

Invasive *Drosophila suzukii* outnumbers native controphics and causes substantial damage to fruits of forest plants

Irene Bühlmann¹, Martin M. Gossner^{2,3}

1 Ökobüro Biotopia, Obertalacher 1, CH-6319 Allenwinden, Switzerland **2** Forest Entomology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland **3** ETH Zurich, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, 8092 Zurich, Switzerland

Corresponding author: Martin M. Gossner (martin.gossner@wsl.ch)

Academic editor: Deepa Pureswaran | Received 3 June 2022 | Accepted 3 October 2022 | Published 18 October 2022

Citation: Bühlmann I, Gossner MM (2022) Invasive *Drosophila suzukii* outnumbers native controphics and causes substantial damage to fruits of forest plants. NeoBiota 77: 39–77. <https://doi.org/10.3897/neobiota.77.87319>

Abstract

Impacts of biological invasions are diverse and can have far-reaching consequences for ecosystems. The spotted wing drosophila, *Drosophila suzukii*, is a major invasive pest of fruits, which negatively affects fruit and wine production. However, little is known about the ecological impact of this fly species on more natural ecosystems it has invaded, such as forests. In this study, we investigated the use of potential host plants by *D. suzukii* at 64 sites in different forest communities in Switzerland from mid-June to mid-October 2020. We examined more than 12,000 fruits for egg deposits of *D. suzukii* to assess its direct impact on the plants. We recorded symptoms of fruit decay after egg deposition to determine if *D. suzukii* attacks trigger fruit decay. In addition, we monitored the drosophilid fauna with cup traps baited with apple cider vinegar, as we expected that *D. suzukii* would outnumber and potentially outcompete native controphics, especially other drosophilids. Egg deposits of *D. suzukii* were found on the fruits of 31 of the 39 potential host plant species studied, with 18 species showing an attack rate > 50%. Overall, fruits of *Cotoneaster divaricatus* (96%), *Atropa bella-donna* (91%), *Rubus fruticosus corylifolius* aggr. (91%), *Frangula alnus* (85%) and *Sambucus nigra* (83%) were attacked particularly frequently, resulting also in high predicted attack probabilities that varied among forest communities. Later and longer fruiting, black fruit colour, larger fruit size and higher pulp pH all positively affected attack rates. More than 50% of the plant species showed severe symptoms of decay after egg deposition, with higher pulp sugar content leading to more severe symptoms. The high fruit attack rate observed was reflected in a high abundance and dominance of *D. suzukii* in trap catches, independent of forest community and elevation. *Drosophila suzukii* was by far the most abundant species, accounting for 86% (81,395 individuals) of all drosophilids. The abundance of *D. suzukii* was negatively associated with the abundance of the native drosophilids. Our results indicate that the invasive *D. suzukii* competes strongly with other frugivorous species and

that its presence might have far-reaching ecosystem-level consequences. The rapid decay of fruits attacked by *D. suzukii* leads to a loss of resources and may disrupt seed-dispersal mutualisms through the reduced consumption of fruits by dispersers such as birds.

Keywords

Alien species, drosophilid, ecological impact, frugivore, fruit decay, host plant range, insect

Introduction

Biotic exchange and subsequent invasions by non-native species in natural and human-modified ecosystems are among the greatest threats to biodiversity worldwide (Wilcove et al. 1998; Pyšek et al. 2020). They can have far-reaching consequences for ecosystems (Vilà et al. 2010), including their functioning (Mack et al. 2000; Ehrenfeld 2010), and for human well-being (Shackleton et al. 2019), and they can cause extraordinary economic costs (Pimentel et al. 2005; Diagne et al. 2021). The perception and recognition of impacts of biological invasions, as well as how they are measured, are diverse and depend on the variables and scales considered (Jeschke et al. 2014). While assessments of economic impacts are measured in terms of economic costs, ecological impacts are evaluated as measurable changes to the properties of an ecosystem by a non-native species. However, the ecological impact of an invader is not easy to define or quantify, due to the context dependency of impacts, the variation in the per capita effect within and across species, and the complex interactions between invaders and their biotic and abiotic environments (Pyšek and Richardson 2010; Ricciardi et al. 2013).

Invasive non-native species may affect native species on the level of individuals (e.g. fecundity, mortality), populations (e.g. abundance, genetic diversity), communities (e.g. species richness and composition, trophic structure) and ecosystems (e.g. nutrient cycling, physical habitat, overall structure and function) (Parker et al. 1999). The impact of a non-native species on native populations and communities varies greatly in temporal (Strayer et al. 2006) and spatial (Mollot et al. 2017) terms and depends critically on the abundance and trophic position of the invasive species (Bradley et al. 2019). This explains why the extent of ecological impact varies greatly between invaders (Kumschick et al. 2015; Lapin et al. 2021).

Insects make up a large proportion of introduced species (DAISIE 2009; Seebens et al. 2017). They are usually introduced accidentally, rarely reach large populations, and/or are often not noticed. However, a small minority become highly abundant and ecologically significant (Liebhold and Tobin 2008). Impacts of non-native insects on native species and ecosystems have many potential mechanisms, but only a very small proportion of non-native insects have been studied regarding their ecological impacts (Kenis et al. 2009). While direct impacts through mechanisms such as predation or competition are more obvious, indirect impacts, such as apparent and exploitative competition or alteration of interactions between native species, often remain unexplored (Traveset and Richardson 2006; White et al. 2006). For example, a meta-analysis of the effects of the invasions of the Argentine ant (*Linepithema humile*) showed that areas with *L. humile*

had 92% fewer native ant seed dispersers than areas where *L. humile* was not present. In addition, the meta-analysis indicated that *L. humile* did not replace native seed dispersers in their functional role, as rates of seed removal and seedling establishment were lower in the presence of *L. humile* (Rodríguez-Cabal et al. 2009). A disruption of seed-dispersal mutualisms affects seedling recruitment, species populations and distributions, plant-community composition, and gene flow (Howe and Smallwood 1982). Such indirect effects of non-native species on plant species can have far-reaching ecological consequences.

For frugivorous insects, the most significant effect on plants is thought to be indirect, namely the reduction of seed dispersal far from the mother plant by vertebrates (Sallabanks and Courtney 1992). Among frugivorous insects, *Drosophila suzukii* (Matsumura 1931; Diptera: Drosophilidae), also known as the spotted wing drosophila, is of particular importance. It is an invasive *Drosophila* species originating from Southeast Asia (Asplen et al. 2015). The presence of the species outside of its native range was first recorded in Japan (Matsumura 1931), 1980 in Hawaii (Leblanc et al. 2009) and in 2008 synchronously in southwestern USA (Hauser 2011) and southern Europe (Cini et al. 2012). The species has spread rapidly and is now widespread on the Asian, European, and North and South American continents (dos Santos et al. 2017). The family Drosophilidae comprises more than 3,900 species, with more than 1,500 of the described species belonging to the genus *Drosophila*. These small flies are widespread in a variety of climates and environments throughout the world (Markow and O'Grady 2005a; Bächli 2021). To date, around 36 species of the genus *Drosophila* and more than 30 species of other genera of the family Drosophilidae are distributed in Switzerland (Bächli et al. 2004; personal communication G. Bächli 2021). The habitat of most of these species is mainly restricted to forest areas (so-called wild species). In contrast, a few species of *Drosophila*, so-called domestic species, mainly occur in settlements and are mostly cosmopolitan in distribution (Atkinson and Shorrocks 1977; Shorrocks 1977; Burla and Bächli 1991). Oviposition and larval development of *Drosophila* are usually restricted to decaying organic resources such as slime flux, fruits, flowers and mushrooms (Markow and O'Grady 2008), but the degree of substrate specialisation varies widely, from generalists to obligate specialists (Mitsui and Kimura 2000b; Markow and O'Grady 2005b; Anholt et al. 2020). This variability is also related to host location, host acceptance, and host use (Markow 2019), with chemical recognition playing a crucial role (Anholt 2020). Most *Drosophila* show some degree of fidelity in oviposition site selection, which often depends more on the decay state of the substrate, than on the identity of the plant or fungus (e.g. Kambysellis and Heed 1971; Nunney 1990; Karageorgi et al. 2017). For example, *D. suzukii* prefers fruits that are more intact (Kienzle and Rohlf 2021), firmer (Sato et al. 2021) and in an earlier maturation stage (Dweck et al. 2021) compared with *D. melanogaster*, another frugivore. *Drosophila* species inoculate their oviposition substrate with microorganisms. They are considered important vectors, especially of yeasts but also of bacteria, and transport viable microbes to new substrates where they grow (Gilbert 1980; Rohlf and Hoffmeister 2005; Stamps et al. 2012; Hamby and Becher 2016). Adults and larvae feed mainly on the microbes that decompose organic material, but also on the decomposing material itself (Markow and O'Grady 2008). Flies additionally benefit

from the dispersal of such microbes, as they obtain signals from their metabolic products for finding sugar resources (Madden et al. 2018).

Drosophila suzukii exploits resources that usually consist of small separate units and are patchy and ephemeral, i.e. they support only one generation. The temporal and spatial constraints of these unpredictable resources may favour generalists (Jaenike 1990). Niche breadth usually correlates positively with geographical range size (Slatyer et al. 2013), but does not necessarily explain invasion success (Carscadden et al. 2020). Following this general rule, the temporal and spatial niche breadth of the invasive *D. suzukii* have been shown to be relatively large compared with other *Drosophila* species in Japan (Yamamoto 1984). Besides using fruits as its preferred substrate for oviposition, it has also been found to develop on fungi (Kimura 1976) and can even complete development on chicken manure (Stockton et al. 2019). Within its invasive range, *D. suzukii* can use the fleshy fruits of many crops and wild plants (e.g. Poyet et al. 2015; Arnó et al. 2016; Kenis et al. 2016). In the year 2020, 198 plant species representing 40 families were already confirmed as host plants (Little et al. 2020), so the fly can be considered extremely polyphagous (sensu Normark and Johnson 2011).

Polyphagous herbivores (or generalists) are more impacted by plant toxicity than specialists (Ali and Agrawal 2012), as specialisation in phytophagous insects is thought to assist in the evolution of adaptations to overcome plant defences (Ehrlich and Raven 1964). However, *D. suzukii* hardly needs to specialise to overcome plant defences. On the one hand, because fleshy fruits are generally intended to be eaten by vertebrates (Lei et al. 2021), the pulp of such ripe fruits is rather easily digested (Cipollini 2000). On the other hand, the association with microbes may help with detoxification and digestion (Douglas 2009, 2015). Fruits share particular volatiles across plant species (Prasanna et al. 2007). As a resource specialist utilising particular plant structures, i.e. fruits, with predictable odour cues, it may not be crucial for *D. suzukii* to specialise on particular plant species in order to increase host location, because olfactory responses to substrate-relevant volatiles of a resource instead of a plant species enables coping with a much narrower range of odours (e.g. Becher et al. 2012; Cunningham and Zalucki 2014; Cunningham et al. 2016).

Drosophila suzukii's attacks on the fruits of agricultural crops cause considerable economic damage to fruit growers through yield losses and the need to take measures to prevent attacks and minimise damage (Bolda et al. 2010; Knapp et al. 2020). Research on *D. suzukii* as a fruit crop pest is therefore ongoing and diverse. In recent studies, the occurrence of *D. suzukii* outside agricultural crops has been investigated to assess pest pressure from adjacent habitats. Woodlands have been shown to be suitable refugia and overwintering habitats (Briem et al. 2016; Pelton et al. 2016; Thistlewood et al. 2018; Wallingford et al. 2018) and can provide a large reservoir of hosts that produce fruits, ensuring continuity of resource availability over time (Poyet et al. 2015; Arnó et al. 2016; Elsensohn and Loeb 2018; Thistlewood et al. 2019). Therefore, large numbers of *D. suzukii* can be expected in forests, as has also been shown in trapping case studies (e.g. Briem et al. 2018; Haro-Barchin et al. 2018; Santoiemma et al. 2018), and population densities are likely to be more constant and higher than in semi-open habitats such as agricultural landscapes. So far, almost no research has been conducted

to address the ecological impact of this fly on the ecosystems it has invaded. Roche et al. (2021) highlighted how *D. suzukii* may produce ecological changes to eastern forests in the USA. Invasion by *D. suzukii* may have consequences for food resources and, consequently, on species with which they compete for fruits. Competitive interactions, i.e. competition for shared resources or interference between species, generally increase with increasing phylogenetic relatedness (Li et al. 2015) and functional similarity (Dick et al. 2017) between the invader and the native species. Accordingly, *D. suzukii* could affect native drosophilids due to two main mechanisms. First, *D. suzukii* can use a wide range of substrates for oviposition, which gives it a competitive advantage over native drosophilids (Karageorgi et al. 2017; Silva-Soares et al. 2017). Unlike other drosophilids that use damaged and overripe fruits, *D. suzukii* has an enlarged, serrated ovipositor which makes it possible for females to pierce the skin of fruits (Atallah et al. 2014). It thus can use undamaged fruit, i.e. it can occupy fruits earlier than other drosophilids. Second, according to the enemy release hypothesis, a lower parasitisation rate leads to a larger population size (Keane 2002; Shea 2002), and parasitisation is an important cause of mortality for drosophilid larvae (Janssen et al. 1988; Fleury et al. 2009).

In this study, we assessed the use of potential host plants in forests by examining egg depositions of *D. suzukii*, reflecting its direct effect on the plants. Since there is a diverse abundance and varying availability of host plants within a plant community, which affects the choice of host plants for *D. suzukii*, we selected different forest communities and forest edges as study sites. We addressed the following questions: (1) Are there differences in the potential host plants of *D. suzukii* growing in different forest communities? (2) To what extent are the potential host plants attacked by *D. suzukii*, and what are the factors influencing the attack rates?

Due to the large numbers of *D. suzukii* trapped in previous studies, we expected that this species would outnumber and potentially outcompete native controphics, especially drosophilids. To test this hypothesis, we trapped drosophilids during the study period and addressed the following questions: (3) What proportion of drosophilid individuals are *D. suzukii*? (4) Does the proportion of *D. suzukii* differ among forest communities? (5) Does the abundance of *D. suzukii* affect the abundance of other drosophilids?

Materials and methods

Study area

We conducted our study in the adjacent cantons of Zug (47.092440–47.218600°N, 8.407940–8.680231°E; elevation 400–1200 m a.s.l.) and Zurich (47.163290–47.365790°N, 8.424865–8.687711°E; 440–1165 m a.s.l.) in Switzerland from June to November in 2020 (Fig. 1). In both regions, the annual average temperature ranges between 4–6 °C at higher elevation sites to 10–12 °C at lower elevation sites and the annual precipitation ranges between 1100–1300 mm and 1700–2000 mm at sites in the canton Zug and 900–1100 mm and 1100–1300 mm at sites in the canton Zurich (climate norm values 1991–2020; Federal Office of Meteorology and Climatology

MeteoSwiss; extracted from <https://map.geo.admin.ch/>). We selected the forest communities 7a (*GALIO ODORATI-FAGETUM TYPICUM*), 19a (*ABIETI-FAGETUM LUZULETOSUM*) and 26f/g (*ACERI-FRAXINETUM MERCURIALIDETOSUM*) (see Ellenberg and Klötzli 1972) for our study, as they include a comparable range of fruiting plants. In addition, we investigated forest edges, as they serve as important habitat for a large range of fruiting plants. We examined the three forest communities at four sites ≥ 1 km apart, from 400 to 1165 m a.s.l. At each site, we selected four 25 m \times 25 m plots of the particular forest community from the available grid cells (also 25 m \times 25 m) in a stratified random design, using a vegetation mapping GIS in the canton of Zurich (Kanton Zürich 2020) and vegetation maps in the canton of Zug. We applied the following criteria in selecting plots: (1) distance between plots ≥ 150 m, (2) distance to the forest edge ≥ 150 m (due to the shape of the area, only a distance of ≥ 70 m was possible at the site “Zollischlag”). We measured the distances between sites, between plots and to the edge of the forest using the mapping platform of the Swiss Confederation (www.map.geo.admin.ch) and subsequently checked them in the field. We reviewed the forest community classification in the field based on indicator plant species. We defined the centre of the plots as the tree nearest to the actual centre point of the 25 m \times 25 m area. We moved a selected plot to the adjacent grid cell if the area was temporarily unstocked (n=2), was covered with logging residues (n=1), or had no characteristics of the respective forest communities (n=3). We investigated forest edges at four sites with four plots each in the canton of Zug. We selected two sites at low elevations (400–600 m a.s.l.) and two at high elevations (800–1000 m a.s.l.). We defined these plots as areas of 12.5 m \times 50 m along the forest edge (instead of 25 m \times 25 m). Where possible, the forest edges were orientated in different cardinal directions. Forest edge sites were ≥ 1 km apart and plots were separated by ≥ 250 m. All sites were located in managed forests.

