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

Irene Bühlmann, [ID] Martin Gossner

1 **Invasive *Drosophila suzukii* outnumbers native controphics and causes**

2 **substantial damage to fruits of forest plants**

3

4 Irene Bühlmann[1] & Martin M. Gossner[2,3]

5

6 **Affiliations:**

7 [1] Ökobüro Biotopia, Obertalacher 1, CH-6319 Allenwinden, Switzerland

8 [2] Forest Entomology, Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf,
9 Switzerland

10 [3] ETH Zurich, Department of Environmental Systems Science, Institute of Terrestrial Ecosystems, 8092 Zurich,
11 Switzerland

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

13 **Running title:** Impact of Drosophila suzukii on forests

14

15 **Author contributions:**

16 I.B. and M.M.G. developed the ideas for the manuscript, acquired the funding and defined the
17 design and methods used in the study; I.B. conducted the field assessments and identified the
18 species; M.M.G. analyzed the data; I.B. wrote the first draft of the manuscript, I.B. and
19 M.M.G. edited, revised and finalized it.

20   ## Abstract

21   Impacts of biological invasions are diverse and can have far-reaching consequences for

22   ecosystems. The spotted wing drosophila, *Drosophila suzukii*, is a major invasive pest of

23   fruits, which negatively affects fruit and wine production. However, little is known about the

24   ecological impact of this fly species on the ecosystems it has invaded. In this study, we

25   investigated the use of potential host plants by *D. suzukii* at 64 sites in different forest

26   communities in Switzerland from mid-June to mid-October 2020. We examined more than

27   12,000 fruits for egg deposits of *D. suzukii* to assess its direct impact on the plants. We

28   recorded symptoms of fruit decay after egg deposition to determine if *D. suzukii* attacks

29   trigger fruit decay. In addition, we monitored the drosophilid fauna with cup traps baited with

30   apple cider vinegar, as we expected that *D. suzukii* would outnumber and potentially

31   outcompete native controphics, especially other drosophilids. Egg deposits of *D. suzukii* were

32   found on the fruit of 31 of the 39 potential host plant species studied, with 18 species showing

33   an attack rate > 50%. Overall, fruits of *Cotoneaster divaricatus* (96%), *Atropa bella-donna*

34   (91%), *Rubus fruticosus corylifolius* aggr. (91%), *Frangula alnus* (85%) and *Sambucus nigra*

35   (83%) were attacked particularly frequently, resulting also in predicted attack probabilities

36   that varied among forest communities. Later and longer fruiting, black fruit colour, larger fruit

37   size and higher pulp pH all positively affected attack rates. More than 50% of the plant

38   species showed severe symptoms of decay after egg deposition, with higher pulp sugar

39   content leading to more severe symptoms. The high fruit attack rate observed was reflected in

40   a high abundance and dominance of *D. suzukii* in trap catches, independent of forest

41   community and elevation. *Drosophila suzukii* was by far the most abundant species,

42   accounting for 86% (81,395 individuals) of all drosophilids. The abundance of *D. suzukii* was

43   negatively associated with the abundance of the native drosophilids. Our results indicate that

44   the invasive *D. suzukii* competes strongly with other frugivorous species and that its presence

45   has far-reaching ecosystem-level consequences. The rapid decay of fruits attacked by *D.*

46   *suzukii* leads to a loss of resources and may disrupt seed-dispersal mutualisms through the

47   reduced consumption of fruits by dispersers such as birds.

48   **Key words**

Introduction

51 Biotic exchange and subsequent invasions by non-native species in natural and human-

52 modified ecosystems are among the greatest threats to biodiversity worldwide (Wilcove et al.

53 1998, Pyšek et al. 2020). They can have far-reaching consequences for ecosystems (Vilà et al.

54 2010), including their functioning (Mack et al. 2000, Ehrenfeld 2010), and for human well-

55 being (Shackleton et al. 2019), and they can have extraordinary economic costs (Pimentel et

56 al. 2005, Diagne et al. 2021). The perception and recognition of impacts of biological

57 invasions, as well as how they are measured, are diverse and depend on the variables and

58 scales considered (Jeschke et al. 2014). While assessments of economic impacts are measured

59 in terms of economic costs, ecological impacts are evaluated as measurable changes to the

60 properties of an ecosystem by a non-native species. However, the ecological impact of an

61 invader is not easy to define or quantify, due to the context dependency of impacts, the

62 variation in the per capita effect within and across species, and the complex interactions

63 between invaders and their biotic and abiotic environments (Pyšek and Richardson 2010,

64 Ricciardi et al. 2013).

65 Invasive non-native species may affect native species on the level of individuals (e.g.

66 fecundity, mortality), populations (e.g. abundance, genetic diversity), communities (e.g.

67 species richness and composition, trophic structure) and ecosystems (e.g. nutrient cycling,

68 physical habitat, overall structure and function) (Parker et al. 1999). The impact of a non-

69 native species on native populations and communities varies greatly in temporal (Strayer et al.

70 2006) and spatial (Mollot et al. 2017) terms and depends critically on the abundance and

71 trophic position of the invasive species (Bradley 2019). This explains why the extent of

72 ecological impact varies greatly between invaders (Kumschick et al. 2015, Lapin et al. 2021).

73 Insects make up a large proportion of introduced species (DAISIE 2009, Seebens et al. 2017).

74 They are usually introduced accidentally, rarely reach large populations, and/or are often not

75 noticed. However, a small minority become highly abundant and ecologically significant

76 (Liebhold and Tobin 2008). Impacts of non-native insects on native species and ecosystems

77 have many potential mechanisms, but only a very small proportion of non-native insects have

78 been studied regarding their ecological impacts (Kenis et al. 2009). While direct impacts

79 through mechanisms such as predation or competition are more obvious, indirect impacts,

80 such as apparent and exploitative competition or alteration of interactions between native

1

81   species, often remain unexplored (Traveset and Richardson 2006, White et al. 2006). For

82   example, a meta-analysis of the effects of the invasions of the Argentine ant (*Linepithema*

83   *humile*) showed that areas with *L. humile* had 92% fewer native ant seed dispersers than areas

84   where *L. humile* was not present. In addition, the meta-analysis indicated that *L. humile* did

85   not replace native seed dispersers in their functional role, as rates of seed removal and

86   seedling establishment were lower in the presence of *L. humile* (Rodriguez-Cabal et al. 2009).

87   A disruption of seed-dispersal mutualisms affects seedling recruitment, species populations

88   and distributions, plant-community composition, and gene flow (Howe and Smallwood 1982).

89   Such indirect effects of non-native species on plant species can have far-reaching ecological

90   consequences.

91   For frugivorous insects, the most significant effect on plants is thought to be indirect, namely

92   the reduction of seed dispersal far from the mother plant by vertebrates (Sallabanks and

93   Courtney 1992). Among frugivorous insects, *Drosophila suzukii* (Matsumura 1931; Diptera:

94   Drosophilidae), also known as the spotted wing drosophila, is of particular importance. It is an

95   invasive *Drosophila* species originating from Southeast Asia (Asplen et al. 2015). The

96   presence of the species outside of its native range was first recorded in Japan (Matsumura

97   1931), 1980 in Hawaii (Leblanc et al. 2009) and in 2008 synchronously in southwestern USA

98   (Hauser 2011) and southern Europe (Cini et al. 2012). The species has spread rapidly and is

99   now widespread on the Asian, European, and North and South American continents (dos

100 Santos et al. 2017). The family Drosophilidae comprises more than 3,900 species, with more

101 than 1,500 of the described species belonging to the genus *Drosophila.* These small flies are

102 widespread in a variety of climates and environments throughout the world (Markow and

103 O'Grady 2005, Bächli 2021). To date, around 36 species of the genus *Drosophila* and more

104 than 30 species of other genera of the family Drosophilidae are distributed in Switzerland

105 (personal communication G. Bächli 2021; Bächli et al. 2004). The habitat of most of these

106 species is mainly restricted to forest areas (so-called wild species). In contrast, a few species

107 of *Drosophila*, so-called domestic species, mainly occur in settlements and are mostly

108 cosmopolitan in distribution (Atkinson and Shorrocks 1977, Shorrocks 1977, Burla and

109 Bächli 1991). Oviposition and larval development of *Drosophila* are usually restricted to

110 decaying organic resources such as slime flux, fruits, flowers and mushrooms (Markow and

111 O'Grady 2008), but the degree of substrate specialisation varies widely, from generalists to

112 obligate specialists (Mitsui and Kimura 2000, Markow and O'Grady 2005, Anholt et al.

113 2020). This variability is also related to host location, host acceptance, and host use (Markow

114 2019), with chemical recognition playing a crucial role (Anholt 2020). Most *Drosophila* show

2

115 some degree of fidelity in oviposition site selection, which often depends more on the decay

116 state of the substrate, than on the identity of the plant or fungus (e.g. Kambysellis and Heed

117 1971, Nunney 1990, Karageorgi et al. 2017). For example, *D. suzukii* prefers fruits that are

118 more intact (Kienzle and Rohlfs 2021), firmer (Sato, Airi et al. 2021) and in an earlier

119 maturation stage (Dweck et al. 2021) compared with *D. melanogaster*, another frugivore.

