear model (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 crop species present in our sampling as reference levels to determine the number of hosts more or less preferred than each crop. This allows us to estimate approximately if trap cropping would be interesting in other crop species present in our sampling. All LMMs were assessed

with a visual inspection of their residuals for normality and homoscedasticity, as suggested by Zuur et al. (2009). Analysing multiple-choice experiments is challenging, especially as our set of collected plant species is our study changed each week. We therefore only scored fruit species according to the proportion of eggs their fruits received within each replicate and averaged it per week. We averaged the weekly scores per species for plant species collected in several weeks. This allowed us to compare if the preference ranking of species in no-choice is coherent with the ranking of species when SWD is exposed to a larger choice of fruits.

To evaluate the impact of fruit characteristics on pest preference and performance, we fitted LMMs with all possible combinations of predictor variables and followed a multi-model inference approach to select the most meaningful set of explanatory variables (Burnham & Anderson 2002; Grueber *et al.* 2011; Harrison *et al.* 2018). All models falling within six AICc units 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 & Anderson, 2002; Richards, 2005; Symonds & Moussalli, 2011). We analysed the effect of skin hardness and elasticity (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 SWD preference for egg-laying (egg number per gram of fruit with a log transformation), we built models with all combinations of L*a*b parameter values as predictors and used the plant species and the date of the experiment as random factors. Similarly, we analysed separately how the emergence success per plant species (log transformation), SWD wing size and development time was associated with the pH of fruits and their sugar content.

Results

Preference

The preference for egg-laying varied among host plants. Overall, SWD laid eggs in the fruits of 56 of the 60 host plants (Table 1). In the no-choice tests, the average number of eggs laid per gram of fruit varied from 0 in four host plants to 17 ± 5 (mean ± 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 tests, the preference level, i.e. the average proportion of eggs laid, varied between 0 in 12 plant hosts to 1 in *Cestrum fasciculatum* and *Prunus lusitanica* (Table 1). Plant species ranked according to SWD average preference in no-choice and multiple-choice tests were strongly correlated (*r*

$_{Spearman} = 0.78$, $p\text{-}value < 0.001$), suggesting consistent preference under no-choice and multiple-choice laboratory experiments.

Table 1 Mean ± confidence interval (CI) of 4 response variables. Plant species are ordered according to the emergence success. 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 light grey correspond to plant species identified as potential traditional trap crops; plant species highlighted in medium grey correspond to plant species identified as potential dead-end trap crops, plant species highlighted in dark grey correspond to plant species identified as potential pest sources

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]
Cornus controversa variegata	=	< 10%	0.1 ± 0.2	0	0	0
Viburnum tinus	=	< 10%	0.11 ± 0.14	0	0	0
Berberis vulgaris	=	< 10%	0.11 ± 0.22	0	0	0
Sorbus aucuparia	=	< 10%	0.12 ± 0.16	0	0	0
Nandina domestica	=	< 10%	0.18 ± 0.23	0.02 ± 0.03	0	0
Sorbus americana Belmonte	=	< 10%	0.21 ± 0.27	0	0	0
Viburnum opulus	=	< 10%	0.26 ± 0.29	0.01 ± 0.01	0	0
Malus spectabilis	=	< 10%	0.3 ± 0.43	0	0	0
Cotoneaster obscurus	=	< 10%	0.32 ± 0.3	0	0	0
Aronia melanocarpa	=	< 10%	0.36 ± 0.26	0.01 ±	0	0
Cornus capitata	=	< 10%	0.45 ± 0.56	0.14 ± 0.17	0	0
Viburnum rhydotiphyllum	=	< 10%	0.61 ± 0.46	0.03 ± 0.03	0	0
Cotoneaster tomentosus	=	< 10%	0.69 ± 0.77	0	0	0
Myrtus communis	=	< 10%	0.72 ± 0.9	0.05 ± 0.07	0	0
Solanum dulcamara	=	< 10%	0.88 ± 0.88	0.03 ± 0	0	0
Cornus sanguinea winterbeauty	=	< 10%	1.11 ± 1.01	0.07 ± 0.06	0	0
Pyracantha coccinea	>	< 10%	1.18 ± 0.48	0.23 ± 0.07	0	0
Cornus sanguinea	>	< 10%	1.35 ± 0.96	0.03 ± 0.03	0	0
Prunus spinosa	>	< 10%	1.6 ± 2.57	0	0	0
Ligustrum vulgare	>	< 10%	2.5 ± 1.59	0.23 ± 0.16	0	0
Viburnum lantana	>	< 10%	2.74 ± 1.3	0.04 ± 0.07	0	0
Prunus lusitanica	>	< 10%	7.97 ± 6.38	1 ± 0	0	0
Phytolacca acinosa	>	< 10%	8.44 ± 1.62	0.1 ± 0.08	0	0
Cestrum fasciculatum	>	< 10%	21.7 ± 8.76	1 ± 0	0	0
Hippophae rhamnoides	>	< 10%	4.29 ± 2.29	0.07 ± 0.05	0.08 ± 0.15	1 ± 1
Ampelopsis brevipedunculata	>	< 10%	8.81 ± 6.18	0.59 ± 0.23	0.15 ± 0.29	1 ± 2
Vitis vinifera* cv. *Humagne	=	< 10%	0.47 ± 0.56	0.02 ± 0.02	0.14 ± 0.28	2 ± 5
Cotoneaster divaricatus	>	< 10%	2.4 ± 3.11	0.08 ± 0.07	0.28 ± 0.54	3 ± 5
Cornus amonum	>	< 10%	16.76 ± 5.27	0.44 ± 0.29	0.65 ± 0.48	3 ± 3

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]
Phytolacca americana	>	< 10%	6.27 ± 2.09	0.56 ± 0.28	0.08 ± 0.15	4 ± 7
Prunus domestica cv. institia	>	< 10%	7.63 ± 5.32	0.26 ± 0.12	0.14 ± 0.27	6 ± 11
Vitis vinifera* cv. *Mara	=	< 10%	0.24 ± 0.14	0.06 ± 0.04	0.07 ± 0.1	8 ± 12
Eleagnus umbelata	>	< 10%	15.76 ± 4.69	0.24 ± 0.05	1.09 ± 0.97	9 ± 10
Prunus laurocerasus	>	10-30%	3.3 ± 1.58	0.5 ± 0.12	0.68 ± 1.14	11 ± 15
Cornus mas	>	10-30%	2.88 ± 1.64	0.12 ± 0.06	0.8 ± 0.61	14 ± 12
Cornus alba sibirica	>	10-30%	12.27 ± 6.56	0.99 ± 0.03	2.62 ± 1.63	16 ± 7
Symphoricarpos alba	>	10-30%	2.72 ± 2.22	0.07 ± 0.08	0.44 ± 0.49	17 ± 23
Solanum nigrum	>	10-30%	2.69 ± 2.92	0.05 ± 0.04	0.94 ± 0.23	18 ± 8
Taxus baccata	>	10-30%	6.62 ± 2.83	0.17 ± 0.22	1.28 ± 0.76	21 ± 12
Rhamnus cathartica	>	10-30%	7.28 ± 1.93	0.16 ± 0.11	1.81 ± 0.95	23 ± 12
Mahonia aquifolium	>	10-30%	10.16 ± 5.94	0.5 ± 0.32	0.99 ± 0.46	27 ± 25
Lonicera xylosteum	>	10-30%	13.27 ± 6.24	0.3 ± 0.14	2.15 ± 1.29	29 ± 21
Sambucus nigra	>	10-30%	15.24 ± 4.14	0.34 ± 0.16	3.62 ± 1.56	29 ± 11
Sambucus nigra Gold	>	10-30%	8.92 ± 5.12	0.53 ± 0.34	2.12 ± 0.84	30 ± 14
Vaccinium myrtillus	>	31-60%	4.19 ± 1.45	0.45 ± 0.11	1.6 ± 0.53	37 ± 13
Cornus alba	>	31-60%	9.52 ± 5.67	0.36 ± 0.2	3.02 ± 0.85	41 ± 26
Lycium chinense	>	31-60%	4.3 ± 3.2	0.76 ± 0.17	2.18 ± 0.95	50 ± 15
Basella alba	>	31-60%	11.29 ± 3.22	0.99 ± 0.02	5.01 ± 1.17	51 ± 18
Solanum villosum	=	31-60%	0.59 ± 0.67	0.03 ± 0.05	0.68 ± 0.81	56 ± 58
Atropa belladona	>	> 60%	7.49 ± 2.71	0.58 ± 0.3	4.03 ± 1.81	60 ± 27
Sambucus ebulus	>	> 60%	11.93 ± 2.05	0.66 ± 0.21	6.58 ± 0.71	62 ± 13
Cornus kousa	>	> 60%	1.27 ± 0.92	0.29 ± 0.25	1.79 ± 1.38	67 ± 41
Lycium barbarum	>	> 60%	4.92 ± 2.5	0.98 ± 0.04	3 ± 1.66	67 ± 22
Frangula alnus	>	> 60%	6.07 ± 1.41	0.61 ± 0.24	4.13 ± 1.42	69 ± 23
Rubus fruticosus* var. *lockness	>	> 60%	10.46 ± 4.38	0.9 ± 0.2	7.22 ± 3.66	71 ± 24
Rubus idaeus	>	> 60%	11.28 ± 4.38	0.17 ± 0.04	13.07 ± 3.74	86 ± 19
Callicarpa giraldii	NA	NA	0	0	NA	NA
Ilex aquifolium	NA	NA	0	0	NA	NA
Lycopersicum pimpinellifolium	NA	NA	0	0	NA	NA
Polygonatum multiflorum	NA	NA	0	0.01 ± 0.02	NA	NA

Nine of the 60 plant species tested were commercially grown crop species. Crop species with few preferred host plants have little potential for trap cropping as the pool of potential trap crop candidates is strongly restricted. About two-thirds of host plants tested were significantly preferred for egg-laying over crops such as grapes (*Vitis vinifera cv*. *Mara* and *Humagne*) and the black chokeberry (*Aronia melanocarpa*) (Table1, Table S3-5). Around 4 to 90 times fewer eggs were laid on grapes than on the preferred plant species in no-choice preference tests and 7 to 62 times fewer eggs in multiple-choice preference tests. Only a third of host plants were

significantly preferred over blueberries (*Vaccinium myrtillus*), with 1.5 to 5 times fewer eggs laid on blueberries than on the preferred species in no-choice preference tests and 1.3 to 2.2 in multiple-choice preference tests (Table 1, Table S6). Crop species such as goji berries (*Lycium barbarum)*, the European plum (*Prunus domestica* subsp. *Insititia),* blackberries (*Rubus fruticosus* var. l*ockness*), raspberries (*Rubus idaeus)* and the European elderberry (*Sambucus nigra)* had only a few or no preferred host plant species than themselves (Figure 1, Table S7-11).

Developmental performance

Developmental assays demonstrated a variable SWD developmental performance among host plants. SWD completed its life cycle in the fruits of 32 of the 56 host plants that were suitable for oviposition. We identified 24 host plants in which no eggs developed into adults, 9 plant species with an emergence success lower than 10%, 11 plant species with an emergence success between 10 and 30%, 5 species between 31 to 60% and 7 plant species above 60%. The average emergence success and the number of emerged flies per gram of fruits differed significantly, with *Rubus idaeus* showing the highest emergence success (86% ± 19%) (Table 1, Emergence success: $\chi^2_{\text{Anova type II}}$ =634.9, d.f.=56, *p-value* < 0.001, Table S12; Emerges flies per gram of fruits: $\chi^2_{\text{Anova type II}}$ = 917.39, d.f.=56, *p-value* < 0.001, Table S13). Fly development time differed among species but not according to sex, varying between 8 days in *Viburnum lantana* to 18 ± 1 days in *Mahonia aquifolium* and *Prunus laurocerasus* (Anova type II: $\chi 2_{\text{plant species}}$ =307.73, d.f.=32, *p-value* < 0.001; $\chi 2_{\text{sex}}$ =1.71, d.f.=1, *p-value* = 0.2; Table S14). Therefore, the difference in development time in adult can take up to a week (Table S15). Wing length was smaller in males but did not vary significantly among host species. The average length ranged from 1.8 ± 0.13 mm in *Lonicera xylosteum* to 3.35 ± 0.12 mm in *Solanum villosum* (Anova type II: $\chi 2_{\text{plant species}}$ =38.89, d.f.=30, *p-value* 0.13; $\chi 2_{\text{sex}}$ =83.11, d.f.=1, *p-value* = < 0.001;Table S15).

Relationship between preference and developmental performance

Overall, there was a significant correlation between oviposition preference and emergence success (τ_{Kendall}=0.52; *p-value* <0.001), suggesting that some host plants such as *Rubus fruticosus, Rubus idaeus, Frangula alnus, Sambucus ebulus and Atropa belladonna* were strongly preferred over grapes for egg-laying and suitable for SWD development to maturation (Figure 1; Table1). In host plants such as *Ilex aquifolium, Berberis vulgaris, Lycopersicum*

pimpinellifolium and *Sorbus aucuparia,* it was not possible to evaluate their suitability since no eggs were laid during the 24 hours of exposure to SWD. Preferred but unsuitable host plants include *Ampelopsis brevipedunculata, Cestrum fasciculatum, Cornus amomum, Eleagnus umbelata, Phytolacca acinosa, Phytolacca americana, Prunus domesticus* subsp. *insititia* and *Prunus lusitanica*; they would therefore be the primary candidates for developing a trap crop (Figure 1; Table 1). Wing length and development time were practically uncorrelated ($\tau_{Kendall}$=-0.01; *p-value* =0.93) and the same was true for oviposition preference ($\tau_{Kendall\ Wing\ length}$ =-0.23; *p-value* =0.08; $\tau_{Kendall\ Development\ time}$=-0.05; *p-value* =0.7) . They are consequently not helpful pest performance criteria to distinguish between potential trap crop candidates.

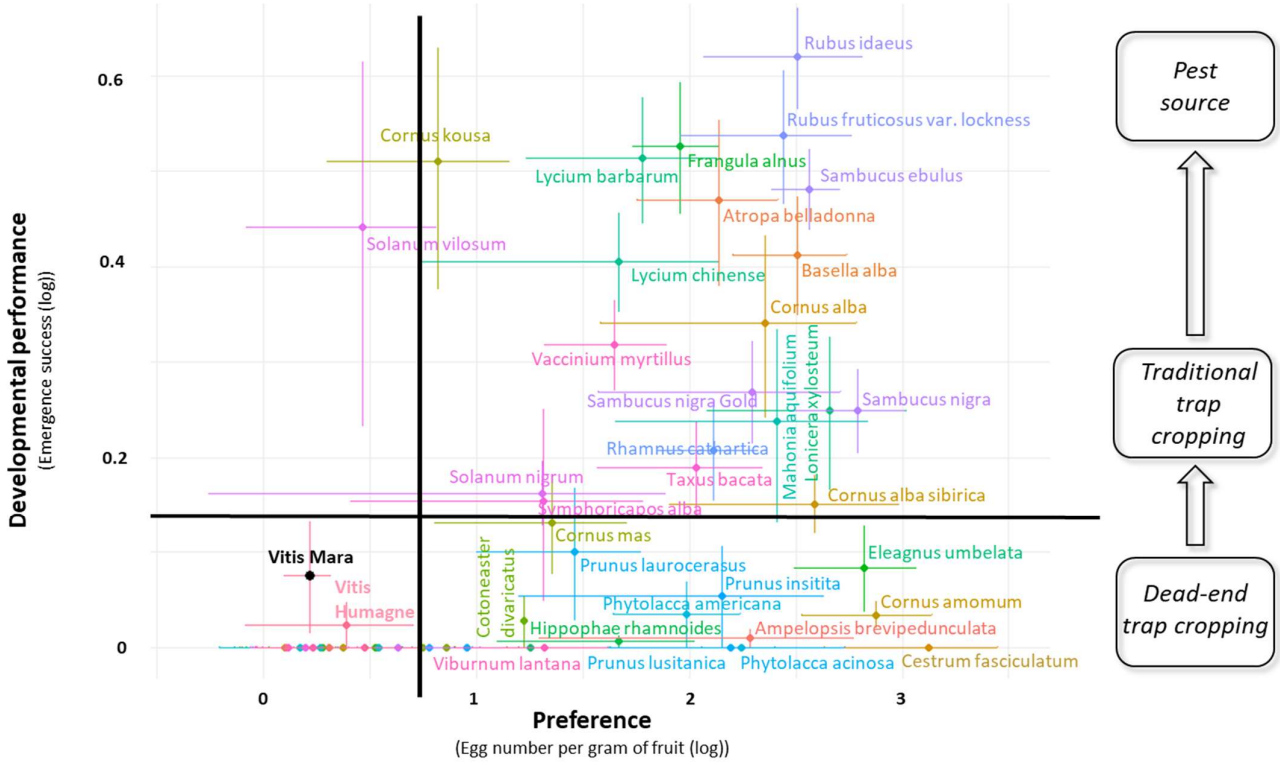

Figure 1: Plant species are indicated with a dot. Horizontal bars are confidence intervals of SWD preference and vertical bars are confidence intervals of the SWD emergence success in the plant species. The black thick vertical and horizontal bars as well the position of the labels (dead-end trap crops, traditional trap crops, pest sources) along the y-axis is arbitrary but describe visually the discussion section.

We found SWD oviposition preference to be associated with fruit skin hardness (R^2 = 0.46; $F_{1, 46}$ = 39.09, *p-value*= < 0.001; Table S16; Figure 2) but not with fruit elasticity (Table 2). The

model predicted a threshold value of 74.5 cN for skin hardness preventing egg-laying. Fruits of seven host plants exceeded this threshold value in ripe fruits (Table S15).

Table 2: Model selection based on AICc between fruit skin hardness and elasticity. (x^2) indicate the test of a quadratic fit of the predictor. * indicate an interaction.

model predictors	df	*AICc*	Δ AICc
hardness	3	271.73	0.00
hardness, hardness (x^2)	4	*273.15*	1.41
hardness*elasticity	5	*274.7759*	3.0426
null model (1)	2	299.26	27.52
elasticity	3	*300.27*	28.54

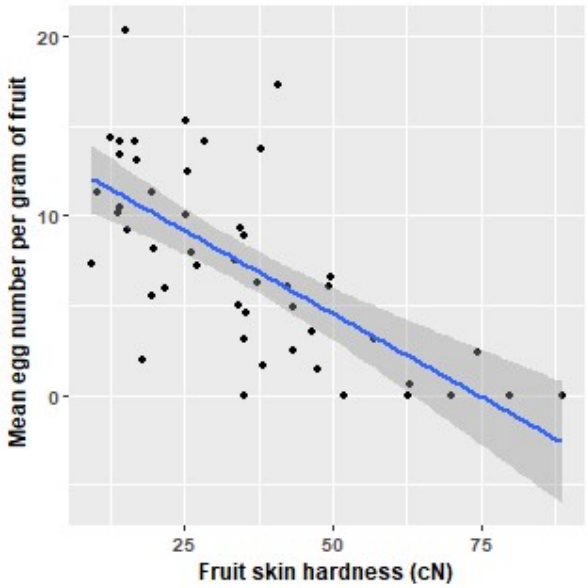

Figure 2: Regression plot between the mean egg number per gram of fruit of each plant species in the no-choice preference test and the skin hardness expressed as centiNewton (cN).

Colour was practically not associated with the preference for egg-laying between a grape berry and the other 11 host plants tested in the two-choice tests (Anova II $_{\text{L parameter}}$ $\chi 2$=0.05, d.f.=1, *p-value* < 0.83, Anova II $_{\text{a parameter}}$ $\chi 2$=0.01, d.f.=1, *p-value* < 0.93, Anova II $_{\text{b parameter}}$ $\chi 2$=0.5, d.f.=1, *p-value* < 0.48; Table 3, Table S17).

Table 3: Model selection based on AICc between preference for egg-laying and fruit colour L, a and b correspond to the parameters used to characterise the colour.

predictors	df	*AICc*	Δ AICc
null model (1)	4.00	1565.73	0.00
b	5.00	1567.24	1.51
L	5.00	1567.68	1.95
a	5.00	1567.73	1.99
a,b	6.00	1568.46	2.73
L,b	6.00	1568.98	3.25
L,a	6.00	1569.68	3.95
L,a,b	7.00	1570.16	4.42

We found no evidence of an association between SWD emergence success and pH or sugar content of fruits (Anova II $_{\text{sugar content}}$: SS= 0.03, d.f. = 1, F-value= 0.89*, p-value* = 0.35; Anova II $_{\text{pH}}$: SS= 0.03, d.f. = 1, F-value= 1.05*, p-value* = 0.31; Table S18).

Development time from egg to adult was shortest in fruits with an acidity level between pH 4 to pH 5.5, similar to the pH level range of e.g. mango, orange or pomelo (Figure 3; Laloknam et al., 2010). Twenty-three of our host plants tested fell in this range (Table 1).

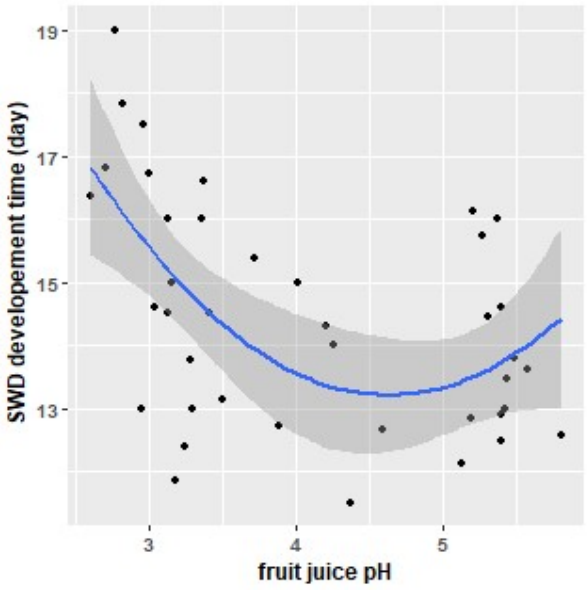

Figure 3: Quadratic regression plot between the mean SWD mean development time in all plant species and the fruit juice pH.

Development time was reduced by circa two days for a pH change from 3 to 4 (Figure 3) and decreased with increasing sugar content (Figure 5). Increased sugar content was correlated with longer wings in SWD offspring (Anova II $\chi 2=8.85$, d.f.=1, *p-value* < 0.01; Table S19). The regression slope indicated that for an increase of 10° Brix, the average wing length of a fly increased by 0.3 mm (Figure 4; Table S20). The pH level of grapes collected between the end of July and mid-September increased on average from 2.7 to 3.3, and the sugar content increased over this period from 14° to 25° Brix.

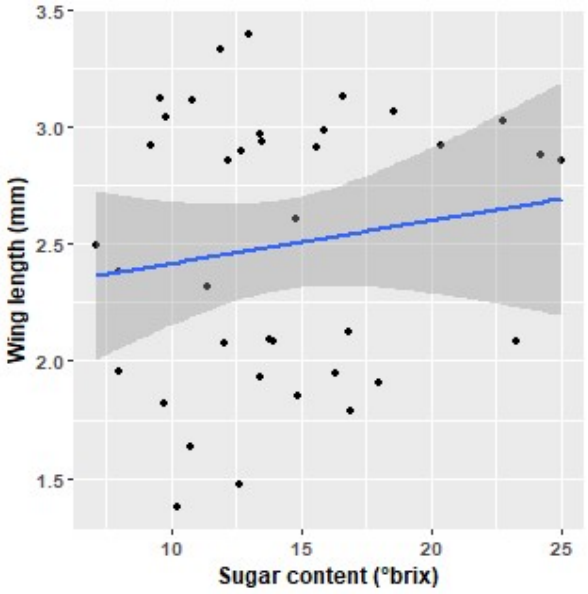

Figure 4: Regression plot between the mean wing length of emerged SWD in each plant species and the fruit juice sugar content, measured in Brix degree (°Brix).

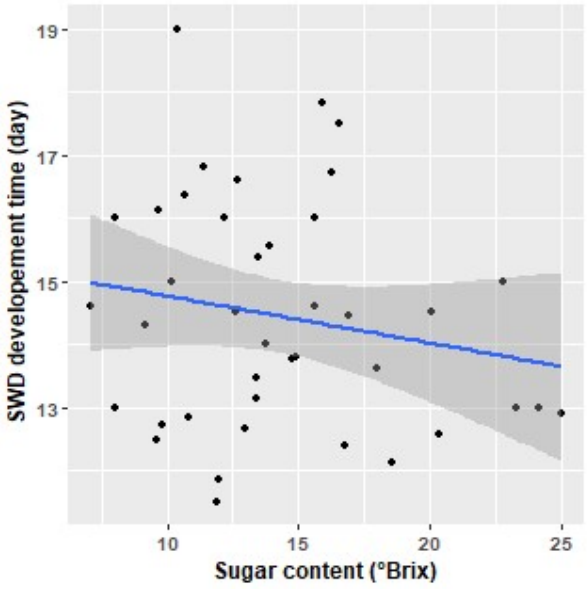

Figure 5: Regression plot between SWD development time in each plant species and the fruit juice sugar content, measured in Brix degree (°Brix).

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 could develop into adults; Table 1, medium grey highlighted). These plants seem therefore to be ecological traps for SWD and are thus candidates for further investigation of their potential as dead-end trap crops against the pest (Figure 1). Ten other host plant species were preferred over grapes for egg-laying but allowed an intermediate level of emergence success between 10 to 30%, namely *Cornus alba sibirica, Cornus mas, Lonicera xylosteum, Mahonia aquifolium, Prunus laucerasus, Rhamnus cathartica, Sambucus nigra, Solanum nigrum, Symphoricarpos alba* and *Taxus baccata* (Table 1, light grey highlighted). These plant species could also be considered interesting candidates for traditional trap cropping provided that additional measures to limit pest spill-over are undertaken, e.g. by insecticide application (Figure 1). Finally, we identified seven host plant species: *Cornus kousa, Frangula alnus, Lycium barbarum, Rubus fruticosus lockness, Rubus idaeus* and *Sambucus ebulus* showing both high preference and performance scores (Table 1, dark grey highlighted). As they are highly preferred compared to grapes and allow over 60% of eggs to develop into adults, they might be considered as a pest source in the vicinity of vineyards (Figure 1).

Preference

SWD laid eggs in most host plants, confirming its strong polyphagous behaviour (Lee *et al.* 2015; Poyet *et al.* 2015; Kenis *et al.* 2016). Previous studies explored a relatively small sample of crop hosts. Despite differences in the experimental modalities and the preference assessment, our results are consistent with the most and least preferred crops already highlighted in previous studies, also confirming that grapes are much less attractive for SWD in comparison to other crops (Lee *et al.* 2011b; Bellamy *et al.* 2013; Burrack *et al.* 2013; Abraham *et al.* 2015; Aly 2018; Olazcuaga *et al.* 2019).

Under laboratory conditions, SWD preference ranking of host plants for egg-laying was similar under no choice vs multiple choice conditions. This suggests that innate SWD preferences are consistent and can guide the selection of plant candidates for trap cropping (Holden *et al.* 2012; Mathews *et al.* 2017). Yet, environmental conditions affecting SWD preference patterns under field conditions are still largely unknown and the realised host range of insects does not always include all hosts they can potentially use (Braga & Janz 2021). Host choice, i.e. whether or not eggs are deposited on a plant, is determined by innate preferences but modulated by the availability of hosts and environmental cues in a sequence of choices, as well as by previous experiences as juvenile or adult (Singer 1986; Schaffner 2001; Carrasco *et al.* 2015; Silva & Clarke 2020). Two-choice preference tests with potted plants in the field could offer a standardised way to study how innate host preferences change under current environmental conditions and determine the actual oviposition choice (Wapshere 1974, 1989; Briese 2005).

SWD preference for host plants as oviposition sites correlated well with fruit skin hardness but not with fruit colour. Although SWD shows preferences for harder artificial substrates in laboratory assays compared to other Drosophila species (Sato *et al.* 2020; Silva & Clarke 2020), our results indicate that SWD lays more eggs in fruit species with softer skin, in line with the results of Burrack et al. (2013). SWD egg-laying has also been shown to decrease with increasing skin hardness in crop cultivars such as grapes (Asplen *et al.* 2015; Kehrli *et al.* 2017a; Tonina *et al.* 2018; Shrader *et al.* 2019; Entling & Hoffmann 2020; Mazzetto *et al.* 2020), cherry (Kamiyama & Guédot 2019) and blueberry (Kinjo *et al.* 2013). In our study, the regression line of the linear model indicates that SWD would not lay any eggs in fruit with a skin hardness of 75 cN and above. Host species with a skin hardness close to this 75cN predicted threshold include the currant tomato (*Lycopersicum 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).* They can be considered non-relevant host plants for SWD as their potential for egg-laying is close to zero, with on average 0.3 eggs per gram of fruit in the no-choice experiment. We sampled ripe fruits based on a visual assessment of their typical ripeness. Yet, colour and skin hardness can evolve during maturation (Lee *et al.* 2011b; Entling & Hoffmann 2020) and observations on host species, which reach their definitive colour early in the ripening stage, such as *Prunus spinosa* or *Sorbus aucuparia*, might need to be considered with more care. For instance, Poyet et al. (2015) demonstrated with infested fruits they collected in nature that *Prunus spinosa* is a suitable host for oviposition and development of SWD. Our

collection period for this species might correspond to a non-attractive stage of the fruit, but this might change with fruit maturation (Lee *et al.* 2011b). Overall, the fruit skin hardness threshold of 75 cN can be used to rapidly estimate the approximate potential of yet untested plant species for oviposition and develop control methods such as fruit coating products (Tait *et al.* 2022). However, it does not alone allow us to predict the preference among hosts as other fruit characteristics and environmental factors influence SWD host choice.

Performance

The three criteria chosen to evaluate host plant suitability for SWD developmental performance were uncorrelated, suggesting that SWD performance in development duration, wing length and emergence success are determined by different components that are not disentangled with the host plant's identity. Still, SWD showed variation among plant species in two of the three criteria, indicating an overall variation of SWD performance among host species.

Although we have identified relationships between fruit traits and SWD development performance across a large range of host plant species, we did not manage to identify fruit traits fundamentally affecting emergence success. Such a relationship between SWD performance and fruit traits could also not be shown between closely related host species, such as grape cultivars (Pelton *et al.* 2017). We found that lower fruit acidity was associated with a longer egg-to-adult development duration until an optimum between pH 4 and 5 was reached (lowest development time). Longer development time at lower fruit acidity has been found for two other vinegar fly species, namely *D. melanogaster* and *D. hydei* (Hodge *et al.* 1996). SWD development time was also longer in fruits with less sugar, in line with the results for tart cherries (*Prunus cerasus)* (Kamiyama & Guédot 2019). Moreover, sugar content was also affecting SWD wing length. Fruits with a higher sugar content led to the emergence of flies with longer wings and thus larger flies, as the size of the different body parts is usually correlated (Carreira *et al.* 2009). It has been reported for *D. melanogaster* that being larger is associated with higher fecundity, higher courtship success and longer survival (Partridge *et al.* 1987; Rodrigues *et al.* 2015). Still, smaller males could have greater territorial success (Zamudio *et al.* 1995) and smaller females showed a higher survival rate and lifetime reproductive success under colder environmental conditions (McCabe & Partridge 1997). For technical reasons, we did not identify the different sugar compounds and sugar molecules in our fruit extracts and we are aware that they might have various effects on larval development and adult traits (Morimoto *et al.* 2020). In addition, Burke & Waddel (2011) showed that *D.*

melanogaster sweetness perception was not systematically related to high-quality nutrition. The availability and the ratio between carbohydrates and protein in the food sources were shown to influence SWD survival, egg production (Plantamp et al., 2017) and reproductive success (Young & Long 2020). Assessing host quality might thus require understanding the role and the balance of macronutrients other than sugars (Wetzel *et al.* 2016; Olazcuaga *et al.* 2019). Host plants inducing a shorter development time, i.e. with optimal acidity or high sugar content, might however allow more pest generations to develop over the season, thereby increasing SWD populations in the landscape or extending the period over which pest control measures have to be implemented.