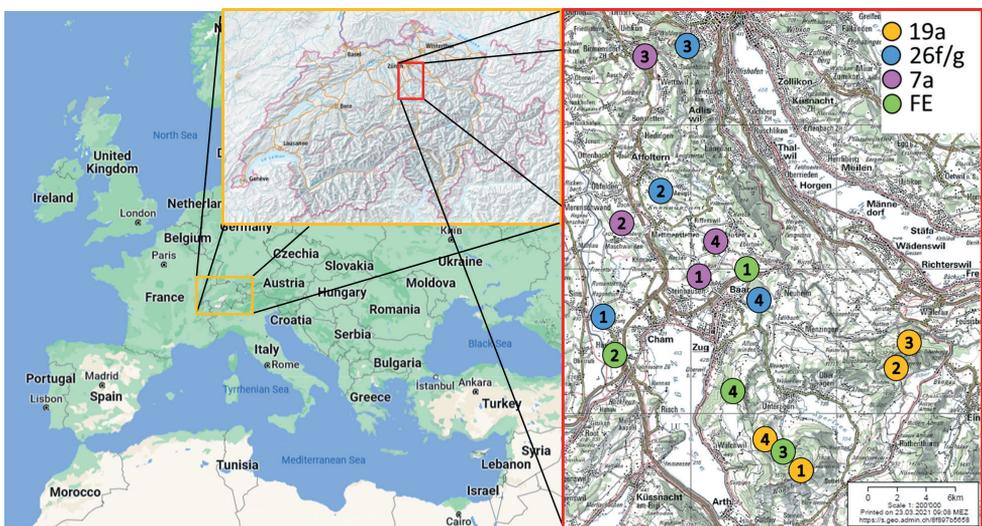


Figure 1. Map showing the locations of the 16 sites (forest communities 7a, 26f/g and 19a; forest edges (FE)) (European map data 2021 Google maps, Switzerland map data 2021 Swiss Confederation).

Field surveys of potential host plants

We considered any fleshy-fruited species, characterised by a high fruit water content, a potential host plant. We used the term “fruit” for all fruit types (i.e. berries, drupes, aggregate drupelets, aggregate nutlets and pomes), independent of the tissue of origin of the pulp. We also examined the aril of European yew (*Taxus baccata*) for egg deposition and included it under the term “fruit” below.

We carried out the field surveys in all plots during six observation sessions (interval of 20 days) over the study period, starting on 22/06/2020 and ending on 15/10/2020: 4 plant communities (3 forest communities + forest edge) × 4 study sites × 4 plots (64 plots) × 6 periods = 384 assessments.

We mapped all potential reproducing host plant species in each plot (25 m × 25 m or 12.5 m × 50 m = 625 m²) and noted its occurrence. We used an estimated dominance value to determine the area (m²) covered by a plant species, and used this value and the recorded height to calculate the plant species' volume. For each potential host plant at each field survey per plot, we estimated the seasonal phenology and the number of ripe fruits present, assigning maturation stage between 0 and 2, corresponding to the majority of plant individuals: 0 = no ripe fruits, 0.25–0.75 = before main fruit maturity (some ripe fruits), 1.0–1.25 mainly ripe fruits, 1.5–1.75 = after main fruit maturity (more over-ripe, fermented fruits than ripe fruits), 2 = no more fruits. Since fruit ripening is usually associated with a change in colour, we used colour change as an indicator of the maturity of the examined fruits. In some species, such as European fly honeysuckle (*Lonicera xylosteum*), rowan (*Sorbus aucuparia*) or alder buckthorn (*Frangula alnus*), changes in fruit flesh firmness during ripening were not advanced at the time of colour change. We judged these fruits to be ripe when they also softened. After maturity, fruits enter senescence (the period during which chemical synthesis pathways give way to degradation processes). As an indicator of the “overripe” stage, we used loss of moisture, which becomes visible as a loss of turgor. At the end of the field survey, we calculated the maturity period with the unit of half a month and estimated the amount of fruit, both per potential host plant species per plot. The exact method used for these estimates depended on the species and was based on counts (e.g. all observed fruits, fruits per square metre, fruits per individual plant, or infructescence). We then extrapolated counts to the plot level. The number of fruits was likely underestimated by this approach and was thus a rather conservative estimate. Fruits that were removed, destroyed or lost due to drought stress near the end of the ripening process were not subtracted from the estimated numbers (see Suppl. material 1: Table S1 for month of fruit maturity, number of fruits, and occurrence (volume) of potential host plant species of *Drosophila suzukii* in the study plots).

Near the plots and in the same forest communities, we additionally examined native potential host plants that occurred in less than three plots (*Lonicera alpigena*, *Taxus baccata*, *Prunus spinosa*, *Crataegus laevigata*, *Lonicera periclymenum*, *Viburnum lantana*). We conducted this additional investigation to estimate the average attack rate of plants with infrequent occurrence on the plots, but we excluded these fruits from the statistical analyses.

European brambles (*Rubus* L. subg. *Rubus*) are taxonomically divided into three sections: *Rubus*, *Corylifolii* and *Caesii* (with one species, *Rubus caesius*). The most

abundant species in our plots were *R. hirtus* agg. (sect. *Rubus*), occurring in the plots of forest community 19a, and *R. villarsianus* (sect. *Corylifolii*), occurring in the plots of forest communities 7a and 26f/g. Especially at the forest edges, but also in the forest communities 26f/g and 7a, more than one species of the sections *Rubus* and/or *Corylifolii* occurred in the plots. We did not identify the described and named species of the sections *Rubus* and *Corylifolii* in the plots and therefore used the term *Rubus fruticosus corylifolius* agg. as the taxonomic unit.

Investigation of fruit attacks by *Drosophila suzukii*

We examined ripe fruits at an accessible height (up to 2 m) for egg deposition using a hand lens (10× magnification). If we observed at least one *D. suzukii* egg on the fruit, we considered the fruit “attacked”, regardless of the number of egg deposits or larvae (for literature on the number of eggs per host plant, see e.g. Lee et al. 2015; Poyet et al. 2015; Olazcuaga et al. 2019; for development potential in different hosts see e.g. Arnó et al. 2016; Kenis et al. 2016; Tonina et al. 2016). We examined at least 10 fruits per population or individual of a potential host plant per plot, and we removed the examined fruits from the plants. If multiple individuals of a plant species occurred in the plot, we examined several individuals. In the case of large populations of brambles (*R. fruticosus corylifolius* agg.) or bilberry (*Vaccinium myrtillus*), i.e. covering > 25% of the plot area, we randomly selected 5 areas of 1 m² for investigating egg deposition. Egg deposition by *D. suzukii* is detectable for only a limited time, due to decay of the fruit substance, rotting, development of the larvae, feeding by other animals, or secondary infections such as grey mould. No larvae in a damaged fruit does not allow inference of non-infestation. Further, damaged fruits may in turn be used as egg-laying substrate by other drosophilids. Therefore, we used only ripe, undamaged fruits to study egg deposition on potential host plants.

We investigated the fruits of European holly (*Ilex aquifolium*) for egg deposition after the field surveys because they had not yet reached fruit maturity during the study period. To check the oviposition activity of *D. suzukii*, we simultaneously examined fruits of the European dwarf elder (*Sambucus ebulus*) and brambles (*Rubus fruticosus corylifolius* agg.) occurring near the European hollies under investigation. We did not examine European mistletoe (*Viscum album*) and common ivy (*Hedera helix*), which were also present in the plots, for *D. suzukii* attacks, as their fruit ripening period fell well outside our study period. The ripe fruits of the wild strawberry (*Fragaria vesca*) often showed numerous feeding marks and damage, such that egg deposition by *D. suzukii* could rarely be detected. We therefore decided not to investigate attacks further and excluded wild strawberry from the analyses. We could confirm its use as a host, however, as adults hatched from collected fruits and we found numerous drosophilid larvae in otherwise intact fruits.

Fruit and decay traits

We compiled fruit traits of the investigated plant species from Herrera (1987), Snow and Snow (1988), Eriksson and Ehrlen (1991), and Stiebel (2003) and from databases

(eFloras 2021, TRY 2021). When the records of fruit traits were comparable or convertible, we included the data from several literature references and used the average value. We included the fruit traits: type, colour, diameter (mm), mass (g), water content of the pulp (%), sugar content of the pulp (glucose and fructose, % of dry mass), lipid content of the pulp (% of dry mass), protein content of the pulp (% of dry mass), pH, persistence of individual fruits (days) and “attacked by non-dispersal frugivores” (%). In addition, we used the amount of ripe fruit and the maturation start and duration, based on our field assessments (see section “Field surveys of potential host plants”), as fruit traits in the analyses.

Fruit decay is a complex natural phenomenon that is co-determined by numerous conditions. It occurs as a result of physical and chemical damage, enzymatic digestion, and especially microbial activity. The fruit skin, which serves as an external barrier, is damaged by the egg deposition of *D. suzukii*. We documented the fruit response to egg deposition, i.e. decay, to determine if attacks trigger fruit decay. We recorded the following symptoms of fruit decay: oviposition scar, denting, oozing of pulp, reduction of fruit substance/loss of shape, and colour change. We categorised the symptoms as mild (1), moderate (2) or severe (3).

Adult trapping

At each site of the forest communities (including forest edges), we installed two baited (80–100 ml) transparent plastic cup traps covered by a red lid with 3 mm diameter entry holes (Profatec AG, Malans, Switzerland) to trap Drosophilidae including *D. suzukii*. As an attractant, we used a mixture of apple cider vinegar and water (3:1; apple cider vinegar IP-Suisse, Denner AG, 8045 Zurich, Switzerland; acetic acid 50 g/l) with 1–2 drops of liquid soap (Oecoplan Abwaschmittel, Coop, 4002 Basel, Switzerland) per 5 dl. We positioned the traps at a height of 1.2–1.5 m on branches of plants that do not bear fleshy fruits, mostly beech (*Fagus sylvatica*), at a distance of 150–200 m from the field survey plots. We installed the traps from 22/06/2020 to 07/07/2020, during the first session of the egg deposition assessment. At the forest edges, we placed the traps approx. 3 m inside the forest (from the shrub belt). We kept the traps in the same positions throughout the experiment and visited them on the same dates as the egg deposition assessments. Therefore, each sampling period of adult drosophilids also lasted 20 days.

During each sampling session, we removed the contents of the traps and preserved them in ethanol, and we renewed the bait. We sorted the trap content into different taxa, which we identified to different taxonomic levels. We identified the non-native *D. suzukii* and other drosophilids to the species level using the identification key of Bächli et al. (2004). “Domestic species”, in particular *Drosophila simulans* and *Drosophila immigrans*, and other non-native species (e.g. *Drosophila curvispina* and *Chymomyza amoena*) were occasionally trapped. Other non-native drosophilid species accounted for < 1% of all trapped individuals. Therefore, we used the term “native drosophilids” for all drosophilids other than *D. suzukii*. We identified other Diptera to the family level following Oosterbroek (2006). See Suppl. material 2: Table S2 for a list of the

trap catches. Since trap captures of a single trap during our study period should not be considered as replicates, especially because of varying phenology in different species (e.g. Bahder et al. 2016), we used the totals of trap captures per trap for the analysis.

Statistical analyses

We carried out all statistical analyses using R version 4.0.2 (R Core Team 2020). We tested all models for multicollinearity using the ‘check_collinearity’ function of the *performance* package (Lüdtke et al. 2021). We performed a test for dispersion, zero inflation and residual diagnostics with the *DHARMA* package (Hartig 2022).

Differences in fruiting plant communities

To test whether the composition of the plant communities differed between the forest communities with respect to the plants with fruits relevant for *D. suzukii*, we conducted non-metric multidimensional scaling (NMDS) based on a Bray-Curtis distance matrix (function ‘metaMDS’, package *vegan*; Oksanen et al. 2020). We defined the abundance of plant species as the estimated number of fruits per study plot and season, square-root transformed. We used the ‘adonis’ function in *vegan* (permutational multivariate analysis of variance, PERMANOVA) to test for statistical differences between the forest communities.

Attack rate and probability of fruits of different plant species

We applied a binomial generalised mixed effects model (package *glmmTMB*; (Brooks et al. 2017)) to test for differences in fruit attacks between forest communities (including forest edges) and plant species. The ratio of attacked to unattacked fruits per study plot and time of recording (cbind(N attacked, N not attacked)) was the response variable, whereas the forest community, the plant species, the elevation (m a.s.l.), the number of ripe fruits, the fruit maturity status, and the canton were the predictor variables. We included study plot as a random term to account for the nested study design. We used an additional observation-level random factor due to dispersion issues.

We simplified our model stepwise by excluding the factor with the highest *p*-value and comparing the two models with the *anova* function based on a CHI²-test. If the more complex model did not differ significantly in model performance from the simpler model, we used the latter. This procedure resulted in the exclusion of canton and elevation (height_NN) from the final model.

We calculated the attack probabilities (LS-means ± SE) of the different plant species in the forest communities and plotted them using the *emmeans* package (Lenth 2022) based on the final model.

The role of fruit traits in fruit attack and decay

We explored whether fruit traits could explain observed differences in attack rates. We first used NMDS to illustrate the fruit trait space of the 39 studied plant species. See

the section “fruit traits” for a list of the fruit traits considered. We treated each plant species in each forest community separately to relate it to attack rate and phenology, which both differed between forest communities for a given plant species. We used the Gower dissimilarity coefficient (Gower 1971) with Podani’s (Podani 1999) extension for ordinal variables to create a distance matrix from our fruit trait data (‘gowdis’ function in the *FD* package (Laliberté and Legendre 2010; Laliberté et al. 2014)).

We performed NMDS (with two axes) on the Gower distance matrix using the ‘metaMDS’ function in the *vegan* package (Oksanen et al. 2020). For illustration, we plotted attack rates of the fruits with different circle sizes and the phenology (month of maturation start) in different colours. We plotted traits post-hoc using the ‘envfit’ function in *vegan*, with 1000 permutations.

We used a binomial generalised mixed effects model (package *glmmTMB*; (Brooks et al. 2017) to test whether fruit attacks were related to fruit traits. The ratio of attacked to unattacked fruits per study plot and time of recording (cbind(N attacked, N not attacked)) was the response variable, whereas fruit availability (amount of fruit per plot), start of ripe fruit availability and duration of ripe fruit availability (both 0.5 month resolution), fruit colour, fruit diameter, sugar content of the pulp, and pulp pH were the predictor variables. We excluded fruit type and mass as well as water content of the pulp because of multicollinearity issues, and lipid and protein content of the pulp, as well as persistence and “attacked by non-dispersal frugivores”, because they had too many missing values. We defined study plot and plant species as random terms to respect the nested study design and the repeated measures on plant species. We used an additional observation-level random factor due to dispersion issues. We standardised all quantitative variables to zero mean and unit variance using the ‘deconstand’ function in the *vegan* package (Oksanen et al. 2020) to allow comparisons of effect sizes.