120 *Drosophila* species inoculate their oviposition substrate with microorganisms. They are

121 considered important vectors, especially of yeasts but also of bacteria, and transport viable

122 microbes to new substrates where they grow (Gilbert 1980, Rohlfs and Hoffmeister 2005,

123 Stamps et al. 2012, Hamby and Becher 2016). Adults and larvae feed mainly on the microbes

124 that decompose organic material, but also on the decomposing material itself (Markow and

125 O'Grady 2008). Flies additionally benefit from the dispersal of such microbes, as they obtain

126 signals from their metabolic products for finding sugar resources (Madden et al. 2018).

127 *Drosophila suzukii* exploits resources that usually consist of small separate units and are

128 patchy and ephemeral, i.e. they support only one generation. The temporal and spatial

129 constraints of these unpredictable resources may favour generalists (Jaenike 1990). Niche

130 breadth usually correlates positively with geographical range size (Slatyer et al. 2013), but

131 does not necessarily explain invasion success (Carscadden et al. 2020). Following this general

132 rule, the temporal and spatial niche breadth of the invasive *D. suzukii* have been shown to be

133 relatively large compared with other *Drosophila* species in Japan (Yamamoto 1984). Besides

134 using fruits as its preferred substrate for oviposition, it has also been found to develop on

135 fungi (Kimura 1976) and can even complete development on chicken manure (Stockton et al.

136 2019). Within its invasive range, *D. suzukii* can use the fleshy fruits of many crops and wild

137 plants (e.g. Poyet et al. 2015, Arnó et al. 2016, Kenis et al. 2016). In the year 2020, 198 plant

138 species representing 40 families were already confirmed as host plants (Little et al. 2020), so

139 the fly can be considered extremely polyphagous (sensu Normark and Johnson 2011).

140 Polyphagous herbivores (or generalists) are more impacted by plant toxicity than specialists

141 (Ali and Agrawal 2012), as specialisation in phytophagous insects is thought to assist in the

142 evolution of adaptations to overcome plant defences (Ehrlich and Raven 1964). However, *D.*

143 *suzukii* hardly needs to specialise to overcome plant defences. On the one hand, because

144 fleshy fruits are generally intended to be eaten by vertebrates (Lei et al. 2021), the pulp of

145 such fruits is often of low toxicity when ripe (Cipollini 2000). On the other hand, the

146 association with microbes may help with detoxification and digestion (Douglas 2009, 2015).

147 Fruits share particular volatiles across plant species (Prasanna et al. 2007). As a resource

3

148   specialist utilising particular plant structures, i.e. fruits, with predictable odour cues, it may

149   not be crucial for *D. suzukii* to specialise on particular plant species in order to increase host

150   location, because olfactory responses to substrate-relevant volatiles of a resource instead of a

151   plant species enables coping with a much narrower range of odours (e.g. Becher et al. 2012,

152   Cunningham and Zalucki 2014, Cunningham et al. 2016).

153   *Drosophila suzukii* attacks on the fruits of agricultural crops cause considerable economic

154   damage to fruit growers through yield losses and the need to take measures to prevent attacks

155   and minimise damage (Bolda et al. 2010, Knapp et al. 2020). Research on *D. suzukii* as a fruit

156   crop pest is therefore ongoing and diverse. In recent studies, the occurrence of *D. suzukii*

157   outside agricultural crops has been investigated to assess pest pressure from adjacent habitats.

158   Woodlands have been shown to be suitable refugia and overwintering habitats (Briem et al.

159   2016, Pelton et al. 2016, Thistlewood et al. 2018, Wallingford et al. 2018) and can provide a

160   large reservoir of hosts that produce fruits, ensuring continuity of resource availability over

161   time (Poyet et al. 2015, Arnó et al. 2016, Elsensohn and Loeb 2018, Thistlewood et al. 2019).

162   Therefore, large numbers of *D. suzukii* can be expected in forests, as has also been shown in

163   trapping case studies (e.g. Briem et al. 2018, Haro-Barchin et al. 2018, Santoiemma et al.

164   2018), and population densities are likely to be more constant and higher than in semi-open

165   habitats such as agricultural landscapes. So far, almost no research has been conducted to

166   address the ecological impact of this fly on the ecosystems it has invaded. Roche et al. (2021)

167   highlighted how *D. suzukii* may produce ecological changes to eastern forests in the USA.

168   Invasion by *D. suzukii* may have consequences for food resources and, consequently, on

169   species with which they compete for fruits. Competitive interactions, i.e. competition for

170   shared resources or interference between species, generally increase with increasing

171   phylogenetic relatedness (Li et al. 2015) and functional similarity (Dick et al. 2017) between

172   the invader and the native species. Accordingly, *D. suzukii* could affect native drosophilids

173   due to two main mechanisms. First, *D. suzukii* can use a wide range of substrates for

174   oviposition, which gives it a competitive advantage over native drosophilids (Karageorgi et al.

175   2017, Silva-Soares et al. 2017). Unlike other drosophilids that use damaged and overripe

176   fruits, *D. suzukii* has an enlarged, serrated ovipositor which makes it possible for females to

177   pierce the skin of fruits (Atallah et al. 2014). It thus can use undamaged fruit, i.e. it can

178   occupy fruits earlier than other drosophilids. Second, according to the enemy release

179   hypothesis, a lower parasitisation rate leads to a larger population size (Keane 2002, Shea

180   2002), and parasitisation is an important cause of mortality for drosophilid larvae (Janssen et

181   al. 1988, Fleury et al. 2009).

182   In this study, we assessed the use of potential host plants in forests by examining egg

183   depositions of *D. suzukii*, reflecting its direct effect on the plants. Since there is a diverse

184   abundance and varying availability of host plants within a plant community, which affects the

185   choice of host plants for *D. suzukii*, we selected different forest communities and forest edges

186   as study sites. We addressed the following questions: (1) Are there differences in the potential

187   host plants of *D. suzukii* growing in different forest communities? (2) To what extent are the

188   potential host plants attacked by *D. suzukii*, and what are the factors influencing the attack

189   rates?

190   Due to the large numbers of *D. suzukii* trapped in previous studies, we expected that this

191   species would outnumber and potentially outcompete native controphics, especially

192   drosophilids. To test this hypothesis, we trapped drosophilids during the study period and

193   addressed the following questions: (3) What proportion of drosophilid individuals are *D.*

194   *suzukii*? (4) Does the proportion of *D. suzukii* differ among forest communities? (5) Does the

195   abundance of *D. suzukii* affect the abundance of other drosophilids?

196

Materials and Methods

Study area

199   We conducted our study in the adjacent cantons of Zug (47.092440 – 47.218600 N, 8.407940

200   – 8.680231 E; elevation 400-1200 m a.s.l) and Zurich (47.163290 – 47.365790 N, 8.424865 –

201   8.687711 E; 440-1165 m a.s.l) in Switzerland from June to November in 2020 Figure 1). In

202   both regions, the annual average temperature ranges between 4-6°C at higher elevation sites

203   to 10-12°C at lower elevation sites and the annual precipitation ranges between 1100-1300

204   mm and 1700-2000 mm at sites in the canton Zug and 900-1100 mm and 1100-1300 mm at

205   sites in the canton Zurich (climate norm values 1991-2020; Federal Office of Meteorology

206   and Climatology MeteoSwiss; extracted from https://map.geo.admin.ch/). We selected the

207   forest communities 7a (*GALIO ODORATI-FAGETUM TYPICUM*), 19a (*ABIETI-FAGETUM*

208   *LUZULETOSUM*) and 26f/g (*ACERI-FRAXINETUM MERCURIALIDETOSUM*) (see

209   Ellenberg and Klötzli 1972) for our study, as they include a comparable range of fruiting

210   plants. In addition, we investigated forest edges, as they serve as important habitat for a large

211   range of fruiting plants. We examined the three forest communities at four sites ≥ 1 km apart,

212   from 400 to 1165 m a.s.l. At each site, we selected four 25 m × 25 m plots of the particular

213   forest community from the available grid cells (also 25 m × 25 m) in a stratified random