Bottom-up forces have been shown to explain a considerable variation of herbivore population abundances (Ylioja *et al.* 1999). It appears that the quality and the abundance of host plants are crucial explaining such pattern (West & Cunningham 2002; Underwood 2009). However, pest individuals' performance is not necessarily correlated with changes in the 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 will be critical to identify the host plant's role in creating source or sink habitat patches and recognise possible "ecological traps" (Delibes et al., 2001). How SWD preference for and performance in host plants contribute to SWD population dynamics has still to be investigated, but we suggest that this information might be helpful to anticipate better pest abundance and movement in the crops' vicinity. This knowledge might also complement models that use the quantity and distribution of wild host plants and crops to predict pest densities in susceptible agricultural fields (Choquenot & Parkes 2001; Carrière *et al.* 2012).

Trap cropping

Not all crop species of our SWD host plant samples are similarly suitable for a trap cropping strategy. We show that grapes are less attractive for SWD egg-laying compared to many other host plant species and present a low SWD developmental performance, i.e. a low emergence success. The 16 plant species we identified here with high preference but low SWD performance are therefore potential candidates that could be used for developing a trap cropping strategy to protect vineyards and thus promote bottom-up pest control (Simon *et al.* 2011). The black chokeberry (*Aronia melanocarpa*) which scored similarly to grapes regarding SWD preference and developmental performance might be another potential crop species that trap

crops could protect from SWD damage. Its cultivation is not frequent in Europe but it has gained popularity in North America where it is native (Shahin *et al.* 2019). If SWD damage becomes problematic in this crop, suitable candidates for trap cropping could be identified with our dataset.

Highly preferred crop species such as blackberries (*Rubus fruticosus*), raspberries (*Rubus idaeus*) or black elderberries (*Sambucus nigra*) lack host plants that are more attractive than themselves. Therefore, even if a potential trap crop plant could be planted in their surroundings, it would likely have little effect in successfully mitigating spill-over and pest damage. As a crop, they are locally abundant and strongly favour SWD development in the area thereby probably driving local SWD population dynamics (Santoiemma *et al.* 2019). Similarly, crop species such as blueberry (*Vaccinium myrtillus*), Goji berries (*Lycium barbarum*) or plums (*Prunus domestica subsp. Insititia*) had too few host plants being preferred for oviposition. Consequently, it will be challenging to discover a suitable trap crop species offering protection against SWD.

We used emergence success to further rank trap crop candidate plant species and to choose the most appropriate type of trap cropping to protect grapes. Since the implications of developmental performance on population growth are yet unclear, we recommend starting to test candidate trap crops with the lowest emergence success first. Nibouche, Tibère, and Costet (2012) reported from a small-scale field experiment a survival rate of the stem borer *Chilo sacchariphagus* larvae on *Erianthus arundinaceus* below 10%, which they considered sufficiently low to categorise *E. arundinaceus* as a dead-end trap crop. The plantation of this trap crop successfully decreased sugarcane pest infestation at commercial field scale. We suggest therefore that host plants highly preferred over grapes for egg-laying and with emergence success <10% could be further tested as promising candidates for dead-end trap cropping. Yet, the definition of "dead-end" is currently arbitrary and vague and should be better defined as authors use the adjective dead-end to qualify trap crops from which pest emergence success varies from 0 to 40 % (Shelton & Nault 2004; Veromann *et al.* 2014; Nibouche *et al.* 2019; Ulmer *et al.* 2020; Gyawali *et al.* 2021).

Trap crop candidates preferred over grapes for egg-laying could be considered candidate host plants for traditional trap cropping independent of their developmental success. They should be applied with additional measures that increase pest retention in the trap crop area to limit pest spill-over (Blitzer *et al.* 2012). As SWD eggs and larvae develop within the trap crop fruits,

insecticide treatments are often of low efficacy before emergence. Therefore, the mechanical destruction of infested fruits or regular vacuuming of emerged adults might be more appropriate to decrease spill-over. We identified an additional 10 plant species that are highly attractive for SWD oviposition and have an intermediate emergence success varying between 10 and 30%. This provides a list of 25 candidate trap crops suitable for trap cropping strategies. The remaining host plants with a high emergence success might create habitat patches that are potential sources of SWD allowing the spill-over of pest individuals into crops (Kristan III 2003). Their presence might therefore be limited in the surrounding of vulnerable crops thereby guiding the management of semi-natural habitats.

To further develop a trap cropping strategy, the choice of the candidates should be adapted to the local environment (Asgarzadeh *et al.* 2014). For instance, several of the candidates mentioned above, such as *Phytolacca americana* or *Prunus laurocerasus*, are invasive plant species in Switzerland (Info Flora 2014). If they are considered for further experimental field tests, appropriate measures should be taken to avoid their dispersal.

Next steps

To develop further trap cropping, the phenology of the trap crop candidates should be followed under field conditions to more accurately estimate the period of grape protection. A combination of different trap crop plant species might be a valuable approach, since complementing candidates might more easily cover the long ripening period of grapes. Such species-rich trap crops were most efficient in decreasing beetle damage in broccoli (Parker *et al.* 2016). This approach might consequently allow selecting the most appropriate candidates to be tested under field conditions. Moreover, the optimal ratio between trap crops and grapevines to decrease pest damage and the most suitable spatial arrangement of the trap crop are currently unknown. Such experiments might ultimately help figure out the practical potential of trap cropping to protect grapes. They will also provide data to conduct cost-benefit estimations linked to the expenses for trap crop maintenance and the loss of viticultural crop area.

Supplementary material

Table S1: List of candidate plant species from literature

List of plant species retrieved from the literature, which flowering period might correspond to a fruiting period overlapping grape maturation. Months of the year are indicated with a number between 1 to 12 (January to December) in the flowering period column.

Family	Plant species	Flowering period (month)
Actinidiaceae	*Actinidia arguta*	6
Adoxaceae	*Sambucus ebulus*	7-8
	Sambucus nigra	5-6
	Viburnum dilatatum	4-6
	Viburnum lantana	5
	Viburnum opulus	5-6
	Viburnum x rhytidophyllum	5-6
Annonaceae	*Asimina triloba*	4
Aquifoliaceae	*Ilex aquifolium*	5
Araliaceae	*Hedera helix*	9-10
Asparagaceae	*Asparagus acutifolius*	7
	Asparagus officinalis	5-6
Beberidaceae	*Berberis julianae*	5-6
	Berberis thunbergii	5-6
	Berberis vulgaris	5-6
	Berberis x media	5-6
	Nandina domestica	7-8
Caprifoliaceae	*Lonicera alpigena*	4-6
	Lonicera caprifolium	5-6
	Lonicera etrusca	5-6
	Lonicera ferdinandii	5-6
	Lonicera henryi	6-8
	Lonicera nigra	5-6
	Lonicera nitida	5
	Lonicera periclymenum	6-8
	Lonicera pileata	6
	Lonicera xylosteum	5-6
	Symphoricarpos albus	6-7
	Symphoricarpos doorenbosii	6
	Symphoricarpos orbiculatus	6-7
Celastraceae	*Euonymus europaeus*	6-7
Cephalotaxaceae	*Cephalotaxus harringtonia*	5-6
Cornaceae	*Aucuba japonica*	5-6
	Cornus alba	5-7
	Cornus amomum	6
	Cornus controversa	7-8
	Cornus foemina	7

Family	Plant species	Flowering period (month)
	Cornus kousa	6-7
	Cornus mas	3
	Cornus sanguinea	5
	Cornus sanguinea	5
	Cornus sericea	5-6
Cucurbitaceae	*Bryonia dioica*	6-7
Dioscoreaceae	*Tamus communis*	5-6
Ebenaceae	*Diospyros kaki*	5-6
Elaeagnaceae	*Elaeagnus umbellata*	5-6
	Gaultheria x wisleyensis	5-6
	Vaccinium myrtilloides	6
	Vaccinium myrtillus	4-6
	Vaccinium praestans	6-7
	Vaccinium uliginosum	5-6
	Vaccinium vitis-idaea	5-6
Hypericaceae	*Hypericum androsaemum*	6
Lamiaceae	*Callicarpa bodinieri*	7
Liliaceae	*Polygonatum multiflorum*	5-7
	Polygonatum verticillatum	5-7
Lythraceae	*Punica granatum*	6
Moraceae	*Ficus carica*	5-8
	Morus alba	5
	Morus australis	5-6
	Morus nigra	5
	Morus rubra	5
Myrtaceae	*Myrtus communis*	6-10
Nolinoideae	*Convallaria majalis*	5
Oleaceae	*Ligustrum lucidum*	8-9
	Ligustrum vulgare	5-7
	Olea europaea	5
	Phillyrea angustifollia	5-6/9-10
	Phillyrea latifolia	5-6/9-10
Phytolaccaceae	*Phytolacca americana*	7
	Phytolacca esculentaVan	7
Ranunculaceae	*Actaea spicata*	5-7
Rhamnaceae	*Frangula alnus*	5-6
	Rhamnus alpina spp. *Fallax*	5-6
	Rhamnus cathartica	5
	Rhamnus pumila	6-7
Rosaceae	*Aronia arbutifolia*	5-6
	Aronia melanocarpa	5
	Aronia x prunifolia	5
	Cotoneaster acutifolius	6-7/9-10
	Cotoneaster dammeri	5-6
	Cotoneaster horizontalis	5
	Cotoneaster lacteus	1-2/6-7/10-11-12
	Cotoneaster rehderi	4-6
	Cotoneaster salicifolius	5-6

Family	Plant species	Flowering period (month)
	Cotoneaster suecicus	6-7
	Cotoneaster x watereri	6-7
	Crataegus chrysocarpa	5-6
	Crataegus coccinea	5
	Crataegus crus-galli	5
	Crataegus kansuensis	5
	Crataegus monogyna	5-6
	Duchesnea indica	4-7
	Fragaria ananassa	4-7
	Fragaria vesca	4-6
	Malus floribunda	5
	Malus pumila	5
	Mespilus germanica	5-6
	Photinia fraseri	5-6
	Photinia prunifolia	6-7
	Photinia villosa	5
	Prunus donarium	5
	Prunus japonica	5
	Prunus lusitanica	6
	Prunus padus	4-6
	Prunus serotina	5-6
	Rhodotypos scandens	5-6
	Ribes alpinum	4-6
	Rosa acicularis	5-7
	Rosa canina	6
	Rosa glauca	6-7
	Rosa pendulina	6-7
	Rosa rugosa	6-8
	Rosa spinosissima	5
	Rubus armeniacus	6-7
	Rubus caesius	6-9
	Rubus fruticosus	5-8
	Sorbus aria	5
	Rubus idaeus	5-7
	Rubus laciniatus	6-7
	Rubus phoenicolasius	6-7
	Rubus saxatilis	5-7
	Sorbus aucuparia	5-6
	Sorbus chamaemespilus	6-7
	Sorbus domestica	4-5
Rubiaceae	*Rubia tinctorum*	6-7
Rutaceae	*Skimmia japonica*	1-2-3-4-5-6-/11-12
Smilacaceae	*Smilax aspera*	9-11
Solanaceae	*Atropa Bella-donna*	6-8
	Lycium barbarum	6-8
	Physalis alkekengi	5-8
	Solanum dulcamara	6-8
	Solanum nigrum	6-10

Family	Plant species	Flowering period (month)
	Solanum pseudocapsicum	5-8
	Withania somnifera	6-9
Vitaceae	*Ampelopsis brevipedunculatatata*	5-9
	Ampelopsis glandulosa	6-8
	Parthenocissus quinquefolia	6-8
	Parthenocissus tricuspidata	6-8
	Vitis labrusca	5-6
	Vitis vinifera	6

Table S2: Weekly fruit sampling 2018

Lists of plant species collected each week for the experiments. Vitis vinifera cv. Mara was added to all samples.

July	August	
week 31	**week 32**	**week 33**
Aronia melanocarpa	*Aronia melanocarpa*	*Cornus amomum*
Cornus mas	*Cestrum fasciculatum*	*Cornus mas*
Cornus sanguinea	*Hippophae rhamnoides*	*Cornus sanguinea*
Lonicera xylosteum	*Lonicera xylosteum*	*Mahonia aquifolium*
Prunus spinosa	*Phytolacca acinosa*	*Rhamnus cathartica*
Sambucus ebulus	*Rubus Idaeus*	*Rubus fruticosus lockness*
Sambucus nigra	*Sambucus ebulus*	*Sorbus americana Belmonte*
Solanum dulcamara	*Sorbus aucuparia*	*Sorbus aucuparia*
	Taxus baccata	*Viburnum lantana*
	Vaccinium myrtillus	*Viburnum rhydotiphyllum*
	Viburnum tinus	

August		September
week 34	**week 35**	**week 36**
Atropa belladona	*Cornus capitata*	*Berberis vulgaris*
Basella alba	*Cornus controversa variegata*	*Lycium barbarum*
Phytolacca americana	*Cornus sanguinea winterbeauty*	*Lycium chinense*
Polygonatum multiflorum	*Cotoneaster tomentosus*	*Lycopersicum pimpinellifolium*
Prunus domesticus subsp. *institia*	*Symphoricarpos alba*	*Pyracantha coccinea*
Vaccinium myrtillus	*Vaccinium myrtillus*	*Solanum nigrum*
	Viburnum opulus	*Solanum villosum*
		Vaccinium myrtillus

September		
week 37	**week 38**	**week 39**
Callicarpa giraldii	*Ampelopsis brevipedunculatata*	*Cotoneaster obscurus*
Ilex aquifolium	*Aronia melanocarpa*	*Myrtus communis*
Ligustrum vulgare	*Cornus alba*	*Nandina domestica*
Malus spectabilis	*Cornus alba sibirica*	*Prunus lusitanica*
Cornus kousa	*Cotoneaster divaricatus*	*Vaccinium myrtillus*
Frangula alnus	*Eleagnus umbelata*	*Vitis vinifera cv. humagne*
Hippophae rhamnoides	*Vaccinium myrtillus*	
Vaccinium myrtillus	*Vitis vinifera cv. humagne*	
Viburnum tinus		

October
week 40
Ilex aquifolium
Ligustrum vulgare
Vaccinium myrtillus

Table S3: Linear model estimate table of egg-laying preference among plant species with *Vitis vinifera cv. Mara* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Vitis vinifera cv. Mara* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.96	0.02	63.44	53.30	< 0.001
Ampelopsis brevipedunculatata	-0.31	0.06	279.34	-5.30	< 0.001
Aronia melanocarpa	-0.02	0.04	395.58	-0.50	0.62
Atropa belladona	-0.46	0.06	111.43	-7.75	< 0.001
Basella alba	-0.52	0.06	111.43	-8.81	< 0.001
Berberis vulgaris	0.02	0.06	187.72	0.40	0.69
Callicarpa giraldii	0.03	0.06	294.77	0.55	0.58
Cestrum fasciculatum	-0.58	0.06	335.04	-9.91	< 0.001
Cornus alba	-0.39	0.06	279.34	-6.77	< 0.001
Cornus alba sibirica	-0.45	0.06	279.34	-7.76	< 0.001
Cornus amomum	-0.56	0.06	284.98	-8.99	< 0.001
Cornus capitata	-0.05	0.07	387.90	-0.71	0.48
Cornus controversa variegata	0.02	0.06	234.80	0.31	0.76
Cornus kousa	-0.16	0.06	294.77	-2.69	0.01
Cornus mas	-0.22	0.04	294.93	-5.08	< 0.001
Cornus sanguinea	-0.11	0.04	294.93	-2.50	0.01
Cornus sanguinea winterbeauty	-0.13	0.06	275.80	-2.07	0.04
Cotoneaster divaricatus	-0.16	0.06	321.64	-2.57	0.01
Cotoneaster obscurus	-0.02	0.06	220.21	-0.28	0.78
Cotoneaster tomentosus	-0.07	0.06	234.80	-1.19	0.24
Eleagnus umbelata	-0.56	0.06	279.34	-9.65	< 0.001
Frangula alnus	-0.44	0.06	294.77	-7.55	< 0.001
Hippophae rhamnoides	-0.31	0.05	364.88	-6.86	< 0.001
Ilex aquifolium	0.03	0.04	292.53	0.69	0.49
Ligustrum vulgare	-0.21	0.04	292.53	-4.98	< 0.001
Lonicera xylosteum	-0.46	0.04	340.76	-10.76	< 0.001
Lycium barbarum	-0.35	0.06	187.72	-6.01	< 0.001
Lycium chinense	-0.30	0.06	187.72	-5.21	< 0.001
Lycopersicum pimpinellifolium	0.05	0.06	187.72	0.83	0.41
Mahonia aquifolium	-0.44	0.06	243.56	-7.51	< 0.001
Malus spectabilis	-0.03	0.06	294.77	-0.46	0.65
Myrtus communis	-0.05	0.06	220.21	-0.87	0.39
Nandina domestica	0.01	0.06	220.21	0.23	0.82
Phytolacca acinosa	-0.48	0.06	335.04	-8.24	< 0.001
Phytolacca americana	-0.43	0.06	111.43	-7.25	< 0.001
Polygonatum multiflorum	0.04	0.06	111.43	0.60	0.55

Fixed effects	Estimate	SE	DF	t value	*p value*
Prunus laucerasus	-0.33	0.06	111.43	-5.51	< 0.001
Prunus lusitanica	-0.35	0.06	220.21	-6.00	< 0.001
Prunus spinosa	-0.07	0.06	338.97	-1.17	0.24
Prunus domestica subsp. institia	-0.39	0.06	111.43	-6.58	< 0.001
Pyracantha coccinea	-0.16	0.06	187.72	-2.76	0.01
Rhamnus cathartica	-0.44	0.06	243.56	-7.63	< 0.001
Rubus fruticosus var. lockness	-0.48	0.06	243.56	-8.29	< 0.001
Rubus idaeus	-0.49	0.06	335.04	-8.43	< 0.001
Sambucus ebulus	-0.51	0.04	388.44	-13.05	< 0.001
Sambucus nigra	-0.53	0.04	187.59	-12.20	< 0.001
Sambucus nigra Gold	-0.46	0.06	234.80	-7.80	< 0.001
Solanum dulcamara	-0.07	0.06	338.97	-1.28	0.20
Solanum nigrum	-0.15	0.06	187.72	-2.56	0.01
Solanum villosum	-0.06	0.06	225.15	-0.93	0.35
Sorbus americana Belmonte	0.00	0.06	243.56	-0.06	0.95
Sorbus aucuparia	0.02	0.04	322.15	0.43	0.67
Symphoricarpos alba	-0.20	0.06	234.80	-3.43	< 0.001
Taxus baccata	-0.42	0.06	335.04	-7.17	< 0.001
Vaccinium myrtillus	-0.27	0.03	532.39	-9.34	< 0.001
Viburnum lantana	-0.27	0.06	243.56	-4.55	< 0.001
Viburnum opulus	0.00	0.04	310.96	0.12	0.91
Viburnum rhydotiphyllum	-0.08	0.06	243.56	-1.29	0.20
Viburnum tinus	0.01	0.05	364.88	0.25	0.80
Vitis humagne	-0.03	0.04	335.84	-0.71	0.48

Table S4: Linear model estimate table of egg-laying preference among plant species with *Aronia melanocarpa* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Aronia melanocarpa* as reference level (intercept). Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	p value
(Intercept)	0.94	0.03	140.09	28.87	< 0.001
Vitis vinifera cv. Mara	0.02	0.04	395.58	0.50	0.62
Ampelopsis brevipedunculatata	-0.29	0.06	425.09	-4.59	< 0.001
Atropa belladona	-0.44	0.07	128.09	-6.77	< 0.001
Basella alba	-0.50	0.07	128.09	-7.75	< 0.001
Berberis vulgaris	0.04	0.07	150.72	0.64	0.52
Callicarpa giraldii	0.05	0.06	238.04	0.77	0.44
Cestrum fasciculatum	-0.56	0.06	481.36	-8.84	< 0.001
Cornus alba	-0.38	0.06	425.09	-5.94	< 0.001
Cornus alba sibirica	-0.43	0.06	425.09	-6.86	< 0.001
Cornus amomum	-0.54	0.07	252.76	-7.95	< 0.001
Cornus capitata	-0.04	0.08	329.00	-0.44	0.66
Cornus controversa variegata	0.04	0.06	200.46	0.55	0.58
Cornus kousa	-0.14	0.06	238.04	-2.14	0.03
Cornus mas	-0.20	0.05	363.13	-3.97	< 0.001
Cornus sanguinea	-0.09	0.05	363.13	-1.78	0.08
Cornus sanguinea winterbeauty	-0.11	0.07	232.17	-1.63	0.10
Cotoneaster divaricatus	-0.14	0.07	452.92	-2.12	0.03
Cotoneaster obscurus	0.00	0.06	180.18	0.03	0.98
Cotoneaster tomentosus	-0.05	0.06	200.46	-0.80	0.43
Eleagnus umbelata	-0.54	0.06	425.09	-8.60	< 0.001
Frangula alnus	-0.42	0.06	238.04	-6.53	< 0.001
Hippophae rhamnoides	-0.29	0.05	369.12	-5.57	< 0.001
Ilex aquifolium	0.05	0.05	201.93	0.93	0.36
Ligustrum vulgare	-0.20	0.05	201.93	-3.81	< 0.001
Lonicera xylosteum	-0.44	0.05	554.44	-8.95	< 0.001
Lycium barbarum	-0.33	0.07	150.72	-5.13	< 0.001
Lycium chinense	-0.29	0.07	150.72	-4.42	< 0.001
Lycopersicum pimpinellifolium	0.07	0.07	150.72	1.02	0.31
Mahonia aquifolium	-0.42	0.06	219.76	-6.50	< 0.001
Malus spectabilis	-0.01	0.06	238.04	-0.13	0.89
Myrtus communis	-0.03	0.06	180.18	-0.51	0.61
Nandina domestica	0.03	0.06	180.18	0.48	0.63
Phytolacca acinosa	-0.46	0.06	481.36	-7.30	< 0.001
Phytolacca americana	-0.41	0.07	128.09	-6.32	< 0.001
Polygonatum multiflorum	0.05	0.07	128.09	0.82	0.42
Prunus laucerasus	-0.31	0.07	128.09	-4.74	< 0.001
Prunus lusitanica	-0.33	0.06	180.18	-5.13	< 0.001
Prunus spinosa	-0.05	0.06	480.38	-0.79	0.43

Fixed effects	Estimate	SE	DF	t value	p value
Prunus domesticus subsp. institia	-0.37	0.07	128.09	-5.71	< 0.001
Pyracantha coccinea	-0.14	0.07	150.72	-2.21	0.03
Rhamnus cathartica	-0.43	0.06	219.76	-6.61	< 0.001
Rubus fruticosus var. lockness	-0.47	0.06	219.76	-7.21	< 0.001
Rubus idaeus	-0.47	0.06	481.36	-7.47	< 0.001
Sambucus ebulus	-0.49	0.05	547.50	-10.58	< 0.001
Sambucus nigra	-0.51	0.05	287.78	-10.11	< 0.001
Sambucus nigra Gold	-0.44	0.06	200.46	-6.76	< 0.001
Solanum dulcamara	-0.06	0.06	480.38	-0.89	0.37
Solanum nigrum	-0.13	0.07	150.72	-2.04	0.04
Solanum villosum	-0.04	0.07	177.63	-0.59	0.56
Sorbus americana Belmonte	0.01	0.06	219.76	0.22	0.82
Sorbus aucuparia	0.04	0.05	389.80	0.72	0.47
Symphoricarpos alba	-0.18	0.06	200.46	-2.82	0.01
Taxus baccata	-0.40	0.06	481.36	-6.31	< 0.001
Vaccinium myrtillus	-0.25	0.04	353.58	-6.30	< 0.001
Viburnum lantana	-0.25	0.06	219.76	-3.83	< 0.001
Viburnum opulus	0.02	0.05	357.42	0.45	0.65
Viburnum rhydotiphyllum	-0.06	0.06	219.76	-0.89	0.37
Viburnum tinus	0.03	0.05	369.12	0.55	0.58
Vitis vinifera cv. Humagne	-0.01	0.05	295.68	-0.17	0.86

Table S5: Linear model estimate table of egg-laying preference among plant species with *Vitis vinifera cv. Humagne* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Vitis vinifera cv. Humagne* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.93	0.03	115.40	28.53	< 0.001
Lycium barbarum	-0.33	0.07	146.40	-5.01	< 0.001
Aronia melanocarpa	0.01	0.05	295.70	0.17	0.86
Vitis vinifera cv. Mara	0.03	0.04	335.80	0.71	0.48
Ampelopsis brevipedunculatata	-0.28	0.06	423.50	-4.47	< 0.001
Atropa belladona	-0.43	0.07	115.50	-6.64	< 0.001
Basella alba	-0.50	0.07	115.50	-7.61	< 0.001
Berberis vulgaris	0.05	0.07	146.40	0.76	0.45
Callicarpa giraldii	0.06	0.06	235.10	0.90	0.37
Cestrum fasciculatum	-0.55	0.06	235.80	-8.51	< 0.001
Cornus alba	-0.37	0.06	423.50	-5.82	< 0.001
Cornus alba sibirica	-0.43	0.06	423.50	-6.73	< 0.001
Cornus amomum	-0.53	0.07	199.30	-7.81	< 0.001
Cornus capitata	-0.03	0.08	296.30	-0.34	0.73
Cornus controversa variegata	0.04	0.06	173.10	0.67	0.50
Cornus kousa	-0.13	0.06	235.10	-2.02	0.04
Cornus mas	-0.19	0.05	163.60	-3.73	< 0.001
Cornus sanguinea	-0.08	0.05	163.60	-1.59	0.11
Cornus sanguinea winterbeauty	-0.10	0.07	202.40	-1.51	0.13
Cotoneaster divaricatus	-0.13	0.07	451.50	-2.00	0.05
Cotoneaster obscurus	0.01	0.06	403.30	0.15	0.88
Cotoneaster tomentosus	-0.04	0.06	173.10	-0.67	0.50
Eleagnus umbelata	-0.54	0.06	423.50	-8.47	< 0.001
Frangula alnus	-0.41	0.06	235.10	-6.40	< 0.001
Hippophae rhamnoides	-0.29	0.05	233.00	-5.35	< 0.001
Ilex aquifolium	0.06	0.05	342.20	1.10	0.27
Ligustrum vulgare	-0.19	0.05	342.20	-3.73	< 0.001
Lonicera xylosteum	-0.43	0.05	191.00	-8.46	< 0.001
Lycium chinense	-0.28	0.07	146.40	-4.29	< 0.001
Lycopersicum pimpinellifolium	0.07	0.07	146.40	1.14	0.26
Mahonia aquifolium	-0.41	0.06	170.30	-6.35	< 0.001
Malus spectabilis	0.00	0.06	235.10	-0.01	0.99
Myrtus communis	-0.03	0.06	403.30	-0.40	0.69
Nandina domestica	0.04	0.06	403.30	0.62	0.54
Phytolacca acinosa	-0.45	0.06	235.80	-7.01	< 0.001
Phytolacca americana	-0.40	0.07	115.50	-6.19	< 0.001
Polygonatum multiflorum	0.06	0.07	115.50	0.93	0.35

Fixed effects	Estimate	SE	DF	t value	*p value*
Prunus laucerasus	-0.30	0.07	115.50	-4.61	< 0.001
Prunus lusitanica	-0.32	0.06	403.30	-5.13	< 0.001
Prunus spinosa	-0.04	0.06	231.50	-0.65	0.52
Prunus domesticus subsp. institia	-0.36	0.07	115.50	-5.58	< 0.001
Pyracantha coccinea	-0.14	0.07	146.40	-2.09	0.04
Rhamnus cathartica	-0.42	0.06	170.30	-6.46	< 0.001
Rubus fruticosus var. lockness	-0.46	0.06	170.30	-7.05	< 0.001
Rubus idaeus	-0.46	0.06	235.80	-7.18	< 0.001
Sambucus ebulus	-0.49	0.05	192.80	-10.05	< 0.001
Sambucus nigra	-0.50	0.05	148.10	-9.76	< 0.001
Sambucus nigra Gold	-0.43	0.06	173.10	-6.62	< 0.001
Solanum dulcamara	-0.05	0.06	231.50	-0.75	0.45
Solanum nigrum	-0.12	0.07	146.40	-1.91	0.06
Solanum villosum	-0.03	0.07	172.70	-0.47	0.64
Sorbus americana Belmonte	0.02	0.06	170.30	0.35	0.73
Sorbus aucuparia	0.04	0.05	176.30	0.86	0.39
Symphoricarpos alba	-0.17	0.06	173.10	-2.69	0.01
Taxus baccata	-0.39	0.06	235.80	-6.04	< 0.001
Vaccinium myrtillus	-0.24	0.04	529.20	-6.20	< 0.001
Viburnum lantana	-0.24	0.06	170.30	-3.69	< 0.001
Viburnum opulus	0.03	0.05	175.00	0.60	0.55
Viburnum rhydotiphyllum	-0.05	0.06	170.30	-0.77	0.45
Viburnum tinus	0.04	0.05	233.00	0.69	0.49

Table S6: Linear model estimate table of egg-laying preference among plant species with *Vaccinium myrtillus* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Vaccinium myrtillus* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.69	0.02	118.02	29.02	< 0.001
Vitis vinifera cv. Humagne	0.24	0.04	529.22	6.20	< 0.001
Lycium barbarum	-0.09	0.06	199.34	-1.41	0.16
Aronia melanocarpa	0.25	0.04	353.58	6.30	< 0.001
Vitis vinifera cv. Mara	0.27	0.03	532.39	9.34	< 0.001
Ampelopsis brevipedunculatata	-0.04	0.06	340.40	-0.70	0.48
Atropa belladona	-0.19	0.06	145.42	-3.17	< 0.01
Basella alba	-0.26	0.06	145.42	-4.21	< 0.001
Berberis vulgaris	0.29	0.06	199.34	4.79	< 0.001
Callicarpa giraldii	0.30	0.06	311.38	4.96	< 0.001
Cestrum fasciculatum	-0.31	0.06	307.08	-5.13	< 0.001
Cornus alba	-0.13	0.06	340.40	-2.13	0.03
Cornus alba sibirica	-0.19	0.06	340.40	-3.09	< 0.01
Cornus amomum	-0.29	0.06	222.64	-4.54	< 0.001
Cornus capitata	0.21	0.08	382.93	2.80	0.01
Cornus controversa variegata	0.28	0.06	237.65	4.70	< 0.001
Cornus kousa	0.11	0.06	311.38	1.83	0.07
Cornus mas	0.05	0.05	195.10	1.06	0.29
Cornus sanguinea	0.16	0.05	195.10	3.45	< 0.001
Cornus sanguinea winterbeauty	0.14	0.06	276.14	2.13	0.03
Cotoneaster divaricatus	0.11	0.06	378.82	1.68	0.09
Cotoneaster obscurus	0.25	0.06	295.58	4.17	< 0.001
Cotoneaster tomentosus	0.20	0.06	237.65	3.26	< 0.01
Eleagnus umbelata	-0.30	0.06	340.40	-4.93	< 0.001
Frangula alnus	-0.17	0.06	311.38	-2.87	< 0.01
Hippophae rhamnoides	-0.05	0.05	356.40	-0.94	0.35
Ilex aquifolium	0.30	0.05	378.66	6.54	< 0.001
Ligustrum vulgare	0.05	0.05	378.66	1.18	0.24
Lonicera xylosteum	-0.19	0.05	262.24	-4.21	< 0.001
Lycium chinense	-0.04	0.06	199.34	-0.64	0.52
Lycopersicum pimpinellifolium	0.31	0.06	199.34	5.19	< 0.001
Mahonia aquifolium	-0.17	0.06	187.95	-2.82	0.01
Malus spectabilis	0.24	0.06	311.38	3.98	< 0.001
Myrtus communis	0.22	0.06	295.58	3.59	< 0.001
Nandina domestica	0.28	0.06	295.58	4.66	< 0.001
Phytolacca acinosa	-0.21	0.06	307.08	-3.52	< 0.001
Phytolacca americana	-0.16	0.06	145.42	-2.69	0.01
Polygonatum multiflorum	0.30	0.06	145.42	4.95	< 0.001