We used a general linear model (‘glm’) with a Poisson distribution to test whether fruit traits determined the decay status of the fruits after the attack by *D. suzukii*. We used the sum of decay traits (see section “fruit and decay traits”) as the response variable and fruit traits (fruit diameter, pulp pH, pulp water, sugar, lipid and protein content) as predictors. We excluded fruit type and mass because of multicollinearity issues. We standardised all quantitative variables to zero mean and unit variance using the ‘deconstand’ function in the *vegan* package (Oksanen et al. 2020) to allow comparisons of effect sizes.

Effects of *D. suzukii* on native Drosophilidae

To test for the effects of forest community and canton on the abundance of *D. suzukii* adults captured in traps, we used a binomial generalised mixed effects model (package *glmmTMB*; (Brooks et al. 2017) with the ratio of *D. suzukii* and native Drosophilidae (cbind(N *D. suzukii*, N native Drosophilidae)) as response variable and study plot as random term. We calculated the predicted proportions of *D. suzukii* (LS-means \pm 95% CI) of the Drosophilidae species caught in the traps in the forest communities and plotted them using the *emmeans* package (Lenth 2022) based on the above model. To predict the abundance of native Drosophilidae as a function of the abundance of *D. suzukii*, we used a generalised mixed effects model with a Poisson distribution (package *glmmTMB*;

Brooks et al. 2017) and defined forest community and canton as additional fixed effect and study plot as random term. We then plotted the predicted effect of *N. D. suzukii* on *N* native Drosophilidae using the *effects* package (Fox and Weisberg 2018).

For all GLMs and GLMMS, we performed a type II Wald chi-square test using the R package *car* (Fox and Weisberg 2019). For most analyses we plotted the standardised estimates (effect sizes) using the ‘plot_model’ function in the sjPlot package (Lüdtke et al. 2021).

Results

Attacks on potential host plants

The composition of the potential host plants of *D. suzukii* differed among forest communities (PERMANOVA, $F=5.432$, $R^2=0.22$, $P=0.001$). The effect of forest community in structuring the plant communities is illustrated by the clustering of the forest communities in the ordination plot, except for the plant community of the study site of a former alluvial forest (site 26_1), which was more similar to forest community 7a than to 26f/g (Fig. 2). The greatest differences in the potential host plant composition were evident between forest communities 19a and 26f/g (pairwise adonis, $R^2=0.21$, $P=0.001$). Forest community 26f/g and the forest edge community were most similar ($R^2=0.07$, $P=0.08$).

At the study sites of forest community 19a, 7 potential host plant species with an estimated 34,000 fruits were recorded. At the study sites of the forest community 26f/g, there were 30 potential host plant species and an estimated 60,200 fruits; in forest community 7a there were 21 potential host plant species and 140,500 fruits, and at the forest edge study sites 32 potential host plant species and 161,000 fruits were observed (Suppl. material 1: Table S1).

Of the 39 potential host plants investigated, attacks were observed on 31 species. Overall, fruits of *Cotoneaster divaricatus* (96%), *Atropa bella-donna* (91%), *Rubus fruticosus corylifolius* aggr. (91%), *Frangula alnus* (85%) and *Sambucus nigra* (83%) were attacked particularly frequently (Suppl. material 1: Fig. S1, proportions of fruits attacked by *Drosophila suzukii* per plant species, separated by forest community). Based on the standardised assessments within the plots, the attack rates differed significantly between plant species and forest communities (Table 1), with forest edges exhibiting particularly high rates, followed by 7a. *Lonicera alpigena*, *Taxus baccata* and *Atropa bella-donna* had the highest probability of being attacked (Fig. 3). Larger numbers of ripe fruits and fruits in a later maturation stage corresponded to higher attack rates (Table 1). Canton and elevation did not have a significant effect on the attack rate and were dropped during model simplification.

The fruit trait space covered by the studied fruits was quite large (Fig. 4, left). The ordination plot illustrates that the attack rate differed greatly among plant species and was determined by the maturation start. Later maturation and longer availability of ripe fruits had a positive effect on attack rate (Table 2, Fig. 4 right). In addition, fruit

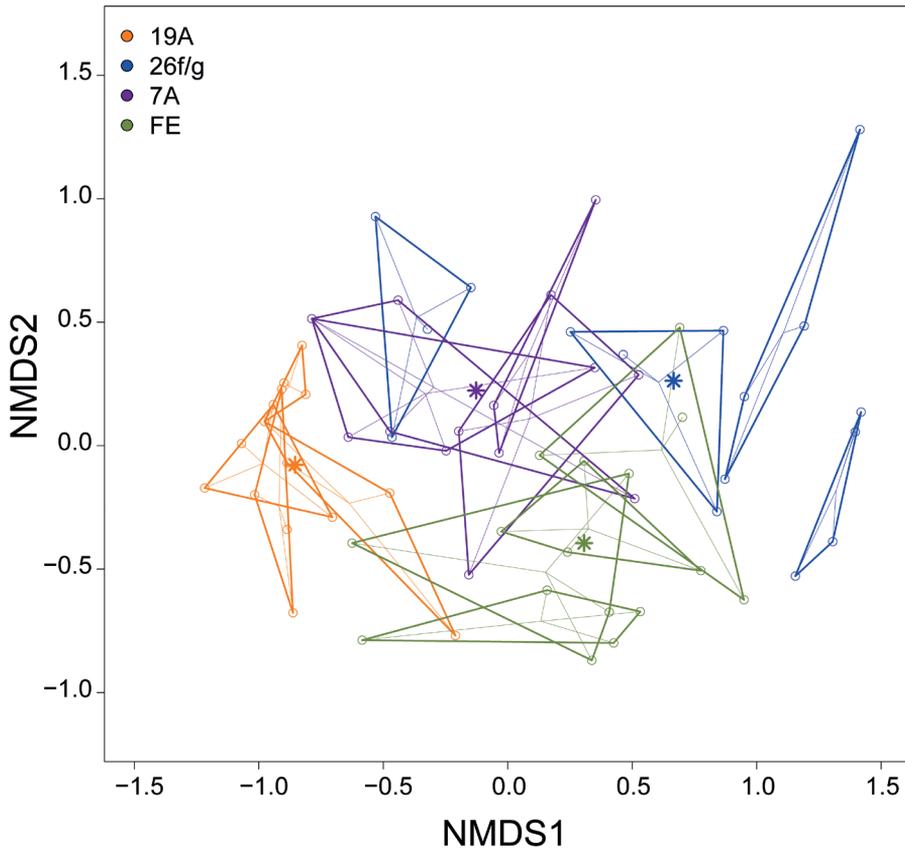


Figure 2. Non-metric multidimensional scaling (NMDS) based on Bray-Curtis distances, showing the host plant composition with its estimated number of fruits for *Drosophila suzukii* at the study sites (four plots each) of the different forest communities. Different forest communities are indicated by different colours. Each dot represents the community in one plot. All the plots in a given site are connected by thick lines, and centroids are indicated by thin lines. The asterisks indicate the centroids of the forest communities. Stress=0.145 (k=3). Forest communities: 7a – *GALIO ODORATI-FAGETUM TYPICUM*, 19a – *ABIETI-FAGETUM LUZULETOSUM*, 26f/g – *ACERI-FRAXINETUM MERCURIALIDETOSUM* (see Ellenberg and Klötzli 1972), FE = forest edge.

Table 1. Results of the binomial generalised mixed effects model (glmmTMB) testing the drivers of attack rates of fruits by *Drosophila suzukii*. Plot nested in study site was defined as a random term. Results of the Wald Chi-square test are given. For continuous variables the direction of the effect (+) is given.

	Ch^2	Degrees of freedom	P
Forest community	34.385	3	<0.001
Plant species	396.861	36	<0.001
Number of ripe fruits	7.513	1	0.006125 (+)
Status of maturation	69.353	1	<0.001 (+)
R ² conditional	0.840		
R ² marginal	0.826		

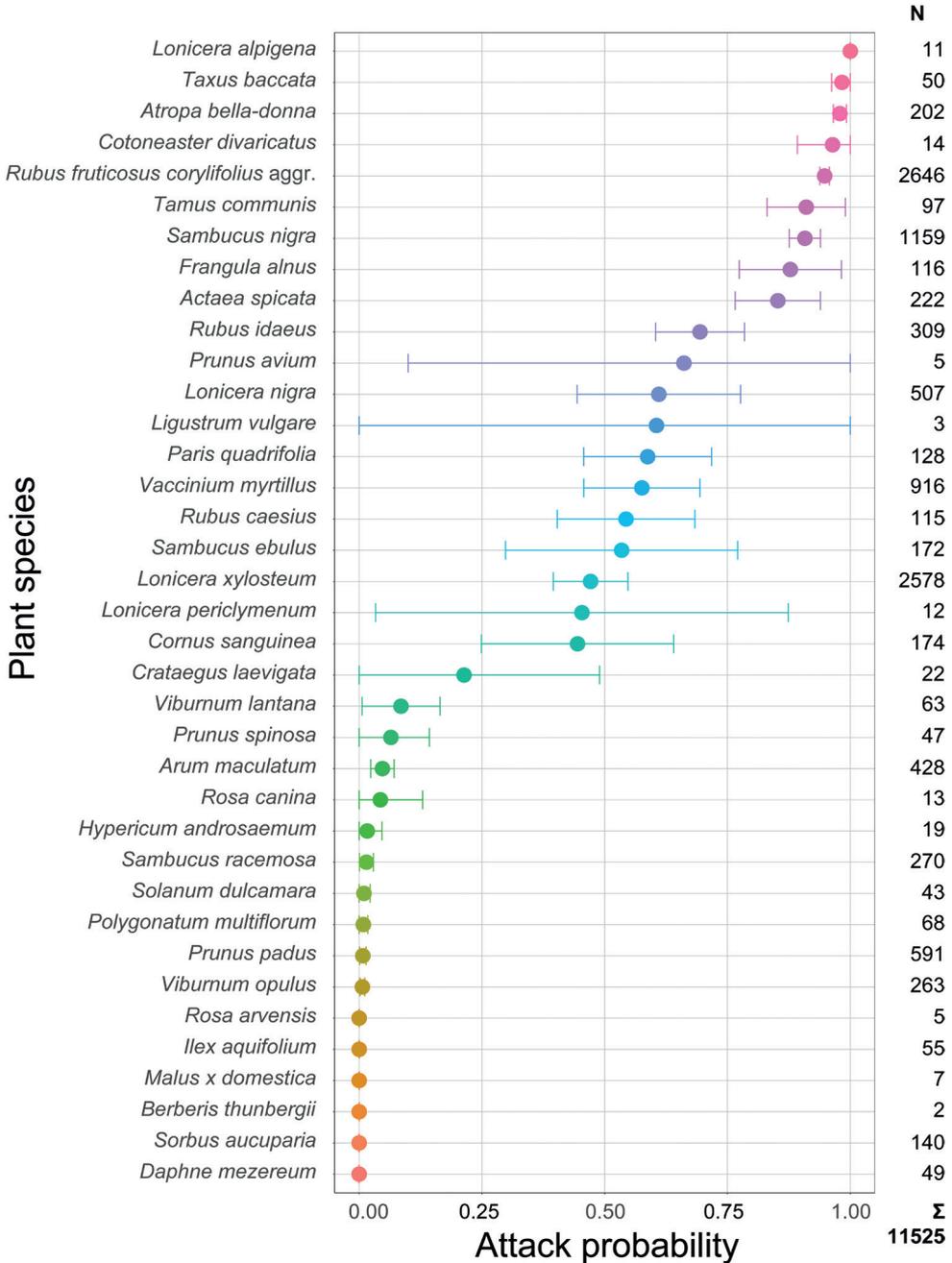


Figure 3. Attack probabilities of fruits of different plant species by *Drosophila suzukii*. Model-derived (for model results, see Table 1) probability estimates are shown (LS-means ± SE, back-transformed from the logit scale to the original probability scale). Only fruits observed within the plots were considered. N refers to the number of observations. For average attack rates per species, including fruits outside the plots, see Suppl. material 1: Fig. S1.

colour affected attack rate, with orange fruits having a lower attack rate than black fruits, and blue and red ones tending to be attacked less than black fruits. In addition, larger fruits and fruits with a higher pulp pH had higher attack rates.

Of the studied fruit traits, only pulp sugar content affected fruit decay status after an attack by *D. suzukii*, with a higher sugar content leading to more severe symptoms of decay (Table 3, Fig. 5).

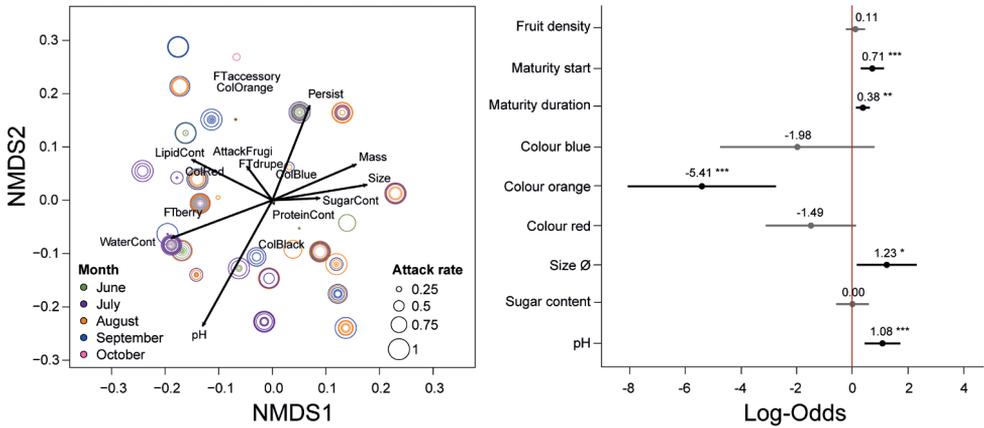


Figure 4. Left: Ordination plot of a non-metric multidimensional scaling (NMDS) analysis illustrating the fruit trait space of the 39 studied plant species (stress-value 0.198). The centre of each circle represents the position of a plant species in the fruit trait space. Attack rates by *Drosophila suzukii* are represented by the size of the circles, and the maturation start month of a plant species in a forest community is illustrated by the colour. FT = fruit type, Col = fruit color, Cont = content of the pulp, Persist = persistence of individual fruits (days), AttackFrugi = “attacked by non-dispersal frugivores” (%). Right: Effect size plot of a generalised linear mixed effects model (binomial glmmTMB) testing the effects of fruit traits, including fruit density and maturation start and duration (both 0.5-month resolution), on the attack rate by *D. suzukii*. Please note that some traits shown in the figure were excluded from the model due to multicollinearity issues or a large number of missing values (see Materials and Methods). The asterisks indicate significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 2. Results of a binomial generalised mixed effects model (binomial glmmTMB) testing the effects of fruit traits on the attack rates of fruits by *Drosophila suzukii*. Plot nested in study site, as well as plant species and an observation-level random factor, were included as random terms. Results of a Wald Chi-squared test are given. For continuous variables the direction of the effect (+) is given.