5

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 × 25 m area. We moved a selected plot 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 × 50 m along the forest edge (instead of 25 m × 25 m). Where possible, the
forest edges were orientated in different cardinal directions. Forest edge sites were ≥ 1 km
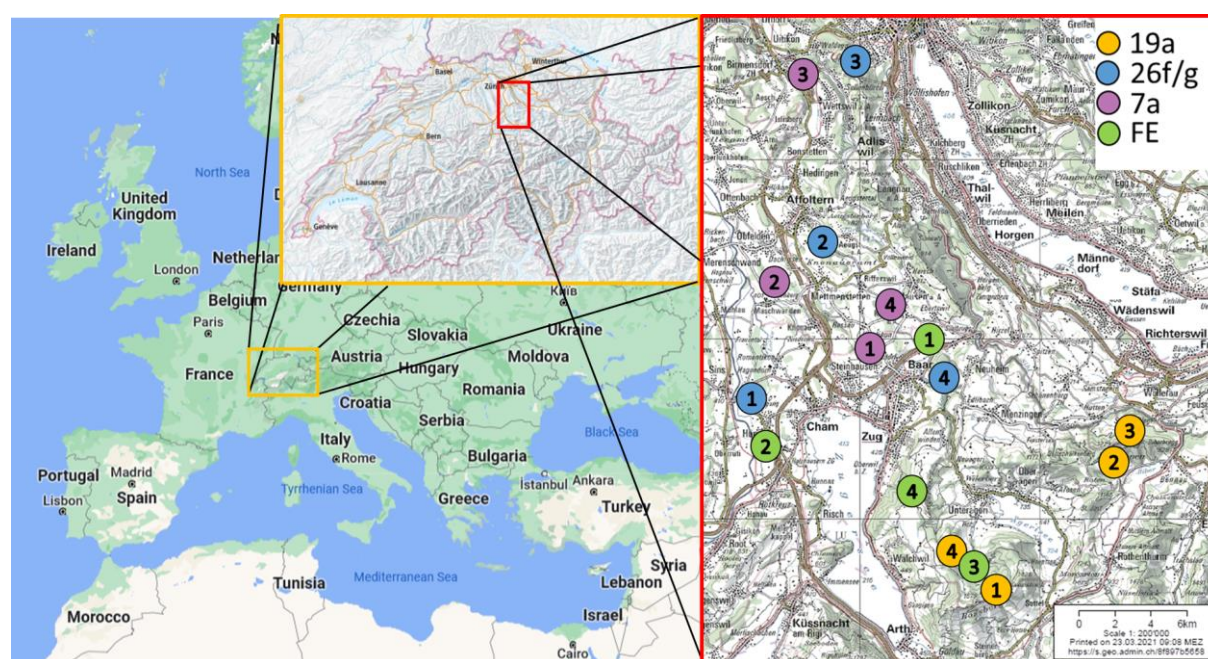apart and plots were separated by ≥ 250 m. All sites were located in managed forests.

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

6

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

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

245   We mapped all potential reproducing host plant species in each plot (25 m × 25 m or 12.5 m ×
246   50 m = 625 m^2) and noted its occurrence. We used an estimated dominance value to
247   determine the area (m^2) covered by a plant species, and used this value and the recorded
248   height to calculate the plant species' volume. For each potential host plant at each field survey
249   per plot, we estimated the seasonal phenology and the number of ripe fruits present, assigning
250   maturation stage between 0 and 2, corresponding to the majority of plant individuals: 0 = no
251   ripe fruits, 0.25–0.75 = before main fruit maturity (some ripe fruits), 1.0–1.25 mainly ripe
252   fruits, 1.5–1.75 = after main fruit maturity (more overripe, fermented fruits than ripe fruits), 2
253   = no more fruits. Since fruit ripening is usually associated with a change in colour, we used
254   colour change as an indicator of the maturity of the examined fruits. In some species, such as
255   European fly honeysuckle (*Lonicera xylosteum*), rowan (*Sorbus aucuparia*) or alder
256   buckthorn (*Frangula alnus*), changes in fruit flesh firmness during ripening were not
257   advanced at the time of colour change. We judged these fruits to be ripe when they also
258   softened. After maturity, fruits enter senescence (period during which chemical synthesis
259   pathways give way to degradation processes). As an indicator of the "overripe" stage, we used
260   loss of moisture, which becomes visible as a loss of turgor. At the end of the field survey, we
261   calculated the maturity period with the unit of half a month and estimated the amount of fruit,
262   both per potential host plant species per plot. The exact method used for these estimates
263   depended on the species and was based on counts (e.g. all observed fruits, fruits per square
264   metre, fruits per individual plant, or infructescence). We then extrapolated counts to the plot
265   level. The number of fruits was likely underestimated by this approach and was thus a rather
266   conservative estimate. Fruits that were removed, destroyed or lost due to drought stress near
267   the end of the ripening process were not subtracted from the estimated numbers.

268   Near the plots and in the same forest communities, we additionally examined native potential

269   host plants that occurred in less than three plots (*Lonicera alpigena*, *Taxus baccata*, *Prunus*

270   *spinosa*, *Crataegus laevigata*, *Lonicera periclymenum*, *Viburnum lantana*). We conducted

271   this additional investigation to estimate the average attack rate of plants with infrequent

272   occurrence on the plots, but we excluded these fruits from the statistical analyses.

273   European brambles (*Rubus* L. subg. *Rubus*) are taxonomically divided into three sections:

274   *Rubus*, *Corylifolii* and *Caesii* (with one species, *Rubus caesius*). The most abundant species in

275   our plots were *R. hirtus* agg. (sect. *Rubus*), occurring in the plots of forest community 19a,

276   and *R. villarsianus* (sect. *Corylifolii*), occurring in the plots of forest communities 7a and

277   26f/g. Especially at the forest edges, but also in the forest communities 26f/g and 7a, more

278   than one species of the sections *Rubus* and/or *Corylifolii* occurred in the plots. We did not

279   identify the described and named species of the sections *Rubus* and *Corylifolii* in the plots and

280   therefore used the term *Rubus fruticosus corylifolius* aggr. as the taxonomic unit.

281   ***Investigation of fruit attacks by* Drosophila suzukii**

282   We examined ripe fruits at an accessible height (up to 2 m) for egg deposition using a hand

283   lens (10× magnification). If we observed at least one *D. suzukii* egg on the fruit, we

284   considered the fruit "attacked", regardless of the number of egg deposits or larvae. We

285   examined at least 10 fruits per population or individual of a potential host plant per plot, and

286   we removed the examined fruits from the plants. If multiple individuals of a plant species

287   occurred in the plot, we examined several individuals. In the case of large populations of

288   brambles (*R. fruticosus corylifolius* agg.) or bilberry (*Vaccinium myrtillus*), i.e. covering >

289   25% of the plot area, we randomly selected ≥ 5 areas of 1 m^2 for investigating egg deposition.

290   Egg deposition by *D. suzukii* is detectable for only a limited time, due to decay of the fruit

291   substance, rotting, development of the larvae, feeding by other animals, or secondary

292   infections such as grey mould. No larvae in a damaged fruit does not allow inference of non-

293   infestation. Further, damaged fruits may in turn be used as egg-laying substrate by other

294   drosophilids. Therefore, we used only ripe, undamaged fruits to study egg deposition on

295   potential host plants.

296   We investigated the fruits of European holly (*Ilex aquifolium*) for egg deposition after the

297   field surveys because they had not yet reached fruit maturity during the study period. To

298   check the oviposition activity of *D. suzukii*, we simultaneously examined fruits of the

299   European dwarf elder (*Sambucus ebulus*) and brambles (*Rubus fruticosus corylifolius* aggr.)

300   occurring near the European hollies under investigation. We did not examine European

301   mistletoe (*Viscum album*) and common ivy (*Hedera helix*), which were also present in the

302   plots, for *D. suzukii* attacks, as their fruit ripening period fell well outside our study period.

303   The ripe fruits of the wild strawberry (*Fragaria vesca*) often showed numerous feeding marks

304   and damage, such that egg deposition by *D. suzukii* could rarely be detected. We therefore

305   decided not to investigate attacks further and excluded wild strawberry from the analyses. We

306   could confirm its use as a host, however, as adults hatched from collected fruits and we found

307   numerous drosophilid larvae in otherwise intact fruits.

308   ***Fruit and decay traits***

309   We compiled fruit traits of the investigated plant species from Herrera (1987), Snow and

310   Snow (1988), Eriksson and Ehrlen (1991), and Stiebel (2003) and from databases (eFloras

311   2021, TRY 2021). When the records of fruit traits were comparable or convertible, we

312   included the data from several literature references and used the average value. We included

313   the fruit traits: type, colour, diameter (mm), mass (g), water content of the pulp (%), sugar

314   content of the pulp (glucose and fructose, % of dry mass), lipid content of the pulp (% of dry

315   mass), protein content of the pulp (% of dry mass), pH, persistence of individual fruits (days)

316   and "attacked by non-dispersal frugivores" (%). In addition, we used the amount of ripe fruit

317   and the maturation start and duration, based on our field assessments (see section "Field

318   surveys of potential host plants"), as fruit traits in the analyses.

319   Fruit decay is a complex natural phenomenon that is co-determined by numerous conditions.

320   It occurs as a result of physical and chemical damage, enzymatic digestion, and especially

321   microbial activity. The fruit skin, which serves as an external barrier, is damaged by the egg

322   deposition of *D. suzukii*. We documented the fruit response to egg deposition, i.e. decay, to

323   determine if attacks trigger fruit decay. We recorded the following symptoms of fruit decay:

324   oviposition scar, denting, oozing of pulp, reduction of fruit substance/loss of shape, and

325   colour change. We categorised the symptoms as mild (1), moderate (2) or severe (3).