Fixed effects	Estimate	SE	DF	t value	*p value*
Prunus laucerasus	-0.06	0.06	145.42	-1.00	0.32
Prunus lusitanica	-0.08	0.06	295.58	-1.40	0.16
Prunus spinosa	0.20	0.06	274.17	3.28	< 0.01
Prunus domesticus subsp. institia	-0.12	0.06	145.42	-2.03	0.04
Pyracantha coccinea	0.10	0.06	199.34	1.72	0.09
Rhamnus cathartica	-0.18	0.06	187.95	-2.93	< 0.01
Rubus fruticosus var. lockness	-0.22	0.06	187.95	-3.57	< 0.001
Rubus idaeus	-0.22	0.06	307.08	-3.70	< 0.001
Sambucus ebulus	-0.25	0.04	296.53	-5.76	< 0.001
Sambucus nigra	-0.26	0.05	208.51	-5.68	< 0.001
Sambucus nigra Gold	-0.19	0.06	237.65	-3.13	< 0.01
Solanum dulcamara	0.19	0.06	274.17	3.18	< 0.01
Solanum nigrum	0.12	0.06	199.34	1.92	0.06
Solanum villosum	0.21	0.06	235.34	3.23	< 0.01
Sorbus americana Belmonte	0.26	0.06	187.95	4.32	< 0.001
Sorbus aucuparia	0.28	0.05	232.12	6.20	< 0.001
Symphoricarpos alba	0.07	0.06	237.65	1.09	0.28
Taxus baccata	-0.15	0.06	307.08	-2.48	0.01
Viburnum lantana	0.00	0.06	187.95	0.02	0.99
Viburnum opulus	0.27	0.05	258.33	5.92	< 0.001
Viburnum rhydotiphyllum	0.19	0.06	187.95	3.13	< 0.01
Viburnum tinus	0.28	0.05	356.40	5.77	< 0.001

Table S7: Linear model estimate table of egg-laying preference among plant species with *Lycium barbarum* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Lycium barbarum* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference leve.l

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.60	0.06	130.31	10.72	< 0.001
Aronia melanocarpa	0.33	0.07	150.72	5.13	< 0.001
Vitis vinifera cv. Mara	0.35	0.06	187.72	6.01	< 0.001
Ampelopsis brevipedunculatata	0.04	0.08	171.28	0.55	0.58
Atropa belladona	-0.11	0.08	125.05	-1.35	0.18
Basella alba	-0.17	0.08	125.05	-2.14	0.03
Berberis vulgaris	0.38	0.08	561.53	4.96	< 0.001
Callicarpa giraldii	0.38	0.08	182.54	4.84	< 0.001
Cestrum fasciculatum	-0.22	0.08	186.87	-2.82	0.01
Cornus alba	-0.04	0.08	171.28	-0.53	0.60
Cornus alba sibirica	-0.10	0.08	171.28	-1.25	0.21
Cornus amomum	-0.21	0.08	182.31	-2.53	0.01
Cornus capitata	0.30	0.09	244.76	3.24	< 0.01
Cornus controversa variegata	0.37	0.08	162.17	4.65	< 0.001
Cornus kousa	0.20	0.08	182.54	2.46	0.01
Cornus mas	0.13	0.07	152.06	1.95	0.05
Cornus sanguinea	0.24	0.07	152.06	3.55	< 0.001
Cornus sanguinea winterbeauty	0.22	0.08	181.01	2.70	0.01
Cotoneaster divaricatus	0.19	0.08	190.78	2.33	0.02
Cotoneaster obscurus	0.34	0.08	154.63	4.22	< 0.001
Cotoneaster tomentosus	0.28	0.08	162.17	3.55	< 0.001
Eleagnus umbelata	-0.21	0.08	171.28	-2.64	0.01
Frangula alnus	-0.09	0.08	182.54	-1.10	0.27
Hippophae rhamnoides	0.04	0.07	172.31	0.57	0.57
Ilex aquifolium	0.38	0.07	155.17	5.53	< 0.001
Ligustrum vulgare	0.14	0.07	155.17	2.01	0.05
Lonicera xylosteum	-0.11	0.07	157.48	-1.56	0.12
Lycium chinense	0.05	0.08	561.53	0.62	0.54
Lycopersicum pimpinellifolium	0.40	0.08	561.53	5.29	< 0.001
Mahonia aquifolium	-0.09	0.08	163.37	-1.08	0.28
Malus spectabilis	0.33	0.08	182.54	4.10	< 0.001
Myrtus communis	0.30	0.08	154.63	3.78	< 0.001
Nandina domestica	0.36	0.08	154.63	4.58	< 0.001
Phytolacca acinosa	-0.13	0.08	186.87	-1.59	0.11
Phytolacca americana	-0.08	0.08	125.05	-0.98	0.33
Polygonatum multiflorum	0.39	0.08	125.05	4.85	< 0.001
Prunus laucerasus	0.02	0.08	125.05	0.31	0.76
Prunus lusitanica	0.00	0.08	154.63	0.02	0.99
Prunus spinosa	0.28	0.08	187.98	3.58	< 0.001

Fixed effects	Estimate	SE	DF	t value	*p value*
Prunus domesticus subsp. institia	-0.04	0.08	125.05	-0.48	0.63
Pyracantha coccinea	0.19	0.08	561.53	2.51	0.01
Rhamnus cathartica	-0.09	0.08	163.37	-1.17	0.24
Rubus fruticosus var. lockness	-0.13	0.08	163.37	-1.66	0.10
Rubus idaeus	-0.14	0.08	186.87	-1.73	0.09
Sambucus ebulus	-0.16	0.07	158.14	-2.39	0.02
Sambucus nigra	-0.18	0.07	143.48	-2.55	0.01
Sambucus nigra Gold	-0.10	0.08	162.17	-1.30	0.19
Solanum dulcamara	0.28	0.08	187.98	3.50	< 0.001
Solanum nigrum	0.20	0.08	561.53	2.66	0.01
Solanum villosum	0.29	0.08	561.53	3.73	< 0.001
Sorbus americana Belmonte	0.35	0.08	163.37	4.38	< 0.001
Sorbus aucuparia	0.37	0.07	156.61	5.37	< 0.001
Symphoricarpos alba	0.15	0.08	162.17	1.91	0.06
Taxus baccata	-0.06	0.08	186.87	-0.81	0.42
Vaccinium myrtillus	0.09	0.06	199.34	1.41	0.16
Viburnum lantana	0.09	0.08	163.37	1.09	0.28
Viburnum opulus	0.36	0.07	155.83	5.17	< 0.001
Viburnum rhydotiphyllum	0.28	0.08	163.37	3.48	< 0.001
Viburnum tinus	0.36	0.07	172.31	5.14	< 0.001
Vitis vinifera cv. Humagne	0.33	0.07	146.36	5.01	< 0.001

Table S8: Linear model estimate table of egg-laying preference among plant species with *Prunus domesticus subsp. institia* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Prunus domesticus subsp. institia* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	p value
(Intercept)	0.57	0.06	105.12	10.00	< 0.001
Rubus fruticosus var. lockness	-0.09	0.08	140.92	-1.17	0.24
Vaccinium myrtillus	0.12	0.06	145.42	2.03	0.04
Vitis vinifera cv. Humagne	0.36	0.07	115.47	5.58	< 0.001
Lycium barbarum	0.04	0.08	125.05	0.48	0.63
Aronia melanocarpa	0.37	0.07	128.09	5.71	< 0.001
Vitis vinifera cv. Mara	0.39	0.06	111.43	6.58	< 0.001
Ampelopsis brevipedunculatata	0.08	0.08	144.83	1.03	0.31
Atropa belladona	-0.07	0.08	561.53	-0.92	0.36
Basella alba	-0.13	0.08	561.53	-1.75	0.08
Berberis vulgaris	0.41	0.08	125.05	5.18	< 0.001
Callicarpa giraldii	0.42	0.08	153.12	5.30	< 0.001
Cestrum fasciculatum	-0.19	0.08	160.52	-2.33	0.02
Cornus alba	0.00	0.08	144.83	-0.04	0.97
Cornus alba sibirica	-0.06	0.08	144.83	-0.77	0.44
Cornus amomum	-0.17	0.08	158.05	-2.06	0.04
Cornus capitata	0.34	0.09	214.73	3.65	< 0.001
Cornus controversa variegata	0.41	0.08	138.82	5.12	< 0.001
Cornus kousa	0.23	0.08	153.12	2.94	< 0.01
Cornus mas	0.17	0.07	135.69	2.50	0.01
Cornus sanguinea	0.28	0.07	135.69	4.10	< 0.001
Cornus sanguinea winterbeauty	0.26	0.08	155.77	3.16	< 0.01
Cotoneaster divaricatus	0.23	0.08	162.30	2.79	0.01
Cotoneaster obscurus	0.37	0.08	131.06	4.69	< 0.001
Cotoneaster tomentosus	0.32	0.08	138.82	4.02	< 0.001
Eleagnus umbelata	-0.17	0.08	144.83	-2.15	0.03
Frangula alnus	-0.05	0.08	153.12	-0.62	0.54
Hippophae rhamnoides	0.08	0.07	140.59	1.11	0.27
Ilex aquifolium	0.42	0.07	124.72	6.07	< 0.001
Ligustrum vulgare	0.18	0.07	124.72	2.56	0.01
Lonicera xylosteum	-0.07	0.07	140.59	-1.00	0.32
Lycium chinense	0.09	0.08	125.05	1.07	0.29
Lycopersicum pimpinellifolium	0.44	0.08	125.05	5.49	< 0.001
Mahonia aquifolium	-0.05	0.08	140.92	-0.60	0.55
Malus spectabilis	0.36	0.08	153.12	4.57	< 0.001
Myrtus communis	0.34	0.08	131.06	4.25	< 0.001
Nandina domestica	0.40	0.08	131.06	5.05	< 0.001

Fixed effects	Estimate	SE	DF	t value	p value
Phytolacca acinosa	-0.09	0.08	160.52	-1.10	0.27
Phytolacca americana	-0.04	0.08	561.53	-0.53	0.60
Polygonatum multiflorum	0.43	0.08	561.53	5.62	< 0.001
Prunus laucerasus	0.06	0.08	561.53	0.83	0.41
Prunus lusitanica	0.04	0.08	131.06	0.50	0.62
Prunus spinosa	0.32	0.08	182.70	4.07	< 0.001
Pyracantha coccinea	0.23	0.08	125.05	2.86	0.01
Rhamnus cathartica	-0.05	0.08	140.92	-0.69	0.49
Rubus idaeus	-0.10	0.08	160.52	-1.24	0.22
Sambucus ebulus	-0.12	0.07	137.79	-1.81	0.07
Sambucus nigra	-0.14	0.07	478.64	-2.06	0.04
Sambucus nigra Gold	-0.07	0.08	138.82	-0.82	0.41
Solanum dulcamara	0.32	0.08	182.70	3.98	< 0.001
Solanum nigrum	0.24	0.08	125.05	3.00	< 0.01
Solanum villosum	0.33	0.08	140.74	4.01	< 0.001
Sorbus americana Belmonte	0.39	0.08	140.92	4.85	< 0.001
Sorbus aucuparia	0.41	0.07	129.47	5.91	< 0.001
Symphoricarpos alba	0.19	0.08	138.82	2.38	0.02
Taxus baccata	-0.03	0.08	160.52	-0.32	0.75
Viburnum lantana	0.12	0.08	140.92	1.57	0.12
Viburnum opulus	0.39	0.07	138.17	5.72	< 0.001
Viburnum rhydotiphyllum	0.31	0.08	140.92	3.95	< 0.001
Viburnum tinus	0.40	0.07	140.59	5.67	< 0.001

Table S9: Linear model estimate table of egg-laying preference among plant species with *Rubus fruticosus cv. lockness* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Rubus fruticosus cv. lockness* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.47	0.06	167.50	8.42	< 0.001
Prunus domesticus subsp. institia	0.09	0.08	140.92	1.17	0.24
Vaccinium myrtillus	0.22	0.06	187.95	3.57	< 0.001
Vitis vinifera cv. Humagne	0.46	0.06	170.26	7.05	< 0.001
Lycium barbarum	0.13	0.08	163.37	1.66	0.10
Aronia melanocarpa	0.47	0.06	219.76	7.21	< 0.001
Vitis vinifera cv. Mara	0.48	0.06	243.56	8.29	< 0.001
Ampelopsis brevipedunculatata	0.18	0.08	192.87	2.21	0.03
Atropa belladona	0.02	0.08	140.92	0.30	0.76
Basella alba	-0.04	0.08	140.92	-0.49	0.62
Berberis vulgaris	0.51	0.08	163.37	6.38	< 0.001
Callicarpa giraldii	0.52	0.08	207.30	6.51	< 0.001
Cestrum fasciculatum	-0.09	0.08	247.82	-1.16	0.25
Cornus alba	0.09	0.08	192.87	1.13	0.26
Cornus alba sibirica	0.03	0.08	192.87	0.41	0.69
Cornus amomum	-0.08	0.08	561.53	-0.97	0.33
Cornus capitata	0.43	0.09	273.96	4.68	< 0.001
Cornus controversa variegata	0.50	0.08	186.17	6.32	< 0.001
Cornus kousa	0.33	0.08	207.30	4.13	< 0.001
Cornus mas	0.27	0.07	528.43	4.01	< 0.001
Cornus sanguinea	0.38	0.07	528.43	5.66	< 0.001
Cornus sanguinea winterbeauty	0.35	0.08	206.64	4.30	< 0.001
Cotoneaster divaricatus	0.32	0.08	213.73	3.94	< 0.001
Cotoneaster obscurus	0.47	0.08	169.90	5.88	< 0.001
Cotoneaster tomentosus	0.41	0.08	186.17	5.22	< 0.001
Eleagnus umbelata	-0.08	0.08	192.87	-0.98	0.33
Frangula alnus	0.04	0.08	207.30	0.56	0.57
Hippophae rhamnoides	0.17	0.07	218.70	2.45	0.02
Ilex aquifolium	0.51	0.07	179.59	7.46	< 0.001
Ligustrum vulgare	0.27	0.07	179.59	3.93	< 0.001
Lonicera xylosteum	0.02	0.07	242.87	0.36	0.72
Lycium chinense	0.18	0.08	163.37	2.25	0.03
Lycopersicum pimpinellifolium	0.53	0.08	163.37	6.69	< 0.001
Mahonia aquifolium	0.05	0.08	561.53	0.61	0.55
Malus spectabilis	0.46	0.08	207.30	5.77	< 0.001
Myrtus communis	0.43	0.08	169.90	5.45	< 0.001
Nandina domestica	0.50	0.08	169.90	6.25	< 0.001

Fixed effects	Estimate	SE	DF	t value	*p value*
Phytolacca acinosa	0.01	0.08	247.82	0.07	0.94
Phytolacca americana	0.05	0.08	140.92	0.67	0.50
Polygonatum multiflorum	0.52	0.08	140.92	6.51	< 0.001
Prunus laucerasus	0.16	0.08	140.92	1.96	0.05
Prunus lusitanica	0.13	0.08	169.90	1.67	0.10
Prunus spinosa	0.42	0.08	278.20	5.28	< 0.001
Pyracantha coccinea	0.32	0.08	163.37	4.04	< 0.001
Rhamnus cathartica	0.04	0.08	561.53	0.51	0.61
Rubus idaeus	-0.01	0.08	247.82	-0.07	0.95
Sambucus ebulus	-0.03	0.07	239.45	-0.42	0.68
Sambucus nigra	-0.04	0.07	198.87	-0.64	0.52
Sambucus nigra Gold	0.03	0.08	186.17	0.35	0.72
Solanum dulcamara	0.41	0.08	278.20	5.19	< 0.001
Solanum nigrum	0.33	0.08	163.37	4.19	< 0.001
Solanum villosum	0.43	0.08	182.31	5.16	< 0.001
Sorbus americana Belmonte	0.48	0.08	561.53	6.34	< 0.001
Sorbus aucuparia	0.50	0.07	516.32	7.55	< 0.001
Symphoricarpos alba	0.28	0.08	186.17	3.57	< 0.001
Taxus baccata	0.07	0.08	247.82	0.86	0.39
Viburnum lantana	0.22	0.08	561.53	2.89	< 0.01
Viburnum opulus	0.49	0.07	218.97	7.13	< 0.001
Viburnum rhydotiphyllum	0.41	0.08	561.53	5.39	< 0.001
Viburnum tinus	0.49	0.07	218.70	7.03	< 0.001

Table S10: Linear model estimate table of egg-laying preference among plant species with *Rubus idaeus* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Rubus idaeus* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.47	0.06	230.09	8.37	< 0.001
Prunus domesticus subsp. institia	0.10	0.08	160.52	1.24	0.22
Rubus fruticosus var. lockness	0.01	0.08	247.82	0.07	0.95
Vaccinium myrtillus	0.22	0.06	307.08	3.70	< 0.001
Vitis vinifera cv. Humagne	0.46	0.06	235.77	7.18	< 0.001
Lycium barbarum	0.14	0.08	186.87	1.73	0.09
Aronia melanocarpa	0.47	0.06	481.36	7.47	< 0.001
Vitis vinifera cv. Mara	0.49	0.06	335.04	8.43	< 0.001
Ampelopsis brevipedunculatata	0.18	0.08	249.68	2.29	0.02
Atropa belladona	0.03	0.08	160.52	0.37	0.71
Basella alba	-0.03	0.08	160.52	-0.43	0.67
Berberis vulgaris	0.51	0.08	186.87	6.46	< 0.001
Callicarpa giraldii	0.52	0.08	285.23	6.61	< 0.001
Cestrum fasciculatum	-0.09	0.08	561.53	-1.14	0.25
Cornus alba	0.10	0.08	249.68	1.21	0.23
Cornus alba sibirica	0.04	0.08	249.68	0.48	0.64
Cornus amomum	-0.07	0.08	270.99	-0.87	0.38
Cornus capitata	0.44	0.09	318.34	4.75	< 0.001
Cornus controversa variegata	0.51	0.08	225.39	6.40	< 0.001
Cornus kousa	0.33	0.08	285.23	4.22	< 0.001
Cornus mas	0.27	0.07	289.89	3.98	< 0.001
Cornus sanguinea	0.38	0.07	289.89	5.60	< 0.001
Cornus sanguinea winterbeauty	0.36	0.08	247.83	4.38	< 0.001
Cotoneaster divaricatus	0.33	0.08	272.91	4.02	< 0.001
Cotoneaster obscurus	0.47	0.08	205.02	5.97	< 0.001
Cotoneaster tomentosus	0.42	0.08	225.39	5.30	< 0.001
Eleagnus umbelata	-0.07	0.08	249.68	-0.92	0.36
Frangula alnus	0.05	0.08	285.23	0.63	0.53
Hippophae rhamnoides	0.18	0.07	497.55	2.59	0.01
Ilex aquifolium	0.52	0.07	254.16	7.58	< 0.001
Ligustrum vulgare	0.28	0.07	254.16	4.03	< 0.001
Lonicera xylosteum	0.03	0.07	544.59	0.45	0.65
Lycium chinense	0.18	0.08	186.87	2.32	0.02
Lycopersicum pimpinellifolium	0.54	0.08	186.87	6.77	< 0.001
Mahonia aquifolium	0.05	0.08	247.82	0.65	0.52
Malus spectabilis	0.46	0.08	285.23	5.87	< 0.001

Fixed effects	Estimate	SE	DF	t value	*p value*
Myrtus communis	0.44	0.08	205.02	5.53	< 0.001
Nandina domestica	0.50	0.08	205.02	6.34	< 0.001
Phytolacca acinosa	0.01	0.08	561.53	0.15	0.88
Phytolacca americana	0.06	0.08	160.52	0.74	0.46
Polygonatum multiflorum	0.52	0.08	160.52	6.59	< 0.001
Prunus laucerasus	0.16	0.08	160.52	2.03	0.04
Prunus lusitanica	0.14	0.08	205.02	1.75	0.08
Prunus spinosa	0.42	0.08	332.61	5.36	< 0.001
Pyracantha coccinea	0.33	0.08	186.87	4.12	< 0.001
Rhamnus cathartica	0.04	0.08	247.82	0.56	0.58
Sambucus ebulus	-0.02	0.06	522.88	-0.35	0.73
Sambucus nigra	-0.04	0.07	245.93	-0.56	0.57
Sambucus nigra Gold	0.03	0.08	225.39	0.42	0.67
Solanum dulcamara	0.41	0.08	332.61	5.28	< 0.001
Solanum nigrum	0.34	0.08	186.87	4.27	< 0.001
Solanum villosum	0.43	0.08	207.40	5.23	< 0.001
Sorbus americana Belmonte	0.49	0.08	247.82	6.15	< 0.001
Sorbus aucuparia	0.51	0.07	516.32	7.63	< 0.001
Symphoricarpos alba	0.29	0.08	225.39	3.65	< 0.001
Taxus baccata	0.07	0.08	561.53	0.97	0.33
Viburnum lantana	0.22	0.08	247.82	2.83	0.01
Viburnum opulus	0.49	0.07	281.15	7.24	< 0.001
Viburnum rhydotiphyllum	0.41	0.08	247.82	5.24	< 0.001
Viburnum tinus	0.50	0.07	497.55	7.30	< 0.001

Table S11: Linear model estimate table of egg-laying preference among plant species with *Sambucus nigra* as reference level

Linear model estimate table of the egg number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Sambucus nigra* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.43	0.04	130.43	10.77	< 0.001
Rubus idaeus	0.04	0.07	245.93	0.56	0.57
Prunus domesticus subsp. institia	0.14	0.07	478.64	2.06	0.04
Rubus fruticosus var. lockness	0.04	0.07	198.87	0.64	0.52
Vaccinium myrtillus	0.26	0.05	208.51	5.68	< 0.001
Vitis vinifera cv. Humagne	0.50	0.05	148.12	9.76	< 0.001
Lycium barbarum	0.18	0.07	143.48	2.55	0.01
Aronia melanocarpa	0.51	0.05	287.78	10.11	< 0.001
Vitis vinifera cv. Mara	0.53	0.04	187.59	12.20	< 0.001
Ampelopsis brevipedunculatata	0.22	0.07	189.14	3.19	< 0.01
Atropa belladona	0.07	0.07	478.64	1.02	0.31
Basella alba	0.00	0.07	478.64	0.07	0.95
Berberis vulgaris	0.55	0.07	143.48	7.98	< 0.001
Callicarpa giraldii	0.56	0.07	195.96	8.15	< 0.001
Cestrum fasciculatum	-0.05	0.07	245.93	-0.70	0.49
Cornus alba	0.13	0.07	189.14	1.95	0.05
Cornus alba sibirica	0.08	0.07	189.14	1.11	0.27
Cornus amomum	-0.03	0.07	227.03	-0.46	0.65
Cornus capitata	0.47	0.08	298.16	5.72	< 0.001
Cornus controversa variegata	0.55	0.07	184.57	7.93	< 0.001
Cornus kousa	0.37	0.07	195.96	5.41	< 0.001
Cornus mas	0.31	0.05	327.86	5.64	< 0.001
Cornus sanguinea	0.42	0.05	327.86	7.65	< 0.001
Cornus sanguinea winterbeauty	0.40	0.07	211.66	5.52	< 0.001
Cotoneaster divaricatus	0.37	0.07	216.60	5.11	< 0.001
Cotoneaster obscurus	0.51	0.07	155.82	7.42	< 0.001
Cotoneaster tomentosus	0.46	0.07	184.57	6.67	< 0.001
Eleagnus umbelata	-0.03	0.07	189.14	-0.49	0.62
Frangula alnus	0.09	0.07	195.96	1.29	0.20
Hippophae rhamnoides	0.22	0.06	206.02	3.71	< 0.001
Ilex aquifolium	0.56	0.06	157.84	9.90	< 0.001
Ligustrum vulgare	0.31	0.06	157.84	5.59	< 0.001
Lonicera xylosteum	0.07	0.05	354.56	1.25	0.21
Lycium chinense	0.22	0.07	143.48	3.22	< 0.01
Lycopersicum pimpinellifolium	0.58	0.07	143.48	8.34	< 0.001
Mahonia aquifolium	0.09	0.07	198.87	1.31	0.19
Malus spectabilis	0.50	0.07	195.96	7.30	< 0.001
Myrtus communis	0.48	0.07	155.82	6.92	< 0.001

Fixed effects	Estimate	SE	DF	t value	*p value*
Nandina domestica	0.54	0.07	155.82	7.84	< 0.001
Phytolacca acinosa	0.05	0.07	245.93	0.72	0.47
Phytolacca americana	0.10	0.07	478.64	1.46	0.14
Polygonatum multiflorum	0.56	0.07	478.64	8.45	< 0.001
Prunus laucerasus	0.20	0.07	478.64	3.01	< 0.01
Prunus lusitanica	0.18	0.07	155.82	2.57	0.01
Prunus spinosa	0.46	0.07	478.64	6.90	< 0.001
Pyracantha coccinea	0.37	0.07	143.48	5.30	< 0.001
Rhamnus cathartica	0.08	0.07	198.87	1.20	0.23
Sambucus ebulus	0.02	0.05	342.60	0.31	0.76
Sambucus nigra Gold	0.07	0.07	184.57	1.05	0.30
Solanum dulcamara	0.45	0.07	478.64	6.80	< 0.001
Solanum nigrum	0.38	0.07	143.48	5.47	< 0.001
Solanum villosum	0.47	0.07	166.63	6.48	< 0.001
Sorbus americana Belmonte	0.52	0.07	198.87	7.64	< 0.001
Sorbus aucuparia	0.55	0.06	208.69	9.75	< 0.001
Symphoricarpos alba	0.33	0.07	184.57	4.76	< 0.001
Taxus baccata	0.11	0.07	245.93	1.63	0.10
Viburnum lantana	0.26	0.07	198.87	3.82	< 0.001
Viburnum opulus	0.53	0.05	324.80	9.68	< 0.001
Viburnum rhydotiphyllum	0.45	0.07	198.87	6.59	< 0.001
Viburnum tinus	0.538629	0.058196	206.018943	9.255	< 0.001

Table S12: Linear model estimate table of the SWD emergence success among plant species

Linear model estimate table of the emergence success (Box-cox transformed) according to candidate trap crop plant species. We used *Vitis vinifera cv. Mara* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.89	0.07	71.33	13.69	< 0.001
Ampelopsis brevipedunculatata	0.10	0.14	270.60	0.74	0.46
Aronia melanocarpa	0.13	0.12	274.60	1.15	0.25
Atropa belladona	-0.52	0.13	98.63	-4.16	< 0.001
Basella alba	-0.54	0.13	98.63	-4.32	< 0.001
Berberis vulgaris	0.05	0.24	307.45	0.19	0.85
Cestrum fasciculatum	0.04	0.12	252.20	0.35	0.73
Cornus alba	-0.49	0.12	239.02	-4.05	< 0.001
Cornus alba sibirica	-0.26	0.12	239.02	-2.14	0.03
Cornus amomum	-0.10	0.12	246.41	-0.79	0.43
Cornus capitata	0.03	0.18	298.70	0.15	0.88
Cornus controversa variegata	0.03	0.24	309.68	0.11	0.91
Cornus kousa	-0.48	0.13	227.87	-3.69	< 0.001
Cornus mas	-0.15	0.10	250.62	-1.56	0.12
Cornus sanguinea	0.13	0.11	273.33	1.20	0.23
Cornus sanguinea winterbeauty	0.03	0.14	260.33	0.19	0.85
Cotoneaster divaricatus	0.05	0.15	287.63	0.33	0.75
Cotoneaster obscurus	0.15	0.15	284.91	0.98	0.33
Cotoneaster tomentosus	0.03	0.15	280.07	0.17	0.86
Eleagnus umbelata	-0.07	0.12	225.75	-0.58	0.56
Frangula alnus	-0.58	0.12	196.19	-4.87	< 0.001
Hippophae rhamnoides	0.14	0.10	225.95	1.43	0.15
Ligustrum vulgare	0.18	0.10	161.10	1.74	0.08
Lonicera xylosteum	-0.26	0.09	225.56	-2.72	0.03
Lycium barbarum	-0.75	0.12	169.74	-6.29	< 0.001
Lycium chinense	-0.69	0.12	184.79	-5.57	< 0.001
Mahonia aquifolium	-0.41	0.11	233.74	-3.58	< 0.001
Malus spectabilis	0.23	0.18	294.05	1.27	0.20
Myrtus communis	0.15	0.15	284.91	0.98	0.33
Nandina domestica	0.15	0.18	301.20	0.84	0.40
Phytolacca acinosa	0.04	0.12	252.20	0.35	0.73
Phytolacca americana	0.10	0.13	98.63	0.78	0.44
Prunus laucerasus	0.00	0.13	98.63	-0.03	0.97
Prunus lusitanica	0.15	0.12	234.37	1.23	0.22
Prunus spinosa	0.18	0.15	295.87	1.20	0.23
Prunus domestica subsp. institia	0.07	0.13	110.17	0.53	0.60
Pyracantha coccinea	0.05	0.12	184.79	0.37	0.71

Fixed effects	Estimate	SE	DF	t value	*p value*
Rhamnus cathartica	-0.45	0.11	233.74	-3.90	< 0.001
Rubus fruticosus var. lockness	-0.80	0.11	233.74	-6.94	< 0.001
Rubus idaeus	-0.86	0.12	252.20	-7.48	< 0.001
Sambucus ebulus	-0.68	0.09	235.29	-7.84	< 0.001
Sambucus nigra	-0.33	0.10	137.47	-3.44	< 0.001
Sambucus nigra Gold	-0.55	0.12	212.48	-4.62	< 0.001
Solanum dulcamara	0.18	0.14	283.14	1.33	0.19
Solanum nigrum	-0.38	0.15	254.40	-2.48	0.03
Solanum villosum	-0.54	0.15	254.40	-3.48	< 0.001
Sorbus americana Belmonte	0.01	0.18	304.17	0.07	0.94
Sorbus aucuparia	0.03	0.17	309.99	0.15	0.88
Symphoricarpos alba	-0.27	0.14	260.33	-1.94	0.05
Taxus baccata	-0.39	0.12	252.20	-3.42	< 0.001
Vaccinium myrtillus	-0.40	0.07	301.38	-5.47	< 0.001
Viburnum lantana	0.01	0.12	246.41	0.10	0.92
Viburnum opulus	0.18	0.15	295.87	1.20	0.23
Viburnum rhydotiphyllum	0.01	0.14	275.82	0.09	0.93
Viburnum tinus	0.04	0.18	306.87	0.23	0.82
Vitis cv. Humagne	0.08	0.11	281.53	0.74	0.46

Table S13: Linear model estimate table of the SWD emergence number per gram of fruit among plant species

Linear model estimate table of the emergence number per gram of fruit (Box-cox transformed) according to candidate trap crop plant species. We used *Vitis vinifera cv. Mara* as reference level (intercept). SE stands for standard error and DF for degrees of freedom. Unintuitively, negative estimates express an increase in egg number per gram of fruit compared to the reference level. This is due the negative Box-Cox transformation factor.