	<i>Chi</i> ²	Degrees of freedom	<i>P</i>
Amount of ripe fruit	0.375	1	0.5404119
Maturation start	11.334	1	<0.001 (+)
Maturation duration	8.967	1	0.0027495 (+)
Fruit colour	16.944	3	<0.001
Fruit size Ø	5.024	1	0.0249951 (+)
Pulp sugar content	<0.001	1	0.9955224
Pulp pH	11.090	1	<0.001 (+)
R ² conditional	0.678		
R ² marginal	0.461		

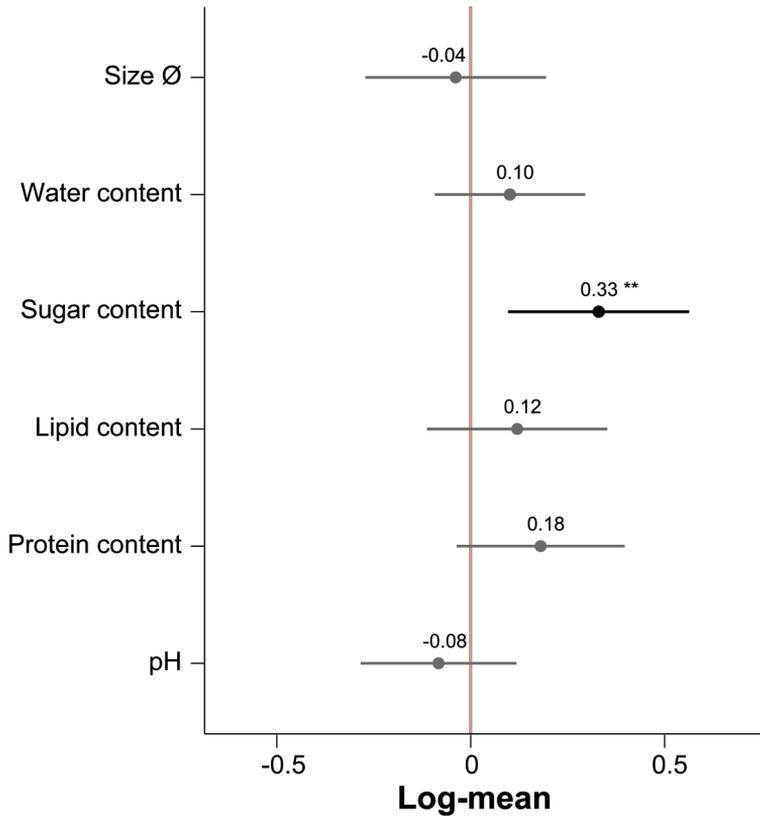


Figure 5. Effect size plot of a generalised linear model (poisson glm) testing the effects of fruit traits (size of the fruits and contents and pH of the pulp) on the decay status of fruits attacked by *Drosophila suzukii*. The asterisks indicate significance level: ** $p < 0.01$.

Table 3. Results of a generalised linear model (poisson glm) testing for the effects of fruit traits on fruit decay status after an attack by *Drosophila suzukii*. Results of a Wald Chi-squared test are given.

	Chi^2	Degrees of freedom	P
Fruit size Ø	0.108	1	0.742903
Pulp water content	1.0408	1	0.307632
Pulp sugar content	7.967	1	0.004763 (+)
Pulp lipid content	1.004	1	0.316309
Pulp protein content	2.591	1	0.107493
Pulp pH	0.655	1	0.418313
R^2 Nagelkerke	0.547		

Adult trapping

During the investigation period, the traps captured 99,366 insects from four orders, each with at least 75 individuals (97,965 Diptera, 751 Hymenoptera, 552 Coleoptera, 75 Dermaptera) (160 traps). Hemiptera, Lepidoptera, Blattodea and Thysanoptera

occurred less frequently. Within the Diptera, species from 27 families were found, with Drosophilidae accounting for almost all observed individuals (97%; 94,624 individuals), followed by Anisopodidae (1%; 1399), Heleomyzidae (<1%; 486), Mycetophilidae (<1%; 310), Phoridae (<1%; 278), Scatopsidae (<1%; 247), Sciaridae (<1%; 127), Chloropidae (<1%; 118), and Dryomyzidae (<1%; 103) etc. *Drosophila suzukii* was by far the most abundant species (82% of all trapped insects, 81,395 individuals) and accounted for 86% of all drosophilids (Suppl. material 2: Table S2).

The species composition of drosophilids in the different forest communities differed, e.g. *D. alpina* was only found in forest community 19a and species of the genus *Amiota* were mainly caught in forest community 26f/g. However, the drosophilid assemblages were dominated by *D. suzukii*, independent of forest community (Fig. 6). We trapped 21,758 (84%) *D. suzukii* and 4,117 (16%) native drosophilids in the forest community 19a, 17,031 (81%) and 4,054 (19%) in 26f/g, 15,708 (86%) and 2,528 (14%) in 7a, and 26,871 (91%) and 2,530 (9%) at the forest edge. The ratio of *D. suzukii* to native drosophilids did not differ significantly between forest communities (Wald Chi-squared test, $Chi^2=3.053$, $DF=1$, $P=0.384$) and cantons ($Chi^2=0.036$, $DF=1$, $P=0.849$). The proportion of *D. suzukii* predicted by the models (purple symbols) was between 0.81 and 0.95 (Fig. 6).

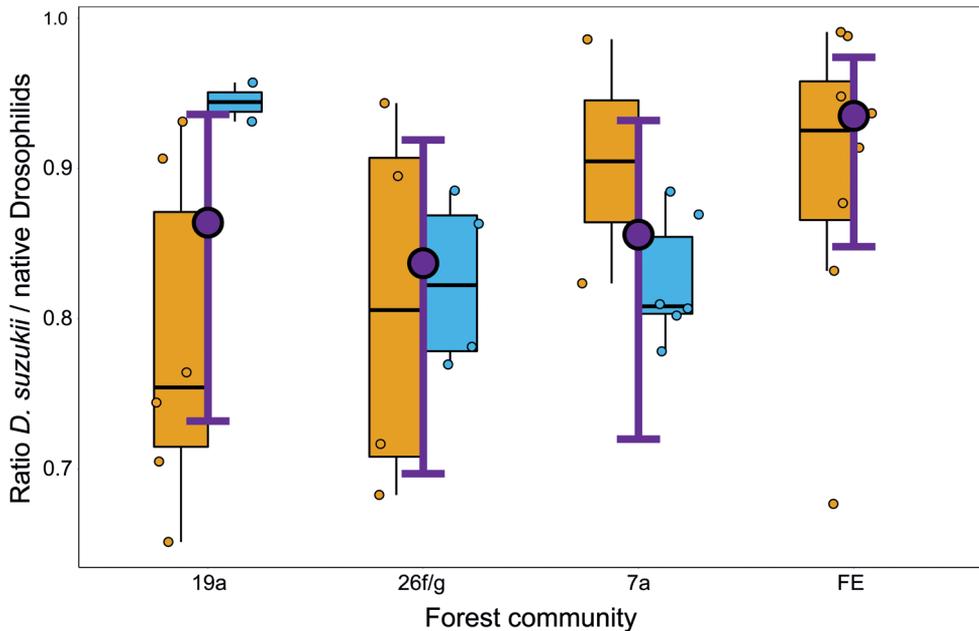


Figure 6. Ratio of *Drosophila suzukii* to native Drosophilidae species adults captured in traps in different forest communities. The boxplots (median, 25%/75% quantiles, min and max values) show raw values for the cantons Zug (orange) and Zurich (blue). Model-derived predicted estimates are shown in purple (LS-means \pm 95% CI, back-transformed from the logit scale to the original probability scale). Forest communities: 7a – *GALIO ODORATI-FAGETUM TYPICUM*, 19a – *ABIETI-FAGETUM LUZULETOSUM*, 26f/g – *ACERI-FRAXINETUM MERCURIALIDETOSUM*) (see Ellenberg and Klötzli 1972), FE = forest edge.

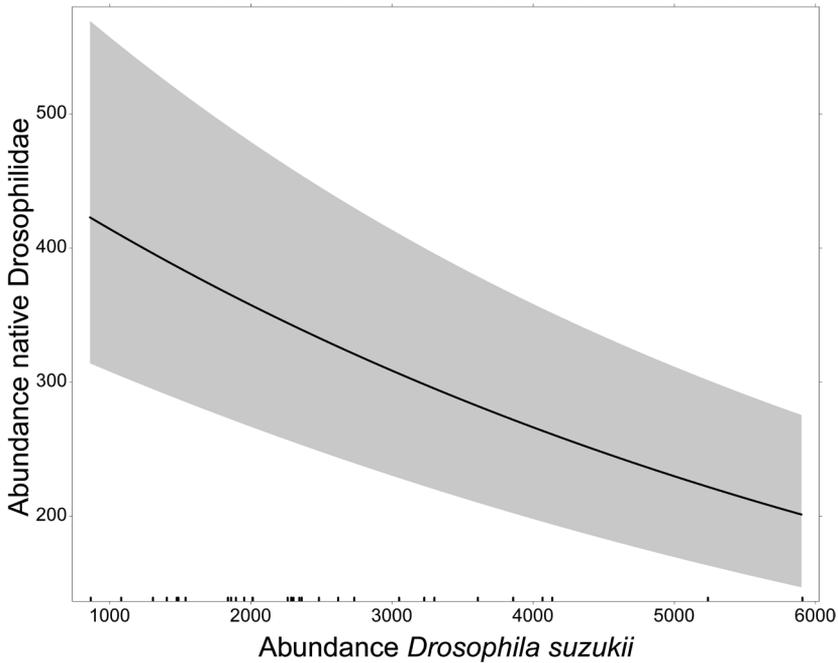


Figure 7. Predicted abundance of other drosophilids as function of the abundance of *Drosophila sukukii* (LS-means \pm 95% CI) from a generalised linear model including forest community and canton as covariates.

The abundance of *D. sukukii* significantly affected the abundance of native drosophilids captured in the traps (Wald Chi-squared Test, $Chi^2=74.072$, $DF=1$, $P<0.001$). The higher the abundance of *D. sukukii*, the smaller the abundance of native drosophilids predicted (Fig. 7). The forest community ($Chi^2=2.445$, $DF=3$, $P=0.485$) and the canton ($Chi^2=0.192$, $DF=1$, $P=0.661$) did not affect the abundance of native drosophilids.

Discussion

Drosophila sukukii, an invasive parasite of forest fruits, attacked 31 species from 15 different plant families (79% of all potential host plants investigated) in the forests of cantons Zug and Zurich. This not only confirms the broad host plant spectrum described in previous studies, but points towards a broad host use for reproduction. A broad host plant spectrum was to be expected, as *D. sukukii* is specialised on fruits and not on plant species per se. Furthermore, *D. sukukii* has been shown to have high plasticity in its host choice (Kienzle et al. 2020; Little et al. 2020). Our results suggest that a large number of fruiting plant species in forests are affected by *D. sukukii*, with likely far-reaching consequences for ecosystem processes (e.g. plant recruitment, resource availability for frugivores) and services (e.g. berry picking).

What influences attacks on the forest plants studied?

The observed broad host plant spectrum raises the question of what limits the host spectrum. Species of *Rosa* or *Sorbus*, which bear rather hard fruits, were hardly infested. We assume that the pulp and skin firmness act as a barrier to egg deposition, as insects have a limited ability to penetrate the skin of the fruit and to lay an egg in hard fruit flesh. It has been reported that the probability of oviposition increases as the force required to penetrate fruit skin decreases (Burrack et al. 2013; Lee et al. 2016). Further, within grape cultivars and single berries, berry skin resistance was found to explain the oviposition preferences of *D. suzukii* (Entling et al. 2019; Tonina et al. 2020). The fact that *Ilex aquifolium* was not infested was probably because its maturity coincides with the reproductive diapause of the fly (Grassi et al. 2018). We found that the red or blue, soft-skinned fruits of *Polygonatum* (Asparagaceae) were hardly used as a host, although this genus is widespread in the fly's area of origin (eFloras 2021). *Drosophila suzukii* may not detect all of the numerous potential host plants because its ability to process multiple sensory inputs is limited (Bernays 2001). Polyphagous herbivores have been shown to be attentive to the volatiles that are shared across host species (Silva and Clarke 2020). As the Asparagaceae are relatively distantly related to other host plants, the fruits and their microbial association with Asparagaceae species might not share certain volatiles with other host plants, making them undetectable to the fly.

The fruits of our 39 potential forest host plants differed in several characteristics that affect host location and oviposition site selection (Markow 2019), reflected by differences in observed attack rates in our study. Within the host plant range of *D. suzukii*, preferences (disproportionate use of potential host plants, i.e. egg deposits) have also been shown for crops in agricultural systems (Lee et al. 2011; Burrack et al. 2013; Olazuaga et al. 2019) and for wild and ornamental non-crop hosts (Poyet et al. 2015) when fruits were exposed to flies in laboratory assays. These preferences may be due to numerous characteristics of the fruit, such as colour, diameter, shape, volatile compound content, firmness, skin texture, or chemical composition, such as sugar content. In the field, several plant characteristics and the diverse abundance and fluctuating availability of host plants, as well as other biotic and abiotic factors of the host site, may also affect the choice of hosts, which makes comparisons of our findings with laboratory assays difficult.

Our non-metric multidimensional scaling (NMDS) indicated high variability in fruit traits and phenology in relation to attack rate. The attack rate varied among fruit colours, with black fruits being most frequently attacked. *Drosophila suzukii* has previously been shown to use colour as visual cue, but that colour contrast rather than colour appearance may be of greater importance (Little et al. 2019). While visual cues are of some importance, especially in behaviours such as courtship (Anholt et al. 2020), the olfactory and gustatory systems of *Drosophila* are crucial for host localisation and selection (Anholt 2020). We therefore expect that other factors correlated with colour might be decisive. For example, the fruit type “pome” or “hips”, which usually has high pulp firmness, mostly had a low attack rate and was often orange or red in colour. Larger fruit size also had a positive effect on attack rate. This could be because a larger

surface area, especially with aggregated fruits such as brambles, makes it easier for *D. suzukii* to find a preferred substrate, e.g. one without damage (mechanical or due to infection) or in an earlier maturation state. We also found that the attack rate increased with higher pulp pH (from pH 2.89 to 6.48). During host location and oviposition site selection, the fly can hardly detect a pH value, and thus this effect might be indirect. Microbes can act as the interface between insect herbivores and their hosts (Jansson et al. 2008; Hansen and Moran 2014; Ljunggren et al. 2019). *Drosophila suzukii*, like other *Drosophila*, is strongly attracted to volatiles produced by microorganisms in particular yeasts associated with fruits (Wright 2015; Hamby and Becher 2016; Bueno et al. 2020). It has also been shown that yeast volatiles, not fruit volatiles, mediate attraction and oviposition in *D. melanogaster* (Becher et al. 2012). In general, within the range of the fruit pulp pH, yeast and bacteria thrive better at higher pH values (Barth et al. 2009; Howell 2016). Fruits with a higher pH may host more microbes and could therefore be more attractive and easier to locate. In addition, moulds (filamentous fungi), an important competitor of *Drosophila* larvae (Wertheim et al. 2002; Rohlf et al. 2005; Trienens et al. 2010), generally exhibit better growth in a lower pH environment (Zhao et al. 2020). This could have led to a lower attractiveness for *D. suzukii* in our study, as decreased egg deposition in response to grey mould (*Botrytis cinerea*) was observed in a recent study (Chakraborty et al. 2022).

Host preferences are considered evidence of specialisation (Loxdale and Harvey 2016). In this case, however, we would expect phylogenetic relatedness in the preferred hosts, which we did not find, as the plant species with the highest observed attack rate belong to very distinct plant clades. Since the larvae feed in particular on microbes, host preferences, unlike those of folivorous insects, are determined more by the quality of the substrate in promoting the yeasts and bacteria associated with *D. suzukii* than by the phylogeny of the host plants. Our results suggest that *D. suzukii* responds to common cues from multiple host species, as well as specific cues from individual host species, as has been shown for other polyphagous herbivores (Silva and Clarke 2020). Other polyphagous herbivores also exhibit preference hierarchies for their hosts (e.g. Clarke et al. 2011; Wang et al. 2017), which may change through learning (West and Paul Cunningham 2002). Preferences should evolve toward maximising offspring fitness (Jaenike 1978), although preferences do not always correlate positively with offspring performance (e.g. Valladares and Lawton 1991; Clark et al. 2011), because other ecological, behavioural and physiological factors additionally influence host choice and host use (Jaenike 1990). While *D. suzukii* deposited its eggs on fruits from 16 different plant families in our study, we do not expect its offspring to perform equally well across the host spectrum, because preferences of insects with a broader host plant spectrum are less strongly associated with better offspring performance than insects specialised on plants within a certain family (Gripenberg et al. 2010). However, invasions are biologically unusual situations, and *D. suzukii* cannot be expected to show strong adaptive patterns of host use yet, as it was only recently introduced. Thus, some differences in larval performance might be expected and have also been shown between many non-crop hosts of *D. suzukii* (e.g. Poyet et al. 2015; Kenis et al. 2016; Olazcuaga et al. 2019).