326   ***Adult trapping***

327   At each site of the forest communities (including forest edges), we installed two baited (80–

328   100 ml) transparent plastic cup traps covered by a red lid with 3 mm diameter entry holes

329   (Profatec AG, Malans, Switzerland) to trap Drosophilidae including *D. suzukii*. As an

330   attractant, we used a mixture of apple cider vinegar and water (3:1; apple cider vinegar IP-

331   Suisse, Denner AG, 8045 Zurich, Switzerland; acetic acid 50 g/l) with 1–2 drops of liquid

332   soap (Oecoplan Abwaschmittel, Coop, 4002 Basel, Switzerland) per 5 dl. We positioned the

333   traps at a height of 1.2–1.5 m on branches of plants that do not bear fleshy fruits, mostly

334   beech (*Fagus sylvatica*), at a distance of 150–200 m from the field survey plots. We installed

335   the traps from 22/06/2020 to 07/07/2020, during the first session of the egg deposition

336   assessment. At the forest edges, we placed the traps approx. 3 m inside the forest (from the

337   shrub belt). We kept the traps in the same positions throughout the experiment and visited

338   them on the same dates as the egg deposition assessments. Therefore, each sampling period of

339   adult drosophilids also lasted 20 days.

340   During each sampling session, we removed the contents of the traps and preserved them in

341   ethanol, and we renewed the bait. We sorted the trap content into different taxa, which we

342   identified to different taxonomic levels. We identified the non-native *D. suzukii* and other

343   drosophilids to the species level using the identification key of Bächli et al. (2004). "Domestic

344   species", in particular *Drosophila simulans* and *Drosophila immigrans*, and other non-native

345   species (e.g. *Drosophila curvispina* and *Chymomyza amoena*) were occasionally trapped.

346   Other non-native drosophilid species accounted for < 1% of all trapped individuals.

347   Therefore, we used the term "native drosophilids" for all drosophilids other than *D. suzukii*.

348   We identified other Diptera to the family level following Oosterbroek (2006). See

349   Supplementary Material Table S1 for a list of the trap catches.

350   ***Statistical analysis***

351   We carried out all statistical analyses using R version 4.0.2 (R Core Team 2020). We tested

352   all models for multicollinearity using the 'check_collinearity' function of the *performance*

353   package (Lüdecke et al. 2021) . We performed a tests for dispersion, zero inflation and

354   residual diagnostics with the *DHARMa* package (Hartig 2022).

355   *Differences in fruiting plant communities*

356   To test whether the composition of the plant communities differed between the forest

357   communities with respect to the plants with fruits relevant for *D. suzukii*, we conducted non-

358   metric multidimensional scaling (NMDS) based on a Bray-Curtis distance matrix (function

359   'metaMDS', package *vegan*; Oksanen et al. 2020). We defined the abundance of plant species

360   as the estimated number of fruits per study plot and season, square-root transformed. We used

361   the 'adonis' function in *vegan* (permutational multivariate analysis of variance,

362   PERMANOVA) to test for statistical differences between the forest communities.

363   *Attack rate and probability of fruits of different plant species*

364   We applied a binomial generalised mixed effects model (package *glmmTMB*; Brooks et al.

365   2017) to test for differences in fruit attacks between forest communities (including forest

366   edges) and plant species. The ratio of attacked to unattacked fruits per study plot and time of

367   recording (cbind(N attacked, N not attacked)) was the response variable, whereas the forest

368   community, the plant species, the elevation (m a.s.l.), the number of ripe fruits, the fruit

369   maturity status, and the canton were the predictor variables. We included study plot as a

370   random term to account for the nested study design. We used an additional observation-level

371   random factor due to dispersion issues.

372   We simplified our model stepwise by excluding the factor with the highest *p*-value and

373   comparing the two models with the *anova* function based on a CHI^2-test. If the more complex

374   model did not differ significantly in model performance from the simpler model, we used the

375   latter. This procedure resulted in the exclusion of canton and elevation (height_NN) from the

376   final model.

377   We calculated the attack probabilities (LS-means ± SE) of the different plant species in the

378   forest communities and plotted them using the *emmeans* package (Lenth 2022) based on the

379   final model.

380   *The role of fruit traits in fruit attack and decay*

381   We explored whether fruit traits could explain observed differences in attack rates. We first

382   used NMDS to illustrate the fruit trait space of the 39 studied plant species. See the section

383   "fruit traits" for a list of the fruit traits considered. We treated each plant species in each forest

384   community separately to relate it to attack rate and phenology, which both differed between

385   forest communities for a given plant species. We used the Gower dissimilarity coefficient

386   (Gower 1971) with Podani's (Podani 1999) extension for ordinal variables to create a distance

387   matrix from our fruit trait data ('gowdis' function in the *FD* package (Laliberté and Legendre

388   2010, Laliberté et al. 2014).

389   We performed NMDS (with two axes) on the Gower distance matrix using the 'metaMDS'

390   function in the *vegan* package (Oksanen et al. 2020). For illustration, we plotted attack rates

391   of the fruits with different circle sizes and the phenology (month of maturation start) in

392   different colours. We plotted traits post-hoc using the 'envfit' function in *vegan*, with 1000

393   permutations.

394   We used a binomial generalised mixed effects model (package *glmmTMB*; Brooks et al. 2017)

395   to test whether fruit attacks were related to fruit traits. The ratio of attacked to unattacked

396   fruits per study plot and time of recording (cbind(N attacked, N not attacked)) was the

397   response variable, whereas fruit availability (amount of fruit per plot), start of ripe fruit

398   availability and duration of ripe fruit availability (both 0.5 month resolution), fruit colour,

399   fruit diameter, sugar content of the pulp, and pulp pH were the predictor variables. We

400   excluded fruit type and mass as well as water content of the pulp because of multicollinearity

401   issues, and lipid and protein content of the pulp, as well as persistence and "attacked by non-

402   dispersal frugivores", because they had too many missing values. We defined study plot and

403   plant species as random terms to respect the nested study design and the repeated measures on

404   plant species. We used an additional observation-level random factor due to dispersion issues.

405   We standardised all quantitative variables to zero mean and unit variance using the

406   'decostand' function in the *vegan* package (Oksanen et al. 2020) to allow comparisons of

407   effect sizes.

408   We used a general linear model ('glm') with a Poisson distribution to test whether fruit traits

409   determined the decay status of the fruits after the attack by *D. suzukii*. We used the sum of

410   decay traits (see section "fruit and decay traits") as the response variable and fruit traits (fruit

411   diameter, pulp pH, pulp water, sugar, lipid and protein content) as predictors. We excluded

412   fruit type and mass because of multicollinearity issues. We standardised all quantitative

413   variables to zero mean and unit variance using the 'decostand' function in the *vegan* package

414   (Oksanen et al. 2020) to allow comparisons of effect sizes.

415

416   *Effects of* D. suzukii *on native Drosophilidae*

417   To test for the effects of forest community and canton on the abundance of *D. suzukii* adults

418   captured in traps, we used a binomial generalised mixed effects model (package *glmmTMB*;

419   Brooks et al. 2017) with the ratio of *D. suzukii* and native Drosophilidae (cbind(N *D. suzukii*,

420   N native Drosophilidae)) as response variable and study plot as random term. We calculated

421   the predicted proportions of *D. suzukii* (LS-means ± 95% CI) of the Drosophilidae species

422   caught in the traps in the forest communities and plotted them using the *emmeans* package

423   (Lenth 2022) based on the above model. To predict the abundance of native Drosophilidae as

424   a function of the abundance of *D. suzukii*, we used a generalised mixed effects model with a

425   Poisson distribution (package *glmmTMB*; Brooks et al. 2017) and defined forest community

426   and canton as additional fixed effect and study plot as random term. We then plotted the

427   predicted effect of N *D. suzukii* on N native Drosophilidae using the *effects* package (Fox and

428   Weisberg 2018).

429   For all GLMs and GLMMS, we performed a type II Wald chi-square test using the R package

430   *car* (Fox and Weisberg 2019). For most analyses we plotted the standardised estimates (effect

431   sizes) using the 'plot_model' function in the sjPlot package (Lüdecke et al. 2021).