Fixed effects	Estimate	SE	DF	t value	*p value*
(Intercept)	0.96	0.05	102.42	21.31	< 0.001
Ampelopsis brevipeduncula	-0.03	0.10	251.11	-0.26	0.80
Aronia melanocarpa	0.06	0.08	261.08	0.75	0.45
Atropa belladona	-0.51	0.09	84.20	-5.84	< 0.001
Basella alba	-0.62	0.09	84.20	-7.13	< 0.001
Berberis vulgaris	0.01	0.17	304.61	0.08	0.94
Cestrum fasciculatum	-0.02	0.08	222.59	-0.19	0.85
Cornus alba	-0.56	0.09	211.98	-6.58	< 0.001
Cornus alba sibirica	-0.45	0.09	211.98	-5.22	< 0.001
Cornus amonum	-0.23	0.09	221.24	-2.69	< 0.01
Cornus capitata	-0.01	0.13	287.91	-0.07	0.94
Cornus controversa variegata	-0.01	0.17	307.85	-0.05	0.96
Cornus kousa	-0.35	0.09	199.36	-3.77	< 0.001
Cornus mas	-0.16	0.07	236.94	-2.29	0.02
Cornus sanguinea	0.08	0.08	261.72	0.97	0.33
Cornus sanguinea winterbeauty	-0.01	0.10	233.61	-0.09	0.93
Cotoneaster divaricatus	-0.07	0.11	273.93	-0.66	0.51
Cotoneaster obscurus	0.07	0.11	268.70	0.67	0.51
Cotoneaster tomentosus	-0.01	0.11	260.27	-0.08	0.94
Eleagnus umbelata	-0.24	0.08	196.49	-2.88	< 0.01
Frangula alnus	-0.59	0.08	164.20	-7.03	< 0.001
Hippophae rhamnoides	0.00	0.07	200.65	0.05	0.96
Ligustrum vulgare	0.06	0.07	145.14	0.81	0.42
Lonicera xylosteum	-0.34	0.07	203.23	-5.07	< 0.001
Lycium barbarum	-0.53	0.08	143.20	-6.33	< 0.001
Lycium chinense	-0.50	0.09	158.76	-5.75	< 0.001
Mahonia aquilefolium	-0.33	0.08	206.19	-4.04	< 0.001
Malus spectabilis	0.06	0.13	283.16	0.50	0.62
Myrtus communis	0.07	0.11	268.70	0.67	0.51
Nandina domestica	0.07	0.13	292.76	0.57	0.57
Phytolacca acinosa	-0.02	0.08	222.59	-0.19	0.85
Phytolacca americana	0.04	0.09	84.20	0.48	0.63
Prunus laucerasus	-0.06	0.09	84.20	-0.70	0.49
Prunus lusitanica	0.07	0.09	203.94	0.84	0.40
Prunus spinosa	0.10	0.11	286.45	0.94	0.35
Prunus tenellus	0.02	0.09	95.47	0.23	0.82
Pyracantha coccinea	0.01	0.09	158.76	0.16	0.87

Fixed effects	Estimate	SE	DF	t value	*p value*
Rhamnus cathartica	-0.43	0.08	206.19	-5.34	< 0.001
Rubus fruticosus lockness	-0.71	0.08	206.19	-8.73	< 0.001
Rubus idaeus	-0.84	0.08	222.59	-10.29	< 0.001
Sambucus ebulus	-0.72	0.06	216.42	-11.56	< 0.001
Sambucus nigra	-0.49	0.07	125.02	-7.23	< 0.001
Sambucus nigra fruitjaune	-0.53	0.08	176.04	-6.35	0.00
Solanum dulcamara	0.10	0.10	269.00	1.04	0.30
Solanum nigrum	-0.35	0.11	236.31	-3.21	< 0.01
Solanum villosum	-0.24	0.11	236.31	-2.14	0.03
Sorbus americana belmonte	0.01	0.13	298.30	0.10	0.92
Sorbus aucuparia	0.00	0.13	309.83	-0.01	0.99
Symphoricarpos alba	-0.19	0.10	233.61	-1.87	0.06
Taxus baccata	-0.39	0.08	222.59	-4.82	< 0.001
Vaccinium myrtillus	-0.35	0.05	299.75	-6.70	< 0.001
Viburnum lantana	0.01	0.09	221.24	0.15	0.88
Viburnum opulus	0.10	0.11	286.45	0.94	0.35
Viburnum rhydotiphyllum	0.01	0.10	258.25	0.13	0.89
Viburnum tinus	-0.02	0.13	301.64	-0.12	0.90
Vitis humagne	0.00	0.08	275.69	0.06	0.95

Table S14: Multiple pairwise comparison for SWD development time among plant species

Multiple pairwise comparison following the linear model between SWD development time among plant species. Results are averaged over the level sex.

Plant species comparison		Estimate	*SE*	*df*	*p-value*
Viburnum lantana	*Ampelopsis brevipedunculata*	-8.06	2.27	351.2	0.24
	Atropa belladona	-7.15	1.74	281.3	0.03
	Basella alba	-8.26	1.74	282.5	< 0.01
	Cornus alba	-7.07	1.89	224	0.12
	Cornus alba sibirica	-7.43	1.92	234	0.07
	Cornus amonum	-7.28	1.51	496.5	< 0.01
	Cornus kousa	-8.08	1.83	229.2	0.01
	Cornus mas	-8.77	1.63	436.9	< 0.001
	Cotoneaster divaricatus	-8.95	2.27	350.1	0.05
	Eleagnus umbelata	-7.19	1.96	240	0.16
	Frangula alnus	-7.64	1.81	227.7	0.02
	Hippophae rhamnoides	-11.06	2.25	364.2	< 0.001
	Lonicera xylosteum	-7.25	1.70	317.3	0.01
	Lycium barbarum	-6.23	1.82	222.9	0.40
	Lycium chinense	-6.28	1.84	227.2	0.39
	Mahonia aquilfolium	-9.86	1.47	507.1	< 0.001
	Phytolacca americana	-7.71	2.21	421.5	0.27
	Prunus laucerasus	-10.49	1.90	258.3	<.0001
	Prunus domesticus subsp. institia	-9.71	2.21	421.5	0.01
	Rhamnus cathartica	-7.80	1.45	483.1	< 0.001
	Rubus fruticosus var. lockness lockness	-5.88	1.42	475.1	0.02
	Rubus Idaeus	-5.19	1.72	286.5	1.00
	Sambucus ebulus	-5.73	1.68	302.4	0.40
	Sambucus nigra	-6.67	1.70	302.3	0.06
	Sambucus nigra Gold	-7.50	1.76	277.1	0.02
	Solanum nigrum	-6.38	1.96	271.6	0.66
	Solanum villosum	-5.26	1.98	266	1.00
	Symphoricarpos alba	-9.21	1.98	354.5	<0.01
	Taxus baccata	-7.73	1.76	303.7	0.01
	Vaccinium myrtillus	-10.05	1.71	248.3	<.0001
	Vitis vinifera cv. Humagne	-7.58	2.10	273.9	0.19
	Vitis vinifera cv. Mara	-8.11	1.85	296	0.01
Ampelopsis brevipedunculata	*Atropa belladona*	0.90	1.64	387.9	1.00
	Basella alba	-0.20	1.63	392.8	1.00
	Cornus alba	0.99	1.50	430.4	1.00
	Cornus alba sibirica	0.63	1.53	443.7	1.00
	Cornus amonum	0.78	1.90	238.1	1.00
	Cornus kousa	-0.02	1.66	388.2	1.00
	Cornus mas	-0.71	1.65	392.4	1.00
	Cotoneaster divaricatus	-0.89	1.96	533.7	1.00
	Eleagnus umbelata	0.87	1.58	413.8	1.00
	Frangula alnus	0.42	1.64	408.3	1.00
	Hippophae rhamnoides	-3.00	2.12	489.1	1.00
	Lonicera xylosteum	0.81	1.61	409.8	1.00
	Lycium barbarum	1.83	1.66	390.3	1.00
	Lycium chinense	1.78	1.67	394.8	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Mahonia aquilfolium	-1.80	1.87	229.5	1.00
	Phytolacca americana	0.34	2.12	482.5	1.00
	Prunus laucerasus	-2.43	1.80	290.7	1.00
	Prunus domesticus subsp. institia	-1.66	2.12	482.5	1.00
	Rhamnus cathartica	0.26	1.85	219.8	1.00
	Rubus fruticosus var. lockness lockness	2.18	1.83	212.8	1.00
	Rubus Idaeus	2.87	1.61	398.8	1.00
	Sambucus ebulus	2.33	1.58	428.7	1.00
	Sambucus nigra	1.39	1.60	418.1	1.00
	Sambucus nigra Gold	0.56	1.65	403.3	1.00
	Solanum nigrum	1.68	1.80	442.2	1.00
	Solanum villosum	2.80	1.83	405.8	1.00
	Symphoricarpos alba	-1.15	1.88	462.5	1.00
	Taxus baccata	0.32	1.65	416.6	1.00
	Vaccinium myrtillus	-1.99	1.53	478.3	1.00
	Vitis vinifera cv. Humagne	0.48	1.96	368	1.00
	Vitis vinifera cv. Mara	-0.05	1.65	489.7	1.00
Atropa belladona	*Basella alba*	-1.11	0.45	80.6	1.00
	Cornus alba	0.09	1.04	140.7	1.00
	Cornus alba sibirica	-0.27	1.09	163.4	1.00
	Cornus amonum	-0.13	1.22	97.9	1.00
	Cornus kousa	-0.92	0.92	127.5	1.00
	Cornus mas	-1.61	0.73	140.4	1.00
	Cotoneaster divaricatus	-1.79	1.64	388.4	1.00
	Eleagnus umbelata	-0.03	1.16	169.6	1.00
	Frangula alnus	-0.48	0.87	127	1.00
	Hippophae rhamnoides	-3.91	1.61	394.1	1.00
	Lonicera xylosteum	-0.09	0.64	119	1.00
	Lycium barbarum	0.92	0.90	126	1.00
	Lycium chinense	0.87	0.93	137.4	1.00
	Mahonia aquilfolium	-2.71	1.17	84.3	1.00
	Phytolacca americana	-0.56	1.43	469.6	1.00
	Prunus laucerasus	-3.34	0.89	86.9	0.17
	Prunus domesticus subsp. institia	-2.56	1.43	469.6	1.00
	Rhamnus cathartica	-0.65	1.13	73.7	1.00
	Rubus fruticosus var. lockness lockness	1.27	1.10	65.3	1.00
	Rubus Idaeus	1.96	0.69	102.1	1.00
	Sambucus ebulus	1.42	0.59	111.9	1.00
	Sambucus nigra	0.49	0.45	94.1	1.00
	Sambucus nigra Gold	-0.35	0.79	123.9	1.00
	Solanum nigrum	0.77	1.15	250.3	1.00
	Solanum villosum	1.90	1.19	220.1	1.00
	Symphoricarpos alba	-2.05	1.21	307.5	1.00
	Taxus baccata	-0.58	0.78	151.2	1.00
	Vaccinium myrtillus	-2.90	0.63	129.1	< 0.01
	Vitis vinifera cv. Humagne	-0.43	1.38	217.4	1.00
	Vitis vinifera cv. Mara	-0.95	0.97	227	1.00
Basella alba	*Cornus alba*	1.19	1.03	142.1	1.00
	Cornus alba sibirica	0.83	1.08	165.2	1.00
	Cornus amonum	0.98	1.21	97.2	1.00
	Cornus kousa	0.18	0.91	129.2	1.00
	Cornus mas	-0.51	0.72	144.9	1.00
	Cotoneaster divaricatus	-0.69	1.63	393.2	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Eleagnus umbelata	1.07	1.15	171.7	1.00
	Frangula alnus	0.62	0.87	128.7	1.00
	Hippophae rhamnoides	-2.80	1.60	399.6	1.00
	Lonicera xylosteum	1.01	0.63	123.5	1.00
	Lycium barbarum	2.03	0.90	127.4	1.00
	Lycium chinense	1.98	0.92	139.2	1.00
	Mahonia aquilfolium	-1.60	1.16	83.5	1.00
	Phytolacca americana	0.55	1.42	479.1	1.00
	Prunus laucerasus	-2.23	0.88	87.9	1.00
	Prunus domesticus subsp. institia	-1.45	1.42	479.1	1.00
	Rhamnus cathartica	0.46	1.13	72.9	1.00
	Rubus fruticosus var. lockness lockness	2.38	1.09	64.5	1.00
	Rubus Idaeus	3.07	0.68	104.7	0.01
	Sambucus ebulus	2.53	0.58	116.2	0.02
	Sambucus nigra	1.59	0.44	99.4	0.23
	Sambucus nigra Gold	0.76	0.79	126.8	1.00
	Solanum nigrum	1.88	1.14	254.7	1.00
	Solanum villosum	3.00	1.19	223.7	1.00
	Symphoricarpos alba	-0.95	1.20	314.8	1.00
	Taxus baccata	0.53	0.77	156.1	1.00
	Vaccinium myrtillus	-1.79	0.62	133	1.00
	Vitis vinifera cv. Humagne	0.68	1.37	220.2	1.00
	Vitis vinifera cv. Mara	0.15	0.97	233.4	1.00
Cornus alba	*Cornus alba sibirica*	-0.36	0.87	170.8	1.00
	Cornus amonum	-0.21	1.42	90	1.00
	Cornus kousa	-1.01	1.08	156.6	1.00
	Cornus mas	-1.70	1.06	142.3	1.00
	Cotoneaster divaricatus	-1.88	1.50	429.3	1.00
	Eleagnus umbelata	-0.12	0.95	170.9	1.00
	Frangula alnus	-0.57	1.04	159.4	1.00
	Hippophae rhamnoides	-3.99	1.70	381.1	1.00
	Lonicera xylosteum	-0.18	1.00	144.3	1.00
	Lycium barbarum	0.84	1.07	152.5	1.00
	Lycium chinense	0.79	1.09	161.2	1.00
	Mahonia aquilfolium	-2.79	1.38	80.6	1.00
	Phytolacca americana	-0.65	1.70	372.8	1.00
	Prunus laucerasus	-3.42	1.28	129.7	1.00
	Prunus domesticus subsp. institia	-2.65	1.70	372.8	1.00
	Rhamnus cathartica	-0.73	1.34	73.1	1.00
	Rubus fruticosus var. lockness lockness	1.19	1.32	67.2	1.00
	Rubus Idaeus	1.88	1.00	138.5	1.00
	Sambucus ebulus	1.34	0.95	141.8	1.00
	Sambucus nigra	0.40	0.98	143.9	1.00
	Sambucus nigra Gold	-0.43	1.05	154.5	1.00
	Solanum nigrum	0.69	1.29	251.3	1.00
	Solanum villosum	1.81	1.32	225.1	1.00
	Symphoricarpos alba	-2.14	1.39	296.2	1.00
	Taxus baccata	-0.67	1.06	169.7	1.00
	Vaccinium myrtillus	-2.98	0.85	168.9	0.30
	Vitis vinifera cv. Humagne	-0.51	1.49	222.9	1.00
	Vitis vinifera cv. Mara	-1.04	1.06	267.8	1.00
Cornus alba sibirica	*Cornus amonum*	0.15	1.46	99.4	1.00
	Cornus kousa	-0.65	1.13	178.7	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Cornus mas	-1.34	1.11	164.6	1.00
	Cotoneaster divaricatus	-1.52	1.53	443.9	1.00
	Eleagnus umbelata	0.24	1.01	197.4	1.00
	Frangula alnus	-0.21	1.09	183.9	1.00
	Hippophae rhamnoides	-3.63	1.73	393.7	1.00
	Lonicera xylosteum	0.18	1.06	169.1	1.00
	Lycium barbarum	1.20	1.12	174.7	1.00
	Lycium chinense	1.15	1.14	183.4	1.00
	Mahonia aquilfolium	-2.43	1.41	89.8	1.00
	Phytolacca americana	-0.29	1.73	384.5	1.00
	Prunus laucerasus	-3.06	1.33	142.9	1.00
	Prunus domesticus subsp. institia	-2.29	1.73	384.5	1.00
	Rhamnus cathartica	-0.37	1.38	82	1.00
	Rubus fruticosus var. lockness lockness	1.55	1.36	75.8	1.00
	Rubus Idaeus	2.24	1.05	162.8	1.00
	Sambucus ebulus	1.70	1.01	169.3	1.00
	Sambucus nigra	0.76	1.04	169.9	1.00
	Sambucus nigra Gold	-0.07	1.10	178	1.00
	Solanum nigrum	1.05	1.33	271.3	1.00
	Solanum villosum	2.17	1.36	243.3	1.00
	Symphoricarpos alba	-1.78	1.43	313.8	1.00
	Taxus baccata	-0.31	1.11	193.8	1.00
	Vaccinium myrtillus	-2.62	0.91	206.2	1.00
	Vitis vinifera cv. Humagne	-0.15	1.53	236.4	1.00
	Vitis vinifera cv. Mara	-0.68	1.11	296.2	1.00
Cornus amonum	*Cornus kousa*	-0.79	1.34	84.5	1.00
	Cornus mas	-1.48	1.05	173.2	1.00
	Cotoneaster divaricatus	-1.66	1.90	237.8	1.00
	Eleagnus umbelata	0.09	1.51	110	1.00
	Frangula alnus	-0.35	1.31	78.8	1.00
	Hippophae rhamnoides	-3.78	1.88	251	1.00
	Lonicera xylosteum	0.04	1.15	104.5	1.00
	Lycium barbarum	1.05	1.33	79	1.00
	Lycium chinense	1.00	1.35	83.2	1.00
	Mahonia aquilfolium	-2.58	0.79	341.3	0.60
	Phytolacca americana	-0.43	1.82	310.5	1.00
	Prunus laucerasus	-3.21	1.44	126.7	1.00
	Prunus domesticus subsp. institia	-2.43	1.82	310.5	1.00
	Rhamnus cathartica	-0.52	0.73	269.1	1.00
	Rubus fruticosus var. lockness lockness	1.40	0.68	230.7	1.00
	Rubus Idaeus	2.09	1.18	94.7	1.00
	Sambucus ebulus	1.55	1.13	90.6	1.00
	Sambucus nigra	0.61	1.15	95.1	1.00
	Sambucus nigra Gold	-0.22	1.24	99.3	1.00
	Solanum nigrum	0.90	1.51	126.9	1.00
	Solanum villosum	2.03	1.54	130.4	1.00
	Symphoricarpos alba	-1.92	1.54	201.2	1.00
	Taxus baccata	-0.45	1.24	112.5	1.00
	Vaccinium myrtillus	-2.77	1.17	70.2	1.00
	Vitis vinifera cv. Humagne	-0.30	1.69	156.6	1.00
	Vitis vinifera cv. Mara	-0.82	1.37	127.4	1.00
Cornus kousa	*Cornus mas*	-0.69	0.95	133.2	1.00
	Cotoneaster divaricatus	-0.87	1.66	388.6	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Eleagnus umbelata	0.89	1.19	181.3	1.00
	Frangula alnus	0.44	0.56	106.1	1.00
	Hippophae rhamnoides	-2.99	1.46	445.9	1.00
	Lonicera xylosteum	0.83	0.88	132.2	1.00
	Lycium barbarum	1.85	0.95	139.1	1.00
	Lycium chinense	1.79	0.98	149.4	1.00
	Mahonia aquilfolium	-1.78	1.29	74.4	1.00
	Phytolacca americana	0.36	1.63	381.2	1.00
	Prunus laucerasus	-2.42	1.19	117.3	1.00
	Prunus domesticus subsp. institia	-1.64	1.63	381.2	1.00
	Rhamnus cathartica	0.28	1.26	66.6	1.00
	Rubus fruticosus var. lockness lockness	2.20	1.23	60.4	1.00
	Rubus Idaeus	2.88	0.88	124.1	0.69
	Sambucus ebulus	2.35	0.83	128.5	1.00
	Sambucus nigra	1.41	0.86	131.3	1.00
	Sambucus nigra Gold	0.58	0.94	142.9	1.00
	Solanum nigrum	1.69	1.19	253	1.00
	Solanum villosum	2.82	1.23	221.1	1.00
	Symphoricarpos alba	-1.13	1.31	302.2	1.00
	Taxus baccata	0.34	0.95	160.5	1.00
	Vaccinium myrtillus	-1.98	0.69	139.6	1.00
	Vitis vinifera cv. Humagne	0.49	1.41	216.4	1.00
	Vitis vinifera cv. Mara	-0.03	0.98	261.3	1.00
Cornus mas	*Cotoneaster divaricatus*	-0.18	1.65	392.2	1.00
	Eleagnus umbelata	1.58	1.18	173.3	1.00
	Frangula alnus	1.13	0.90	130.6	1.00
	Hippophae rhamnoides	-2.29	1.62	403.5	1.00
	Lonicera xylosteum	1.52	0.58	162.5	1.00
	Lycium barbarum	2.54	0.94	127.4	1.00
	Lycium chinense	2.49	0.96	138.5	1.00
	Mahonia aquilfolium	-1.09	0.99	146.2	1.00
	Phytolacca americana	1.05	1.53	439.7	1.00
	Prunus laucerasus	-1.72	1.05	112.6	1.00
	Prunus domesticus subsp. institia	-0.95	1.53	439.7	1.00
	Rhamnus cathartica	0.97	0.95	122.6	1.00
	Rubus fruticosus var. lockness lockness	2.89	0.91	104.5	1.00
	Rubus Idaeus	3.58	0.66	122.3	< 0.001
	Sambucus ebulus	3.04	0.55	150.6	< 0.001
	Sambucus nigra	2.10	0.60	172.6	0.30
	Sambucus nigra Gold	1.27	0.77	140.8	1.00
	Solanum nigrum	2.39	1.18	248.7	1.00
	Solanum villosum	3.51	1.22	223.9	1.00
	Symphoricarpos alba	-0.44	1.19	338.3	1.00
	Taxus baccata	1.03	0.75	183.2	1.00
	Vaccinium myrtillus	-1.29	0.69	140.1	1.00
	Vitis vinifera cv. Humagne	1.18	1.40	224.6	1.00
	Vitis vinifera cv. Mara	0.66	0.98	248.9	1.00
Cotoneaster divaricatus	*Eleagnus umbelata*	1.76	1.59	415.3	1.00
	Frangula alnus	1.31	1.64	408.3	1.00
	Hippophae rhamnoides	-2.12	2.12	488.2	1.00
	Lonicera xylosteum	1.70	1.62	410.3	1.00
	Lycium barbarum	2.72	1.66	390.6	1.00
	Lycium chinense	2.66	1.67	394.3	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Mahonia aquilfolium	-0.91	1.87	229.2	1.00
	Phytolacca americana	1.23	2.12	483.9	1.00
	Prunus laucerasus	-1.54	1.80	290.8	1.00
	Prunus domesticus subsp. institia	-0.77	2.12	483.9	1.00
	Rhamnus cathartica	1.15	1.85	219.4	1.00
	Rubus fruticosus var. lockness lockness	3.07	1.83	212.4	1.00
	Rubus Idaeus	3.76	1.61	399.1	1.00
	Sambucus ebulus	3.22	1.59	429.1	1.00
	Sambucus nigra	2.28	1.60	418.9	1.00
	Sambucus nigra Gold	1.45	1.65	403.8	1.00
	Solanum nigrum	2.56	1.81	442.8	1.00
	Solanum villosum	3.69	1.83	404.9	1.00
	Symphoricarpos alba	-0.26	1.88	464.3	1.00
	Taxus baccata	1.21	1.65	417.7	1.00
	Vaccinium myrtillus	-1.11	1.53	478.4	1.00
	Vitis vinifera cv. Humagne	1.36	1.96	368.9	1.00
	Vitis vinifera cv. Mara	0.84	1.65	490.3	1.00
Eleagnus umbelata	*Frangula alnus*	-0.45	1.16	187.2	1.00
	Hippophae rhamnoides	-3.87	1.78	377.5	1.00
	Lonicera xylosteum	-0.06	1.13	176.4	1.00
	Lycium barbarum	0.96	1.19	179.1	1.00
	Lycium chinense	0.91	1.21	187.2	1.00
	Mahonia aquilfolium	-2.67	1.47	100.5	1.00
	Phytolacca americana	-0.53	1.78	368.7	1.00
	Prunus laucerasus	-3.30	1.38	146	1.00
	Prunus domesticus subsp. institia	-2.53	1.78	368.7	1.00
	Rhamnus cathartica	-0.61	1.44	92.7	1.00
	Rubus fruticosus var. lockness lockness	1.31	1.41	86.4	1.00
	Rubus Idaeus	2.00	1.12	169.7	1.00
	Sambucus ebulus	1.46	1.08	178.5	1.00
	Sambucus nigra	0.52	1.11	177.8	1.00
	Sambucus nigra Gold	-0.31	1.17	183.3	1.00
	Solanum nigrum	0.81	1.38	264.7	1.00
	Solanum villosum	1.93	1.42	239.8	1.00
	Symphoricarpos alba	-2.02	1.48	302.6	1.00
	Taxus baccata	-0.55	1.18	196.7	1.00
	Vaccinium myrtillus	-2.86	1.00	205.7	1.00
	Vitis vinifera cv. Humagne	-0.39	1.58	232.1	1.00
	Vitis vinifera cv. Mara	-0.92	1.18	277.8	1.00
Frangula alnus	*Hippophae rhamnoides*	-3.43	1.43	481.9	1.00
	Lonicera xylosteum	0.39	0.83	130.7	1.00
	Lycium barbarum	1.41	0.91	140.8	1.00
	Lycium chinense	1.35	0.94	152.6	1.00
	Mahonia aquilfolium	-2.22	1.26	68.6	1.00
	Phytolacca americana	-0.08	1.61	402.2	1.00
	Prunus laucerasus	-2.86	1.16	118.2	1.00
	Prunus domesticus subsp. institia	-2.08	1.61	402.2	1.00
	Rhamnus cathartica	-0.16	1.23	61	1.00
	Rubus fruticosus var. lockness lockness	1.76	1.20	55	1.00
	Rubus Idaeus	2.45	0.83	122.9	1.00
	Sambucus ebulus	1.91	0.78	124.7	1.00
	Sambucus nigra	0.97	0.81	129.1	1.00
	Sambucus nigra Gold	0.14	0.90	143.5	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Solanum nigrum	1.25	1.15	268.7	1.00
	Solanum villosum	2.38	1.19	232.3	1.00
	Symphoricarpos alba	-1.57	1.28	321.1	1.00
	Taxus baccata	-0.10	0.90	164.3	1.00
	Vaccinium myrtillus	-2.42	0.63	147.2	0.10
	Vitis vinifera cv. Humagne	0.05	1.38	225.1	1.00
	Vitis vinifera cv. Mara	-0.47	0.93	292.2	1.00
Hippophae rhamnoides	*Lonicera xylosteum*	3.82	1.59	419.4	1.00
	Lycium barbarum	4.83	1.62	394.3	1.00
	Lycium chinense	4.78	1.64	397.8	1.00
	Mahonia aquilfolium	1.20	1.84	242.4	1.00
	Phytolacca americana	3.35	2.10	484.2	1.00
	Prunus laucerasus	0.57	1.77	287.1	1.00
	Prunus domesticus subsp. institia	1.35	2.10	484.2	1.00
	Rhamnus cathartica	3.26	1.82	231.9	1.00
	Rubus fruticosus var. lockness lockness	5.18	1.80	224.5	1.00
	Rubus Idaeus	5.87	1.58	405.3	0.12
	Sambucus ebulus	5.33	1.55	440.1	0.35
	Sambucus nigra	4.39	1.57	428.8	1.00
	Sambucus nigra Gold	3.56	1.62	409.1	1.00
	Solanum nigrum	4.68	1.77	446.2	1.00
	Solanum villosum	5.80	1.80	404.9	0.71
	Symphoricarpos alba	1.86	1.86	467	1.00
	Taxus baccata	3.33	1.62	424.1	1.00
	Vaccinium myrtillus	1.01	1.49	475.8	1.00
	Vitis vinifera cv. Humagne	3.48	1.93	366.4	1.00
	Vitis vinifera cv. Mara	2.96	1.64	484.1	1.00
Lonicera xylosteum	*Lycium barbarum*	1.02	0.87	127.3	1.00
	Lycium chinense	0.96	0.90	140.3	1.00
	Mahonia aquilfolium	-2.61	1.10	88.2	1.00
	Phytolacca americana	-0.47	1.49	444.9	1.00
	Prunus laucerasus	-3.25	0.99	101.8	0.76
	Prunus domesticus subsp. institia	-2.47	1.49	444.9	1.00
	Rhamnus cathartica	-0.55	1.06	75.8	1.00
	Rubus fruticosus var. lockness lockness	1.37	1.02	65.9	1.00
	Rubus Idaeus	2.06	0.52	94.7	0.08
	Sambucus ebulus	1.52	0.40	106.1	0.12
	Sambucus nigra	0.58	0.48	138.2	1.00
	Sambucus nigra Gold	-0.25	0.68	122.8	1.00
	Solanum nigrum	0.86	1.12	264.9	1.00
	Solanum villosum	1.99	1.17	232.9	1.00
	Symphoricarpos alba	-1.96	1.13	344.2	1.00
	Taxus baccata	-0.49	0.63	173.6	1.00
	Vaccinium myrtillus	-2.81	0.59	141.2	< 0.01
	Vitis vinifera cv. Humagne	-0.34	1.36	227.8	1.00
	Vitis vinifera cv. Mara	-0.86	0.91	254.2	1.00
Lycium barbarum	*Lycium chinense*	-0.05	0.57	169.6	1.00
	Mahonia aquilfolium	-3.63	1.28	69.2	1.00
	Phytolacca americana	-1.48	1.62	393.1	1.00
	Prunus laucerasus	-4.26	1.18	119.2	0.24
	Prunus domesticus subsp. institia	-3.48	1.62	393.1	1.00
	Rhamnus cathartica	-1.57	1.25	61.8	1.00
	Rubus fruticosus var. lockness lockness	0.35	1.22	55.9	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Rubus Idaeus	1.04	0.86	121.1	1.00
	Sambucus ebulus	0.50	0.82	120.7	1.00
	Sambucus nigra	-0.44	0.84	126.4	1.00
	Sambucus nigra Gold	-1.27	0.94	135.5	1.00
	Solanum nigrum	-0.15	0.88	408	1.00
	Solanum villosum	0.97	0.94	292.1	1.00
	Symphoricarpos alba	-2.98	1.31	298.9	1.00
	Taxus baccata	-1.50	0.94	158.8	1.00
	Vaccinium myrtillus	-3.82	0.66	147.5	<.0001
	Vitis vinifera cv. Humagne	-1.35	1.40	223.4	1.00
	Vitis vinifera cv. Mara	-1.88	1.05	239.8	1.00
Lycium chinee	*Mahonia aquilfolium*	-3.58	1.30	73.3	1.00
	Phytolacca americana	-1.43	1.64	397.9	1.00
	Prunus laucerasus	-4.21	1.20	125.1	0.33
	Prunus domesticus subsp. institia	-3.43	1.64	397.9	1.00
	Rhamnus cathartica	-1.52	1.27	65.7	1.00
	Rubus fruticosus var. lockness lockness	0.40	1.24	59.7	1.00
	Rubus Idaeus	1.09	0.89	133.4	1.00
	Sambucus ebulus	0.55	0.85	135.1	1.00
	Sambucus nigra	-0.39	0.87	140.1	1.00
	Sambucus nigra Gold	-1.22	0.97	146.7	1.00
	Solanum nigrum	-0.10	0.91	420.2	1.00
	Solanum villosum	1.03	0.96	303.3	1.00
	Symphoricarpos alba	-2.92	1.33	307.2	1.00
	Taxus baccata	-1.45	0.96	171.4	1.00
	Vaccinium myrtillus	-3.77	0.70	169.4	< 0.001
	Vitis vinifera cv. Humagne	-1.30	1.41	229.4	1.00
	Vitis vinifera cv. Mara	-1.82	1.07	250.8	1.00
Mahonia aquilfolium	*Phytolacca americana*	2.14	1.78	302.6	1.00
	Prunus laucerasus	-0.63	1.39	117.1	1.00
	Prunus domesticus subsp. institia	0.14	1.78	302.6	1.00
	Rhamnus cathartica	2.06	0.64	251.3	0.78
	Rubus fruticosus var. lockness lockness	3.98	0.58	202	<.0001
	Rubus Idaeus	4.67	1.13	80.5	0.04
	Sambucus ebulus	4.13	1.07	75.1	0.13
	Sambucus nigra	3.19	1.10	79.8	1.00
	Sambucus nigra Gold	2.36	1.19	86.2	1.00
	Solanum nigrum	3.48	1.47	116	1.00
	Solanum villosum	4.60	1.50	120.3	1.00
	Symphoricarpos alba	0.65	1.50	188.7	1.00
	Taxus baccata	2.12	1.18	97.8	1.00
	Vaccinium myrtillus	-0.19	1.12	58.5	1.00
	Vitis vinifera cv. Humagne	2.28	1.65	147.9	1.00
	Vitis vinifera cv. Mara	1.75	1.32	114.4	1.00
Phytolacca americana	*Prunus laucerasus*	-2.78	1.62	303	1.00
	Prunus domesticus subsp. institia	-2.00	1.96	532.7	1.00
	Rhamnus cathartica	-0.09	1.76	289.6	1.00
	Rubus fruticosus var. lockness lockness	1.83	1.74	281.1	1.00
	Rubus Idaeus	2.52	1.51	409.8	1.00
	Sambucus ebulus	1.99	1.47	457.9	1.00
	Sambucus nigra	1.05	1.42	493.2	1.00
	Sambucus nigra Gold	0.22	1.56	400.9	1.00
	Solanum nigrum	1.33	1.77	445.7	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Solanum villosum	2.46	1.80	407.1	1.00
	Symphoricarpos alba	-1.49	1.81	456.4	1.00
	Taxus baccata	-0.02	1.55	428.2	1.00
	Vaccinium myrtillus	-2.34	1.49	478.2	1.00
	Vitis vinifera cv. Humagne	0.13	1.93	366.6	1.00
	Vitis vinifera cv. Mara	-0.39	1.66	443.7	1.00
Prunus laucerasus	*Prunus domesticus subsp. institia*	0.78	1.62	303	1.00
	Rhamnus cathartica	2.69	1.36	106.8	1.00
	Rubus fruticosus var. lockness lockness	4.61	1.33	99.5	0.43
	Rubus Idaeus	5.30	1.02	96.5	< 0.001
	Sambucus ebulus	4.76	0.96	99.1	< 0.01
	Sambucus nigra	3.82	0.88	91.7	0.02
	Sambucus nigra Gold	2.99	1.10	108.1	1.00
	Solanum nigrum	4.11	1.38	185.8	1.00
	Solanum villosum	5.23	1.41	170.8	0.15
	Symphoricarpos alba	1.29	1.43	205.8	1.00
	Taxus baccata	2.76	1.09	116.9	1.00
	Vaccinium myrtillus	0.44	0.99	109.8	1.00
	Vitis vinifera cv. Humagne	2.91	1.57	175.8	1.00
	Vitis vinifera cv. Mara	2.39	1.23	155.6	1.00
Prunus domesticus subsp. institia	*Rhamnus cathartica*	1.91	1.76	289.6	1.00
	Rubus fruticosus var. lockness lockness	3.83	1.74	281.1	1.00
	Rubus Idaeus	4.52	1.51	409.8	1.00
	Sambucus ebulus	3.99	1.47	457.9	1.00
	Sambucus nigra	3.05	1.42	493.2	1.00
	Sambucus nigra Gold	2.22	1.56	400.9	1.00
	Solanum nigrum	3.33	1.77	445.7	1.00
	Solanum villosum	4.46	1.80	407.1	1.00
	Symphoricarpos alba	0.51	1.81	456.4	1.00
	Taxus baccata	1.98	1.55	428.2	1.00
	Vaccinium myrtillus	-0.34	1.49	478.2	1.00
	Vitis vinifera cv. Humagne	2.13	1.93	366.6	1.00
	Vitis vinifera cv. Mara	1.61	1.66	443.7	1.00
Rhamnus cathartica	*Rubus fruticosus var. lockness lockness*	1.92	0.50	117.1	0.11
	Rubus Idaeus	2.61	1.09	69.6	1.00
	Sambucus ebulus	2.07	1.03	63.9	1.00
	Sambucus nigra	1.13	1.06	68.5	1.00
	Sambucus nigra Gold	0.30	1.16	75.8	1.00
	Solanum nigrum	1.42	1.44	107	1.00
	Solanum villosum	2.54	1.47	111.3	1.00
	Symphoricarpos alba	-1.41	1.47	175.8	1.00
	Taxus baccata	0.07	1.15	86	1.00
	Vaccinium myrtillus	-2.25	1.08	50.3	1.00
	Vitis vinifera cv. Humagne	0.22	1.63	139.2	1.00
	Vitis vinifera cv. Mara	-0.31	1.29	103.5	1.00
Rubus fruticosus var. lockness var. lockness	*Rubus Idaeus*	0.69	1.06	61	1.00
	Sambucus ebulus	0.15	1.00	55	1.00
	Sambucus nigra	-0.79	1.03	59.5	1.00
	Sambucus nigra Gold	-1.62	1.13	67.6	1.00
	Solanum nigrum	-0.50	1.41	99.9	1.00
	Solanum villosum	0.62	1.45	104.3	1.00
	Symphoricarpos alba	-3.33	1.45	166.2	1.00
	Taxus baccata	-1.86	1.12	76.8	1.00