Plant communities differ floristically and phytophysiognomically (Braun-Blanquet 1932) because species traits and an interacting milieu affect performance across environmental gradients such as temperature, moisture and soil chemistry (Mcgill et al. 2006). Therefore, the abundance and availability of host plants among forest communities must also differ. In our NMDS of available fruits of potential host plants in the plots, the forest communities were clustered. This finding and our model results indicated that the availability of different plant species determines the use of the host plants, as the forest community affected the attack rate. In addition to the diversity of host plants in an area, other associational effects, such as the density and frequency of neighbouring host plants, can influence the likelihood of a particular plant being used as a host, as can the density of the particular host plant (Underwood et al. 2014). As stated by the resource concentration hypothesis (Root 1973), a high density of host plants may increase the likelihood that the fly will find the fruits and remain on the host plant. This was supported by our results, as the number of ripe fruits present in our plots strongly affected the attack rate. Furthermore, since optimal oviposition behaviour depends not only on the suitability of the substrate, but also on the probability of finding a more suitable host in the time available (Jaenike 1978), adherence to a particular host plant species might be advantageous. A large amount of fruits may be more obvious to *D. suzukii* and thus increase the attack rate. A strong preference for more apparent resources in complex environments has also been shown for *D. melanogaster* (Verschut et al. 2016).

Our results further show that a longer fruit duration of fruits present increased the attack rate. Plants with more fruits, and especially plants such as brambles that produce ripe fruits over a long period, ensure continuous availability of resources without the need to search for new hosts, thus promoting the presence of overlapping generations of *D. suzukii* on the same host, further increasing attack rate. In Switzerland, between four and eight generations of *D. suzukii* per year are expected (Wiman et al. 2014). In addition, prior experience with olfactory and visual cues can enhance host location (Silva and Clarke 2020). Furthermore, a later ripening date was related to a higher attack rate, which may occur when the peak of abundance of *D. suzukii* and the period of fruit maturity coincide. The predominant maturity status of the plants in the plots also affected the attack rate. The more advanced the maturity, the greater the attack rate of the ripe fruits investigated. An advanced maturity status attracts more flies (Keeseey et al. 2015), but also indicates overlapping generations on the same plant.

Adult trapping revealed *Drosophila suzukii* as a dominant species

The high fruit attack rate observed in our study was also reflected in a high abundance and dominance of *D. suzukii* in trap catches, independent of forest community and elevation. This indicates the broad environmental tolerance of the fly. However, frequent occurrence in mountainous regions does not necessarily mean that *D. suzukii* inhabits these regions year-round, as studies from Japan and the Italian Alps suggest that the fly exhibits extensive movements between low and high elevations (Mitsui et al. 2010; Tait et al. 2018) and is capable of travelling distances of up to 9 km (Tait et al. 2018). However, it can be assumed

that the fly can survive the winter at these sites, as *D. suzukii* is firmly established on the island of Hokkaido in Japan, where winters average -4 to -12 °C (Kimura 2004).

Although our forest communities differed significantly in host composition, there were no differences in the proportion of *D. suzukii* between the forest communities. *Drosophila suzukii* accounted for 86% of the drosophilids caught during our study period. Recent snapshot studies of trap catches in forests also showed a high proportion of *D. suzukii*. In a survey in native riparian and non-riparian chestnut forest patches in northwestern Spain in August, *D. suzukii* accounted for 30% and 27% of the drosophilids caught in beer traps (Maceda-Veiga et al. 2021). Kremmer et al. (2017) reported 56% *D. suzukii* of the summed trap catches across natural habitat and crops in February (baited with apple cider vinegar). Studies in agricultural areas similar to our sites in terms of trapping period, climate and sampling method do not confirm *D. suzukii* as the most abundant taxon: *D. suzukii* accounted for 7% in Apulia, Italy (Antonacci et al. 2017), 11% in Kansas, USA (but baited with mashed banana; Gleason et al. 2019), and 18% in Washington, USA) (but some unmanaged habitats included; Bahder et al. 2016). Several factors could have caused these differences. First, agricultural and forested areas differ in biotic and abiotic factors, and species composition thus also differs (Burla and Bächli 1991). The assemblages of drosophilids, excluding *D. suzukii*, trapped in these agricultural areas were dominated by domestic species (distributed worldwide), while native species dominated in our area. Similarly, the occurrence of controphics, such as other insects, vertebrates or mould, and the occurrence of predators differ. Second, competition between *D. suzukii* and native species might be different in the two habitat types, due to differences in the occurrence of ecologically related species and available resources. Third, different measures taken to control the fly in agricultural fields might have reduced the populations of *D. suzukii*. However, these measures usually also affect other drosophilids. Fourth, forests can be expected to be the preferred habitat of *D. suzukii*, resulting in high overall proportions. Numerous forest fruits are suitable for the development of *D. suzukii*, due to its wide host niche (Little et al. 2020), and forests may offer preferred climatic conditions for *D. suzukii*, especially higher humidity (Hamby et al. 2016; Tochen et al. 2016; Eben et al. 2018).

Unlike in our study, surveys of drosophilid assemblages from trapping studies in various habitats in Asia, where *D. suzukii* is native or has been established for many years, do not show *D. suzukii* to be a dominant species: its proportion in relation to other drosophilids is reported to be up to 0.02 (e.g. Kaneko and Tokumitsu 1969; Toda 1992; Hirai et al. 2000; Guruprasad et al. 2010) and reached a value of 0.05 in a study in Korea (Lee 1964). Parasitisation is, however, an important mortality factor for drosophilid larvae (Janssen et al. 1988; Fleury et al. 2009), and the abundance of potential hosts is one factor determining the evolution of parasitoid host use (Novković et al. 2012). The degree of parasitisation is much higher in native populations (Torchin et al. 2003). The expected lower parasitisation of *D. suzukii* could be one of the main factors contributing to its frequent occurrence outside its native range, as escape from natural enemies can explain the success of introduced species (Keane 2002; Shea 2002).

Impact on native drosophilids

Our trap catches revealed that the abundance of *D. suzukii* was significantly negatively associated with the abundance of other drosophilids. Its dominance indicates a superiority over the native species. The heavily sclerotised, serrated ovipositor serves as a competitively unique trait (Karageorgi et al. 2017; Silva-Soares et al. 2017). Besides the capability of using a wider range of substrates for oviposition, we propose that the broader temporal niche of resource use is a competitive advantage. *Drosophila suzukii* can use substrates for oviposition earlier than other drosophilid species. Consequently, oviposition by *D. suzukii* induces substrate decay, rendering the substrate time-limited for the larval development of other fruit pulp consumers. While ripe fruits are inherently a temporally limited resource, this limitation is probably enhanced in forests compared with agricultural areas, because the fleshy fruits of wild plants are usually much smaller than those of cultivated plants. However, oviposition of *D. suzukii* on long-lasting larval habitats such as cultivated fruits may allow further use by other drosophilids (Rombaut et al. 2017; but see Entling and Hoffmann 2020).

Furthermore, *D. suzukii* may outcompete native drosophilids, due to different development times. This might lead to different competitiveness in forests and agriculture. Cold adaptation in *Drosophila* to colonise temperate climates appears to be associated with longer development times (Santos et al. 2006; Kinzner et al. 2018), and cosmopolitan human commensals (“domestic species”) such as *D. melanogaster*, which originated in central equatorial Africa (Lachaise and Silvain 2004), have comparatively short development times (Markow and O’Grady 2005a). In laboratory experiments, it has been found that the presence of *D. melanogaster* on the substrate significantly reduced adult *D. suzukii* emergence, reflecting a difference in minimum development time (7 days for *D. melanogaster* and 11 days for *D. suzukii* at 25 °C; (Dancu et al. 2017; Shaw et al. 2018). Presumably, the presence of *D. suzukii* reduces native drosophilid emergence as well. Coexistence of drosophilids across food-limited resource patches is facilitated by aggregation over patches (eggs in clutches of more than one egg, as well as non-random distributions of ovipositing females), which creates partial refuges and allows inferior species to exist (Rosewell et al. 1990; Jaenike and James 1991; Sevenster and Alphen 1996; Rohlfs and Hoffmeister 2003). In addition, parasitism facilitates the coexistence of drosophilid species (Mitsui and Kimura 2000a). However, as an invasive species, *D. suzukii* is expected to be exposed to lower pressure from parasitoids (Torchin et al. 2003), resulting in larger populations. Unlike other drosophilids, *D. suzukii* has been shown not to aggregate over patches (Mitsui et al. 2006). Therefore, we suggest that it may exclude and outcompete other drosophilids in the exploitation of resource patches, which is supported by our results: higher abundance of *D. suzukii* was associated with lower abundance of other drosophilids.

Potential impact on host plants

Piercing of the skin of undamaged fruit by *D. suzukii* provides an entry point for infestation by pathogens, and inoculated microbes can act as a jump-start for decay.

Microbes that infect fruits have been hypothesised to make fruits unattractive to vertebrate frugivores that potentially compete for fruit pulp (Janzen 1977; Ruxton et al. 2014). Just as humans respond to infested fruit with rejection, birds have been shown to prefer intact fruit to infested fruit (e.g. Manzur and Courtney 1984; Jordano 1987; Borowicz 1988; Buchholz and Levey 1990; Cipollini and Stiles 1993; Traveset et al. 1995; but see Valburg 1992). Attacks by *D. suzukii* alter the attractiveness of the fruit because it changes the chemical composition and visual cues, such as colour, shape and reflective patterns. Since the choice of fruits by birds depends on visual perception (Schaefer and Ruxton 2011), we assume that attacks on fruits by *D. suzukii* could reduce the attractiveness for birds, resulting in reduced seed dispersal. This is because many host plants of *D. suzukii* rely especially on frugivorous birds for dispersal (Garcia et al. 2010). Negative effects on seeds are unexpected because attacks occur after seed set.

In the field, when we observed symptoms of fruit decay after *D. suzukii* attacks, we noticed that fruit decay progressed at very different rates among plant species, which may be due to their different compounds and compositions. For example, the bright red fruits of *Lonicera alpigena* were found to change into dry, brown fruit mummies (rotten fruits) within a short time, while fruits of *Prunus padus* had hardly any symptoms of decay and hung intact on the bushes for more than 40 days without decaying. On *Prunus padus*, a significant reduction in the number of emerged *D. suzukii* adults and a significant delay in the larval-pupal development time was detected when compared with *Prunus avium* (Alhmedi et al. 2019), where oviposition by *D. suzukii* is known to trigger microbial development (Ayyanath et al. 2018). Because larval development depends on the development of microbes (Sang 1956; Schwarz et al. 2014; Hamby and Becher 2016), decay within a short time indicates a strong response of microbial growth and development and better host suitability to *D. suzukii* offspring development. Among the fruit traits we studied, we found that the pulp sugar content determined the severity of the symptoms of decay after an attack by *D. suzukii*. The rapid decomposition of simple carbohydrates leads to rapid microbial growth (Zhao et al. 2020), explaining why more severe symptoms of decay were evident at higher sugar levels. Nutrient levels deplete over time as microbes and larvae consume the resources, so rapid fruit decay after an attack by *D. suzukii* means a loss of resources for other frugivores.

Conclusion

Almost half of the 39 studied forest plant species showed attack rates by *D. suzukii* of > 50%, with a high percentage showing severe symptoms of fruit decay after egg deposition. This may lead to reduced fruit consumption by vertebrate seed dispersers. *Drosophila suzukii* is a damaging agent for plants, and if the fly reproduces in large numbers, dispersal agents and host plants may both suffer. Besides the direct effect of parasitism of forest fruits by *D. suzukii*, leading to competition with other frugivorous species, the indirect effect of disrupting seed-dispersal mutualisms can have far-reaching consequences for ecosystems. With ongoing climate change, these potentially

severe ecological impacts might be amplified in temperate forests, as higher average and winter temperatures will most likely lead to shorter generation times and lower winter mortality, which will eventually further increase the pressure on forest fruits and the competitiveness of *D. suzukii* over native drosophilids.

Acknowledgements

We are grateful to Gerhard Bächli for his helpful input and comments, Lea Bernath, Martin Ziegler and Urs Kamm for their continuous support of the study, Melissa Dawes for English editing, and the Cantons of Zug and Zurich for their financial support. MMG was supported by the HOMED project (<http://homed-project.eu/>), which received funding from the European Union's Horizon 2020 research and innovation programme under grant agreement No. 771271.

References

- Alhmedi A, Clymans R, Van Kerckvoorde V, Bylemans D, Beliën T (2019) Preference and performance of *Drosophila suzukii* on *Prunus* species: A potential eco-friendly pest management tool. *Crop Protection* 122: 35–41. <https://doi.org/10.1016/j.cropro.2019.04.018>
- Ali JG, Agrawal AA (2012) Specialist versus generalist insect herbivores and plant defense. *Trends in Plant Science* 17(5): 293–302. <https://doi.org/10.1016/j.tplants.2012.02.006>
- Anholt RRH (2020) Chemosensation and Evolution of *Drosophila* Host Plant Selection. *iScience* 23(1): 100799. <https://doi.org/10.1016/j.isci.2019.100799>
- Anholt RRH, O'Grady P, Wolfner MF, Harbison ST (2020) Evolution of Reproductive Behavior. *Genetics* 214(1): 49–73. <https://doi.org/10.1534/genetics.119.302263>
- Antonacci R, Tritto P, Cappucci U, Fanti L, Piacentini L, Berloco M (2017) Drosophilidae monitoring in Apulia (Italy) reveals *Drosophila suzukii* as one of the four most abundant species. *Bulletin of Insectology* 70: 139–146.
- Arnó J, Solà M, Riudavets J, Gabarra R (2016) Population dynamics, non-crop hosts, and fruit susceptibility of *Drosophila suzukii* in Northeast Spain. *Journal of Pest Science* 89(3): 713–723. <https://doi.org/10.1007/s10340-016-0774-3>
- Asplen MK, Anfora G, Biondi A, Choi D-S, Chu D, Daane KM, Gibert P, Gutierrez AP, Hoelmer KA, Hutchison WD, Isaacs R, Jiang Z-L, Kárpáti Z, Kimura MT, Pascual M, Philips CR, Plantamp C, Ponti L, Véték G, Vogt H, Walton VM, Yu Y, Zappalà L, Desneux N (2015) Invasion biology of spotted wing Drosophila (*Drosophila suzukii*): A global perspective and future priorities. *Journal of Pest Science* 88(3): 469–494. <https://doi.org/10.1007/s10340-015-0681-z>
- Atallah J, Teixeira L, Salazar R, Zaragoza G, Kopp A (2014) The making of a pest: The evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species. *Proceedings. Biological Sciences* 281(1781): 20132840–20132840. <https://doi.org/10.1098/rspb.2013.2840>
- Atkinson W, Shorrocks B (1977) Breeding site specificity in the domestic species of *Drosophila*. *Oecologia* 29(3): 223–232. <https://doi.org/10.1007/BF00345697>