Results

432

Attacks on potential host plants

433

434   The composition of the potential host plants of *D. suzukii* differed among forest communities

435   (PERMANOVA, F=5.432, R^2=0.22, P=0.001). The effect of forest community in structuring

436   the plant communities is illustrated by the clustering of the forest communities in the

437   ordination plot, except for the plant community of the study site of a former alluvial forest

438   (site 26_1), which was more similar to forest community 7a than to 26f/g (Figure 2). The

439   greatest differences in the potential host plant composition were evident between forest

440   communities 19a and 26f/g (pairwise adonis, R^2=0.21, P=0.001). Forest community 26f/g and

441   the forest edge community were most similar (R^2=0.07, P=0.08).
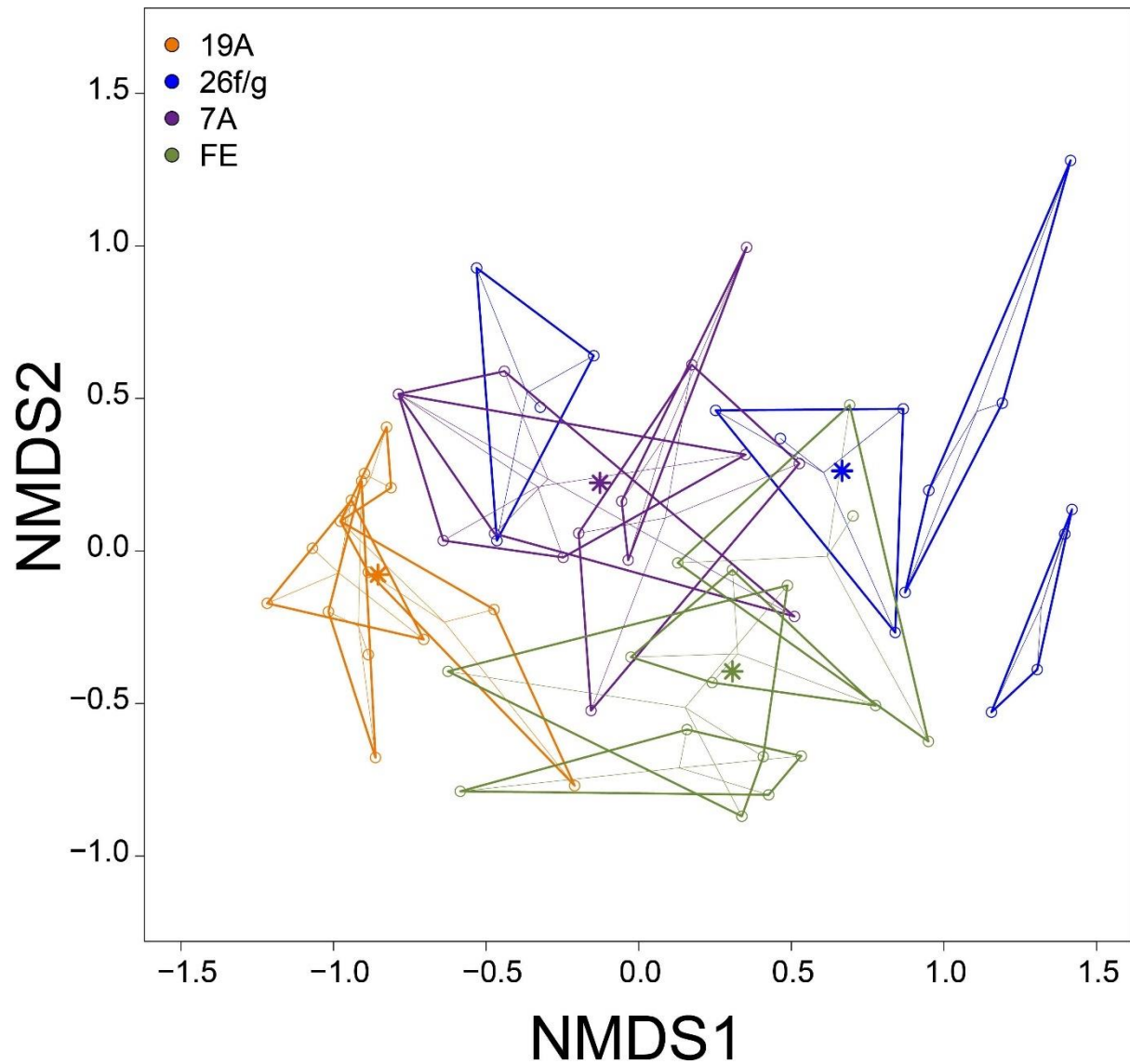
442

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.

452

453   At the study sites of forest community 19a, 7 potential host plant species with an estimated

454   34,000 fruits were recorded. At the study sites of the forest community 26f/g, there were 30

455   potential host plant species and an estimated 60,200 fruits; in forest community 7a there were

456   21 potential host plant species and 140,500 fruits, and at the forest edge study sites 32

457   potential host plant species and 161,000 fruits were observed (Supplementary Material Table

458   S1).

459   Of the 39 potential host plants investigated, attacks were observed on 31 species. Overall,

460   fruits of *Cotoneaster divaricatus* (96%), *Atropa bella-donna* (91%), *Rubus fruticosus*

461   *corylifolius* aggr. (91%), *Frangula alnus* (85%) and *Sambucus nigra* (83%) were attacked

462   particularly frequently (Supplementary Material Figure S1, proportions of fruits attacked by

463   *Drosophila suzukii* per plant species, separated by forest community). Based on the

464   standardised assessments within the plots, the attack rates differed significantly between plant

465   species and forest communities (**Table 1**), with forest edges exhibiting particularly high rates,

466   followed by 7a. *Lonicera alpigena*, *Taxus baccata* and *Atropa bella-donna* had the highest

467   probability of being attacked (Figure 3). Larger numbers of ripe fruits and fruits in a later

468   maturation stage corresponded to higher attack rates (**Table 1**). Canton and elevation did not

469   have a significant effect on the attack rate and were dropped during model simplification.

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

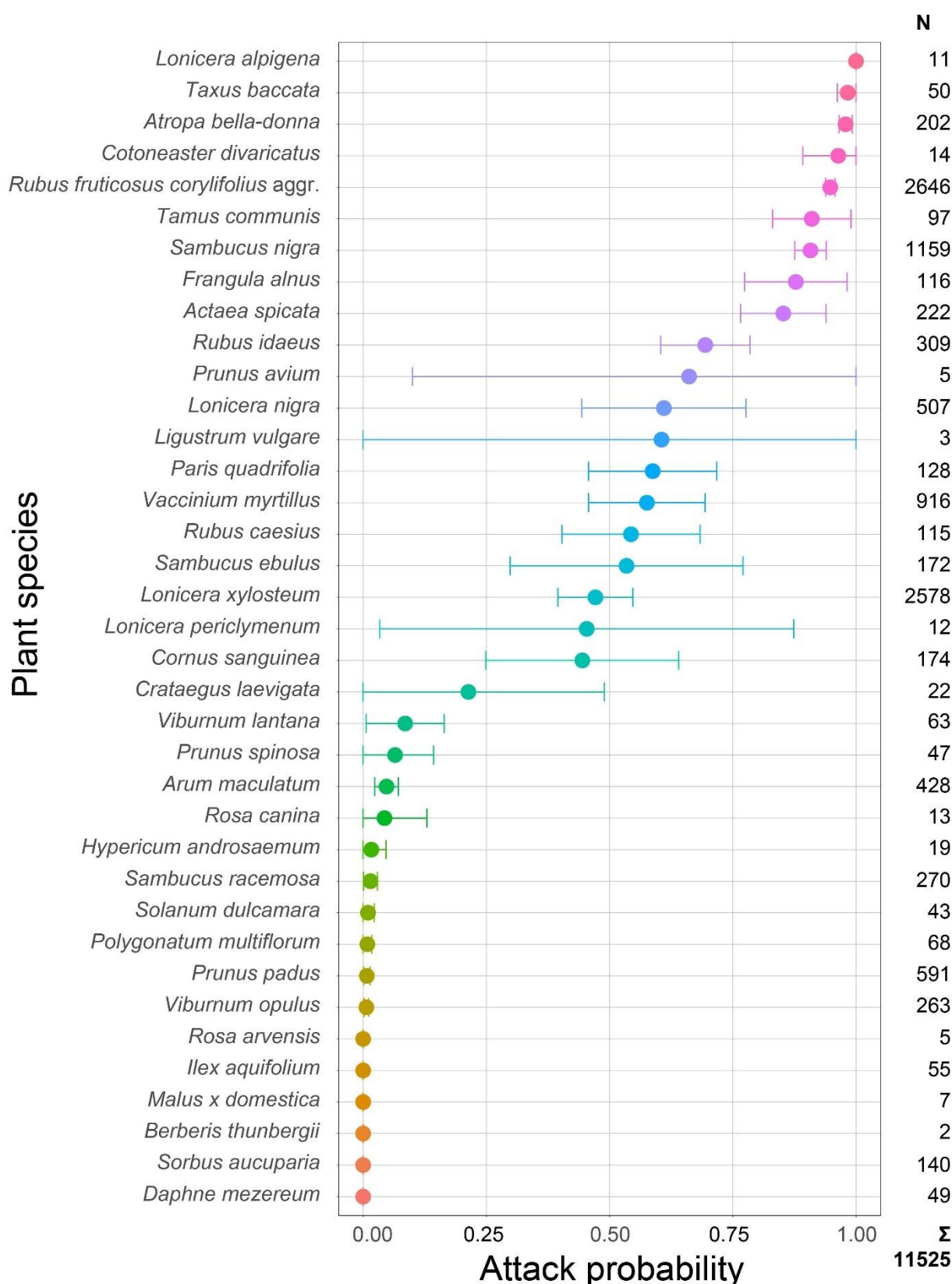|	Chi^2	Degrees of freedom	P
Forest community	34.385	3	<0.001
Plant species	396.861	36	<0.001
Number of ripe fruits	7.513	1	<0.01 (+)
Status of maturation	69.353	1	<0.001 (+)
R^2 conditional	0.840		
R^2 marginal	0.826		

474

15

475

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. For average attack rates per species, including
fruits outside the plots, see Supplementary Material Figure S1.