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Vaccinium myrtillus	-4.17	1.05	43.7	0.13
	Vitis vinifera cv. Humagne	-1.70	1.60	132.6	1.00
	Vitis vinifera cv. Mara	-2.23	1.26	95	1.00
Rubus Idaeus	*Sambucus ebulus*	-0.54	0.40	72.1	1.00
	Sambucus nigra	-1.48	0.56	102.9	1.00
	Sambucus nigra Gold	-2.31	0.68	105.5	0.49
	Solanum nigrum	-1.19	1.12	254.5	1.00
	Solanum villosum	-0.07	1.16	222.4	1.00
	Symphoricarpos alba	-4.02	1.13	318.7	0.24
	Taxus baccata	-2.54	0.54	153.8	< 0.01
	Vaccinium myrtillus	-4.86	0.58	121.6	<.0001
	Vitis vinifera cv. Humagne	-2.39	1.35	219.2	1.00
	Vitis vinifera cv. Mara	-2.92	0.91	228.7	0.80
Sambucus ebulus	*Sambucus nigra*	-0.94	0.44	124.6	1.00
	Sambucus nigra Gold	-1.77	0.56	120.2	1.00
	Solanum nigrum	-0.65	1.08	274.7	1.00
	Solanum villosum	0.47	1.13	239.6	1.00
	Symphoricarpos alba	-3.48	1.07	395.7	0.64
	Taxus baccata	-2.01	0.54	184.7	0.13
	Vaccinium myrtillus	-4.32	0.50	125.8	<.0001
	Vitis vinifera cv. Humagne	-1.85	1.32	233.3	1.00
	Vitis vinifera cv. Mara	-2.38	0.84	283	1.00
Sambucus nigra	*Sambucus nigra - Sambucus nigra Gold*	-0.83	0.69	131.6	1.00
	Solanum nigrum	0.29	1.10	272.7	1.00
	Solanum villosum	1.41	1.15	238	1.00
	Symphoricarpos alba	-2.54	1.14	355.9	1.00
	Taxus baccata	-1.07	0.67	176.2	1.00
	Vaccinium myrtillus	-3.38	0.54	137.8	<.0001
	Vitis vinifera cv. Humagne	-0.91	1.34	231.3	1.00
	Vitis vinifera cv. Mara	-1.44	0.90	265.8	1.00
Sambucus nigra Gold	*Solanum nigrum*	1.12	1.18	256.6	1.00
	Solanum villosum	2.24	1.22	227.9	1.00
	Symphoricarpos alba	-1.71	1.05	455.4	1.00
	Taxus baccata	-0.24	0.77	156.4	1.00
	Vaccinium myrtillus	-2.55	0.69	154.4	0.16
	Vitis vinifera cv. Humagne	-0.08	1.40	224.4	1.00
	Vitis vinifera cv. Mara	-0.61	0.90	277.4	1.00
Solanum nigrum	*Solanum nigrum - Solanum villosum*	1.13	1.18	420.6	1.00
	Symphoricarpos alba	-2.82	1.49	382.8	1.00
	Taxus baccata	-1.35	1.17	289	1.00
	Vaccinium myrtillus	-3.67	0.97	366.1	0.09
	Vitis vinifera cv. Humagne	-1.20	1.57	289.2	1.00
	Vitis vinifera cv. Mara	-1.72	1.26	356.7	1.00
Solanum villosum	*Symphoricarpos alba*	-3.95	1.52	343.5	1.00
	Taxus baccata	-2.48	1.22	252.4	1.00
	Vaccinium myrtillus	-4.80	1.02	282	< 0.01
	Vitis vinifera cv. Humagne	-2.33	1.60	263.7	1.00
	Vitis vinifera cv. Mara	-2.85	1.30	305.7	1.00
Symphoricarpos alba	*Taxus baccata*	1.47	1.19	350.7	1.00
	Vaccinium myrtillus	-0.85	1.14	407.1	1.00
	Vitis vinifera cv. Humagne	1.62	1.67	311	1.00
	Vitis vinifera cv. Mara	1.10	1.28	435	1.00
Taxus baccata	*Vaccinium myrtillus*	-2.32	0.68	205.7	0.42

Plant species comparison		Estimate	*SE*	*df*	*p-value*
	Vitis vinifera cv. Humagne	0.15	1.40	240.1	1.00
	Vitis vinifera cv. Mara	-0.37	0.98	274.8	1.00
Vaccinium myrtillus	*Vitis vinifera cv. Humagne*	2.47	1.23	250.2	1.00
	itis mara	1.95	0.82	344.2	1.00
Vitis vinifera cv. Humagne	*Vitis vinifera cv. Mara*	-0.52	1.48	276.3	1.00

Table S15: Fruit traits

Mean and confidence interval (CI) of SWD development time, SWD wing length, fruit skin hardness and elasticity, fruit colour parameters (L, a and b) as well as fruit pH and sugar content. Fruit skin hardness is expresses as centiNewton (cN). NA stands for missing data.

Plant species	Mean ± CI development time [days]	Mean ± CI wing length [mm]	Mean ± CI skin hardness [cN]	Mean ± CI skin elasticity [mm]	Mean ± CI L parameter	Mean ± CI a parameter	Mean ± CI b parameter	Mean ± CI fruit pH	Mean ± CI fruit sugar content [°brix]
Viburnum lantana	8 ± NA	2.2 ± NA	35.21 ± 3.88	0.22 ± 0.43	NA	NA	NA	NA	NA
Eleagnus umbelata	11.5 ± 0.98	2.18 ± 0.12	13.81 ± 1.25	0.5 ± 0.99	NA	NA	NA	3.24 ± NA	16.8 ± NA
Solanum villosum	11.67 ± 0.65	3.35 ± 0.12	47.52 ± 4.5	1.27 ± 2.49	NA	NA	NA	4.37 ± NA	11.9 ± NA
Solanum nigrum	12 ± NA	3.4 ± NA	37.23 ± 5.61	1.29 ± 2.52	NA	NA	NA	4.59 ± NA	13 ± NA
Cornus alba	12.2 ± 0.64	2.14 ± 0.16	28.34 ± 4.53	0.89 ± 1.75	NA	NA	NA	3.17 ± NA	12 ± NA
Cornus alba sibirica	12.4 ± 0.78	2.28 ± 0.18	16.75 ± 2.25	0.59 ± 1.15	NA	NA	NA	NA	11.5 ± NA
Lycium chinense	12.47 ± 0.54	3.12 ± 0.13	34.27 ± 2.69	1.26 ± 2.46	NA	NA	NA	5.19 ± NA	10.8 ± NA
Frangula alnus	12.5 ± 0.58	2.79 ± 0.22	42.3 ± 18.59	1.69 ± 3.31	NA	NA	NA	5.8 ± NA	20.4 ± NA
Lycium barbarum	12.62 ± 0.61	3.05 ± 0.11	43.45 ± 0.71	1.22 ± 2.39	60.7 ± 1.38	35.95 ± 1.92	47.27 ± 3.29	5.39 ± NA	9.6 ± NA
Cornus kousa	12.96 ± 0.53	2.81 ± 0.23	17.95 ± 2.62	1.4 ± 2.74	NA	NA	NA	5.4 ± NA	25 ± NA
Ampelopsis brevipedunculatata	13 ± NA	1.95 ± NA	25.21 ± 3.12	0.78 ± 1.53	63.2 ± 1.32	-5.77 ± 0.46	13.23 ± 1.39	5.42 ± NA	8 ± NA
Rubus idaeus	13.48 ± 0.16	1.88 ± 0.07	10.25 ± 2.92	0.53 ± 1.05	NA	NA	NA	3.5 ± NA	13.4 ± NA
Sambucus ebulus	13.53 ± 0.23	2.11 ± 0.1	15.95 ± 1.79	0.74 ± 1.44	35.65 ± 1.46	1.16 ± 0.22	-0.03 ± 0.14	5.39 ± 0.26	17.17 ± 2.25
Sambucus nigra	13.65 ± 0.36	2.44 ± 0.18	38.03 ± 3.48	1.11 ± 2.17	36.2 ± 2.29	1.84 ± 0.48	0.64 ± 0.36	3.95 ± 0.13	10.39 ± NA
Atropa belladona	13.71 ± 0.35	2.88 ± 0.16	27.01 ± 5.42	1.24 ± 2.42	NA	NA	NA	5.44 ± NA	13.4 ± NA
Vitis vinifera cv. Mara	14 ± 1.13	2.75 ± 0.44	70.71 ± 2.74	1.52 ± 2.99	37.2 ± 0.54	1.55 ± 0.15	-2.72 ± 0.21	3.01 ± 0.12	21.15 ± 2.11
Cotoneaster divaricatus	14 ± NA	2.1 ± NA	25.22 ± 2.62	0.24 ± 0.47	NA	NA	NA	4.25 ± NA	13.8 ± NA
Phytolacca americana	14 ± NA	2.88 ± NA	31.87 ± 2.95	1.31 ± 2.56	31.8 ± 1.52	1.27 ± 0.2	0.27 ± 0.35	5.25 ± NA	18.2 ± NA
Rubusu fruticosus var. lockness	14.03 ± 0.26	2.72 ± 0.09	14.12 ± 5.06	1.08 ± 2.12	44.85 ± 3.63	35.95 ± 1.92	47.27 ± 3.29	3.28 ± NA	14.8 ± NA
Basella alba	14.43 ± 0.2	2.44 ± 0.19	19.46 ± 4.13	0.57 ± 1.12	NA	NA	NA	5.4 ± NA	7.1 ± NA
Sambucus nigra Gold	14.45 ± 0.72	2.85 ± 0.25	35.12 ± 3.85	0.86 ± 1.69	NA	NA	NA	4.2 ± NA	9.2 ± NA
Vitis vinifera cv. Humagne	14.5 ± 2.94	NA	58.14 ± 8.94	1.7 ± 3.33	NA	NA	NA	3.44 ± 0.05	20 ± 0.41
Lonicera xylosteum	15.32 ± 0.69	1.8 ± 0.13	13.41 ± 2.17	0.84 ± 1.64	42.57 ± 2.28	27.91 ± 2.01	15.87 ± 1.97	5.25 ± 0.1	13.3 ± 7.06
Cornus amomum	15.4 ± 1.18	2.94 ± 0.17	14.96 ± 1.44	0.24 ± 0.47	40.04 ± 1.5	4.21 ± 0.63	-6.83 ± 0.99	3.72 ± NA	13.5 ± NA
Taxus baccata	15.56 ± 0.93	2.12 ± 0.19	9.4 ± 2.89	0.41 ± 0.81	NA	NA	NA	6.53 ± NA	13.9 ± NA
Rhamnus cathartica	15.71 ± 0.58	3.11 ± 0.19	19.74 ± NA	0.61 ± NA	35.63 ± 3.27	3.05 ± 0.72	0.45 ± 0.38	5.27 ± NA	29.7 ± NA
Vaccinium myrtillus	15.88 ± 0.58	2.43 ± 0.19	32.26 ± 2.16	0.76 ± 1.49	NA	NA	NA	3.03 ± 0.27	12.71 ± 1.59
Symphoricarpos alba	16 ± 3.92	2.38 ± 1.01	46.59 ± 3.71	1.25 ± 2.45	NA	NA	NA	5.37 ± NA	8 ± NA
Hippophae rhamnoides	16 ± NA	NA	44.18 ± 15.58	1.1 ± 2.16	NA	NA	NA	3.35 ± NA	16.85 ± NA
Prunus domesticus subsp. institia	16 ± NA	2.86 ± NA	43.37 ± 2.69	1 ± 1.96	NA	NA	NA	3.12 ± NA	12.2 ± NA
Cornus mas	16.58 ± 1.31	2.11 ± 0.32	53.39 ± 5.91	0.61 ± 1.19	NA	NA	NA	2.98 ± 0.04	16.45 ± 0.29
Prunus laucerasus	17.38 ± 1.23	3.16 ± 0.12	19.4 ± 4.25	0.42 ± 0.81	NA	NA	NA	NA	NA
Mahonia aquifolium	17.78 ± 1.17	3.01 ± 0.15	26.13 ± 3.96	0.46 ± 0.89	NA	NA	NA	2.82 ± NA	15.9 ± NA
Callicarpa giraldii	NA	NA	51.04 ± 5.58	0.46 ± 0.9	NA	NA	NA	5.4 ± NA	14.4 ± NA

Plant species	Mean ± CI development time [days]	Mean ± CI wing length [mm]	Mean ± CI skin hardness [cN]	Mean ± CI skin elasticity [mm]	Mean ± CI L parameter	Mean ± CI a parameter	Mean ± CI b parameter	Mean ± CI fruit pH	Mean ± CI fruit sugar content [°brix]
Ilex aquifolium	NA	NA	69.9 ± 7.87	0.31 ± 0.61	NA	NA	NA	5.27 ± NA	15.2 ± NA
Lycopersicum pimpinellifolium	NA	NA	86.85 ± 3.8	1.03 ± 2.02	NA	NA	NA	4.45 ± NA	7.4 ± NA
Polygonatum multiflorum	NA	NA	169.22 ± 14	0.37 ± 0.72	NA	NA	NA	NA	NA
Cornus controversa variegata	NA	NA	28.03 ± 2.5	0.18 ± 0.36	NA	NA	NA	NA	NA
Viburnum tinus	NA	NA	105.18 ± 15.81	0.32 ± 0.63	NA	NA	NA	NA	NA
Berberis vulgaris	NA	NA	29.76 ± 1.95	0.28 ± 0.55	NA	NA	NA	2.84 ± NA	14.75 ± NA
Sorbus aucuparia	NA	NA	75.29 ± 4.69	0.55 ± 1.07	NA	NA	NA	3.26 ± 0.07	22.6 ± 9.41
Nandina domestica	NA	NA	68.83 ± 26.9	0.33 ± 0.65	NA	NA	NA	5.34 ± NA	10.2 ± NA
Sorbus americana Belmonte	NA	NA	76.89 ± 8.18	0.3 ± 0.58	NA	NA	NA	3.33 ± NA	18.9 ± NA
Viburnum opulus	NA	NA	58.82 ± 16.91	1.4 ± 2.74	NA	NA	NA	3.02 ± NA	10.6 ± NA
Malus spectabilis	NA	NA	76.35 ± 17.63	0.41 ± 0.79	NA	NA	NA	NA	NA
Cotoneaster obscurus	NA	NA	28.88 ± 4.42	0.6 ± 1.18	NA	NA	NA	3.81 ± NA	22.2 ± NA
Aronia melanocarpa	NA	NA	38.88 ± 2.46	0.52 ± 1.01	NA	NA	NA	3.78 ± 0.5	17.8 ± 1.76
Cornus capitata	NA	NA	20.26 ± 1.91	1 ± 1.96	NA	NA	NA	NA	NA
Viburnum rhydotiphyllum	NA	NA	26.12 ± 10.62	0.31 ± 0.6	NA	NA	NA	NA	NA
Cotoneaster tomentosus	NA	NA	43.82 ± 5.32	0.41 ± 0.8	NA	NA	NA	NA	NA
Myrtus communis	NA	NA	35.08 ± 7.28	0.35 ± 0.69	NA	NA	NA	NA	NA
Solanum dulcamara	NA	NA	37.53 ± 1.03	1.6 ± 3.14	NA	NA	NA	4.35 ± NA	13.1 ± NA
Cornus sanguinea winterbeauty	NA	NA	20.52 ± 0.73	0.29 ± 0.57	NA	NA	NA	4.96 ± NA	17 ± NA
Pyracantha coccinea	NA	NA	25.38 ± 1.99	0.29 ± 0.56	NA	NA	NA	NA	NA
Cornus sanguinea	NA	NA	23.92 ± 2.39	0.45 ± 0.89	NA	NA	NA	4.58 ± 0.14	19.2 ± 5.29
Prunus spinosa	NA	NA	93.66 ± 21.13	0.81 ± 1.58	NA	NA	NA	3.11 ± NA	18.5 ± NA
Ligustrum vulgare	NA	NA	29.99 ± 6.84	0.26 ± 0.5	NA	NA	NA	5.36 ± NA	14.8 ± NA
Prunus lusitanica	NA	NA	NA	NA	29.94 ± 2.6	2.45 ± 0.76	0.19 ± 0.39	4.68 ± NA	33.1 ± NA
Phytolacca acinosa	NA	NA	29.35 ± 4.61	1.32 ± 2.59	NA	NA	NA	5.36 ± NA	17.2 ± NA
Cestrum fasciculatum	NA	NA	18.92 ± 3.97	0.35 ± 0.68	44.19 ± 4.15	36.96 ± 4.8	9.54 ± 3.26	5.25 ± NA	8.2 ± NA

Table S16: Effect of hardness on egg-laying

Anova table and linear model estimate table on the egg number per gram of fruit depending on skin hardness. SS = sum of squares, SE = Standard error, DF = degree of freedom.

	SS	**DF**	***F value***	***p value***
hardness	605.90	1.00	39.09	< 0.001
Residuals	712.97	46.00		

	Estimate	**SE**	**t value**	***p value***
(Intercept)	13.83	1.18	11.69	< 0.001
hardness	-0.19	0.03	-6.25	< 0.001

Table S17: Model selection and model averaging of colour impact on egg-laying

Model selection and model averaging table over L, a and b parameters, describing colours. SS= sum of squares, SE = Standard error, DF = degree of freedom.

model selection

predictors	df	*AICc*	Δ AICc
null model (1)	4.00	1565.73	0.00
b	5.00	1567.24	1.51
L	5.00	1567.68	1.95
a	5.00	1567.73	1.99
a,b	6.00	1568.46	2.73
L,b	6.00	1568.98	3.25
L,a	6.00	1569.68	3.95
L,a,b	7.00	1570.16	4.42

model averaging

models	DF	logLik	AICc	Δ	*weight*
null model (1)	4.00	-778.87	1565.80	0.00	0.46
b	5.00	-778.62	1567.34	1.54	0.21
L	5.00	-778.84	1567.78	1.99	0.17
a	5.00	-778.86	1567.83	2.03	0.17

full average

models	Estimate	SE	Adjusted SE	z value	*p value*
(Intercept)	1.43	0.19	0.20	7.34	< 0.001
b	0.00	0.00	0.00	0.27	0.78
L	0.00	0.00	0.00	0.09	0.93
a	0.00	0.00	0.00	0.03	0.98

conditional average

models	Estimate	SE	Adjusted SE	z value	*p value*
(Intercept)	1.43	0.19	0.20	7.34	< 0.001
b	0.00	0.00	0.00	0.70	0.48
L	0.00	0.01	0.01	0.22	0.83
a	0.00	0.01	0.01	0.08	0.94

Table S18: Model selection and model averaging for sugar content and pH of fruits on emergence success

Model selection and model averaging table over fruit sugar content and pH effect on egg-laying. Predictors followed by "(x^2)" represent predictors for which a quadratic fit has been tested. SS= sum of squares, SE = Standard error, DF = degree of freedom

model selection

predictor	DF	*AICc*	Δ AICc
sugar content	3	-17.12	0.00
null model (1)	2	*-16.88*	0.24
pH	3	*-16.39*	0.73
sugar content, sugar content (x^2)	4	-15.47	1.65
pH*sugar content	5	*-14.73*	2.39
pH,pH (x^2)	4	*-14.53*	2.58
pH*sugar content, pH (x^2), sugar content (x^2)	7	*-12.22*	4.90

model averaging

	DF	logLik	AICc	Δ	*weight*
(Null)	2.00	10.44	-16.55	0.00	0.30
sugar content	3.00	11.56	-16.45	0.10	0.29
pH	3.00	11.20	-15.73	0.83	0.20
sugar content, sugar content (x^2)	4.00	11.73	-14.33	2.23	0.10
pH, pH (x^2)	4.00	11.27	-13.39	3.16	0.06
pH*sugar content	5.00	12.36	-12.96	3.59	0.05

full average

	Estimate	SE	Adjusted SE	z value	*p value*
(Intercept)	0.32	0.03	0.03	9.61	< 0.001
sugar content	0.02	0.03	0.03	0.64	0.52
pH	0.01	0.02	0.02	0.47	0.64
sugar content (x^2)	0.00	0.01	0.01	0.15	0.88
pH (x^2)	0.00	0.01	0.01	0.08	0.93
sugar content : pH	0.00	0.01	0.01	0.03	0.98

conditional average

	Estimate	SE	Adjusted SE	z value	*p value*
(Intercept)	0.32	0.03	0.03	9.61	< 0.001
sugar content	0.05	0.03	0.03	1.40	0.16
pH	0.04	0.03	0.03	1.18	0.24
sugar content (x^2)	-0.01	0.02	0.02	0.55	0.58
pH (x^2)	-0.01	0.04	0.04	0.35	0.73
sugar content : pH	0.00	0.03	0.03	0.12	0.91

Table S19: Model selection and model averaging for fruit sugar content and pH on SWD wing length

Model selection and model averaging table over fruit sugar content and pH on SWD wing length. Predictors followed by "(x^2)" represent predictors for which a quadratic fit has been tested. SS= sum of squares, SE = Standard error, DF = degree of freedom

model selection

predictors	df	*AICc*	Δ AICc
sugar content	4	22.40	0.00
sugar content (x^2)	5	*22.45*	0.05
null model (1)	3	27.55	5.15
pH	4	30.06	7.66
pH * sugar content	8	30.26	7.86
pH (x^2)	5	32.58	10.18

model averaging

	Df	logLik	AICc	Δ	*weight*
sugar content	4.00	-6.59	22.40	0.00	0.93
null model (1)	3.00	-10.42	27.55	5.15	0.07

full average

	Estimate	SE	Adjusted SE	z value	*p value*
(Intercept)	2.46	0.16	0.17	14.70	< 0.001
sugar content	0.11	0.05	0.05	2.19	0.03

conditional average

	Estimate	SE	Adjusted SE	z value	*p value*
(Intercept)	2.46	0.16	0.17	14.70	< 0.001
sugar content	0.12	0.04	0.04	2.86	< 0.001

Table S20: Effect of sugar content on wing length

Anova table and linear model estimate table on the egg number per gram of fruit depending on sugar content. SS = sum of squares, SE = Standard error, DF = degree of freedom

Analysis of Deviance Table (Type II)

	X	Df	*p value*	
sugar content	8.8482	1	0.002934	**

Linear model estimate table

	Estimate	Std. Error	df	t value	*p value*	
(Intercept)	2.07	0.22	19.68	9.60	< 0.001	***
sugar content	0.03	0.01	27.45	2.98	0.01	**

Chapter 2 - Testing trap cropping candidates against *Drosophila suzukii* to protect vineyards

Abstract

The spotted wing drosophila (SWD), *Drosophila suzukii*, can cause significant damage to wine production by favouring the development of sour rot disease outbreaks in vineyards. Like in many generalist insects, host preference and performance of SWD are not consistently correlated. Luring SWD with host plants it prefers over grapes might allow the development of an environmentally friendly pest control method, the so-called trap cropping. Depending on the developmental performance of the pest in the trap crop, the trap cropping strategy might be "dead-end" when the development of the pest is low or, if not, combined with an additional measure to reduce the pest spill-over from the trap crop. Here, we evaluated the potential of 11 candidate trap crop species in two-choice preference tests under laboratory and semi-field conditions. We studied the preference of SWD for each candidate plant over grapes to identify host plants capable of luring the pest away from grapevines. Then, we recorded the SWD infestation level on close-by grapes to select candidate plants with highest protection potential. Finally, we evaluated SWD developmental performance in the candidate plants to suggest the most appropriate type of trap cropping. The porcelain berry, *Ampelopsis glandulosa* var. *brevipedunculata,* showed the highest potential for dead-end trap cropping: SWD strongly preferred this plant species over grapes for egg-laying, infestation in adjacent grapes was reduced and SWD emergence success in its fruits was low. Although SWD strongly preferred ten other candidates over grapes for egg-laying, infestation in adjacent grapes was not reduced. Three of these eight candidate species even increased infestation in adjacent grapes. The most promising candidates should be tested under field conditions to evaluate further their potential for trap cropping to protect grapes.

Introduction

Trap cropping is an environmentally friendly management strategy to control polyphagous arthropod pests, altering crop-pest interactions by planting host plants that the pest species strongly prefers in the vicinity of the actual crop (González-Chang et al., 2019). Trap crops are commonly deployed within or alongside the main crop to lure the pest away from the crop and thereby reduce crop damage and yield losses (Hokkanen 1991; Shelton & Badenes-Perez 2006).

For trap cropping to be a successful management strategy, trap crops must be preferred over the crop before or during the critical period when the crop is most vulnerable to pest damage. Moreover, trap crops should prevent or at least limit the pest spill-over back to the crop, i. e. retain the pest within the trap crop (Ludwig & Kok 1998; Boucher *et al.* 2003; Shelton & Badenes-Perez 2006; Holden *et al.* 2012; Blaauw *et al.* 2017).

Two types of trap crops exist. Dead-end trap cropping uses trap crop plants that the pest prefers over the crop to lay eggs but whose fruits do not allow the pest development in adults (Shelton & Nault 2004). This corresponds to the so-called "ecological trap" (Battin 2004). Such suboptimal host choices can arise in many herbivorous insect species as insect preference and performance are not necessarily correlated (Mayhew 2001; Gripenberg *et al.* 2010; Poyet *et al.* 2015; Diepenbrock *et al.* 2016). Dead-end trap cropping has been successfully implemented to control the spotted borer *Chilo sacchariphagus* (Bojer, 1856) (Lepidoptera: Crambidae) in sugarcane crops on Reunion island (Nibouche *et al.* 2012, 2019; Jacob *et al.* 2021) and has promoted interest for controlling other pest species (Grundy *et al.* 2004; Badenes-Perez *et al.* 2014; Rhino *et al.* 2014, 2016; Ulmer *et al.* 2020; Mhatre *et al.* 2021; Sacchi *et al.* 2021).