- Ayyanath M-M, Zurowski CL, Scott IM, Lowery DT, Watson MC, O’Gorman DT, MacKenzie KE, Úrbez-Torres JR (2018) Relationship between *Drosophila suzukii* and postharvest disorders of Sweet Cherry. *Phytobiomes Journal* 2(1): 42–50. <https://doi.org/10.1094/PBIOMES-02-17-0007-R>
- Bächli G, Viljoen F, Escher SA, Saura A (2004) The Drosophilidae (Diptera) of Fennoscandia and Denmark. Brill, Leiden; Boston, 362 pp. <https://doi.org/10.1163/9789047414681>
- Bächli G (2021) TaxoDros: The database on taxonomy of Drosophilidae. <https://www.taxodros.uzh.ch/search/class.php> [March 27, 2021]
- Bahder BW, Bahder LD, Hauser M, Beers E, Walsh DB (2016) Relative abundance and phenology of *Drosophila* Fallén, 1815 (Diptera: Drosophilidae) species in south-central Washington State. *The Pan-Pacific Entomologist* 92(2): 92–99. <https://doi.org/10.3956/2016-92.2.92>
- Barth M, Hankinson TR, Zhuang H, Breidt F (2009) Microbiological Spoilage of Fruits and Vegetables. In: Sperber WH, Doyle MP (Eds) *Compendium of the Microbiological Spoilage of Foods and Beverages*. Springer, New York, 135–183. https://doi.org/10.1007/978-1-4419-0826-1_6
- Becher PG, Flick G, Rozpędowska E, Schmidt A, Hagman A, Lebreton S, Larsson MC, Hansson BS, Piškur J, Witzgall P, Bengtsson M (2012) Yeast, not fruit volatiles mediate *Drosophila melanogaster* attraction, oviposition and development. *Functional Ecology* 26: 822–828. <https://doi.org/10.1111/j.1365-2435.2012.02006.x>
- Bernays EA (2001) Neural limitations in phytophagous insects: Implications for Diet Breadth and Evolution of Host Affiliation. *Annual Review of Entomology* 46(1): 703–727. <https://doi.org/10.1146/annurev.ento.46.1.703>
- Bolda MP, Goodhue RE, Zalom FG (2010) Spotted Wing Drosophila: Potential Economic Impact of a Newly Established Pest. *Agricultural and Resource Economics* 13: 5–8.
- Borowicz VA (1988) Do Vertebrates Reject Decaying Fruit? An Experimental Test with *Cornus amomum* Fruits. *Oikos* 53(1): 74. <https://doi.org/10.2307/3565665>
- Bradley BA, Leginhas BB, Whitlock R, Allen JM, Bates AE, Bernatchez G, Diez JM, Early R, Lenoir J, Vilà M, Sorte CJB (2019) Disentangling the abundance–impact relationship for invasive species. *Proceedings of the National Academy of Sciences* 116: 9919–9924. <https://doi.org/10.1073/pnas.1818081116>
- Braun-Blanquet J (1932) *Plant sociology. The study of plant communities*. 1st Edn. McGraw-Hill Book Co., Inc., New York and London.
- Briem F, Eben A, Gross J, Vogt H (2016) An invader supported by a parasite: Mistletoe berries as a host for food and reproduction of Spotted Wing Drosophila in early spring. *Journal of Pest Science* 89(3): 749–759. <https://doi.org/10.1007/s10340-016-0739-6>
- Briem F, Dominic A, Golla B, Hoffmann C, Englert C, Herz A, Vogt H (2018) Explorative Data Analysis of *Drosophila suzukii* Trap Catches from a Seven-Year Monitoring Program in Southwest Germany. *Insects* 9(4): 125. <https://doi.org/10.3390/insects9040125>
- Brooks ME, Kristensen K, Benthem KJ, van Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9: 378. <https://doi.org/10.32614/RJ-2017-066>

- Buchholz R, Levey DJ (1990) The Evolutionary Triad of Microbes, Fruits, and Seed Dispersers: An Experiment in Fruit Choice by Cedar Waxwings, *Bombycilla cedrorum*. *Oikos* 59(2): 200. <https://doi.org/10.2307/3545535>
- Bueno E, Martin KR, Raguso RA, McMullen JG II, Hesler SP, Loeb GM, Douglas AE (2020) Response of Wild Spotted Wing *Drosophila* (*Drosophila suzukii*) to Microbial Volatiles. *Journal of Chemical Ecology* 46(8): 688–698. <https://doi.org/10.1007/s10886-019-01139-4>
- Burla H, Bächli G (1991) A search for pattern in faunistical records of drosophilid species in Switzerland. *Journal of Zoological Systematics and Evolutionary Research* 29(3): 176–200. <https://doi.org/10.1111/j.1439-0469.1991.tb01630.x>
- Burrack HJ, Fernandez GE, Spivey T, Kraus DA (2013) Variation in selection and utilization of host crops in the field and laboratory by *Drosophila suzukii* Matsumura (Diptera: Drosophilidae), an invasive frugivore. *Pest Management Science* 69(10): 1173–1180. <https://doi.org/10.1002/ps.3489>
- Carscadden KA, Emery NC, Arnillas CA, Cadotte MW, Afkhami ME, Gravel D, Livingstone SW, Wiens JJ (2020) Niche Breadth: Causes and Consequences for Ecology, Evolution, and Conservation. *The Quarterly Review of Biology* 95(3): 179–214. <https://doi.org/10.1086/710388>
- Chakraborty A, Mori B, Rehermann G, Hernández Garcia A, Lemmen-Lechelt J, Hagman A, Khalil S, Håkansson S, Witzgall P, Becher PG (2022) Yeast and fruit fly mutual niche construction and antagonism against mould. *Functional Ecology* 36(7): 1639–1654. <https://doi.org/10.1111/1365-2435.14054>
- Cini A, Ioriatti C, Anfora G (2012) A review of the invasion of *Drosophila suzukii* in Europe and a draft research agenda for integrated pest management. *Bulletin of Insectology* 65(1): 149–160.
- Cipollini M (2000) Secondary metabolites of vertebrate-dispersed fruits: Evidence for adaptive functions. *Revista Chilena de Historia Natural* 73(3): 421–440. <https://doi.org/10.4067/S0716-078X2000000300006>
- Cipollini ML, Stiles EW (1993) Fruit Rot, Antifungal Defense, and Palatability of Fleshy Fruits for Frugivorous Birds. *Ecology* 74(3): 751–762. <https://doi.org/10.2307/1940803>
- Clark KE, Hartley SE, Johnson SN (2011) Does mother know best? The preference-performance hypothesis and parent-offspring conflict in aboveground-belowground herbivore life cycles. *Ecological Entomology* 36(2): 117–124. <https://doi.org/10.1111/j.1365-2311.2010.01248.x>
- Clarke AR, Powell KS, Weldon CW, Taylor PW (2011) The ecology of *Bactrocera tryoni* (Diptera: Tephritidae): what do we know to assist pest management? *Annals of Applied Biology* 158(1): 26–54. <https://doi.org/10.1111/j.1744-7348.2010.00448.x>
- Cunningham JP, Zalucki MP (2014) Understanding Heliethine (Lepidoptera: Heliethinae) Pests: What is a Host Plant? *Journal of Economic Entomology* 107(3): 881–896. <https://doi.org/10.1603/EC14036>
- Cunningham JP, Carlsson MA, Villa TF, Dekker T, Clarke AR (2016) Do Fruit Ripening Volatiles Enable Resource Specialism in Polyphagous Fruit Flies? *Journal of Chemical Ecology* 42(9): 931–940. <https://doi.org/10.1007/s10886-016-0752-5>
- DAISIE [Ed.] (2009) *Handbook of alien species in Europe*. Springer, Dordrecht, 399 pp.

- Dancau T, Stemberger TLM, Clarke P, Gillespie DR (2017) Can competition be superior to parasitism for biological control? The case of spotted wing *Drosophila* (*Drosophila suzukii*), *Drosophila melanogaster* and *Pachycrepoides vindemmiae*. *Biocontrol Science and Technology* 27(1): 3–16. <https://doi.org/10.1080/09583157.2016.1241982>
- Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA, Courchamp F (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592(7855): 571–576. <https://doi.org/10.1038/s41586-021-03405-6>
- Dick JTA, Laverty C, Lennon JJ, Barrios-O’Neill D, Mensink PJ, Robert Britton J, Médoc V, Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017) Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. Souza L (Ed.). *Journal of Applied Ecology* 54: 1259–1267. <https://doi.org/10.1111/1365-2664.12849>
- dos Santos LA, Mendes MF, Krüger AP, Blauth ML, Gottschalk MS, Garcia FRM (2017) Global potential distribution of *Drosophila suzukii* (Diptera, Drosophilidae). *PLoS ONE* 12(3): e0174318. <https://doi.org/10.1371/journal.pone.0174318>
- Douglas AE (2009) The microbial dimension in insect nutritional ecology. *Functional Ecology* 23(1): 38–47. <https://doi.org/10.1111/j.1365-2435.2008.01442.x>
- Douglas AE (2015) Multiorganismal Insects: Diversity and Function of Resident Microorganisms. *Annual Review of Entomology* 60(1): 17–34. <https://doi.org/10.1146/annurev-ento-010814-020822>
- Dweck HK, Talross GJ, Wang W, Carlson JR (2021) Evolutionary shifts in taste coding in the fruit pest *Drosophila suzukii*. *eLife* 10: e64317. <https://doi.org/10.7554/eLife.64317>
- Eben A, Reifenrath M, Briem F, Pink S, Vogt H (2018) Response of *Drosophila suzukii* (Diptera: Drosophilidae) to extreme heat and dryness: Heat wave effects on *Drosophila suzukii*. *Agricultural and Forest Entomology* 20(1): 113–121. <https://doi.org/10.1111/afe.12235>
- eFloras (2021) eFloras. <http://www.efloras.org/> [April 14, 2022]
- Ehrenfeld JG (2010) Ecosystem Consequences of Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics* 41(1): 59–80. <https://doi.org/10.1146/annurev-ecolsys-102209-144650>
- Ehrlich PR, Raven PH (1964) Butterflies and Plants: A Study in Coevolution. *Evolution; International Journal of Organic Evolution* 18(4): 586–608. <https://doi.org/10.1111/j.1558-5646.1964.tb01674.x>
- Ellenberg H, Klötzli F (1972) Waldgesellschaften und Waldstandorte der Schweiz. *Mitteilungen der Schweizerischen Anstalt für das forstliche Versuchswesen* 48: 589–930.
- Elsensohn J, Loeb G (2018) Non-Crop Host Sampling Yields Insights into Small-Scale Population Dynamics of *Drosophila suzukii* (Matsumura). *Insects* 9(1): 5. <https://doi.org/10.3390/insects9010005>
- Entling W, Hoffmann C (2020) Single and combined effects of *Drosophila suzukii* and *Drosophila melanogaster* on sour rot development in viticulture. *Journal of Applied Entomology* 144(3): 153–160. <https://doi.org/10.1111/jen.12721>

- Entling W, Anslinger S, Jarausch B, Michl G, Hoffmann C (2019) Berry skin resistance explains oviposition preferences of *Drosophila suzukii* at the level of grape cultivars and single berries. *Journal of Pest Science* 92(2): 477–484. <https://doi.org/10.1007/s10340-018-1040-7>
- Eriksson O, Ehrlen J (1991) Phenological variation in fruit characteristics in vertebrate-dispersed plants. *Oecologia* 86: 463–470. <https://doi.org/10.1007/BF00318311>
- Fleury F, Gibert P, Ris N, Allemand R (2009) Advances in Parasitology. Chapter 1. Ecology and Life History Evolution of Frugivorous *Drosophila* Parasitoids. Elsevier 70: 3–44. [https://doi.org/10.1016/S0065-308X\(09\)70001-6](https://doi.org/10.1016/S0065-308X(09)70001-6)
- Fox J, Weisberg S (2018) Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *Journal of Statistical Software* 87(9): 1–27. <https://doi.org/10.18637/jss.v087.i09>
- Fox J, Weisberg S (2019) An R Companion to Applied Regression. 3rd edn. Thousand Oaks CA. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Garcia D, Zamora R, Amico GC (2010) Birds as Suppliers of Seed Dispersal in Temperate Ecosystems: Conservation Guidelines from Real-World Landscapes: Seed-Dispersal by Frugivorous Birds. *Conservation Biology* 24(4): 1070–1079. <https://doi.org/10.1111/j.1523-1739.2009.01440.x>
- Gilbert DG (1980) Dispersal of yeasts and bacteria by *Drosophila* in a temperate forest. *Oecologia* 46(1): 135–137. <https://doi.org/10.1007/BF00346979>
- Gleason JM, Roy PR, Everman ER, Gleason TC, Morgan TJ (2019) Phenology of *Drosophila* species across a temperate growing season and implications for behavior. *PLoS ONE* 14(5): e0216601. <https://doi.org/10.1371/journal.pone.0216601>
- Gower JC (1971) A General Coefficient of Similarity and Some of Its Properties. *Biometrics* 27(4): 857. <https://doi.org/10.2307/2528823>
- Grassi A, Gottardello A, Dalton DT, Tait G, Rendon D, Ioriatti C, Gibeaut D, Rossi Stacconi MV, Walton VM (2018) Seasonal Reproductive Biology of *Drosophila suzukii* (Diptera: Drosophilidae) in Temperate Climates. *Environmental Entomology* 47(1): 166–174. <https://doi.org/10.1093/ee/nvx195>
- Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationships in phytophagous insects. *Ecology Letters* 13(3): 383–393. <https://doi.org/10.1111/j.1461-0248.2009.01433.x>
- Guruprasad BR, Hegde SN, Krishna MS (2010) Seasonal and Altitudinal Changes in Population Density of 20 Species of *Drosophila* in Chamundi Hill. *Journal of Insect Science* 10(123): 1–12. <https://doi.org/10.1673/031.010.12301>
- Hamby KA, Becher PG (2016) Current knowledge of interactions between *Drosophila suzukii* and microbes, and their potential utility for pest management. *Journal of Pest Science* 89(3): 621–630. <https://doi.org/10.1007/s10340-016-0768-1>
- Hamby KAE, Bellamy D, Chiu JC, Lee JC, Walton VM, Wiman NG, York RM, Biondi A (2016) Biotic and abiotic factors impacting development, behavior, phenology, and reproductive biology of *Drosophila suzukii*. *Journal of Pest Science* 89: 605–619. <https://doi.org/10.1007/s10340-016-0756-5>
- Hansen AK, Moran NA (2014) The impact of microbial symbionts on host plant utilization by herbivorous insects. *Molecular Ecology* 23(6): 1473–1496. <https://doi.org/10.1111/mec.12421>