481

482   The fruit trait space covered by the studied fruits was quite large (Figure 4, left). The

483   ordination plot illustrates that the attack rate differed greatly among plant species and was

484   determined by the maturation start. Later maturation and longer availability of ripe fruits had

485   a positive effect on attack rate (Table 2, Figure 4 right). In addition, fruit colour affected

486   attack rate, with orange fruits having a lower attack rate than black fruits, and blue and red

487   ones tending to be attacked less than black fruits. In addition, larger fruits and fruits with a

488   higher pulp pH had higher attack rates.

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

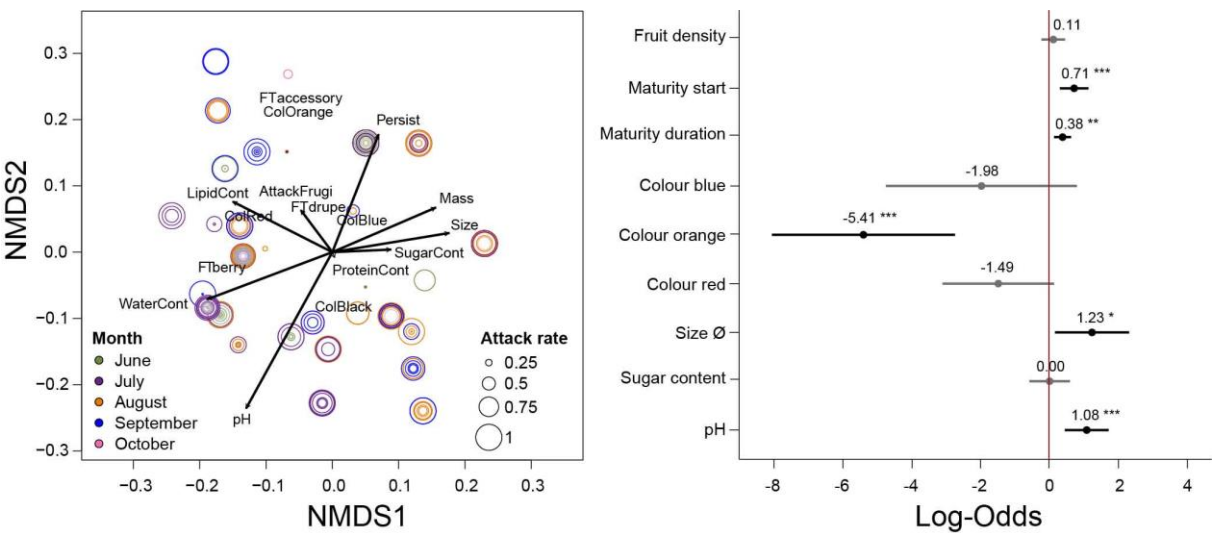|	Chi^2	Degrees of freedom	P
Amount of ripe fruit	0.375	1	0.540
Maturation start	11.334	1	<0.001 (+)
Maturation duration	8.967	1	<0.01 (+)
Fruit colour	16.944	3	<0.001
Fruit size Ø	5.024	1	<0.05 (+)
Pulp sugar content	<0.001	1	0.996
Pulp pH	11.090	1	<0.001 (+)
R^2 conditional	0.678		
R^2 marginal	0.461		

494

495

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.

508

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, Figure 5).

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.

	Chi²	Degrees of freedom	*P*
Fruit size Ø	0.108	1	0.743
Pulp water content	1.0408	1	0.308
Pulp sugar content	7.967	1	<0.01 (+)
Pulp lipid content	1.004	1	0.316

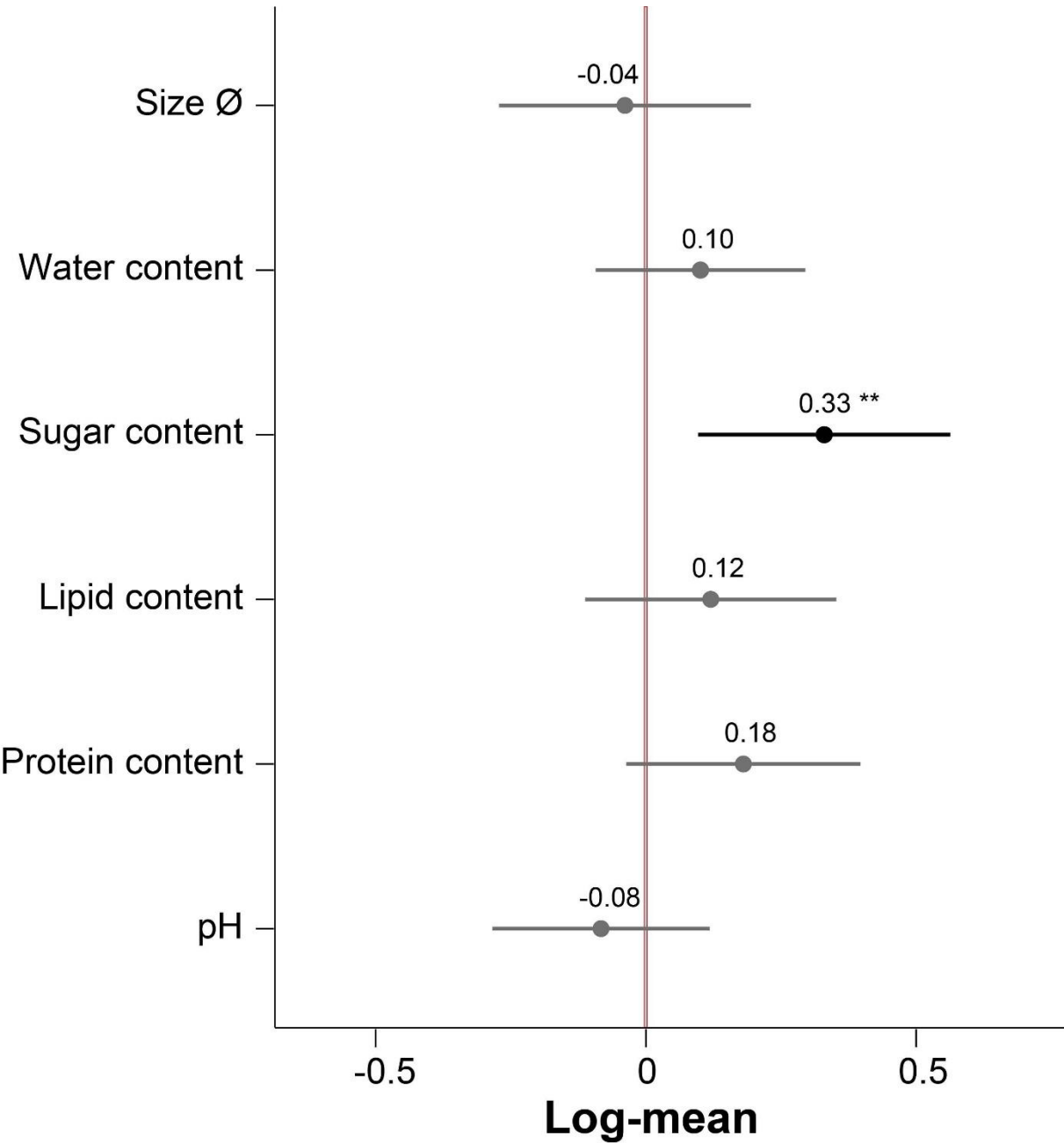|			
Pulp protein content	2.591	1	0.107
Pulp pH	0.655	1	0.418
R^2 Nagelkerke	0.547		

515

516

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

520

521 *Adult trapping*

522   During the investigation period, the traps captured 99,366 insects from four orders, each with

523   at least 75 individuals (97,965 Diptera, 751 Hymenoptera, 552 Coleoptera, 75 Dermaptera)

524   (160 traps). Hemiptera, Lepidoptera, Blattodea and Thysanoptera occurred less frequently.

525   Within the Diptera, species from 27 families were found, with Drosophilidae accounting for

526   almost all observed individuals (97%; 94,624 individuals), followed by Anisopodidae (1%;

527   1399), Heleomyzidae (<1%; 486), Mycetophilidae (<1%; 310), Phoridae (<1%; 278),

528   Scatopsidae (<1%; 247), Sciaridae (<1%; 127), Chloropidae (<1%; 118), and Dryomyzidae

529   (<1%; 103) etc. *Drosophila suzukii* was by far the most abundant species (82% of all trapped

530   insects, 81,395 individuals) and accounted for 86% of all drosophilids (Supplementary

531   Material Table S2).

532   The species composition of drosophilids in the different forest communities differed, e.g. *D.*

533   *alpina* was only found in forest community 19a and species of the genus *Amiota* were mainly

534   caught in forest community 26f/g. However, the drosophilid assemblages were dominated by

535   *D. suzukii,* independent of forest community (Figure 6). We trapped 21,758 (84%) *D. suzukii*

536   and 4,117 (16%) native drosophilids in the forest community 19a, 17,031 (81%) and 4,054

537   (19%) in 26f/g, 15,708 (86%) and 2,528 (14%) in 7a, and 26,871 (91%) and 2,530 (9%) at the

538   forest edge. The ratio of *D. suzukii* to native drosophilids did not differ significantly between

539   forest communities (Wald Chi-squared test, Chi^2=3.053, DF=1, *P*=0.384) and cantons