The second type of trap cropping we refer to as "traditional trap cropping" uses trap crop plants that the pest prefers over the crop to lay eggs too, but whose fruits still allow the pest to develop in adults. Therefore it is usually implemented with other control measures to prevent the pest from recolonising the crop (Ludwig & Kok 1998). For example, attraction to the trap crop can be combined with a killing strategy called the "attract and kill" method. Measures to prevent pest spill-over include the release or support of natural predators (Rust 1977; Virk *et al.* 2004; Rhino *et al.* 2016; Gordon *et al.* 2017), mechanical pest removal or mechanical destruction of the trap crop, decreasing subsequent pest generations (Rust 1977; Swezey *et al.* 2007; Cotes *et al.* 2018) or a local application of insecticides to the trap crop (Ellsworth *et al.* 1992; Mitchell

et al. 2000; Cavanagh *et al.* 2009; Lin *et al.* 2015; Tomaseto *et al.* 2019). Alternatively, trap crops can be utilised in a push-pull strategy. Repellents (e.g. plant species, plant extracts, cultivation techniques) can be applied in the crop area to create adverse conditions that push the pest out of the crop, while the surrounding trap crop attracts the pest (Cook *et al.* 2007; Khan *et al.* 2007; Lamy *et al.* 2018).

To control polyphagous pests, such as the invasive spotted wing drosophila (SWD), *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), management strategies need to integrate multiple control methods to be effective (Vreysen *et al.* 2007; Zhou *et al.* 2011; Haye *et al.* 2016). SWD control is thus challenging, as the pest is ubiquitous across agricultural landscapes, subsisting throughout the year in semi-natural habitats (Cahenzli *et al.* 2018a; Tonina *et al.* 2018). This pest lays eggs in undamaged ripe fruits in a wide range of wild plants and horticultural crops (e.g. cherries, strawberries, raspberries, blackberries, blueberries, grapes), causing considerable economic losses (Goodhue *et al.* 2011; Cini *et al.* 2014; Farnsworth *et al.* 2017). In vineyards, the punctures of grapes caused during egg-laying can favour the development of microorganisms in wounded berries, which triggers the development of sour rot. This grape disease can deteriorate wine quality (Ioriatti *et al.* 2018). In Swiss vineyards, 61 to 72% of winegrowers expect revenue loss due to SWD infestation (Knapp *et al.* 2021). Although preventive and sanitation measures reduce SWD damage on grapes, pest control can still be unsatisfactory. It is presumed that additional management practices could enhance current integrated pest management measures and provide alternatives to insecticide use (Knapp, Mazzi, and Finger, 2019).

Given the relatively weak preference of SWD for grapes in comparison to other crops (Lee *et al.* 2011b; Bellamy *et al.* 2013; Shrader *et al.* 2019; Fragnière *et al.* in prep.) and the extensive host range of SWD (Mitsui *et al.* 2010; Lee *et al.* 2011b; Poyet *et al.* 2015; Kenis *et al.* 2016), trap cropping might be a potentially effective control strategy to protect grapes from SWD infestation. In a previous laboratory study, we found specific plant species whose fruiting period matches the grape maturation period and for which SWD presented a strong egg-laying preference compared to grapes under no-choice and multiple-choice conditions (Fragnière *et al.* in prep.). Given their varying SWD developmental performance (Poyet *et al.* 2015; Fragnière *et al.* in prep.), potential candidates could either be considered for dead-end trap cropping or traditional trap cropping, and complement current preventive control measures repelling SWD from vineyards (Haye *et al.* 2016; Linder *et al.* 2018).

Here, we aim to identify host plant species with a high potential for trap cropping to protect grapes under semi-field conditions that could be suitable for further testing in the field. Using two-choice assays under laboratory and semi-field conditions, we investigated: 1) SWD preference for egg-laying between each trap crop candidate species and grapes, 2) whether the presence of the trap crop impacted the damage level on nearby grapes (protection potential), and 3) what type of trap cropping is possible given the emergence success of the pest in the candidate trap crops. Plant hosts for which SWD has a stronger preference for egg-laying than grapes would be considered as candidate trap crops for traditional trap cropping, while hosts that in addition prevents SWD development in adults would be considered as candidate trap crops for dead-end trap cropping.

Materials and methods

Biological materials

The study occurred at the Swiss Federal Research Institute for Agriculture (Agroscope) in Nyon (Switzerland). We reared SWD under controlled conditions on a homemade banana-yeast medium in our insect rearing facility. To conduct the following experiments, we used mated five to twelve-day-old female SWD.

Young grapevines of the cultivar Mara were ordered from a grapevine plant nursery (Les Frères Dutruy, Founex, Switzerland) and grown outdoors in 25-litre pots. Grapevines were protected against downy and powdery mildew roughly every two weeks with a standard program of conventional fungicides. To ensure that wild SWD did not infest maturing grapes before the start of the experiments, we protected each grape cluster in a closed fine net bag at the beginning of grape ripening until their use.

Based on the results of Fragnière et al. (in prep.), we selected five native plant species (*Lonicera xylosteum*, *Rhamnus cathartica*, *Sambucus ebulus, Sambucus nigra* and *Rubus fruticosus* var. *lockness* (*Rubus fruticosus* in the following)) and six ornamental plant species (*Ampelopsis glandulosa* var. *brevipedunculata* (*Ampelopsis brevipedunculata* in the following), *Cestrum fasciculatum*, *Cornus amomum*, *Lycium barbarum*, *Phytolacca americana* and *Prunus lusitanica*) as candidate trap crops. We purchased potted plants of these 11 species from commercial garden centres in Switzerland or neighbouring countries. Plants were maintained outdoors until the end of their flowering periods. We then transferred them into insect-proof

greenhouses to protect their fruits from wild SWD infestation. Experiments were conducted over the growing seasons of 2019 and 2020, which allowed all plant species to grow fruits.

Experiments

We performed two-choice experiments either under laboratory or semi-field conditions. In each experiment, we studied the egg-laying preference of SWD for fruits of a trap crop candidate species compared to grapevine (Figure 1: arrows in the top row). Since SWD females may lay different numbers of eggs depending on the general suitability of host plants in their environment, we also compared SWD infestation levels among grapevines next to other trap crop species (Figure 1: arrows in the bottom row). We refer to this as protection potential, i.e. we consider that a candidate trap crop triggers a high protection if adjacent grapes are less infested than grapes in the control treatment.

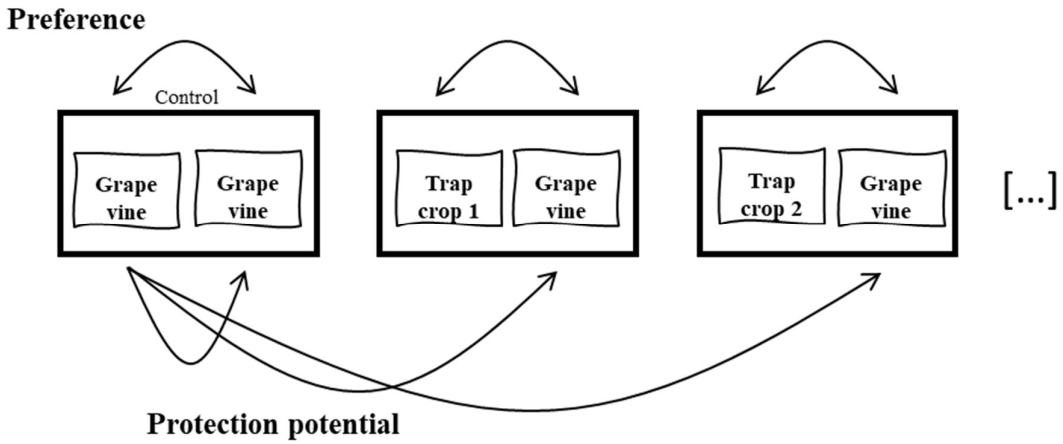

Figure 1: Graphical representation of the statistical analysis in the laboratory and semi-field experiments. Black thick rectangles indicate boxes in the laboratory experiments or cages in the semi-field experiment. Arrows indicate the comparisons for analysing preference (top row) and protection potential (bottom row) in the statistical tests. Preference was analysed by comparing oviposition on a trap crop to a grapevine within the same box/cage. The protection potential was evaluated by comparing grape infestation in the control treatment (Grapevine x Grapevine) with the infestation of grapes in the 11 trap crop treatments.

Laboratory two-choice experiment

We used fruits from our plants reared in the greenhouse to perform two-choice experiments in the laboratory from September 4th to October 31st 2019, and from September 1st until November 10th 2020. We exposed SWD females in rectangular plastic boxes (12 x 8 x 4 cm) to one grape berry and an equivalent weight of berries from one of the 11 trap crop candidate species. As a

control treatment, we also set-up up boxes with two grapes. The two berries were arranged on the opposite sides of the box. We covered the box bottom with filter paper and provided a water-soaked cotton roll to improve humidity and expand SWD life span. We exposed fruits to one SWD female per gram of fruit in each box for 24h under standardised conditions (20°C, 70% RH, 8/16 day/night). We recorded the number of eggs laid on the fruits the following day using a stereomicroscope. The control treatment consisting of two grapes was set up each time we ran the experiment. Depending on the availability of fruits, the 12 treatments were repeated between 22 to 69 times over the two years.

Semi-field two-choice experiment

Two-choice tests were conducted outdoors under semi-field conditions between September 3rd and November 21st 2019, and from August 31st to November 9th 2020. We set up 30 insect-proof cages (1.6 x 1.6 x 1.8 m, Bugdorm©) and placed one potted plant individual of the 11 candidate species and a grapevine of the cultivar Mara 70 cm apart. As a control, we also set up cages with two potted grapevines. Before exposing plants to SWD, we pruned fruits on each potted plant to make fruit availability similar between the two plants within a single cage. After that, we released 50 female and 25 male SWD into each cage. After 42h of exposure, we collected the fruits, recorded the number of laid eggs on each berry using a stereomicroscope and determined the total fruit weight and egg count for each plant. The 12 treatments were repeated 9 to 24 times each over the two years, and at least one cage with two grapevines was set up with the control treatment each time we ran the experiment.

Developmental assays

To assess the suitability of the 11 trap crop candidate species for SWD development into adults, we placed all fruits bearing SWD eggs laid during the laboratory two-choice preference experiments into individual small plastic boxes (2 x 2 x 2 cm). According to the availability of fruit species, 7 to 27 replicates were performed. We stored the boxes under standardised conditions in a climatic chamber (20°C, 70% RH, 16/8 day/night) and monitored them daily to record the number and duration of adult emergences.

Statistical analyses

All statistical analyses were performed in R (version 4.1.1). We ran separate analyses to assess the preference and the protection potential of trap crop candidates, each for the laboratory and

the semi-field two-choice experiment. We generally applied linear mixed effect models with a gaussian error distribution using the library lmerTest (version 3.1.3; Kuznetsova et al., 2017). Preference was evaluated by comparing oviposition on a trap crop to that on the adjacent grapevine (Figure 1 top row). The protection potential was assessed by comparing grape infestation in the control treatment (grape vs grape) with the infestation of grapes in the trap crop treatments. It was sometimes challenging to estimate fruit quantity between plants bearing fruits of different sizes or distributed differently on the branches in the semi-field experiment. Similarly, it was sometimes difficult in the laboratory two-choice experiment to expose precisely the same quantity of trap crop fruits to one grape berry. To correct for the varying availability of fruit, we used the number of eggs per gram of fruit as the response variable in all our analyses. Other possible response variables, such as the absolute number of eggs or the number of eggs per fruit surface, were highly correlated with the number of eggs per gram of fruit (Table S1).

To assess the difference in egg-laying preference between a trap crop candidate and the adjacent grapevine, we used the trap crop candidate as the explanatory variable and the box number nested within the date of the experiment as a random factor in both the semi-field and the laboratory two-choice analyses. To determine the protection potential of each trap crop candidate for grapes, we used the trap crop candidate as the explanatory variable and included the date of the experiment as a random factor. One of the two grapevines from the control treatment (grapevine vs grapevine) designated randomly before the beginning of the experiment was used as the reference level in the analysis. To conform to the assumptions of linearity and homoscedasticity of the linear model residuals, we applied a Box-Cox transformation of the response variables (Zuur *et al.* 2009).

We evaluated the emergence success in the eleven trap crop species using descriptive statistics to characterise trap crop candidate species. The lower the emergence success of SWD in the trap crop candidate plants, the higher its potential for developing a trap crop strategy with minimal spill-over risk.

Results

Laboratory two-choice experiments

There was no statistical difference in the number of eggs laid between the two grapevines in the control treatment, validating thus the experimental set-up (Table 1). The preference of SWD

varied among fruit species (X^2 $_{\text{Anova II}}$ = 943.28, d.f. = 12, *p-value* = < 0.001). All candidate plants were strongly preferred over grapes for oviposition, but preference levels varied: SWD females laid between 1.2 times more eggs per gram of fruit on *Rhamnus cathartica* to 20 times more on *Ampelopsis brevipedunculata* (Figure 2b, Table S2).

Table 1: Linear model of SWD preference for egg-laying, comparing infestation level of the trap crop candidate species with the infestation of the adjacent grapes under laboratory conditions. The intercept value refers to grape infestation. Vitis vinifera cv. Mara row corresponds to the infestation level of the second grapevine plant in the control treatment (the first one being used as the reference level). Because of the Box-Cox transformation of the response variable, negative estimate values indicate a higher infestation than the reference level's infestation.

	Estimate	**SE**	**df**	**t value**	***p-value***
(Intercept)	0.86	0.03	20	33.17	< 0.001
Ampelospsis brevipedunculata	-0.40	0.03	969	-13.61	< 0.001
Cornus amomum	-0.39	0.03	1008	-12.61	< 0.001
Cestrum fasciculatum	-0.25	0.05	910	-5.39	< 0.001
Lycium barbarum	-0.23	0.03	997	-6.56	< 0.001
Lonicera xylosteum	-0.34	0.03	931	-12.07	< 0.001
Phytolacca americana	-0.44	0.03	999	-14.74	< 0.001
Prunus lusitanica	-0.47	0.04	1035	-11.56	< 0.001
Rhamnus cathartica	-0.16	0.05	1076	-3.45	< 0.001
Rubus fruticosus	-0.13	0.04	1041	-3.35	< 0.001
Sambucus ebulus	-0.42	0.03	1002	-14.58	< 0.001
Sambucus nigra	-0.25	0.04	1068	-5.74	< 0.001
Vitis vinifera cv. Mara (control)	0.01	0.02	960	0.28	0.78

The infestation level of grape berries next to the different trap plant candidates (protection potential) was affected by plant species (X^2 $_{\text{Anova II}}$ = 38.87, d.f. = 11, *p-value* = < 0.001). *Sambucus nigra*, *Rhamnus cathartica* and *Lycium barbarum* fruits increased the number of eggs laid on the adjacent grape berries by a factor of 3 compared to the control treatment (Table 2). The infestation of grapes adjacent to *Rubus fruticosus* and *Sambucus ebulus* was very similar to the control. Although statistically not significantly different to the control, the presence of *Ampelopsis brevipedunculata*, *Phytolacca americana* and *Prunus lusitanica* halved the mean number of eggs laid on grapes, while the presence of *Cestrum fasciculatum, Cornus amomum* and *Lonicera xylosteum* increased the mean egg infestation per gram of fruit on the adjacent grape berry around 1.2 times. (Table 2, Figure 2d, Table S2).

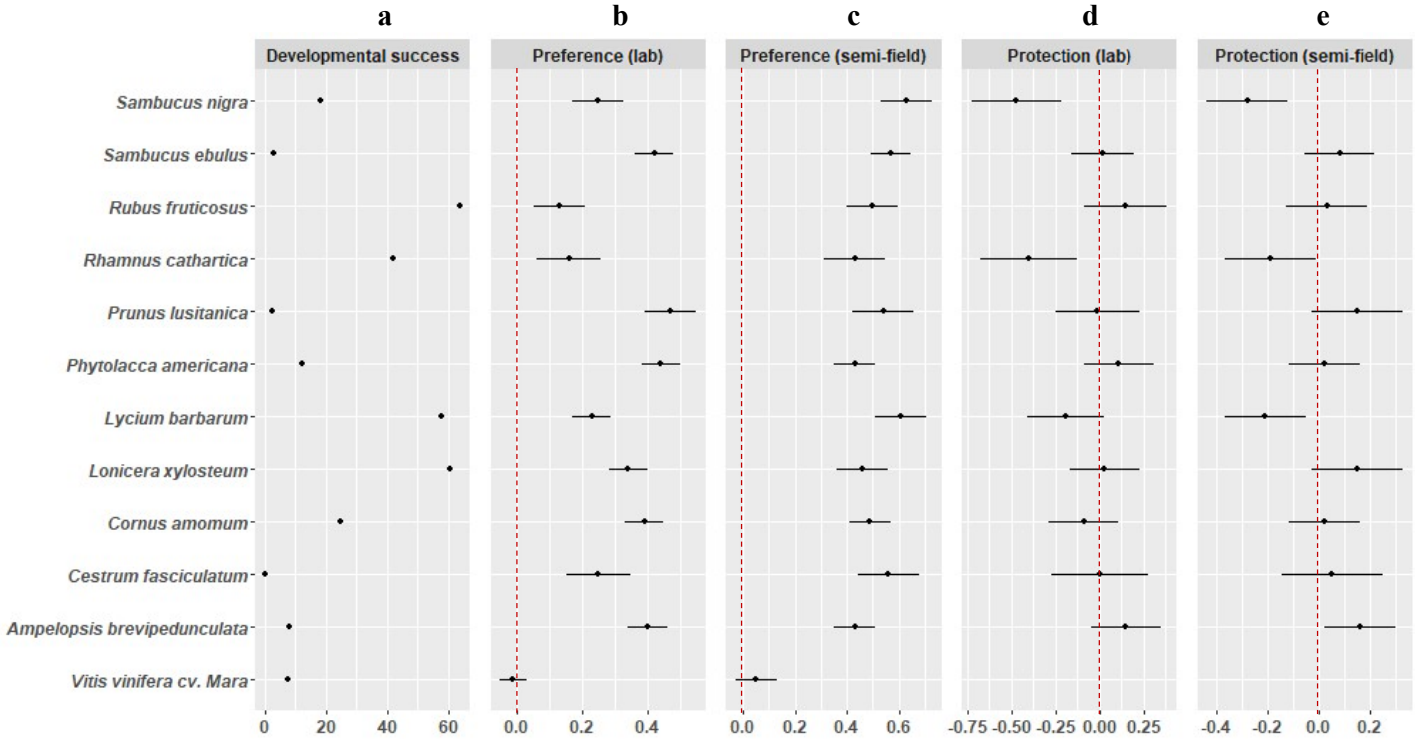

Figure 2: Developmental performance (mean percentage and confidence intervals (CI)) and preference and protection potential (linear model estimate and CI) for each candidate trap crop: a:SWD mean developmental success (%) and the CI around the mean in each plant species. b, c: Linear model estimates and the CI of SWD preference between the trap crop and the grapes under laboratory (b) and semi-field two-choice experiments (c). The reference level of the model (red dashed line) corresponds to grape infestation. d, e: linear model estimates and the CI of the infestation level of grapes in the different trap crop treatments (protection potential) under laboratory (d) and semi-field two-choice experiments (e). The reference level of the model (red dashed line) corresponds to the grape infestation in the control treatment. To simplify the lecture of the graph, the negative estimates seen in Tables 1 to 4 expressing an increase due to the Box-Cox transformation have been multiplied by -1. This way, positive estimates express a stronger preference (b, c) or better protection (d, e).

Table 2: Linear model comparing grapes infestation to determine the protection potential of the candidate trap crop species toward adjacent grapes under laboratory conditions. The intercept refers *to Vitis vinifera cv. Mara*. Negative estimate values correspond to a lower grape infestation compared to the reference level in the presence of the trap crop candidate species.

	Estimate	SE	df	t value	*p-value*
(Intercept)	0.37	0.07	47	5.07	< 0.001
Ampelospsis brevipedunculata	-0.15	0.10	581	-1.54	0.12
Cornus amomum	0.09	0.10	582	0.92	0.36
Cestrum fasciculatum	0.00	0.14	361	-0.02	0.99
Lycium barbarum	0.19	0.11	466	1.67	0.09
Lonicera xylosteum	-0.03	0.10	402	-0.25	0.81
Phytolacca americana	-0.11	0.10	576	-1.12	0.27
Prunus lusitanica	0.01	0.12	590	0.11	0.91
Rhamnus cathartica	0.40	0.14	556	2.78	< 0.01
Rubus fruticosus	-0.15	0.12	535	-1.27	0.21
Sambucus ebulus	-0.02	0.09	584	-0.24	0.81
Sambucus nigra	0.47	0.13	591	3.60	< 0.001

Semi-field two-choice experiments

There was no statistical difference in the number of eggs per fruit weight in the control treatment between the two grapevines under the semi-field conditions (Table 3). The preference of SWD varied among fruit species, but again all were preferred to grapes ($X^2_{\text{Anova II}} = 1023.3$, d.f. = 12, *p-value* = < 0.001, Table 3). The number of eggs per gram of fruits on the trap plant candidates was between 10-times higher for *Rubus fruticosus* and to 50-times for *Prunus lusitanica* (Figure 2c, Table S2).

Table 3: Linear model of SWD preference for egg-laying, comparing infestation level in the trap crop candidate species under semi-field conditions. The intercept refers to *Vitis vinifera cv. Mara*. Because of the Box-Cox transformation of the response variable, negative estimate values correspond to a higher infestation than the reference level's infestation.

	Estimate	SE	df	t value	*p-value*
(Intercept)	0.87	0.01	312	62.71	< 0.001
Ampelospsis brevipedunculata	-0.43	0.04	289	-10.44	< 0.001
Cornus amomum	-0.49	0.04	289	-11.77	< 0.001
Cestrum fasciculatum	-0.56	0.06	299	-9.94	< 0.001
Lycium barbarum	-0.61	0.05	295	-12.65	< 0.001
Lonicera xylosteum	-0.46	0.05	297	-8.93	< 0.001
Phytolacca americana	-0.43	0.04	288	-10.69	< 0.001
Prunus lusitanica	-0.54	0.06	300	-9.02	< 0.001
Rhamnus cathartica	-0.43	0.06	299	-7.52	< 0.001
Rubus fruticosus	-0.50	0.05	293	-10.38	< 0.001
Sambucus ebulus	-0.57	0.04	284	-15.41	< 0.001
Sambucus nigra	-0.63	0.05	296	-12.56	< 0.001
Vitis vinifera cv. Mara (trap)	-0.05	0.04	283	-1.47	0.14

The infestation level between grape berries next to the different trap plant candidates (protection potential) was affected by the plant species ($X^2_{\text{Anova II}} = 53.57$, d.f. = 11, *p-value* = < 0.001). *Ampelopsis brevipedunculata* significantly reduced the number of eggs laid on adjacent gapes by a factor of 0.2 compared to the control treatment. *Lonicera xylosteum* also tended to reduce the infestation in adjacent grapes. Conversely, the presence of *Sambucus nigra, Rhamnus cathartica* and *Lycium barbarum* significantly led to higher egg infestation on adjacent grapes, between 1.2 times for *Sambucus nigra* to 2.8 times for *Lycium barbarum* compared to

grapevines. The other seven candidate trap crop species did not significantly affect the number of eggs laid per gram of fruits on adjacent gapes (Table 4, Figure 2e, Table S2).

Table *4*: Estimate table of the linear model comparing grapes infestation to determine the protection potential of the trap crop candidate species under semi-field conditions. The intercept refers to *Vitis vinifera cv. Mara*. Because of the Box-Cox transformation of the response variable, negative estimate values correspond to a higher grapes infestation compared to the reference level in the presence of the trap crop candidate species.

	Estimate	SE	df	t value	p-value
(Intercept)	0.66	0.06	51	10.85	< 0.001
Ampelospsis brevipedunculata	0.16	0.07	172	2.25	0.03
Cornus amomum	0.02	0.07	175	0.26	0.79
Cestrum fasciculatum	0.05	0.10	180	0.51	0.61
Lycium barbarum	-0.21	0.08	180	-2.44	0.02
Lonicera xylosteum	0.15	0.09	179	1.70	0.09
Phytolacca americana	0.02	0.07	174	0.29	0.77
Prunus lusitanica	0.15	0.09	168	1.62	0.11
Rhamnus cathartica	-0.19	0.09	178	-2.10	0.04
Rubus fruticosus	0.03	0.08	178	0.32	0.75
Sambucus ebulus	0.08	0.07	172	1.22	0.23
Sambucus nigra	-0.28	0.08	172	-3.58	< 0.001

Developmental assays

The 11 trap crop candidate species were differently suitable for the egg-to-adult development of SWD (Figure 3). *Cestrum fasciculatum*, *Prunus lusitanica*, *Sambucus ebulus* and *Ampelopsis brevipedunculata* were of low suitability and allowed only between 0 to 8% of eggs to develop into adult flies. *Phytolacca americana*, *Sambucus nigra* and *Cornus amomum* presented an intermediate egg-to-adult development rate of 12 to 24%. *Rhamnus cathartica*, *Lycium barbarum*, *Lonicera xylosteum* and *Rubus fruticosus* were of higher suitability and between 41 to 63% of eggs laid were able to develop into adults (Figure 2a, Table S2).

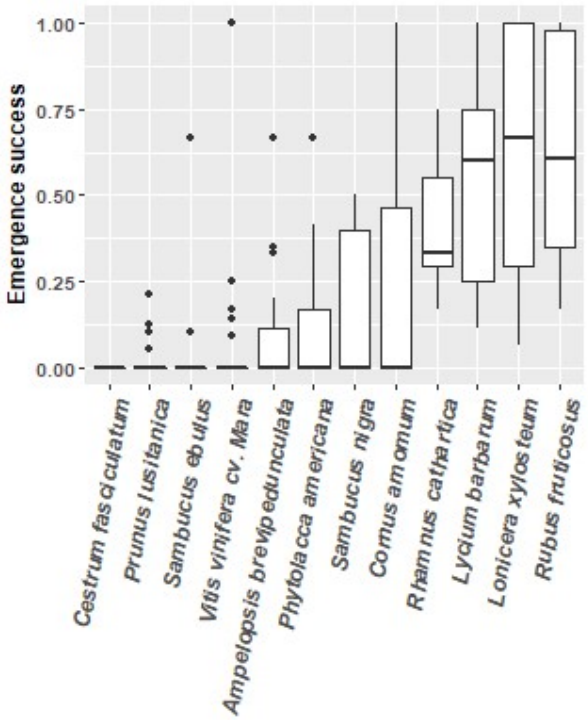

Figure 3: Boxplot of emergence success of each trap crop candidate species.

Discussion

According to our results, the most promising species as dead-end trap crop would be *Ampelopsis brevipedunculata* as it was a strongly preferred over grapes for SWD egg laying and reducing SWD infestation in adjacent grapes. Moreover, *Ampelopsis brevipedunculata* prevented most SWD eggs from developing into adults. No other candidate had a strong profile as dead-end trap crop. Despite a strong preference of SWD to lay its eggs in the other trap crop candidates, none of them showed protection potential, i.e. to reduce infestation in adjacent grapes. Three of them, namely *Sambucus nigra, Rhamnus cathartica* and *Lycium barbarum,* even increased infestation under laboratory and semi-field conditions and thus would increase the risk of a pill-over of the pest to the crop. Therefore, we recommend that they should not be considered any longer as candidate trap crops against SWD in vineyards. Although not reducing infestation, but also not increasing it, four of the 11 candidate trap crops might be of interest for traditional trap cropping as they were nonetheless preferred over grapes for egg-laying.

Preference

The results of the preference tests were consistent under laboratory and semi-field conditions. The preference ranking of the 11 candidate trap plants tested in our study is similar to the preference ranking observed in the no-choice laboratory experiment of Fragnière et al. (in prep.) for most plant species. Exceptions are *Sambucus nigra* and *Prunus lusitanica,* where in our previous study, the first showed a lower and the latter a higher attractivity for SWD egg laying. The preference difference between the trap crop and the crop is one essential component of trap cropping (Mathews et al., 2017). Under field conditions, the presence of various host plant species requires polyphagous pests to permanently choose between different cues emitted by these host plants (Carrasco *et al.* 2015; Silva & Clarke 2020), considering not only different abiotic but also biotic factors such as predation avoidance or the pest's physiological state (Lee *et al.* 2011a; Clymans *et al.* 2019). We increased the complexity of SWD choice compared to our laboratory experiment in our semi-field conditions by having foliated plants and allowing abiotic factors such as light and temperature to vary naturally. Knowing how much SWD preference for host plants differs under simple experimental and natural conditions would help to determine the minimal preference difference that has to be reached by a candidate trap plant over grapevine in our laboratory or semi-field studies (Braga & Janz 2021). Overall, this would greatly simplify the selection of the most appropriate candidates for further field experiments.

Protection effect

To develop an efficient trap crop, preventing pest spill-over from the trap crop to the crop is the second essential element of successful trap cropping (Badenes-Perez et al., 2005; Tscharntke et al., 2005). Our study showed a reduced infestation of grapes adjacent to *Ampelospsis brevipedunculata* and a tendency of reduced infestation next to *Lonicera xylosteum*. This protective effect suggests a low spill-over potential of SWD towards grapevines in the vicinity of these plant species. This could only be observed under our semi-field conditions when whole plants were used, suggesting that SWD is more selective under complex settings. Some candidates, including *Lycium barbarum*, *Rhamnus cathartica* and *Sambucus nigra*, increased infestation on adjacent grapes under laboratory and semi-field conditions, suggesting a larger spill-over of SWD towards grapevines in the vicinity of these plant species. Overall, the effect size of the increased infestation was larger than that of the infestation reduction.

Interestingly, *Lonicera xylosteum* and *Ampelopsis brevipedunculata* had denser foliage than *Lycium barbarum*, *Rhamnus cathartica* and *Sambucus nigra* in the semi-field experiment. Dense foliage might restrain SWD and favour the retention of the pest in architecturally more complex trap crop candidates (Schöneberg et al., 2020). Leaf volatiles are also an essential factor explaining SWD fruit preference for ripening fruits compared to *Drosophila melanogaster* (Keesey *et al.* 2015). Moreover, Plantamp et al. (2017) showed that some fruits that are attractive for SWD egg-laying are not necessarily providing all required nutrients to adult flies, indicating that the fruit status of host plants might not be the only criterium SWD employs. It might be challenging to estimate the importance of fruits offering egg-laying sites compared to other possible triggers.

Developmental performance

We distinguished considerable variation in the developmental performance between our 11 candidate trap crops. In line with Poyet et al. (2015), our study showed that attractive host plants for egg-laying preventing any pest development are scarce. Only *Cestrum fasciculatum* consistently prevented egg development into adults in this study and Fragnière et al. (in prep.). However, many host fruits allow only a weak SWD emergence success, although they do not completely inhibit the development of adults. Compared to the development performance results obtained in Fragnière et al. (in prep.), who used a similar developmental set-up, SWD showed similar developmental performance for five plant species. Yet, in this study, SWD

showed an 8- and 21- times lower emergence success in Sambucus ebulus and Phytolacca americana, respectively. In contrast, emergence success was nearly eight times higher in *Cornus amomum* and *Ampelopsis brevipedunculata* and two to three times higher in *Lonicera xylosteum* and *Phytolacca americana* in this study. We performed development assay replicates over approximately two months, whereas Fragnière et al. (in prep.) replicated development assays from the same sampling events for each plant tested. This allowed them to test a more extensive range of plant species, but a much smaller ripeness range was covered per species. The greater variation in the ripeness stage of our plant species might explain the difference in developmental performance between the two studies. However, how fruit characteristics such as ripeness are linked to developmental performance is still debated (Wetzel *et al.* 2016; Pelton *et al.* 2017; Olazcuaga *et al.* 2019; Morimoto *et al.* 2020).