- Haro-Barchin E, Scheper J, Ganuza C, De Groot GA, Colombari F, van Kats R, Kleijn D (2018) Landscape-scale forest cover increases the abundance of *Drosophila suzukii* and parasitoid wasps. *Basic and Applied Ecology* 31: 33–43. <https://doi.org/10.1016/j.baae.2018.07.003>
- Hartig F (2022) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.5. <https://CRAN.R-project.org/package=DHARMA>
- Hauser M (2011) A historic account of the invasion of *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) in the continental United States, with remarks on their identification. *Pest Management Science* 67(11): 1352–1357. <https://doi.org/10.1002/ps.2265>
- Herrera CM (1987) Vertebrate-Dispersed Plants of the Iberian Peninsula: A Study of Fruit Characteristics. *Ecological Monographs* 57(4): 305–331. <https://doi.org/10.2307/2937089>
- Hirai Y, Goto SG, Yoshida T, Kimura MT (2000) Faunal and Ecological Surveys on Drosophilid Flies in Iriomotejima, a Subtropical Island of Japan. *Entomological Science* 3: 273–284.
- Howe HF, Smallwood J (1982) Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics* 1(1): 201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>
- Howell K (2016) Spoilage: Yeast Spoilage of Food and Beverages. *Encyclopedia of Food and Health*. Elsevier, 113–117. <https://doi.org/10.1016/B978-0-12-384947-2.00650-4>
- Jaenike J (1978) On Optimal Oviposition Behavior in Phytophagous Insects. *Theoretical Population Biology* 14(3): 350–356. [https://doi.org/10.1016/0040-5809\(78\)90012-6](https://doi.org/10.1016/0040-5809(78)90012-6)
- Jaenike J (1990) Host Specialization in Phytophagous Insects. *Annual Review of Ecology and Systematics* 21(1): 243–273. <https://doi.org/10.1146/annurev.es.21.110190.001331>
- Jaenike J, James AC (1991) Aggregation and the Coexistence of Mycophagous *Drosophila*. *Journal of Animal Ecology* 60(3): 913. <https://doi.org/10.2307/5421>
- Janson EM, Stireman JO, Singer MS, Abbot P (2008) Phytophagous insect-microbe mutualism and adaptive evolutionary diversification. *Evolution; International Journal of Organic Evolution* 62(5): 997–1012. <https://doi.org/10.1111/j.1558-5646.2008.00348.x>
- Janssen A, Driessen G, Haan MD, Roodbol N (1988) The Impact of Parasitoids On Natural Populations of Temperate Woodland *Drosophila*. *Netherlands Journal of Zoology* 38(1): 61–73. <https://doi.org/10.1163/156854288X00049>
- Janzen DH (1977) Why Fruits Rot, Seeds Mold, and Meat Spoils. *American Naturalist* 111(980): 691–713. <https://doi.org/10.1086/283200>
- Jeschke JM, Bacher S, Blackburn TM, Dick JTA, Essl F, Evans T, Gaertner M, Hulme PE, Kühn I, Mrugała A, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM, Sendek A, Vilà M, Winter M, Kumschick S (2014) Defining the Impact of Non-Native Species. *Conservation Biology* 28(5): 1188–1194. <https://doi.org/10.1111/cobi.12299>
- Jordano P (1987) Avian fruit removal: Effects of fruit variation, crop size, and insect damage. *Ecology* 68(6): 1711–1723. <https://doi.org/10.2307/1939863>
- Kambysellis MP, Heed WB (1971) Studies of Oogenesis in Natural Populations of Drosophilidae. I. Relation of Ovarian Development and Ecological Habitats of the Hawaiian Species. *American Naturalist* 105(941): 31–49. <https://doi.org/10.1086/282700>
- Kaneko A, Tokumitsu T (1969) *Drosophila* Survey of Hokkaido, XXVII.: On Drosophilid Flies from Seven Localities of the Hidaka District in Southern Hokkaido. *Journal of the Faculty of Science, Hokkaido University* 6: 244–256.
- Karageorgi M, Bräcker LB, Lebreton S, Minervino C, Cavey M, Siju KP, Grunwald Kadow IC, Gompel N, Prud'homme B (2017) Evolution of Multiple Sensory Systems Drives

- Novel Egg-Laying Behavior in the Fruit Pest *Drosophila suzukii*. *Current Biology* 27(6): 847–853. <https://doi.org/10.1016/j.cub.2017.01.055>
- Keane R (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution* 17(4): 164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Keesey IW, Knaden M, Hansson BS (2015) Olfactory Specialization in *Drosophila suzukii* Supports an Ecological Shift in Host Preference from Rotten to Fresh Fruit. *Journal of Chemical Ecology* 41(2): 121–128. <https://doi.org/10.1007/s10886-015-0544-3>
- Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré Ch, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde C (2009) Ecological effects of invasive alien insects. *Biological Invasions* 11: 21–45. <https://doi.org/10.1007/s10530-008-9318-y>
- Kenis M, Tonina L, Eschen R, van der Sluis B, Sancassani M, Mori N, Haye T, Helsen H (2016) Non-crop plants used as hosts by *Drosophila suzukii* in Europe. *Journal of Pest Science* 89(3): 735–748. <https://doi.org/10.1007/s10340-016-0755-6>
- Kienzle R, Rohlf M (2021) Mind the Wound!—Fruit Injury Ranks Higher than, and Interacts with, Heterospecific Cues for *Drosophila suzukii* Oviposition. *Insects* 12(5): 424. <https://doi.org/10.3390/insects12050424>
- Kienzle R, Groß LB, Caughman S, Rohlf M (2020) Resource use by individual *Drosophila suzukii* reveals a flexible preference for oviposition into healthy fruits. *Scientific Reports* 10(1): 3132. <https://doi.org/10.1038/s41598-020-59595-y>
- Kimura MT (2004) Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. *Oecologia* 140: 442–449. <https://doi.org/10.1007/s00442-004-1605-4>
- Kimura MT (1976) *Drosophila* Survey of Hokkaido, XXXII.: A Field Survey of Fungus Preferences of Drosophilid Flies in Sapporo (With 1 Text-figure and 8 Tables). *Journal of the Faculty of Science, Hokkaido University* 20: 288–298.
- Kinzner M, Krapf P, Nindl M, Heussler C, Eisenkölbl S, Hoffmann AA, Seeber J, Arthofer W, Schlick-Steiner BC, Steiner FM (2018) Life-history traits and physiological limits of the alpine fly *Drosophila nigrosparsa* (Diptera: Drosophilidae): A comparative study. *Ecology and Evolution* 8(4): 2006–2020. <https://doi.org/10.1002/ece3.3810>
- Knapp L, Mazzi D, Finger R (2020) The economic impact of *Drosophila suzukii*: perceived costs and revenue losses of cherry, plum and grape growers. *Pest Management Science* 77(2): 978–1000. <https://doi.org/10.1002/ps.6110>
- Kremmer L, Thaon M, Borowiec N, David J, Poirié M, Gatti J-L, Ris N (2017) Field Monitoring of *Drosophila suzukii* and Associated Communities in South Eastern France as a Pre-Requirement for Classical Biological Control. *Insects* 8(4): 124. <https://doi.org/10.3390/insects8040124>
- Kumschick S, Bacher S, Evans T, Marková Z, Pergl J, Pyšek P, Vaes-Petignat S, van der Veer G, Vilà M, Nentwig W (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. *Journal of Applied Ecology* 52: 552–561. <https://doi.org/10.1111/1365-2664.12427>
- Lachaise D, Silvain J-F (2004) How two Afrotropical endemics made two cosmopolitan human commensals: The *Drosophila melanogaster*–*D. simulans* palaeogeographic riddle. *Genetica* 120(1–3): 17–39. <https://doi.org/10.1023/B:GENE.0000017627.27537.ef>
- Laliberté E, Legendre P, Shipley B (2014) FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12. <https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.494.7392&rep=rep1&type=pdf>

- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91(1): 299–305. <https://doi.org/10.1890/08-2244.1>
- Lapin K, Bacher S, Cech T, Damjanić R, Essl F, Georges F-I, Hoch G, Kavčič A, Koltay A, Kostić S, Lukić I, Marinšek A, Nagy L, Agbaba SN, Oettel J, Orlović S, Poljaković-Pajnik L, Sallmannshofer M, Steinkellner M, Stojnic S, Westergren M, Zlatkovic M, Zolles A, de Groot M (2021) Comparing environmental impacts of alien plants, insects and pathogens in protected riparian forests. *NeoBiota* 69: 1–28. <https://doi.org/10.3897/neobiota.69.71651>
- Leblanc L, O’Grady PM, Rubinoff D, Montgomery SL (2009) New Immigrant Drosophilidae in Hawaii, and a Checklist of the Established Immigrant Species. *Proceedings of the Hawaiian Entomological Society* 41: 121–127.
- Lee TJ (1964) Taxonomy, and geographical distribution of Drosophilidae (Diptera) in Korea. *Chungang University Theses Collection* 9: 424–459.
- Lee JC, Bruck DJ, Curry H, Edwards D, Haviland DR, Van Steenwyk RA, Yorgey BM (2011) The susceptibility of small fruits and cherries to the spotted-wing drosophila, *Drosophila suzukii*. *Pest Management Science* 67(11): 1358–1367. <https://doi.org/10.1002/ps.2225>
- Lee JC, Dreves AJ, Cave AM, Kawai S, Isaacs R, Miller JC, Van Timmeren S, Bruck DJ (2015) Infestation of Wild and Ornamental Noncrop Fruits by *Drosophila suzukii* (Diptera: Drosophilidae). *Annals of the Entomological Society of America* 108(2): 117–129. <https://doi.org/10.1093/aesa/sau014>
- Lee JC, Dalton DT, Swoboda-Bhattarai KA, Bruck DJ, Burrack HJ, Strik BC, Woltz JM, Walton VM (2016) Characterization and manipulation of fruit susceptibility to *Drosophila suzukii*. *Journal of Pest Science* 89(3): 771–780. <https://doi.org/10.1007/s10340-015-0692-9>
- Lei B, Cui J, Newman C, Buesching CD, Xie Z, Macdonald DW, Zhou Y (2021) Seed dispersers shape the pulp nutrients of fleshy-fruited plants. *Proceedings. Biological Sciences* 288(1953): 20210817. <https://doi.org/10.1098/rspb.2021.0817>
- Lenth RV (2022) emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.4.5. <https://cran.r-project.org/web/packages/emmeans/emmeans.pdf>
- Li S, Cadotte MW, Meiners SJ, Hua Z, Shu H, Li J, Shu W (2015) The effects of phylogenetic relatedness on invasion success and impact: deconstructing Darwin’s naturalisation conundrum. *Ecology Letters* 18: 1285–1292. <https://doi.org/10.1111/ele.12522>
- Liebhold AM, Tobin PC (2008) Population Ecology of Insect Invasions and Their Management. *Annual Review of Entomology* 53(1): 387–408. <https://doi.org/10.1146/annurev.ento.52.110405.091401>
- Little CM, Rizzato AR, Charbonneau L, Chapman T, Hillier NK (2019) Color preference of the spotted wing Drosophila, *Drosophila suzukii*. *Scientific Reports* 9(1): 16051. <https://doi.org/10.1038/s41598-019-52425-w>
- Little CM, Chapman TW, Hillier NK (2020) Plasticity Is Key to Success of *Drosophila suzukii* (Diptera: Drosophilidae) Invasion. *Journal of Insect Science* 20: 5. <https://doi.org/10.1093/jisesa/ieaa034>
- Ljunggren J, Borrero-Echeverry F, Chakraborty A, Lindblom TU, Hedenström E, Karlsson M, Witzgall P, Bengtsson M (2019) Yeast volatomes differentially effect larval feeding in an insect herbivore. *Applied and Environmental Microbiology* [preprint]. <https://doi.org/10.1101/721845>

- Loxdale HD, Harvey JA (2016) The ‘generalism’ debate: Misinterpreting the term in the empirical literature focusing on dietary breadth in insects. *Biological Journal of the Linnean Society. Linnean Society of London* 119(2): 265–282. <https://doi.org/10.1111/bij.12816>
- Lüdecke D, Ben-Shachar M, Patil I, Waggoner P, Makowski D (2021) performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open Source Software* 6(60): 3139. <https://doi.org/10.21105/joss.03139>
- Maceda-Veiga A, Albacete S, Carles-Tolrá M, Pujade-Villar J, Máca J, Mac Nally R (2021) Streams and rural abandonment are related to the summer activity of the invasive pest *Drosophila suzukii* in protected European forests. *Forest Ecology and Management* 485: 118942. <https://doi.org/10.1016/j.foreco.2021.118942>
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA (2000) Biotic invasions: Causes, epidemiology, global consequences and control. *Ecological Applications* 10(3): 22. [https://doi.org/10.1890/1051-0761\(2000\)010\[0689:BICEGC\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2)
- Madden AA, Epps MJ, Fukami T, Irwin RE, Sheppard J, Sorger DM, Dunn RR (2018) The ecology of insect–yeast relationships and its relevance to human industry. *Proceedings. Biological Sciences* 285(1875): 20172733. <https://doi.org/10.1098/rspb.2017.2733>
- Manzur MI, Courtney SP (1984) Influence of Insect Damage in Fruits of Hawthorn on Bird Foraging and Seed Dispersal. *Oikos* 43(3): 265. <https://doi.org/10.2307/3544142>
- Markow TA (2019) Host use and host shifts in *Drosophila*. *Current Opinion in Insect Science* 31: 139–145. <https://doi.org/10.1016/j.cois.2019.01.006>
- Markow TA, O’Grady P (2005a) *Drosophila: a guide to species identification and use*. Academic Press, 1–272.
- Markow TA, O’Grady P (2005b) Evolutionary Genetics of Reproductive Behavior in *Drosophila: Connecting the Dots*. *Annual Review of Genetics* 39(1): 263–291. <https://doi.org/10.1146/annurev.genet.39.073003.112454>
- Markow TA, O’Grady P (2008) Reproductive ecology of *Drosophila*. *Functional Ecology* 22(5): 747–759. <https://doi.org/10.1111/j.1365-2435.2008.01457.x>
- Matsumura S (1931) 6000 illustrated insects of Japan-Empire. Toko Shoin, Tokyo, 1694 pp.
- Mcgill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21(4): 178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Mitsui H, Kimura MT (2000a) Coexistence of drosophilid flies: Aggregation, patch size diversity and parasitism. *Ecological Research* 15(1): 93–100. <https://doi.org/10.1046/j.1440-1703.2000.00328.x>
- Mitsui H, Kimura M (2000b) Food preference of Drosophilid Flies in Domestic and Forest Areas of Central Japan. *The Entomological Society of Japan* 3: 285–289.
- Mitsui H, Takahashi KH, Kimura MT (2006) Spatial distributions and clutch sizes of *Drosophila* species ovipositing on cherry fruits of different stages. *Population Ecology* 48(3): 233–237. <https://doi.org/10.1007/s10144-006-0260-5>
- Mitsui H, Beppu K, Kimura MT (2010) Seasonal life cycles and resource uses of flower- and fruit-feeding drosophilid flies (Diptera: Drosophilidae) in central Japan. *Entomological Science* 13(1): 60–67. <https://doi.org/10.1111/j.1479-8298.2010.00372.x>

- Mollot G, Pantel JH, Romanuk TN (2017) The Effects of Invasive Species on the Decline in Species Richness. *Advances in Ecological Research*. Elsevier 56: 61–83. <https://doi.org/10.1016/bs.aecr.2016.10.002>
- Normark BB, Johnson NA (2011) Niche explosion. *Genetica* 139(5): 551–564. <https://doi.org/10.1007/s10709-010-9513-5>
- Novković B, Oikawa A, Murata Y, Mitsui H, Kimura MT (2012) Abundance and host associations of parasitoids attacking frugivorous drosophilids on Iriomote-jima, a subtropical island of Japan. *European Journal of Entomology* 109(4): 517–526. <https://doi.org/10.14411/eje.2012.065>
- Nunney L (1990) *Drosophila* on Oranges: Colonization, Competition, and Coexistence. *Ecology* 71(5): 1904–1915. <https://doi.org/10.2307/1937598>
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solyomos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlenn D, Ouellette M-H, Cunha ER, Smith T, Stier A, Braak CJFT, Weedon J (2020) *vegan*: Community Ecology Package. R package version 2.5–7. <https://CRAN.R-project.org/package=vegan>
- Olazcuaga L, Rode NO, Foucaud J, Facon B, Ravigné V, Ausset A, Leménager N, Loiseau A, Gautier M, Estoup A, Hufbauer RA (2019) Oviposition Preference and Larval Performance of *Drosophila suzukii* (Diptera: Drosophilidae), Spotted-Wing Drosophila: Effects of Fruit Identity and Composition. *Environmental Entomology* 48(4): 867–881. <https://doi.org/10.1093/ee/nvz062>
- Oosterbroek P (2006) The European Families of the Diptera: Identification, Diagnosis, Biology. KNNV Publishing, 1–205. <https://doi.org/10.1163/9789004278066>
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1(1): 3–19. <https://doi.org/10.1023/A:1010034312781>
- Pelton E, Gratton C, Isaacs R, Van Timmeren S, Blanton A, Guédot C (2016) Earlier activity of *Drosophila suzukii* in high woodland landscapes but relative abundance is unaffected. *Journal of Pest Science* 89(3): 725–733. <https://doi.org/10.1007/s10340-016-0733-z>
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52(3): 273–288. <https://doi.org/10.1016/j.ecolecon.2004.10.002>
- Podani J (1999) Extending Gower's general coefficient of similarity to ordinal characters. *Taxon* 48(2): 331–340. <https://doi.org/10.2307/1224438>
- Poyet M, Le Roux V, Gibert P, Meirland A, Prévost G, Eslin P, Chabrierie O (2015) The Wide Potential Trophic Niche of the Asiatic Fruit Fly *Drosophila suzukii*: The Key of Its Invasion Success in Temperate Europe? *PLoS ONE* 10(11): e0142785. <https://doi.org/10.1371/journal.pone.0142785>
- Prasanna V, Prabha TN, Tharanathan RN (2007) Fruit Ripening Phenomena—An Overview. *Critical Reviews in Food Science and Nutrition* 47(1): 1–19. <https://doi.org/10.1080/10408390600976841>