540   (Chi^2=0.036, DF=1, *P*=0.849). The proportion of *D. suzukii* predicted by the models (purple

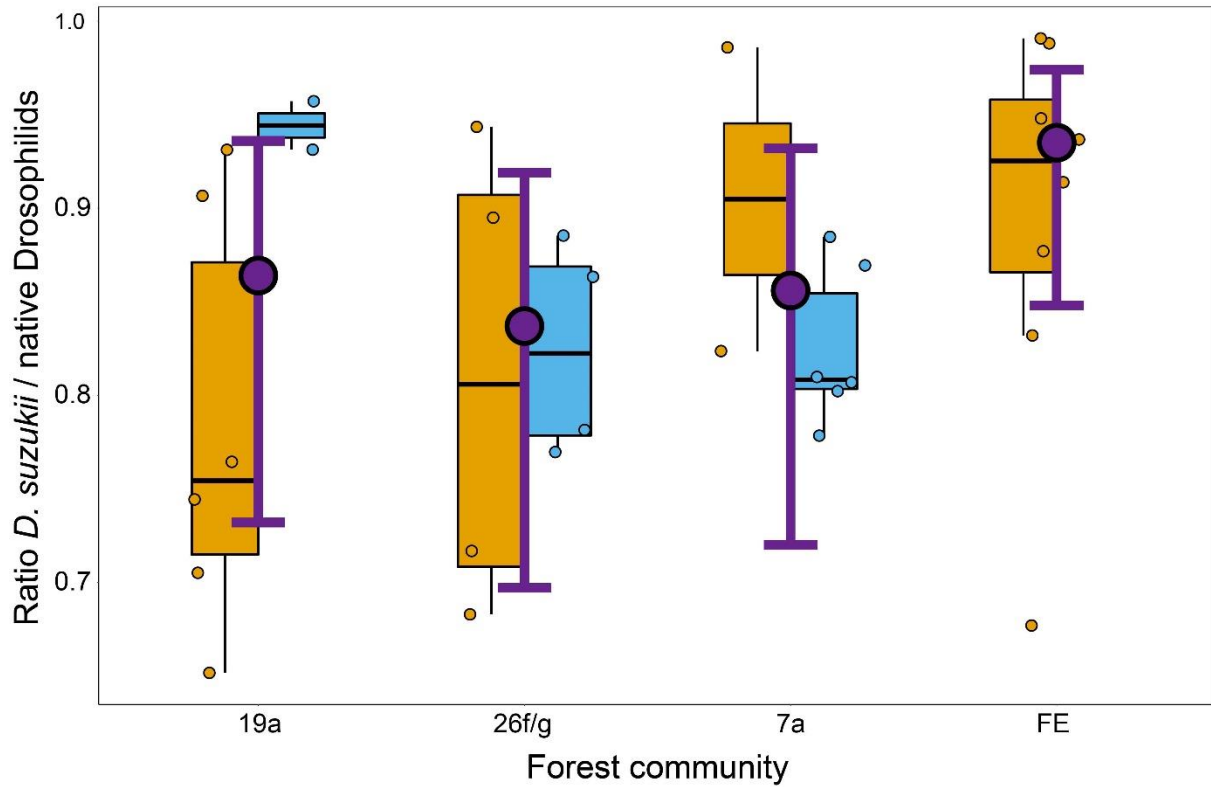541   symbols) was between 0.81 and 0.95 (Figure 6).

542

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 ± 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.

551

552

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

The abundance of *D. suzukii* 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. suzukii*, the smaller the abundance of native drosophilids predicted (Figure 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.

561

Discussion

Drosophila suzukii, 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. suzukii* is specialised on fruits and not on plant species per se. Furthermore, *D.*

568   *suzukii* has been shown to have high plasticity in its host choice (Kienzle et al. 2020, Little et

569   al. 2020). Our results suggest that a large number of fruiting plant species in forests are

570   affected by *D. suzukii*, with likely far-reaching consequences for ecosystem processes (e.g.

571   plant recruitment, resource availability for frugivores) and services (e.g. berry picking).

572

What influences attacks on the forest plants studied?

574   The observed broad host plant spectrum raises the question of what limits the host spectrum.

575   Species of *Rosa* or *Sorbus,* which bear rather hard fruits, were hardly infested. We assume

576   that the pulp and skin firmness act as a barrier to egg deposition, as insects have a limited

577   ability to penetrate the skin of the fruit and to lay an egg in hard fruit flesh. It has been

578   reported that the probability of oviposition increases as the force required to penetrate fruit

579   skin decreases (Burrack et al. 2013, Lee et al. 2016). Further, within grape cultivars and single

580   berries, berry skin resistance was found to explain the oviposition preferences of *D. suzukii*

581   (Entling et al. 2019; Tonina et al. 2020). The fact that *Ilex aquifolium* was not infested was

582   probably because its maturity coincides with the reproductive diapause of the fly (Grassi et al.

583   2018). We found that the red or blue, soft-skinned fruits of *Polygonatum* (Asparagaceae) were

584   hardly used as a host, although this genus is widespread in the fly's area of origin (eFloras

585   2021). *Drosophila suzukii* may not detect all of the numerous potential host plants because its

586   ability to process multiple sensory inputs is limited (Bernays 2001). Polyphagous herbivores

587   have been shown to be attentive to the volatiles that are shared across host species (Silva and

588   Clarke 2020). As the Asparagaceae are relatively distantly related to other host plants, the

589   fruits and their microbial association with Asparagaceae species might not share certain

590   volatiles with other host plants, making them undetectable to the fly.

591   The fruits of our 39 potential forest host plants differed in several characteristics that affect

592   host location and oviposition site selection (Markow 2019), reflected by differences in

593   observed attack rates in our study. Within the host plant range of *D suzukii*, preferences

594   (disproportionate use of potential host plants, i.e. egg deposits) have also been shown for

595   crops in agricultural systems (Lee et al. 2011, Burrack et al. 2013, Olazcuaga et al. 2019) and

596   for wild and ornamental non-crop hosts (Poyet et al. 2015) when fruits were exposed to flies

597   in laboratory assays. These preferences may be due to numerous characteristics of the fruit,

598   such as colour, diameter, shape, volatile compound content, firmness, skin texture, or

599   chemical composition, such as sugar content. In the field, several plant characteristics and the

600   diverse abundance and fluctuating availability of host plants, as well as other biotic and

601   abiotic factors of the host site, may also affect the choice of hosts, which makes comparisons

602   of our findings with laboratory assays difficult.

603   Our non-metric multidimensional scaling (NMDS) indicated high variability in fruit traits and

604   phenology in relation to attack rate. The attack rate varied among fruit colours, with black

605   fruits being most frequently attacked. *Drosophila suzukii* has previously been shown to use

606   colour as visual cue, but that colour contrast rather than colour appearance may be of greater

607   importance.(Little et al. 2019). While visual cues are of some importance, especially in

608   behaviours such as courtship (Anholt et al. 2020), the olfactory and gustatory systems of

609   *Drosophila* are crucial for host localisation and selection (Anholt 2020). We therefore expect

610   that other factors correlated with colour might be decisive. For example, the fruit type "pome"

611   or "hips, which usually has high pulp firmness, mostly had a low attack rate and was often

612   orange or red in colour. Larger fruit size also had a positive effect on attack rate. This could

613   be because a larger surface area, especially with aggregated fruits such as brambles, makes it

614   is easier for *D. suzukii* to find a preferred substrate, e.g. one without damage (mechanical or

615   due to infection) or in an earlier maturation state. We also found that the attack rate increased

616   with higher pulp pH (from pH 2.89 to 6.48). During host location and selection, the fly can

617   hardly detect a pH value, and thus this effect might be indirect. Microbes can act as the

618   interface between insect herbivores and their hosts (Janson et al. 2008, Hansen and Moran

619   2014, Ljunggren et al. 2019). *Drosophila suzukii*, like other *Drosophila*, is strongly attracted

620   to volatiles produced by microorganisms in particular yeasts associated with fruits (Wright

621   2015, Hamby and Becher 2016, Bueno et al. 2020). It has also been shown that yeast

622   volatiles, not fruit volatiles, mediate attraction and oviposition in *D. melanogaster* (Becher et

623   al. 2012). In general, within the range of the fruit pulp pH, yeast and bacteria thrive better at

624   higher pH values (Barth et al. 2009, Howell 2016). Fruits with a higher pH may host more

625   microbes and could therefore be more attractive and easier to locate. In addition, moulds

626   (filamentous fungi), an important competitor of *Drosophila* larvae (Wertheim et al. 2002,

627   Rohlfs et al. 2005, Trienens et al. 2010), generally exhibit better growth in a lower pH

628   environment (Zhao et al. 2020). This could have led to a lower attractiveness for *D. suzukii* in

629   our study, as decreased egg deposition in response to grey mould (*Botrytis cinerea*) was

630   observed in a recent study (Chakraborty et al. 2022).