Implication for trap cropping

In our semi-field experiment, we showed that the candidate trap plant species could affect the infestation level in the adjacent grapes, suggesting that adult spill-over at a small spatial scale affects the infestation of nearby plants. Yet, we have little information about the effect of various levels of pest developmental performance on pest density and potential spill-over toward the main crop. Pest movement between the crop and the crop margins containing highly preferred and suitable host plants, such as *Rubus* spp. or *Lonicera xylosteum* that ensure good larval developmental performance, have been observed. Yet, increased capture rates of SWD flies could only be observed at crop edges without leading to a higher infestation in the crop centre (Leach et al., 2018; Weißinger et al., 2019). This supports the idea that sufficiently preferred host plants for oviposition might be suitable trap crops by increasing pest retention even though they do not completely inhibit SWD development (Blaauw et al., 2017). Most studies developing dead-end trap cropping against SWD were conducted under small temporal and spatial scales. They could therefore not quantify the impact of emergence success on SWD population density nor the possible spill-over of adults. Generally, a high level of pest development can lead to higher pest densities and thus greater damage to the crop (Choquenot & Parkes 2001). In some crop systems, high pest densities in the trap crops did not lead to higher pest densities in the adjacent main crop, suggesting that spill-over may also not only depend on high pest densities (Gordon et al., 2017; Swezey et al., 2013).

Pest development success in hosts is easy to measure and frequently used as a criterion to select trap crops. To protect strawberries in greenhouses, Ulmer et al. (2020) reported promising

results for *Pyracantha coccinea* as a dead-end trap crop against SWD with an emergence success of 0%. Similarly, Shelton and Nault (2004) proposed *Barbarea vulgaris* as a trap crop against *Plutella xylostella* as no egg was able to develop into adults. Yet, several other studies suggest that dead-end trap crops can be used with pest mortality rates ranging from 35% to 60% (Gyawali et al., 2021; Veromann et al., 2014). A successful dead-end trap cropping example was reported at commercial field scale by planting *Erianthus arundinaceus* to control the stem borer *Chilo sacchariphagus* in sugarcane crops (Nibouche et al., 2019). Nibouche et al. (2012) already reported from small-scale field experiments a decrease in sugarcane infestation at a survival rate of the *Chilo sacchariphagus* ranging between 4 to 6%. It is therefore difficult to set an emergence success threshold below which the candidate trap crop should be considered as a dead-end trap crop and above which the use of candidate trap plants should be accompanied by additional control strategies that increase pest retention in the trap crop area and prevent spill-over to the main crop (Holden et al., 2012).

Candidates for dead-end trap cropping

Comparing our candidate's preference, performance and protection potential, we found that *Ampelopsis brevipedunculata, Cestrum fasciculatum* and *Prunus lusitanica* are highly preferred for oviposition. *Prunus lusitanica* is commonly planted in private gardens and parks in Europe. In Switzerland, it is rarely spreading naturally (Info Flora 2022b). *Cestrum fasciculatum* is native to central Mexico and is used as an ornamental plant in Europe. For both species, it was difficult to obtain a sufficient number of ripe fruits on the young potted plants. The number of replicates remained relatively low, roughly around ten replicates per species. The porcelain berry, *Ampelopsis brevipedunculata,* is also widely used as ornamental plant species in Europe. Although it is invasive in the US, we are unaware that this species is particularly problematic in natural areas in Europe (Swearingen *et al.* 2010). Nonetheless, the further development of a suitable trap crop should take into account the invasion potential of these three plant species. The emergence success of SWD on these three species varied between 0 to 8%, which lies in the range of the previously mentioned successful dead-end trap crop, *Erianthus arundinaceus*. Moreover, *Ampelopsis brevipedunculata* reduced SWD infestation levels on adjacent grapes, suggesting a very low spill-over potential, while *Cestrum fasciculatum* and *Prunus lusitanica* neither increased nor decreased infestation on adjacent grapes. Overall, *Ampelopsis brevipedunculata* seems currently to be the most suitable candidate plant species for dead-end trap cropping.

Candidates for traditional trap cropping

The emergence success of the other candidate trap crop plants varied between 12 to 60%. Combined with additional control strategies increasing pest retention within the trap crop area, they might be suitable for traditional trap cropping. In particular, *Cornus amomum* and *Lonicera xylosteum* might be of interest since they did not increase SWD infestations on adjacent grapes in the laboratory and semi-field 2-choice experiments. These candidate trap crops could be tested in combination with other measures increasing either directly the pest retention in the trap crop or indirectly increasing the attractiveness of the trap crop by repelling the pest from the main crop (Hassanali et al., 2008; Khan et al., 2007; Pickett et al., 2010; Wallingford et al., 2018). Currently, repulsive measures such as removing leaves around grape bunches and applying mineral powders are already part of the preventive measures adopted against SWD in Swiss vineyards (Linder *et al.* 2018; Knapp *et al.* 2019). Field experiments testing the efficacy of repellent plant extracts or plant volatiles are rare, but some substances may show interesting repellence potential (Renkema & Smith, 2020; Renkema et al., 2016; Wallingford et al., 2018)

Lonicera xylosteum is an indigenous shrub in Europe, but *Cornus amomum* is an ornamental plant species native to the US. In 2020, it was reported that this species is established along water banks in Lithuania (Petrulaitis & Gudžinskas 2020). We would therefore suggest to carefully test *Cornus amomum* for its invasion potential. Similarly, *Phytolacca americana*, highly invasive in Europe, would have potential in traditional trap cropping only in its native range, North America (Info Flora 2014). Yet, its toxicity for humans and some animals might decrease the interest in this plant as a trap crop (EMEA 2000). The indigenous shrub *Sambucus nigra* increased grape infestation only in the laboratory 2-choice experiment and showed a considerable variation in developmental performance between this study and the results of Fragnière, Bacher and Kehrli (in prep.). We suggest not considering this species for further testing as several other candidate plant species already showed more potential.

Unsuited candidates for trap cropping

Candidate plant species increasing infestation in their immediate vicinities, such as *Sambucus nigra*, *Rhamnus cathartica* and *Lycium barbarum*, should not be considered further in developing a trap cropping management strategy. Interestingly, the potted plants of these three species had very scarce foliage. This might partially explain the higher spill-over and infestation

in adjacent grapes, as SWD might not have found a suitable micro-habitat within that trap crop plant (Tochen *et al.* 2016; Schöneberg *et al.* 2020; Winkler *et al.* 2020).

Rubus fruticosus var. *lockness* did not influence the infestation level in adjacent grapes, but SWD developmental performance was very high at 63%. This plant species is widespread in hedges surrounding vineyards and its presence increases the fly abundance during some seasonal periods (Weißinger *et al.* 2019). We thus suggest that it might increase the SWD population locally.

Next steps

Our study highlighted the potential of several plant species, most of all *Ampelopsis brevipedunculata*, for trap cropping against SWD in vineyards. However, we are still lacking information on how preference for candidate trap crops might change under natural conditions and how SDW emergence success from trap crop fruits affects pest spill-over towards grapes and thus their protection. Given the additional costs associated with the implementation of supporting control measures to limit spill-over in vineyards and increase pest retention in the trap crop area, we suggest that further tests should be conducted first with the dead-end candidate *Ampelopsis brevipedunculata* since it should theoretically not require these extra measures. Additionally, to increase the chances of successful trap cropping, the timing and spatial positioning of the trap crop should be evaluated. For instance, perimeter trap cropping, i.e. trap crops surrounding the crop, has been favourable for managing several mobile pest species (Boucher et al., 2003; Cavanagh et al., 2009; Cohen & Yuval, 2000). We also observed that none of the species tested would bear fruits over the entire grape maturation. We suggest therefore that a trap cropping strategy would be more efficient if several species with straddling fruiting time were associated and could work synergistically (Rhino *et al.* 2014; Parker *et al.* 2016; Gordon *et al.* 2017). Ultimately, the success of the trap crop strategy relies on the economic balance between crop production and protection. The land area dedicated to trap cropping will likely reduce the production land area so that a minimum number of trap crop plants will be used. Depending on local vineyard conditions, the abundance ratio between the trap crop and the main crop will likely affect the successful outcome of trap cropping (West & Cunningham, 2002).

Supplementary material

Table S1: Correlation between possible response variables

Pearson's correlations between the response variable we used in the analysis (egg number per gram of fruits (variable 1) and other response variables that could be used (variable 2). The table above reports the correlations of response variables in the semi-field experiment, the table below reports the correlation of response variables in the laboratory experiments.

Person's correlation						
semi-field experiment						
Variable 1	**Variables 2**	**t-value**	**d.f.**	***p-value***	**CI (95%)**	**cor. Estimate**
egg number per gram of fruit	egg density	13.11	379	<0.001	0.49-0.62	0.56
	egg occupancy	15.6	379	<0.001	0.6-0.68	0.63
	egg number per fruit surface	24.22	379	<0.001	0.74-0.82	0.78
	egg number	11.55	379	<0.001	0.43-0.58	0.51
laboratory experiment						
egg number per gram of fruit	egg number per fruit surface	64.11	601	<0.001	0.92-0.94	0.93
	egg number	64.11	601	<0.001	0.92-0.94	0.93

Table S2 : Raw data measured for each tested plant species in the five different experiments

Mean ± confidence interval (CI) of the developmental success, the trap crop candidate species infestation under laboratory and semi-field conditions (preference) as well as the infestation of grapes adjacent to the trap crop candidate species under laboratory and semi-field conditions (protection).

		Preference		**Protection**	
	developemental success	**laboratory**	**semi-field**	**laboratory**	**semi-field**
Cestrum fasciculatum	0 ± 0	8.59 ± 5.25	3.02 ± 1.15	0.92 ± 1.01	0.2 ± 0.14
Prunus lusitanica	2.44 ± 0.02	9.93 ± 2.55	2.76 ± 1.07	0.53 ± 0.32	0.06 ± 0.05
Sambucus ebulus	2.95 ± 0.05	7.37 ± 1.63	4.82 ± 1.96	0.65 ± 0.31	0.12 ± 0.1
Ampelopsis brevipedunculata	8.13 ± 0.05	7.6 ± 2	2.16 ± 0.86	0.36 ± 0.29	0.06 ± 0.03
Phytolacca americana	12.24 ± 0.07	7.74 ± 1.61	3.27 ± 1.59	0.46 ± 0.24	0.11 ± 0.05
Sambucus nigra	18 ± 0.15	5.59 ± 2.35	7.47 ± 2.69	2.26 ± 1.09	0.4 ± 0.18
Cornus amomum	24.91 ± 0.15	8.07 ± 1.89	7.81 ± 5.22	1.05 ± 0.5	0.08 ± 0.04
Rhamnus cathartica	41.9 ± 0.15	2.54 ± 1.03	8.13 ± 6.25	2.18 ± 1.15	0.58 ± 0.42
Lycium barbarum	57.66 ± 0.14	6.61 ± 2.14	2.73 ± 1.87	2.08 ± 0.97	0.92 ± 0.45
Lonicera xylosteum	60.5 ± 0.14	7.17 ± 1.76	11.04 ± 3.32	0.81 ± 0.41	0.16 ± 0.12
Rubus fruticosus var. *lockness*	63.57 ± 0.2	2.58 ± 1.46	2.95 ± 1.26	0.63 ± 0.69	0.3 ± 0.22
Vitis vinifera* cv. *Mara (trap)	7.5 ± 0.09	0.74 ± 0.27	0.32 ± 0.26		
Vitis vinifera* cv. *Mara		0.72 ± 0.24	0.42 ± 0.26	0.72 ± 0.24	0.32 ± 0.26

Chapter 3 - Testing the efficacy of the fly honeysuckle, *Lonicera xylosteum*, as a perimeter trap crop against *Drosophila suzukii* in small experimental vineyards

Abstract

The development of trap cropping in perennial crops is still uncommon, and we lack scientific-based evidence of trap cropping efficiency potential in the field. We used the fly honeysuckle, *Lonicera xylosteum,* as a trap crop and varied its abundance to identify the most efficient way of protecting grapes from the invasive fruit fly pest *Drosophila suzukii.* Under semi-field conditions, we performed two-choice experiments between grapevines and different *L. xylosteum* abundance. Here, infestation increased in grapes next to a single trap crop plant compared to no trap crops but did not increase in grapes next to two trap crop plants. We also created small-scale vineyards surrounded by different numbers of *L. xylosteum* plants. In this small-scale field experiment, the interaction between the number of *L. xylosteum* plants bearing fruits and the distance from the hedge along our experimental site affected the number of eggs laid in grapes. We have evidence that the abundance of the trap crop has a critical influence as a too low abundance might increase damage instead of providing crop protection.

Introduction

The spotted wing drosophila (SWD), *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), is a mobile and polyphagous invasive pest species in soft fruit crops (Asplen *et al.* 2015). Native to southeast Asia, the SWD has invaded most continents within the last decade (Walsh *et al.* 2011; Cini *et al.* 2012; Deprá *et al.* 2014; Kwadha *et al.* 2021). It lays its eggs in intact ripe berries, thereby damaging many berry crops such as cherries, strawberries, raspberries or grapes, and wild hosts. Berries in which SWD can develop rot prematurely, causing substantial economic damages (Goodhue *et al.* 2011; Farnsworth *et al.* 2017).

In grapes, SWD developmental performance is weak compared to fruits (Pelton *et al.* 2017; Fragnière *et al.* in prep.). Therefore, the development of the larvae into an adult is less problematic than in other fruit crops. However, when SWD lays eggs, it punctures the grape skin allowing subsequent microbial exchanges through the wound. This might trigger the development of the sour rot disease, considerably affecting wine quality (Ioriatti *et al.* 2018) and leading to relevant losses in grape crops. In Switzerland, about two out of three winegrowers expect revenue loss in their vineyards (Knapp *et al.* 2021).

Currently, SWD control in vineyards relies on preventive and sanitation measures (Haye *et al.* 2016; Linder *et al.* 2018). If they are insufficient, farmers have to apply synthetic or biological insecticides (Walsh *et al.* 2011; Knapp *et al.* 2019). As alternative methods are still needed to enhance IPM strategy against SWD, manipulating SWD host plants in the vicinity of vineyards is a suitable biological control option to explore (Vreysen *et al.* 2007; Zhou *et al.* 2011; Tait *et al.* 2021).

Wild hosts in forest edges allow SWD to subsist throughout the year and SWD invades then fruit crops when their fruits start to ripen (Cahenzli *et al.* 2018a; Tonina *et al.* 2018). The proportion of host plants in the landscape is known to modify the local population dynamics of SWD (Santoiemma *et al.* 2019). Moreover, alternative host plants in natural habitats, such as hedges, influence the fly's dispersion in neighbouring crops (Leach *et al.* 2019; Weißinger *et al.* 2019).

Plant host manipulation is used in the pest control method called "trap cropping". This control method seeks to lure a pest away from a crop, deploying host plants that the pest prefers in the

vicinity of the crop (Hokkanen 1991; Shelton & Badenes-Perez 2006). To ensure trap crop efficiency, trap crops also need to retain the pest to limit re-infestation of the nearby crop (Holden *et al.* 2012; Swezey *et al.* 2013). To do so, trap crops are commonly treated with an insecticide, decreasing the quantity used and the surface sprayed compared to a treatment on the main crop and avoiding pesticides residues on the harvest (Ellsworth *et al.* 1992; Mitchell *et al.* 2000; Cavanagh *et al.* 2009; Lin *et al.* 2015; Tomaseto *et al.* 2019). Mechanical alternative measures can also decrease the subsequent pest generation from leaving the trap crop, including vacuuming the trap crop area or destroying the trap crop (Rust 1977; Swezey *et al.* 2007; Cotes *et al.* 2018).

The spatial arrangement of the trap crop contributes to its success (Holden *et al.* 2012). Several studies showed that positioning the trap crop around the main crop, referred to as "perimeter trap cropping", created a natural barrier preventing pest dispersion from semi-natural habitats into the crop while concentrating pest density in the trap crop area (Shelton & Badenes-Perez 2006). This has been favourable in managing several mobile pest species (Mitchell *et al.* 2000; Boucher *et al.* 2003; Adler & Hazzard 2009; Cavanagh *et al.* 2009).

Lonicera xylosteum is a common and native shrub species in Western Switzerland and is abundant in forest edges and hedges (Info Flora 2022a). In laboratory studies, Fragnière et al. (in prep. a, in prep. b) highlighted the potential of *L. xylosteum* as a trap crop against SWD in vineyards. They reported a strong preference of SWD for egg-laying in *L. xylosteum* berries compared to grapes. They also observed a tendency of reduced infestation on grapes adjacent to *L. xylosteum* under semi-field conditions, suggesting a low spill-over potential of adult SWD toward the grapevines.

In this study, we evaluate the potential of *L. xylosteum* as a trap crop to reduce SWD egg-laying in grapes. As SWD invades vineyards from semi-natural edges and its presence decreases with increasing distance from the semi-natural habitats (Cahenzli *et al.* 2018a), we hypothesised that a perimeter trap crop between the vineyard and semi-natural habitats might provide protection against SWD infestation. In the semi-field experiment, we evaluated SWD preference for egg-laying between L. xylosteum and grapes and the effect of trap crop abundance on the grape infestation. In the small-scale field experiment, we assessed the impact of trap crop abundance and distance from the hedge bordering our experimental site on the grape infestation, the trap crop infestation and SWD dispersal within our plots.

Materials and methods

Biological material rearing and maintenance

We used five- to twelve-day-old adult SWD from our insect rearing facility to perform the semi-field experiment. The flies were reared on a homemade banana-yeast growth medium under controlled conditions (22°, 70%RH,16/8 day/night).

To conduct the semi-field and field experiment, grapevines of the grape variety Garanoir were ordered from a plant nursery (Gland, Switzerland) and then grown outdoors in 25-litre pots. Grapevines were treated with synthetic fungicides against downy and powdery mildew roughly every two weeks according to the conventional treatment plan followed in our institute. To ensure that wild SWD did not infest maturing grapes before the start of the experiments, we covered each grape clutch with a fine mesh from the beginning of grape ripening until their use.

L. xylosteum potted plants were purchased from a Swiss garden centre. Two to three years old plants with a height between 1 to 1.5 meters were selected to ensure proper fruiting. Plants were kept outdoors until the end of the flowering period. Subsequently, we transferred them to an insect-proof greenhouse to prevent wild SWD infestation until they were used for the experiments.

Semi-field two-choice test

We performed two-choice preference tests in outdoor insect-proof cages (160 x 160 x 180 cm tents, Bugdorm©) between the 2nd and the 10th of September 2020. We exposed one grapevine plant paired with either no (treatment control), one (treatment 1LX) or two (treatment 2LX) potted *L. xylosteum* plants (n=6 per treatment). We added 50 female and 25 male SWD in each cage and monitored the presence of SWD flies daily. When we no longer observed flies in the cages, we recorded the number of berries, the number of eggs laid and the total berry weight for each potted plant.

To assess SWD preference for egg-laying between *L. xylosteum* and grapevine, we used a linear model to evaluate the effect of the plant species (*L. xylosteum* or grapevine) and the treatment (1LX and 2LX) on the number of eggs laid per gram of fruit (Box-Cox transformed). The control treatment offers no choice. Therefore we included only 1LX and 2LX treatments here.

To test if grapevine infestation depends on the number of *L. xylosteum* plants in the vicinity, we fitted a linear model using only the number of eggs laid per gram of grapes (log-transformed) as the response variable and the treatment (control, 1LX and 2LX) as the explanatory variable.

Field experiment

We set up 18 plots of 16 potted grapevines arranged in a square (Figure 1). Plots were surrounded by zero (control treatment), 8 (treatment 8 LX) or 16 (treatment 16 LX) potted *L. xylosteum* plants (n=6 plots per treatment). *L. xylosteum* was equally distributed around the grapevine plots at a distance of 180cm to the grapevine plants (Figure 1). The 18 plots were separated by at least 10m. Plots were randomly arranged in a grass field surrounded on the northern edge by a hedge and grassland on the other edges. We used the row numbers (1,2 or 3) as a proxy for the distance between the plots and the hedge, with plots of row 1 being the closest to the hedge.

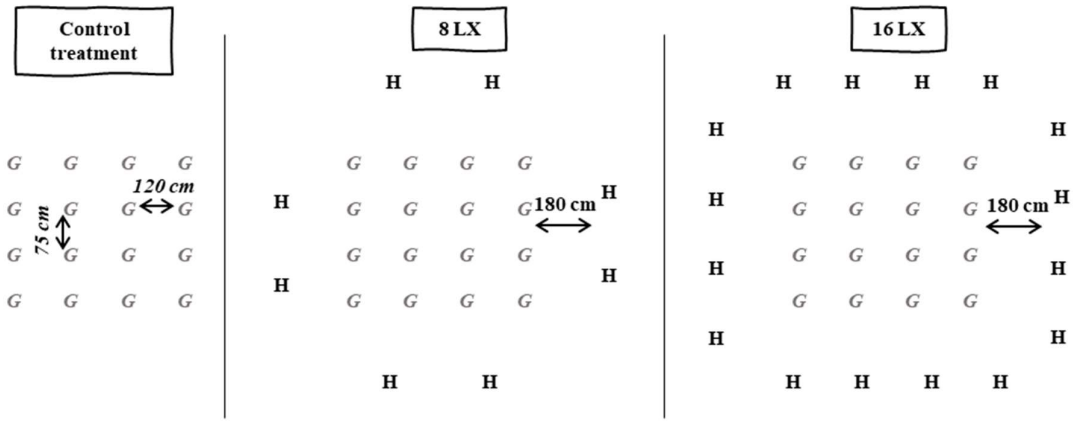

Figure 1: Sketch of the field experiments. The three treatments (control, 8 LX, 16 LX) are composed of 16 grapevine plots surrounded by 0, 16 or 8 L. xylosteum plants. G stands for grapevine, H for L. xylosteum plant.

All plots were covered by a 30 x 30 mm mesh net to prevent birds from eating the berries. The experiment lasted as long as *L. xylosteum* bore fruits, from the 27th of August 2020 until the 30th of September 2020.

We monitored grape infestation on the 4th, 10th, 17th, 24th of September and 1st of October, i.e. once a week during the experiment. We randomly collected 80 grape berries per plot (except during the first sampling, where we collected only three grape berries per plot) and recorded the number of eggs laid on each berry under a stereo microscope. Because of *L. xylosteum* plant transport and windy condition during the experiment, knocking some plants to the ground, some

plants lost all of their berries. Therefore, on the same dates as the grape infestation monitoring, we also recorded in each plot the number of *L. xylosteum* plants bearing fruits as it might be a more accurate descriptor than the treatment categories. On the 4th, 10th and 30th of September 2020, we sampled from each plot six randomly selected *L. xylosteum* berries to evaluate if SWD was actively laying eggs in the trap crop. On the last sampling, we collected and weighted 50 *L. xylosteum* berries from each plot as the experiment ended. The quantity of *L. xylosteum* berries might also be an interesting predictor to test for SWD infestation.

To assess pest pressure, we placed one SWD trap (Drosal pro©, 250ml) in the centre of each grapevine plot and evaluated its content on the 10th, 17th, 24th of September and 1st of October. Traps were filled with a commercial attractant solution. We counted the number of male and female adult SWD captured and refilled traps with fresh attractant solution at each trap evaluation. To evaluate SWD population density, we divided the number of individuals by the days the trap was in the field.

We evaluated the effect of the treatment, the number of *L. xylosteum* plants bearing fruit and the distance from the hedge (predictors) on the grape infestation, the infestation of *L. xylosteum* and the SWD adult capture for both males and females (response variables) with separate generalised mixed effect models (GLMM) for each response variables. The sampling date was set as the random factor in each of them.

To analyse grape infestation, we used the egg number on grapes per plot as the response variable in a GLMM fitted with a Poisson distribution (library lme4, version 1.1.27.1, Bates et al., 2015). We built models with all possible combinations of our explanatory variables under investigation, i.e. treatment (control, 8Lx, 16Lx), the number of *L. xylosteum* plants bearing fruits and distance from the hedge categories. We excluded models combining the treatment and the number of L. xylosteum plants bearing grapes as both predictors describe the same information, i.e. the abundance of trap crop plants around grapevine plots. After that, we ranked the models according to their AICc scores. We considered for model averaging all models falling within six units from the set's best model, except models already containing all predictors of another model with a lower AICc score (library MuMIn version 1.43.17, Barton, 2022).

We used linear mixed effect models with a Box-Cox transformation of the response variables to analyse the effect of the predictors previously cited on the egg number per gram of *L.*

xylosteum berries (*L. xylosteum* infestation) and the number of captured SWD adults per day for both males and females separately (library lmerTest version 3.1.3, Kuznetsova et al., 2017). We followed the same procedure as described above for the model selection. In addition, we also tested for correlation between the number of female SWD captured per day and the grape or *L. xylosteum* infestation using linear mixed models (LMM) (library lmerTest version 3.1.3, (Kuznetsova *et al.* 2017).

All analyses were conducted in R (version 4.1.2).

Results

Semi-field experiment

We observed a strong preference of SWD for egg-laying in *L. xylosteum* berries compared to grapes in the semi-field experiments. The plant species and the treatments (1 Lx and 2 Lx) affected the number of eggs laid per gram of fruit but not their interaction (Table 1). The infestation was higher in *L. xylosteum* compared to grapes and grapes in the cage with the treatment 2Lx had fewer eggs per gram of fruit than grapes in cages with the treatment 1 Lx (Table 2).

Table 1: Analysis of deviance (Type II) of the number of eggs laid per gram of fruit (Box-Cox transformed) according to the plant species and the treatment.

Analysis of deviance table (Type II)

	SS	df	F value	*p-value*
Plant species	1.72	1	216.69	< 0.001
Treatment	0.12	1	15.21	0.001
Plant species : Treatment	0.01	1	1.68	0.212

Table 2: Linear model of the number of eggs laid per gram of fruit (Box-Cox transformed) according to the plant species and the treatment. The intercept of the model referred to *Vitis vinifera cv. Garanoir* infestation and 1 Lx treatment. The model was run without the interaction term between the plant species and the treatment as it was not significant in the Anova type II of the linear model (Table 1). Due to the Box-Cox transformation of the response variable, the sign of the estimates are reversed. A negative estimate corresponds thus to an increase compared to the intercept. SE = standard error.

Linear model estimate table

	Estimate	**SE**	**t value**	***p-value***
(Intercept)	0.77	0.03	22.01	< 0.001
L. xylosteum	-0.57	0.04	-14.45	< 0.001
Treatment 2Lx	0.15	0.04	3.83	0.001

The treatments (control, 1 Lx, 2 Lx) affected overall the infestation level of grapes ($R^2 = 0.35$, Anova type II : SS = 0.22, $F_{2,15}=4$, *p-value* = 0.04). We have moderate evidence that the presence of one *L. xylosteum* plant (treatment 1 Lx) increased the infestation level on adjacent grapes in comparison to the control, whereas the presence of two *L. xylosteum* plants (treatment 2 Lx) did not significantly increase the infestation level on adjacent grapes (Figure 2, Table 3, Table S1)

Table 3: Linear model on the egg number per gram of grapes (log-transformed) according to the treatments (1 Lx, 2 Lx). The intercept refers to the control treatment. SE = standard error.

Linear model estimate table

	Estimate	**SE**	**t value**	***p-value***
Intercept	0.10	0.07	1.47	0.16
1 Lx	0.26	0.10	2.73	0.02
2 Lx	0.07	0.10	0.72	0.48

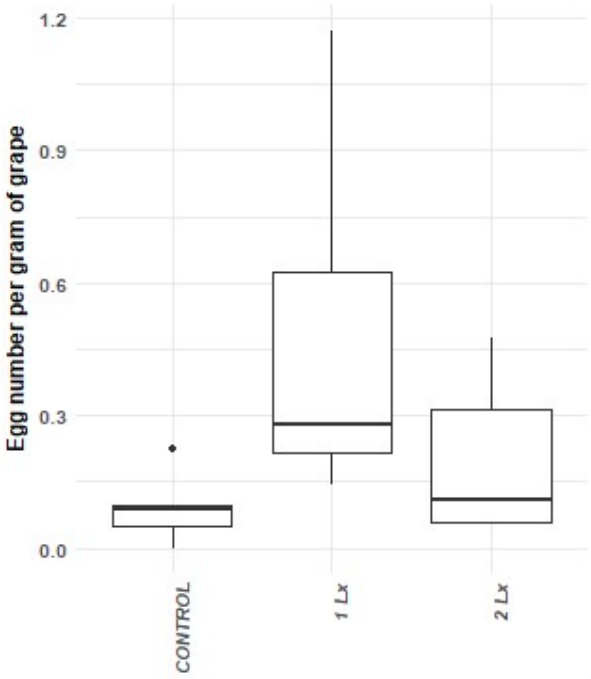

Figure 2: Boxplots of the infestation level in grapes (raw data) for the three treatments in the semi-field experiment.

Field experiment

Over the three sampling dates in the trap crop, the number of *L. xylosteum* plants bearing fruits stayed relatively constant between the two trap crop treatments, with treatment 1 Lx having about half the number of plants bearing fruits (Table S2). Infestation in both grapes and the trap crop increased over time while the number of SWD females decreased in the traps (Figure 3)

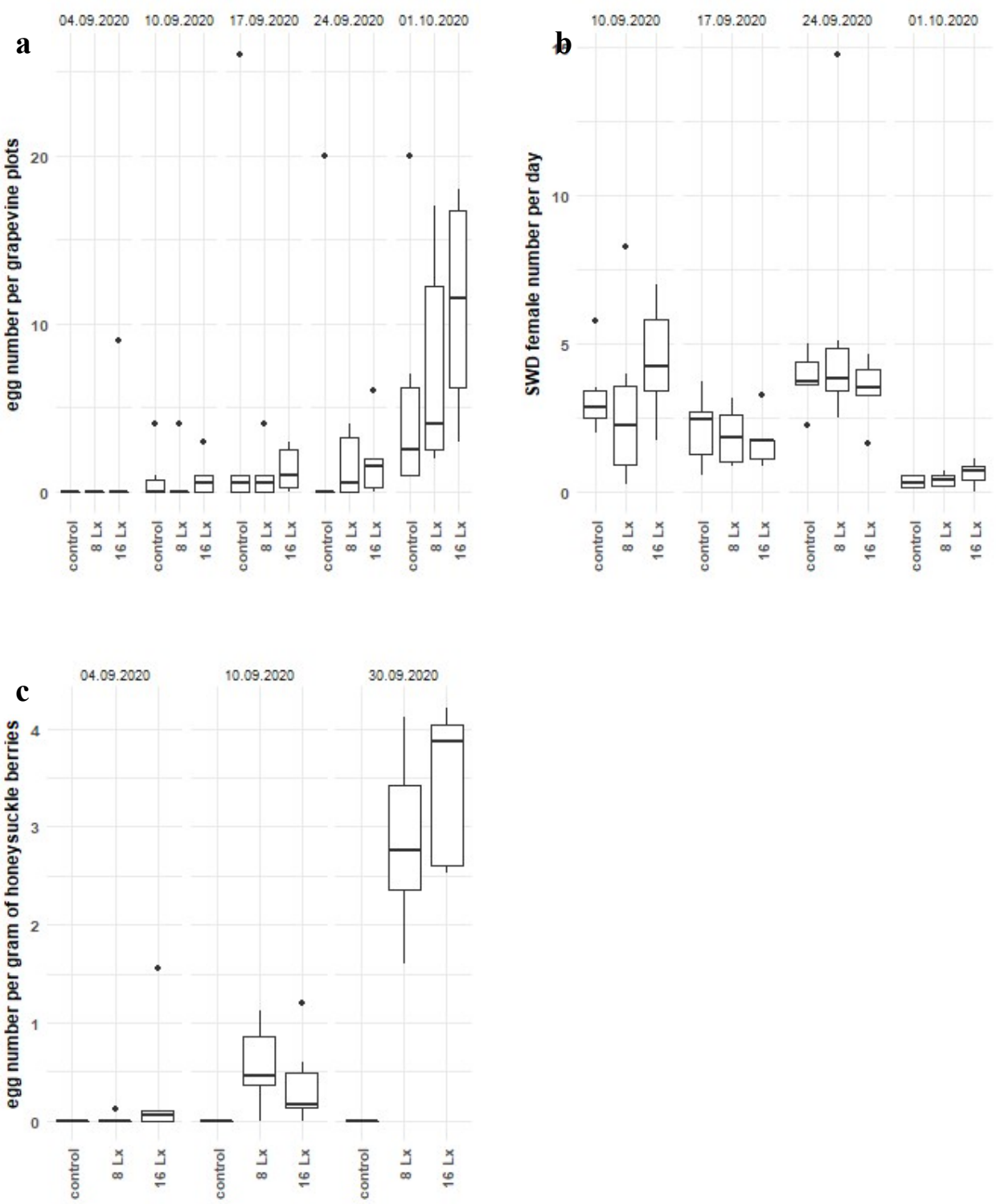

Figure 3: Boxplots of a) the infestation level in grapes, b) the abundance of SWD females per day, and c) the infestation level in L. xylosteum.