- Pyšek P, Richardson DM (2010) Invasive Species, Environmental Change and Management, and Health. *Annual Review of Environment and Resources* 35(1): 25–55. <https://doi.org/10.1146/annurev-environ-033009-095548>
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M, Vilà M, Wingfield MJ, Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews of the Cambridge Philosophical Society* 95(6): 1511–1534. <https://doi.org/10.1111/brv.12627>
- R Core Team (2020) R: A language and environment for statistical computing, version 4.0.2. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* 83(3): 263–282. <https://doi.org/10.1890/13-0183.1>
- Roche DP, Stoleson SH, Lituma CM (2021) Invasion of Eastern Deciduous Forests by the Spotted Wing *Drosophila*: Impacts and Knowledge Gaps. *Wildlife Society Bulletin* 45(4): 711–718. <https://doi.org/10.1002/wsb.1234>
- Rodriguez-Cabal MA, Stuble KL, Nuñez MA, Sanders NJ (2009) Quantitative analysis of the effects of the exotic Argentine ant on seed-dispersal mutualisms. *Biology Letters* 5(4): 499–502. <https://doi.org/10.1098/rsbl.2009.0297>
- Rohlf M, Hoffmeister TS (2003) An evolutionary explanation of the aggregation model of species coexistence. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270(Suppl_1): 1471–2954. <https://doi.org/10.1098/rsbl.2003.0002>
- Rohlf M, Hoffmeister TS (2005) Maternal effects increase survival probability in *Drosophila subobscura* larvae. *Entomologia Experimentalis et Applicata* 117(1): 51–58. <https://doi.org/10.1111/j.1570-7458.2005.00334.x>
- Rohlf M, Obmann B, Petersen R (2005) Competition with filamentous fungi and its implication for a gregarious lifestyle in insects living on ephemeral resources. *Ecological Entomology* 8(5): 556–563. <https://doi.org/10.1111/j.0307-6946.2005.00722.x>
- Rombaut A, Guilhot R, Xuéreb A, Benoit L, Chapuis MP, Gibert P, Fellous S (2017) Invasive *Drosophila suzukii* facilitates *Drosophila melanogaster* infestation and sour rot outbreaks in the vineyards. *Royal Society Open Science* 4(3): 9. <https://doi.org/10.1098/rsos.170117>
- Root RB (1973) Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica Oleracea*). *Ecological Monographs* 43(1): 95–124. <https://doi.org/10.2307/1942161>
- Rosewell J, Shorrocks B, Edwards K (1990) Competition on a Divided and Ephemeral Resource: Testing the Assumptions. I. Aggregation. *Journal of Animal Ecology* 59(3): 977. <https://doi.org/10.2307/5026>
- Ruxton GD, Wilkinson DM, Schaefer HM, Sherratt TN (2014) Why fruit rots: Theoretical support for Janzen's theory of microbe–macrobe competition. *Proceedings. Biological Sciences* 281(1782): 20133320. <https://doi.org/10.1098/rspb.2013.3320>
- Sallabanks R, Courtney SP (1992) Frugivory, Seed Predation, and Insect-Vertebrate Interactions. *Annual Review of Entomology* 37(1): 377–400. <https://doi.org/10.1146/annurev.en.37.010192.002113>

- Sang JH (1956) The quantitative nutritional requirements of *Drosophila melanogaster*. The Journal of Experimental Biology 33(1): 45–72. <https://doi.org/10.1242/jeb.33.1.45>
- Santoïemma G, Trivellato F, Caloi V, Mori N, Marini L (2018) Habitat preference of *Drosophila suzukii* across heterogeneous landscapes. Journal of Pest Science 92: 485–494. <https://doi.org/10.1007/s10340-018-1052-3>
- Santos M, Brites D, Laayouni H (2006) Thermal evolution of pre-adult life history traits, geometric size and shape, and developmental stability in *Drosophila subobscura*. Journal of Evolutionary Biology 19(6): 2006–2021. <https://doi.org/10.1111/j.1420-9101.2006.01139.x>
- Sato A, Tanaka KM, Yew JY, Takahashi A (2021) *Drosophila suzukii* avoidance of microbes in oviposition choice. Royal Society Open Science 8(1): 201601. <https://doi.org/10.1098/rsos.201601>
- Schaefer HM, Ruxton GD (2011) Plant-Animal Communication. Oxford University Press. <https://doi.org/10.1093/acprof:osobl/9780199563609.001.0001>
- Schwarz S, Durisko Z, Dukas R (2014) Food selection in larval fruit flies: Dynamics and effects on larval development. Naturwissenschaften 101(1): 61–68. <https://doi.org/10.1007/s00114-013-1129-z>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): 14435. <https://doi.org/10.1038/ncomms14435>
- Sevenster JG, Alphen JJMV (1996) Aggregation and Coexistence. II. A Neotropical *Drosophila* Community. Journal of Animal Ecology 65(3): 308. <https://doi.org/10.2307/5877>
- Shackleton RT, Shackleton CM, Kull CA (2019) The role of invasive alien species in shaping local livelihoods and human well-being: A review. Journal of Environmental Management 229: 145–157. <https://doi.org/10.1016/j.jenvman.2018.05.007>
- Shaw B, Brain P, Wijnen H, Fountain MT (2018) Reducing *D. suzukii* through competition. Pest Management Science 74: 1466–1471. <https://doi.org/10.1002/ps.4836>
- Shea K (2002) Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution 17(4): 170–176. [https://doi.org/10.1016/S0169-5347\(02\)02495-3](https://doi.org/10.1016/S0169-5347(02)02495-3)
- Shorrocks B (1977) An ecological classification of European *Drosophila* species. Oecologia 26(4): 335–345. <https://doi.org/10.1007/BF00345533>
- Silva R, Clarke AR (2020) The “sequential cues hypothesis”: A conceptual model to explain host location and ranking by polyphagous herbivores. Insect Science 27(6): 1136–1147. <https://doi.org/10.1111/1744-7917.12719>
- Silva-Soares NF, Nogueira-Alves A, Beldade P, Mirth CK (2017) Adaptation to new nutritional environments: Larval performance, foraging decisions, and adult oviposition choices in *Drosophila suzukii*. BMC Ecology 17(1): 21. <https://doi.org/10.1186/s12898-017-0131-2>
- Slatyer RA, Hirst M, Sexton JP (2013) Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16: 1104–1114. <https://doi.org/10.1111/ele.12140>

- Snow BK, Snow D (1988) Birds and Berries: A Study of an Ecological Interaction. T & AD Poyser, Calton, England, 1–268.
- Stamps JA, Yang LH, Morales VM, Boundy-Mills KL (2012) *Drosophila* Regulate Yeast Density and Increase Yeast Community Similarity in a Natural Substrate. PLoS ONE 7(7): e42238. <https://doi.org/10.1371/journal.pone.0042238>
- Stiebel H (2003) Frugivorie bei mitteleuropäischen Vögeln: Der Mutualismus zwischen Vögeln und ornithochoren Pflanzen: Ernährung frugivorer Vögel und Konsequenzen für die Samenausbreitung. PHD Thesis. Carl-von-Ossietzki-Universität, Oldenburg. <http://oops.uni-oldenburg.de/254/2/stifru03.pdf>
- Stockton DG, Brown R, Loeb GM (2019) Not berry hungry? Discovering the hidden food sources of a small fruit specialist, *Drosophila suzukii*. Ecological Entomology 44(6): 810–822. <https://doi.org/10.1111/een.12766>
- Strayer DL, Eviner VT, Jeschke JM, Pace ML (2006) Understanding the long-term effects of species invasions. Trends in Ecology & Evolution 21(11): 645–651. <https://doi.org/10.1016/j.tree.2006.07.007>
- Tait G, Grassi A, Pfab F, Crava CM, Dalton DT, Magarey R, Ometto L, Vezzulli S, Rossi-Stacconi MV, Gottardello A, Pugliese A, Firrao G, Walton VM, Anfora G (2018) Large-scale spatial dynamics of *Drosophila suzukii* in Trentino, Italy. Journal of Pest Science 91(4): 1213–1224. <https://doi.org/10.1007/s10340-018-0985-x>
- Thistlewood HMA, Gill P, Beers EH, Shearer PW, Walsh DB, Rozema BM, Acheampong S, Castagnoli S, Yee WL, Smytheman P, Whitener AB (2018) Spatial Analysis of Seasonal Dynamics and Overwintering of *Drosophila suzukii* (Diptera: Drosophilidae) in the Okanagan-Columbia Basin, 2010–2014. Environmental Entomology 47(2): 221–232. <https://doi.org/10.1093/ee/nvx178>
- Thistlewood HMA, Rozema B, Acheampong S (2019) Infestation and timing of use of non-crop plants by *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) in the Okanagan Basin, Canada. Canadian Entomologist 151(1): 34–48. <https://doi.org/10.4039/tce.2018.47>
- Tochen S, Woltz JM, Dalton DT, Lee JC, Wiman NG, Walton VM (2016) Humidity affects populations of *Drosophila suzukii* (Diptera: Drosophilidae) in blueberry. Journal of Applied Entomology 140(1–2): 47–57. <https://doi.org/10.1111/jen.12247>
- Toda MJ (1992) Three-dimensional dispersion of drosophilid flies in a cool temperate forest of northern Japan. Ecological Research 7(3): 283–295. <https://doi.org/10.1007/BF02347097>
- Tonina L, Mori N, Giomi F, Battisti A (2016) Development of *Drosophila suzukii* at low temperatures in mountain areas. Journal of Pest Science 89(3): 667–678. <https://doi.org/10.1007/s10340-016-0730-2>
- Tonina L, Giomi F, Sancassani M, Ajelli M, Mori N, Giongo L (2020) Texture features explain the susceptibility of grapevine cultivars to *Drosophila suzukii* (Diptera: Drosophilidae) infestation in ripening and drying grapes. Scientific Reports 10(1): 10245. <https://doi.org/10.1038/s41598-020-66567-9>
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. Nature 421(6923): 628–630. <https://doi.org/10.1038/nature01346>
- Traveset A, Richardson D (2006) Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology & Evolution 21(4): 208–216. <https://doi.org/10.1016/j.tree.2006.01.006>

- Traveset A, Willson MF, Gaither JC (1995) Avoidance by Birds of Insect-Infested Fruits of *Vaccinium ovalifolium*. *Oikos* 73(3): 381. <https://doi.org/10.2307/3545962>
- Trienens M, Keller NP, Rohlf M (2010) Fruit, flies and filamentous fungi - experimental analysis of animal-microbe competition using *Drosophila melanogaster* and *Aspergillus* mould as a model system. *Oikos* 119(11): 1765–1775. <https://doi.org/10.1111/j.1600-0706.2010.18088.x>
- TRY (2021) TRY Plant Trait Database. <https://www.try-db.org/TryWeb/Home.php> [April 14, 2022]
- Underwood N, Inouye BD, Hambäck PA (2014) A Conceptual Framework for Associational Effects: When Do Neighbors Matter and How Would We Know? *The Quarterly Review of Biology* 89(1): 1–19. <https://doi.org/10.1086/674991>
- Valburg LK (1992) Eating Infested Fruits: Interactions in a Plant-Disperser-Pest Triad. *Oikos* 65(1): 25. <https://doi.org/10.2307/3544883>
- Valladares G, Lawton JH (1991) Host-Plant Selection in the Holly Leaf-Miner: Does Mother Know Best? *Journal of Animal Ecology* 60(1): 227. <https://doi.org/10.2307/5456>
- Verschut TA, Becher PG, Anderson P, Hambäck PA (2016) Disentangling associational effects: both resource density and resource frequency affect search behaviour in complex environments. *Functional Ecology* 30: 1826–1833. <https://doi.org/10.1111/1365-2435.12670>
- Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S, Roques A, Roy D, Hulme PE (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment* 8(3): 135–144. <https://doi.org/10.1890/080083>
- Wallingford AK, Rice KB, Leskey TC, Loeb GM (2018) Overwintering behavior of *Drosophila suzukii*, and potential springtime diets for egg maturation. *Environmental Entomology* 47(5): 1266–1273. <https://doi.org/10.1093/ee/nvy115>
- Wang Y, Ma Y, Zhou D-S, Gao S-X, Zhao X-C, Tang Q-B, Wang C-Z, van Loon JJA (2017) Higher plasticity in feeding preference of a generalist than a specialist: Experiments with two closely related *Helicoverpa* species. *Scientific Reports* 7(1): 17876. <https://doi.org/10.1038/s41598-017-18244-7>
- Wertheim B, Marchais J, Vet LEM, Dicke M (2002) Allee effect in larval resource exploitation in *Drosophila*: an interaction among density of adults, larvae, and micro-organisms: Allee effect in larval resource exploitation. *Ecological Entomology* 27(5): 608–617. <https://doi.org/10.1046/j.1365-2311.2002.00449.x>
- West SA, Paul Cunningham J (2002) A General Model for Host Plant Selection in Phytophagous Insects. *Journal of Theoretical Biology* 214(3): 499–513. <https://doi.org/10.1006/jtbi.2001.2475>
- White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: A neglected concept in invasion biology. *Diversity & Distributions* 12(4): 443–455. <https://doi.org/10.1111/j.1366-9516.2006.00265.x>
- Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying Threats to Imperiled Species in the United States. *Bioscience* 48(8): 607–615. <https://doi.org/10.2307/1313420>
- Wiman NG, Walton VM, Dalton DT, Anfora G, Burrack HJ, Chiu JC, Daane KM, Grassi A, Miller B, Tochen S, Wang X, Ioriatti C (2014) Integrating Temperature-Dependent Life

- Table Data into a Matrix Projection Model for *Drosophila suzukii* Population Estimation. PLoS ONE 9(9): e106909. <https://doi.org/10.1371/journal.pone.0106909>
- Wright GA (2015) Olfaction: Smells Like Fly Food. *Current Biology* 25(4): 144–146. <https://doi.org/10.1016/j.cub.2014.12.052>
- Yamamoto A (1984) Heat and Cold Resistances of Sixteen *Drosophila* Species from Japan in Relation to Their Field Ecology. *Zoological Society of Japan* 1: 641–652.
- Zhao P, Ndayambaje JP, Liu X, Xia X (2020) Microbial Spoilage of Fruits: A Review on Causes and Prevention Methods. *Food Reviews International*: 1–22. <https://doi.org/10.1080/87559129.2020.1858859>
- Zürich K (2020) Vegetationskundliche Kartierung der Wälder im Kanton Zürich. <http://maps.zh.ch/?scale=37682&srId=2056&topic=WaldVKZH&x=2697548.76&y=1261707.35> [March 31, 2021]

Supplementary material 1

Tables S1, Figure S1

Authors: Irene Bühlmann, Martin M. Gossner

Data type: Docx file.

Explanation note: Supplementary information on potential host plant species of *Drosophila suzukii* in the study plots and Boxplots of proportions of fruits attacked by *Drosophila suzukii* per species, including fruits outside the plots, separated by forest community.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.77.87319.suppl1>

Supplementary material 2

Table S2

Authors: Irene Bühlmann, Martin M. Gossner

Data type: Xlsx file.

Explanation note: Abundances of sampled insect taxa, based on catches from cup traps with 3 mm diameter entry holes baited with apple cider vinegar in different forest communities.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/neobiota.77.87319.suppl2>