The infestation on grapes, i.e. the egg number per grapevine plot, was best described by a model including the number of *L. xylosteum* plants bearing fruits, the distance from the hedge and their interaction (Table 4, Table S3).

Table 4: Analysis of deviance (Type II) of the number of eggs laid per plot according to the number of L. xylosteum plants bearing fruits, the distance between the plot and the hedge and their interaction.

Analysis of Deviance Table (Type II)

	X^2	Df	*p-value*
Number of *L. xylosteum* plants bearing fruits	4.07	1.00	0.04
Distance from hedge	23.51	1.00	< 0.001
Number of *L. xylosteum* plants bearing fruits : Distance from hedge	20.99	1	< 0.001

The model shows that the number of eggs laid on grapes decreases with an increasing number of *L. xylosteum* plants bearing fruits or increasing distance from the hedge. Yet, the significant interaction indicates that these trends might change depending on both predictors (Table 5). We found no correlation between grape infestation and *L. xylosteum* berry weight on the last sampling date ($R^2 = 0.01$, $F_{1,16}=0.22$, *p-value* = 0.65).

We found no predictors explaining *L. xylosteum* infestation, as the best model according to the AICc score was the null model (Table 6).

Table 5: Estimate table of the GLMM fitted with a Poisson distribution. SE stands for the standard error

GLM estimate table

	Estimate	SE	z value	*p-value*
(Intercept)	-0.13	0.76	-0.17	0.86
Number of honeysuckle plants bearing fruits	0.39	0.09	4.14	< 0.001
Distance from hedge	-0.72	0.11	-6.59	< 0.001
Number of *L. xylosteum* plants bearing fruits : Distance from hedge	0.48	0.10	4.58	< 0.001

Table 6: AICc score table of linear models analysing the egg number per gram of L. xylosteum berries according to the different predictor combinations. (x^2) indicate that a quadratic fit of the predictor was tested

Predictors	*df*	*AICc*	Δ AICc
null model (1)	3	*-28.18*	*0.00*
distance to hedge	4	*-26.35*	*1.83*
treatment	*4*	*-25.80*	*2.38*
distance to hedge, treatment	5	*-23.93*	*4.24*
number of honeysuckle plants bearing fruits	*4*	*-22.04*	*6.14*
number of honeysuckle plants bearing fruits, number of honeysuckle plants bearing fruits (x^2)	*5*	*-17.10*	*11.08*
number of honeysuckle plants bearing fruits, distance to hedge	*5*	*-17.00*	*11.18*

The number of captured SWD females per day was not correlated with the number of eggs per grapevines plots or the number of eggs per gram of *L. xylosteum* (Anova type II $_{L.xylosteum}$: $\chi 2$ =0.0729, df=1, *p-value* = 0.79; Anova type II $_{grapes}$: $\chi 2$ =0.54 df=1, *p-value* = 0.45). However, we observed that the distance from the natural hedge better explained the count of captured SWD females than males per day (For females: Anova II: $\chi 2$ =9.46, df=1, *p-value* = 0.002; Table S4; For males: Table S5). The number of females captured decreased with increasing distance from the hedge (Table 7).

Table 7: Estimate table of the linear mixed effect model on the count of captured SWD females (Box-Cox transformed) per day according to the distance from the hedges.). Due to the Box-Cox transformation of the response variable, the sign of the estimates are reversed. A positive estimate corresponds thus to a decrease compared to the intercept.

Linear model estimate table

	Estimate	***Std. Error***	**df**	**t value**	**p-value**
Intercept	0.65	0.07	3.88	9.59	< 0.001
distance from hedge	0.04	0.01	67.00	3.08	0.003

Discussion

We have shown that the relative abundance of trap crop to crops can impact the infestation level of the pest in the crop. In semi-field experiments, grape infestation increased with a single *L. xylosteum* plant. In contrast, with the presence of two *L. xylosteum* plants, it stayed at similar levels compared to infestation levels in the control treatment. In the small-scale field experiment, the interaction between the trap crop abundance and the distance from the hedge affected the grape infestation. This suggests that the appropriate abundance of trap crop plants to protect a crop might depend on the local arrangement of the semi-natural structures bordering it.

We found no evidence of damage reduction when using *L. xylosteum* plants as trap crops in the field with the two trap crop abundances tested. Our experiment did not confirm the potential of *L.* xylosteum to serve as a trap crop in vineyards as suggested in previous laboratory studies (Fragnière et al., in prep. b). Their study assessed SWD preference for egg-laying between *L. xylosteum* and the grape cultivar Mara. We think this modification should not strongly impact the efficiency of *L. xylosteum* as a trap crop. Genetically, the cultivars Garanoir and Mara are close since they both come from the hybridisation of the same parents Gamay x Reichensteiner (Swiss Wine 2016). The sensitivity of different grape cultivars has been found in many studies (Pelton *et al.* 2017; Baser *et al.* 2018; Entling *et al.* 2019; Tonina *et al.* 2020). Still, Kehrli et al. (2017b) observed a similar infestation rate in the cultivars Mara and Garanoir.

L. xylosteum is widespread in Switzerland (Info Flora 2022a) and was present in the hedge bordering the experimental area (unpublished field observations). The phenology of *L. xylosteum* in natural conditions is too early to cover the entire grape maturation period.

Moreover, *L. xylosteum* berries are also frequently eaten by birds therefore their natural densities are not very high at the end of the grape maturation period. When potted, the maturation of *L. xylosteum* is even faster. Thus, the *L. xylosteum* plants used for the experiments bear very ripe fruits when the experiments could start and this might not be representative of *L. xylosteum* in natural conditions. Still, we observed in the semi-field experiment that overripe *L. xylosteum* berries were preferred over grapes to lay eggs even though SWD prefers in general ripening fruit over green or overripe ones (Lee *et al.* 2011b). Therefore, our field experiment might have missed the optimal timing when the preference for *L. xylosteum* berries is maximal compared to grapes. This might consequently impact the efficiency of *L. xylosteum* as a trap crop. To protect grapes during their entire maturation period, we suggest a mixture of several plant species should be considered (Parker *et al.* 2016).

The infestation rate and the number of captured SWD were uncorrelated, in line with the observations of Burrack et al., 2015; Drummond et al., 2019; Hamby et al., 2014 and Pelton et al., 2016. Kirkpatrick et al. (2018b) estimated that a single SWD captured corresponds to roughly 200 SWD in a trapping area of 2,7 ha in tart cherry crops. A female SWD do not acquire enough food from intact fruits acting as oviposition sites to mature their eggs (Plantamp *et al.* 2017). Therefore, SWD responds to different cues according to its physiological state, with fermentation food volatiles attracting flies in search of food while fruit volatiles attract flies in search of oviposition sites (Clymans *et al.* 2019). SWD has also been observed to leave secretion on the fruit during egg-laying, which could stimulate the oviposition in other emigrant female SWD (Tait *et al.* 2020b; Elsensohn *et al.* 2021a, b). Recently, much progress has been made in understanding physiological changes at the fly level (Pool & Scott 2014). However, we still lack knowledge about how these changes impact the daily behaviour of SWD and how this can be used to adapt crop protection strategies.

We observed an infestation increase in the trap crop before seeing an infestation in grapes in the field experiment. Leach et al. (2019) reported a season-long high abundance of SWD in the vicinity of *L. xylosteum* plants bordering blueberry farms. Still, they did not observe significantly higher infestation levels in crops adjacent to *L. xylosteum* plants than in crops adjacent to non-host plant species. As SWD egg-to-adult development time is around 15 days at 20°C in *L. xylosteum* fruits (Fragnière et al., in prep. b, in prep. a; Poyet et al., 2015), our study cannot distinguish damage due to individuals from the second generation hatching from

the trap crop or due to the emigration of adults from semi-natural structures. Potential spill-over from the second generation of pests seems likely (Diepenbrock *et al.* 2016).

We tested in our field experiment a perimeter trap cropping strategy. Perimeter trap cropping has been tested in several studies and is often associated with an insecticide application on the trap crop to improve its efficiency and avoid pest spill-over (Boucher 2003, Aluja 1997; Cavanagh 2009, Potting 2014). Heterogenous patchy habitats may disrupt polyphagous pest movement (Garcia *et al.* 2020), yet vineyards usually cover large homogenous areas. Rows of trap crops placed around the vineyard might be highly attractive but leave a large proportion of the crop without direct protection. Alternatively, trap crop plants which would be scattered within the field might not be of sufficient size to attract an adequate proportion of the pest and thereby fail to protect the crop (Holden et al., 2012). The number of potted *L. xylosteum* plants surrounding the grapevine plots was not creating a dense perimeter trap crop. At the landscape scale, Bahr et al. (1998) suggested that tall and dense vegetation structures, such as hedges, could make pest movement harder in the landscape and enhance regional pest control. Tillman et al. (2014) tested barriers, synthetic or plant-based and dense enough to block the view over the field, to stop adult stink bug dispersal into cotton crops. Their study showed that plant-based and synthetic barriers taller than the cotton crop efficiently prevented bug dispersion. As our trap crop plants were scattered around the grapevine plots, we suggest that this was insufficient to create a barrier-like effect against SWD.

We could perform only a small-sized field experiment even though SWD is a highly mobile pest species. The 18 plots were spread over a 50m x 200m field surface and at least 10m apart. Passive SWD dispersal capabilities are strong, up until 9km away from their marking point (Tait *et al.* 2018). Regarding daily movements, food-based traps are not attractive and capture low numbers of flies when decaying fruits are available in the field (Vacas *et al.* 2019). Still, SWD has a relatively low active dispersal capacity in comparison to other fruit flies and most dispersal happens within 200 to 300m (Vacas *et al.* 2019; Tait *et al.* 2020a). This suggests that one fly could visit several plots each day. With control plots embedded in the same area, we suggest that our experimental field might look like one large complex vineyard, i.e. supporting a higher proportion of semi-natural habitats than a regular vineyard. Scattering the plots over a larger landscape area would prevent flies from actively dispersing to the nearby plots. However, this would simultaneously increase natural variation and possibly cover the potential effect of trap cropping if they are weak.

In semi-field experiments, we showed the importance of trap crop abundance on the infestation level of adjacent grapes. Our study also highlights the importance of considering the distance to natural structures as they might influence the effect of trap crop abundance on crop infestation. Field tests to identify trap crop abundances sufficient to control the pest remain challenging as SWD density fluctuates yearly (Daniela *et al.* 2018). Moreover, they are essential to find an economic balance between the area of land dedicated to trap cropping and production. To avoid too much land loss, farmers involved in the experiment of Nibouche et al. (2019) adopted the trap cropping strategy requiring 8 to 12 % of land for trap cropping (Nibouche *et al.* 2012). Still, they planted the trap crop as discontinuous borders or in uncultivated areas close to their fields. The efficiency of such adaptation by the practitioners was however not scientifically investigated.

As the dispersal of organisms depends in part on the resource abundance (Dwyer & Morris 2006), trap crop abundance and local landscape composition should therefore be examined with caution because a too low abundance especially in simple landscapes might increase damage rather than protect grapes (Chaplin-Kramer & Kremen 2012; Sivakoff *et al.* 2013). Trap cropping, therefore, seems to be a very challenging and demanding control method to develop from a scientific point of view, as many aspects have to be evaluated to offer an effective and safe control method to practitioners.

Supplementary material

Table S1: Raw data of oviposition preference in the semi-field experiment

Mean ± confidence interval (CI) of the egg number per gram of fruit and the fruit weight for L. xylosteum plants and grapevines according to the treatment (1 Lx, 2 Lx, control) in the semi-field experiment.

treatment	plant species	Mean ± CI egg number per gram of fruit	Mean ± CI fruit weight
1 Lx	*L. xylosteum*	14.97 ± 6.18	8.07 ± 4.84
	Vitis vinifera cv. Mara	0.47 ± 0.3	24.56 ± 3.14
2 Lx	*L. xylosteum*	5.22 ± 3	59.42 ± 34.68
	Vitis vinifera cv. Mara	0.2 ± 0.15	26.52 ± 5.86
control	*L. xylosteum*		
	Vitis vinifera cv. Mara	0.11 ± 0.07	26.83 ± 11.02

Table S2: Data summary of *L. xylosteum* in the field experiment

Summary table of the *L. xylosteum* plants and fruit weight over time in the field experiment. **a** = Mean ± confidence interval (CI) of *L. xylosteum* berry weight at the end of the experiment for each treatment. **b**= Mean ± confidence interval (CI) of the number of *L. xylosteum* bearing fruits for each sampling date and treatment.

a

treatment	number of *L. xylosteum* plants	Mean ± CI *L .xylosteum* fruit weight
16 Lx	16	28.93 ± 11.54
8 Lx	8	21.44 ± 11.82
control	0	0 ±0

b

treatment	Mean ± CI number of *L. xylosteum* plants bearing fruits	Sampling date
16 Lx	12.5 ± 1.21	17.09.2020
2 Lx	6.5 ± 0.84	
16 Lx	11.83 ± 2.23	24.09.2020
2 Lx	6 ± 1.34	
16 Lx	10.83 ± 1.92	30.09.2020
2 Lx	6 ± 1.34	

Table S3: Model selection for grape infestation

Each row indicate the predictors and the AICc value of each model tested. (x^2) indicate that a quadratic fit of the predictor was tested.

Predictors	df	*AICc*	Δ AICc
number of *L. xylosteum* plants bearing fruits * distance to hedge	5	415.41	0.00
number of *L. xylosteum* plants bearing fruits, distance to hedge	4	437.21	21.80
number of *L. xylosteum* plants bearing fruits (x^2)	4	474.19	58.78
number of *L. xylosteum* plants bearing fruits	3	479.74	64.33
distance to hedge * treatment	7	504.82	89.41
distance to hedge ,treatment	5	540.70	125.29
distance to hedge	3	548.80	133.39
treatment	4	573.81	158.40
null model (1)	2	578.19	162.78

Table S4: Model selection for captured SWD female per day

Each row indicate the predictors and the AICc value of each model tested. (x^2) indicate that a quadratic fit of the predictor was tested.

model predictors	df	*AICc*	Δ AICc
distance from hedge	4.00	-128.44	0
distance from hedge,treatment	6.00	-125.11	3.32513
null model (1)	3.00	-121.70	6.74475
treatment	5.00	-118.20	10.23577
distance from hedge, number of *L. xylosteum* bearing fruits	5.00	-99.62	28.82354
number of *L. xylosteum* bearing fruits	4.00	-97.47	30.97291
number of *L. xylosteum* bearing fruits, number of *L. xylosteum* bearing fruits^2	5.00	-95.12	33.32312

Table S5: Model selection for captured SWD male per day

Each row indicate the predictors and the AICc value of each model tested. (x^2) indicate that a quadratic fit of the predictor was tested.

model predictors	df	AICc	Δ AICc
distance from hedge	4.00	-27.51	0.00
null model (1)	3.00	-25.78	1.73
distance from hedge,treatment	6.00	-24.03	3.48
treatment	5.00	-22.44	5.07
distance from hedge, number of honeysuckle bearing fruits	5.00	-20.66	6.85
number of honeysuckle bearing fruits	4.00	-18.81	8.70
number of honeysuckle bearing fruits, number of honeysuckle bearing fruits^2	5.00	-16.49	11.02

General Discussion

This thesis presented the shortlisting process to identify potential trap crop species to protect grapes from SWD damage and a small-scale field experiment testing the efficacy as trap crop of one of these candidates, *Lonicera xylosteum*, under natural conditions. In Chapter 1, we performed experimental trials on a range of potential SWD host plants to evaluate SWD preference for egg-laying and its developmental performance in their fruits. We identified 16 plant species with an interesting potential as trap crops. We highlighted substantial variation of SWD emergence success in the fruits of these different plant species, which could not be explained by the fruit pH or sugar content. In Chapter 2, based on the findings of Chapter 1, we selected 11 candidate trap crops that we tested against grapevines in two-choice experiments under semi-field conditions. We found that SWD demonstrated a strong preference for *Ampelopsis brevipedunculata* for oviposition and reduced the infestation of adjacent grapes. In addition, we eliminated from the selection process three candidate plant species, *Lycium barabarum*, *Sambucus nigra* and *Rhamnus cathartica*, which should not be considered further for trap cropping tests as the infestation of adjacent grapes increased in their presence. Based on the results of Chapter 2 and accounting for technical considerations, we tested *Lonicera xylosteum* in Chapter 3 in a small-scale field experiment. Although we could not demonstrate the efficacy of the trap cropping method with this candidate trap crop under field conditions, we showed that semi-natural structures and the abundance of the trap crop impacted the grape infestation. In the semi-field experiment of Chapter 3, low trap crop abundance increased the infestation of adjacent grapes, whereas a higher trap crop abundance did not change the infestation level in comparison to the control treatment.

Two-choice experiments

Our study demonstrated that over three growing seasons, it is possible to test a wide range of potential host species and identify candidate trap crop plants that can then be tested under field conditions. The laboratory experiments of the first year allowed the testing of many plant species and selecting species worth further evaluation. However, the two-choice laboratory experiments did not provide much additional information in the following years than the two-choice semi-field experiment. They thus did not contribute much to the decision-making. Nevertheless, they allowed us to compare SWD responses across two degrees of experimental complexity. They also ensured the obtention of results, as the semi-field experiments are

comparatively more challenging to perform and present more uncertainties. The scientific pertinence of these two-choice laboratory experiments is debatable and I think they might be dispensable when testing selected candidate trap crops are tested under semi-field conditions in a two-choice set-up. With the time gained, I would instead suggest performing two-choice tests using potted plants already under field conditions. This would allow a more accurate picture of the insect preference under natural conditions (Silva & Clarke 2020) and also help evaluate the needs and obstacles for future field experiments. During the second year, we performed two-choice tests with four plant species against grapevines in an open field with the remaining potted plants (Annex 1). As their number was limited, the number of replicates were low and the natural SWD population pressure, was also low (unpublished observations). Since the experiment was inconclusive (infestation level were too low), we chose not to use it in the second chapter. Still, as stated above, I think it might be a better complementary experiment to the semi-field two-choice trials than the laboratory experiments (Diamond 1983).

In addition, when the number of selected candidate trap crop species to perform the two-choice experiments is low, I suggest directly testing an abundance gradient of the tested trap crops. Rather than testing approximately the same quantity of fruits among the candidate trap crops, I suggest that varying the number of fruits (i.e. having an abundance gradient) within a candidate trap crop would allow the identification of the minimal abundance of trap crops to lower infestation on adjacent grapes. Comparisons across candidate trap crop species would still be possible by standardising the infestation with the quantity of fruit available.

SWD behaviour

To accelerate the search for good candidate trap crops against SWD, we tested fruit traits such as pH, sugar content, and skin colour but found that these characteristics did not contribute to the choice patterns nor influence the developmental performance of SWD. When the primary aim of a study is to understand large-scale infestation patterns or evaluate control methods, the traits measured to understand the pest behaviour are often very general and easy to measure, as usually few resources are required to obtain these data (Poyet *et al.* 2015; Kamiyama & Guédot 2019). Evaluating general traits is crucial in the first years of the invasion to understand rapidly fundamental aspects of the pest biology and the potential species that it may affect (Burrack *et al.* 2013; Ioriatti *et al.* 2015; Poyet *et al.* 2015). Later in the invasion process of the crop pest, the study of traits should instead aim at increasing the efficacy of existing trapping techniques (Basoalto *et al.* 2013; Rice *et al.* 2016) or at increasing the specificity of current or future

control methods (Becher *et al.* 2012; Olazcuaga *et al.* 2019; Tait *et al.* 2020b; Bolton *et al.* 2021). To do so, finer analysis of traits might be required. This could bring valuable information as current traps or lures against SWD, lack species-specificity (Cloonan *et al.* 2018).

The semi-field experiment we performed allowed us to evaluate SWD preference of one fly generation. The field experiment, which lasted a month, allowed SWD to complete at least one lifecycle in the trap crop fruits. Yet, we cannot distinguish the damage caused by this second generation from damage caused by the natural immigration of flies from the semi-natural structures. Oviposition and feeding experiences as adults or larvae can improve the host detection capacity of polyphagous insects (Cunningham *et al.* 1999; Cunningham & West 2008; Anderson & Anton 2014) and are therefore likely to exhibit associative learning behaviour (Jones & Agrawal 2017). This would be favourable for trap cropping, as flies emerging from the trap crop could potentially prefer similar hosts as adults. However, SWD lacks host fidelity (Diepenbrock *et al.* 2016), suggesting that the second generation emerging from a trap crop might not be inclined to stay in the trap crop. Retention of flies in the trap crop is consequently crucial to evaluate (Holden *et al.* 2012). Rearing distinct SWD population on different hosts would allow the assessment of trap crop preference and protection effect modifications.

Trap crops are commonly associated with push-pull strategies, so that the push effect, usually deterrent substances, increases the preference for the trap crop (Hassanali *et al.* 2008; Lamy *et al.* 2018). Wallingford et al. (2018) determined that under experimental conditions, octenol and geosmin molecules could deter SWD from the previously attractive smell and that 1-octen-3-ol dispensers decrease SWD infestation within a 10cm radius in a raspberry field. Other substances tested in laboratory conditions did not provide sufficient deterrent effects to expect a deterrent effect under field conditions (Wernicke *et al.* 2020).

Field experiment

Choice of the candidate trap crop

Based on the results of Chapter 2, *A. brevipedunculata* was found to be a superior choice than *L. xylosteum* for testing trap cropping in the field experiment. The two-choice experiments were performed over two years. At the end of the first year (2019), when the field experiment was being planned, the results indicated that *L. xylosteum* was the best candidate trap crop

plant. *A. brevipedunculata* plants and fruits were only ready for testing in our facilities in 2020. The decision to use *L. xylosteum* for the field experiment thus was based on the results of the two-choice experiments of 2019 and its ready availability. *L. xylosteum* is a common indigenous shrub in Switzerland and can be purchased in high number in local garden centres.

From field experiments to trap cropping use

To conduct our field experiments, we used potted grapevines. However, we observed that the phenology of potted plants is often slightly shifted in time compared to planted species. In trap crops, the phenology and thus the development stage of a trap crop plant species plays a crucial role in attracting pest species (Cotes *et al.* 2018). This could not be evaluated in our study. Nevertheless, using potted plants offers the possibility to create simple small-scale plots of a perennial crop and allows the testing of candidate trap crops in a relatively easy manner. Grapevines can be grown for a couple of years in pots and produce enough grape bunches so that experiments can be replicated over several years.

Very few examples of trap cropping experiments in perennial crops exist (but see Aluja et al., 1997; Javaid & Joshi, 1995; Moussa et al., 2019; Tomaseto et al., 2019; Wan et al., 2016). This might be explained partially by the technical difficulties of manipulative studies in perennial crops and also by the risk of increased infestation in the field, as we showed in Chapter 3 where a too low trap crop abundance increases infestation. The majority of studies assessing trap cropping have been conducted for annual crops (see reviews Hokkanen, 1991; Javaid & Joshi, 1995; Sarkar et al., 2018; Sharma et al., 2019; Shelton & Badenes-Perez, 2006), with several positive reports (see for example Boucher et al., 2003; Mitchell et al., 2000; Nibouche et al., 2012; Rea et al., 2002). Whether trap cropping tests led to commercial use is not reported in the scientific literature. Trap cropping is most likely not a standard method in industrialised European or North American farms.

From trap crops to ecological traps

Our field experiment was performed at a small scale, and the structure of semi-natural areas bordering the experimental set up was thus similar for all tested plots except for the distance between the hedge bordering the field and the plots. Therefore, we only evaluated if the trap crop would decrease infestation within field limits, as is the case for most trap crop experiments in annual or perennial crops. To extend the control of SWD beyond the field limits and use trap crops as part of area-wide management — which would lower SWD population at a regional

scale (Kristan III 2003; Schellhorn *et al.* 2008, 2015), —trap crop experiments should be designed over a larger scale to asses if trap cropping can indeed act as an ecological trap and affect pest population dynamics (Donovan & Thompson 2001; Frouz & Kindlmann 2015; Togni *et al.* 2021).

Native vs exotic candidate trap crop species

Out of the 11 selected candidate trap crops in Chapter 2, only five plants were native to Switzerland. Among them, *L. xylosteum* did not provide protection to grapes under field conditions, SWD showed strong developmental performance in *Sambucus ebulus* and *Rubus fruticosus* whereas *Sambucus nigra* and *Rhamnus cathartica* increased infestation in adjacent grapes under semi-field conditions. This indicates that native Swiss species show little potential as a trap crop against SWD. Our best candidate trap crop, *A. brevipedunculata,* is native to eastern Asia and is invasive in the US (Emerine *et al.* 2013).

Our study thus provides an example of a possible positive use of an alien plant species. Using alien plants for positive purposes such as pest control is controversial (Vimercati *et al.* 2020). Deleterious impacts of invasive plants on native flora and fauna are well documented (Pyšek *et al.* 2012). Yet, non-native plant species may be capable of adapting better than native flora to places where environmental conditions change rapidly (Schlaepfer *et al.* 2011). They might also support the conservation of endemic animal species as long as they provide a similar function to the native plants they are replacing, such as offering food resources or egg-laying sites (Graves & Shapiro, 2003; Jakobsson & Padrón, 2014; Severns & Warren, 2008; Williams et al., 2006 but see Yoon & Read, 2016). Many alien plants, sold for years as ornamental plants, become naturalised without becoming invasive. Yet, as we lack understanding of the proportion and the reasons naturalised plant species become invasive, assessing the risk of using alien plant species is challenging (Pyšek & Richardson 2010). Moreover, the sale of invasive plant species to private individuals will soon be prohibited by the Swiss government (Motion Friedl 2020). This might complicate the acceptance of positive impact of alien species.

Trap cropping is a type of biological control with a bottom-up approach instead of the top-down one of classical biological control (Parolin *et al.* 2012). The search for a predator to control an invasive crop pest is frequently not restricted to predators in the invaded range of the pest. Similarly, searching for candidate trap crop species that only are indigenous to the invaded range of the pest is highly restrictive. Here, we demonstrated that some native Swiss

plant species show little potential as trap crops against SWD. A similar problem is known with developing a biological control agent against SWD. Parasitoid wasps found in Europe have shown little success in mitigating SWD damage in the field (Chabert *et al.* 2012; Wolf *et al.* 2020, 2021). However, the exotic parasitoid wasp, *Ganapsis Brasiliensis,* collected in the native range of SWD, has been identified as a potential control agent against SWD (Girod *et al.* 2018). To release this biological control agent in the field in Europe, specificity tests and risk assessments would be required (Seehausen *et al.* 2020, 2022). Similarly, an alien trap crop plant would likely need to be evaluated before being tested and used in the field.

Conclusive remark

Our study illustrates how identifying an effective trap cropping strategy against SWD, from finding suitable candidates to evaluating the correct quantity of trap crop required to offer protection, is a lengthy process. SWD invaded Europe more than a decade ago. The first response to control a new pest is usually insecticide application, as it is a rapid solution to implement (Devine & Furlong 2007). Farmers have also quickly adapted their cultural practices to incorporate preventive measures to mitigate the first impact of SWD invasion. Research can now focus on how to deal with the SWD problem sustainably with a long-term focus, such as implementing trap cropping and other integrated pest management strategies.

As with many current control methods, trap cropping might not be sufficiently efficient on its own to control SWD infestation. However, it might mitigate SWD damage when combined with other control methods (Vreysen *et al.* 2007; Haye *et al.* 2016). Trap cropping has many advantages, such as its low environmental impact or species specificity, yet several general drawbacks can be found. Although trap cropping is species-specific, crops are rarely attacked by only one pest species, so when developing trap cropping, many resources would focus on controlling only one species. Land must also be dedicated to trap crops, which can no longer be used for production. Whether economic balance can be maintained is not yet answered (Shelton & Badenes-Perez 2006; Nibouche *et al.* 2019). In addition, agricultural methods based on diversification strategies, such as trap cropping, might not be easily integrated into the current European farming type (Shennan 2008). Vineyards are farmed in large monocultures. This type of agriculture is relatively simple as it involves only one crop and is also low-risk because of the relative climatic stability of the temperate regions of Europe (Mortensen & Smith 2020). Traditionally, diverse agroecosystems are usually found in risk-prone environments, characterised by smaller farm sizes and focusing on overall crop production

rather than separated crop-related activities(Abate *et al.* 2000). Nevertheless, as wine grapes are a high-value-added crop, the financial cost of trap cropping risk might be bearable for winegrowers in Europe, more so than implementing trap cropping in crops with a lower economic attractiveness. Consequently, investigating trap cropping in high added-value crops might be better tolerated. Whilst some diversification examples exist for vineyards, they are relatively scarce and for now predominantly focusing on supporting arthropod populations, assuming it is enhancing top-down pest control (Altieri & Nicholls 2002; Altieri *et al.* 2005a, b; Rausis 2022). Trap cropping seems a very challenging and demanding control method to develop from a scientific point of view to offer an effective and safe option to practitioners. Still, a successful trap crop development would provide an excellent example of a diversification strategy that mitigates the impact of a targeted pest and could encourage practitioners to test and adopt these strategies in a broader crop range.

Annexe 1

Two-choice experiment under field conditions

We conducted a two-choice field experiment with four candidate trap plants (*Lycium barbarum, Rubus fruticosus, Lonicera xylosteum* and *Rhamnus cathartica*) during the second year. We set pairs of potted plants composed of one candidate trap plant and a grapevine as well as pairs of grapevines as the control treatment in the vicinity of our research station. We randomly placed the pairs in a field of small berry bushes whose fruits were already harvested by the time of our experiment. The field is delimited by a hedge on the east side and surrounds a mix of grass fields and perennials crops on the other edges. After two weeks of exposure to the naturalised SWD population in the area, we assessed the infestation of the candidate trap plants and grapevines. For each plant, we recorded the egg number as well as the count and weight of the berries. As the number of replicates and the infestation were very low, we could not infer much from the analysis of this data (Table 1).

Table 1: Mean and confidence interval of infestation measured in the two-choice field experiment.

Treatment	Plant species	Mean egg number per gram of fruit	CI	Replicate number
Lycium barabarum	*Lycium barabarum*	0.00	0.00	
	Vitis vinifera cv. Mara	0.09	0.16	6
Lonicera xylosteum	*Lonicera xylosteum*	0.15	0.13	
	Vitis vinifera cv. Mara	0.02	0.03	5
Rhamnus cathartica	*Rhamnus cathartica*	0.00	0.00	
	Vitis vinifera cv. Mara	0.04	0.06	4
Rubus fruticosus	*Rubus fruticosus*	1.41	1.02	
	Vitis vinifera cv. Mara	0.15	0.11	8
Control	*Vitis vinifera cv. Mara*	0.01	0.01	
	Vitis vinifera cv. Mara (trap plant)	0.01	0.02	3

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