631   Host preferences are considered evidence of specialisation (Loxdale and Harvey 2016). In this

632   case, however, we would expect phylogenetic relatedness in the preferred hosts, which we did

633 not find, as the plant species with the highest observed attack rate belong to very distinct plant

634 clades. Since the larvae feed in particular on microbes, host preferences, unlike those of

635 folivorous insects, are determined more by the quality of the substrate in promoting the yeasts

636 and bacteria associated with *D. suzukii* than by the phylogeny of the host plants. Our results

637 suggest that *D. suzukii* responds to common cues from multiple host species, as well as

638 specific cues from individual host species, as has been shown for other polyphagous

639 herbivores (Silva and Clarke 2020). Other polyphagous herbivores also exhibit preference

640 hierarchies for their hosts (e.g. Clarke et al. 2011, Wang et al. 2017), which may change

641 through learning (West and Paul Cunningham 2002). Preferences should evolve toward

642 maximising offspring fitness (Jaenike, John 1978), although preferences do not always

643 correlate positively with offspring performance (e.g. Valladares and Lawton 1991, Clark et al.

644 2011), because other ecological, behavioural and physiological factors additionally influence

645 host choice and host use (Jaenike 1990). While *D. suzukii* deposited its eggs on fruits from 16

646 different plant families in our study, we do not expect its offspring to perform equally well

647 across the host spectrum, because preferences of insects with a broader host plant spectrum

648 are less strongly associated with better offspring performance than insects specialised on

649 plants within a certain family (Gripenberg et al. 2010). However, invasions are biologically

650 unusual situations, and *D. suzukii* cannot be expected to show strong adaptive patterns of host

651 use yet, as it was only recently introduced. Thus, some differences in larval performance

652 might be expected and have also been shown between many non-crop hosts of *D. suzukii* (e.g.

653 Poyet et al. 2015, Kenis et al. 2016, Olazcuaga et al. 2019)

654 Plant communities differ floristically and phytophysiognomically (Braun-Blanquet 1932)

655 because species traits and an interacting milieu affect performance across environmental

656 gradients such as temperature, moisture and soil chemistry (Mcgill et al. 2006). Therefore, the

657 abundance and availability of host plants among forest communities must also differ. In our

658 NMDS of available fruits of potential host plants in the plots, the forest communities were

659 clustered. This finding and our model results indicated that the availability of different plant

660 species determines the use of the host plants, as the forest community affected the attack rate.

661 In addition to the diversity of host plants in an area, other associational effects, such as the

662 density and frequency of neighbouring host plants, can influence the likelihood of a particular

663 plant being used as a host, as can the density of the particular host plant (Underwood et al.

664 2014). As stated by the resource concentration hypothesis (Root 1973), a high density of host

665 plants may increase the likelihood that the fly will find the fruits and remain on the host plant.

666 This was supported by our results, as the number of ripe fruits present in our plots strongly

667   affected the attack rate. Furthermore, since optimal oviposition behaviour depends not only on

668   the suitability of the substrate, but also on the probability of finding a more suitable host in

669   the time available (Jaenike, John 1978), adherence to a particular host plant species might be

670   advantageous. A large amount of fruit may be more obvious to *D. suzukii* and thus increase

671   the attack rate. A strong preference for more apparent resources in complex environments has

672   also been shown for *D. melanogaster* (Verschut et al. 2016).

673   Our results further show that a longer fruit duration of fruits present increased the attack rate.

674   Plants with more fruits, and especially plants such as brambles that produce ripe fruits over a

675   long period, ensure continuous availability of resources without the need to search for new

676   hosts, thus promoting the presence of overlapping generations of *D. suzukii* on the same host,

677   further increasing attack rate. In Switzerland, between four and eight generations of *D. suzukii*

678   per year are expected (Wiman et al. 2014). In addition, prior experience with olfactory and

679   visual cues can enhance host location (Silva and Clarke 2020). Furthermore, a later ripening

680   date was related to a higher attack rate, which may occur when the peak of abundance of *D.*

681   *suzukii* and the period of fruit maturity coincide. The predominant maturity status of the plants

682   in the plots also affected the attack rate. The more advanced the maturity, the greater the

683   attack rate of the ripe fruits investigated. An advanced maturity status attracts more flies

684   (Keesey et al. 2015), but also indicates overlapping generations on the same plant.

685   ***Adult trapping revealed* Drosophila suzukii *as a dominant species***

686   The high fruit attack rate observed in our study was also reflected in a high abundance and

687   dominance of *D. suzukii* in trap catches, independent of forest community and elevation. This

688   indicates the broad environmental tolerance of the fly. However, the frequent occurrence in

689   mountainous regions does not necessarily mean that *D. suzukii* inhabits these regions all year

690   round, as the fly has been demonstrated to show extensive movement between low and high

691   elevations in Japan (Mitsui H. et al. 2010) and is able to cover distances of up to 9 km (Tait et

692   al. 2018). However, it can be assumed that the fly can survive the winter at these sites, as *D.*

693   *suzukii* is firmly established on the island of Hokkaido in Japan, where winters average -4 to -

694   12°C (Kimura 2004).

695   Although our forest communities differed significantly in host composition, there were no

696   differences in the proportion of *D. suzukii* between the forest communities. *Drosophila*

697   *suzukii* accounted for 86% of the drosophilids caught during our study period. Recent

698   snapshot studies of trap catches in forests also showed a high proportion of *D. suzukii*. In a

699   survey in native riparian and non-riparian chestnut forest patches in northwestern Spain in

700   August, *D. suzukii* accounted for 30% and 27% of the drosophilids caught in beer traps

701   (Maceda-Veiga et al. 2021). Kremmer et al. (2017) reported 56% *D. suzukii* of the summed

702   trap catches across natural habitat and crops in February (baited with apple cider vinegar).

703   Studies in agricultural areas similar to our sites in terms of trapping period, climate and

704   sampling method do not confirm *D. suzukii* as the most abundant taxon: *D. suzukii* accounted

705   for 7% in Apulia, Italy (Antonacci et al. 2017), 11% in Kansas, USA (but baited with mashed

706   banana; Gleason et al. 2019), and 18% in Washington, USA) (but some unmanaged habitats

707   included; Bahder et al. 2016). Several factors could have caused these differences. First,

708   agricultural and forested areas differ in biotic and abiotic factors, and species composition

709   thus also differs (Burla and Bächli 1991). The assemblages of drosophilids, excluding *D.*

710   *suzukii*, trapped in these agricultural areas were dominated by domestic species (distributed

711   worldwide), while native species dominated in our area. Similarly, the occurrence of

712   controphics, such as other insects, vertebrates or mould, and the occurrence of predators

713   differ. Second, competition between *D. suzukii* and native species might be different in the

714   two habitat types, due to differences in the occurrence of ecologically related species and

715   available resources. Third, different measures taken to control the fly in agricultural fields

716   might have reduced the populations of *D. suzukii*. However, these measures usually also

717   affect other drosophilids. Fourth, forests can be expected to be the preferred habitat of *D.*

718   *suzukii*, resulting in high overall proportions. Numerous forest fruits are suitable for the

719   development of *D. suzukii*, due to its wide host niche (Little et al. 2020), and forests may offer

720   preferred climatic conditions for *D. suzukii*, especially higher humidity (Hamby et al. 2016,

721   Tochen et al. 2016, Eben et al. 2018).

722   Unlike in our study, surveys of drosophilid assemblages from trapping studies in various

723   habitats in Asia, where *D. suzukii* is native or has been established for many years, do not

724   show *D. suzukii* to be a dominant species: its proportion in relation to other drosophilids is

725   reported to be up to 0.02 (e.g. Kaneko and Tokumitsu 1969, Toda 1992, Hirai et al. 2000,

726   Guruprasad et al. 2010) and reached a value of 0.05 in a study in Korea (Lee 1964).

727   Parasitisation is, however, an important mortality factor for drosophilid larvae (Janssen et al.

728   1988, Fleury et al. 2009), and the abundance of potential hosts is one factor determining the

729   evolution of parasitoid host use (Novković et al. 2012). The degree of parasitisation is much

730   higher in native populations (Torchin et al. 2003). The expected lower parasitisation of *D.*

731   *suzukii* could be one of the main factors contributing to its frequent occurrence outside its

732   native range, as escape from natural enemies can explain the success of introduced species

733   (Keane 2002, Shea 2002).

734   ***Impact on native drosophilids***

735   Our trap catches revealed that the abundance of *D. suzukii* was significantly negatively

736   associated with the abundance of other drosophilids. Its dominance indicates a superiority

737   over the native species. The heavily sclerotised, serrated ovipositor serves as a competitively

738   unique trait (Karageorgi et al. 2017, Silva-Soares et al. 2017). Besides the capability of using

739   a wider range of substrates for oviposition, we propose that the broader temporal niche of

740   resource use is a competitive advantage. *Drosophila suzukii* can use substrates for oviposition

741   earlier than other drosophilid species. Consequently, oviposition by *D. suzukii* induces

742   substrate decay, rendering the substrate time-limited for the larval development of other fruit

743   pulp consumers. While ripe fruits are inherently a temporally limited resource, this limitation

744   is probably enhanced in forests compared with agricultural areas, because the fleshy fruits of

745   wild plants are usually much smaller, than those of cultivated plants. Furthermore, *D. suzukii*

746   may outcompete native drosophilids, due to different development times. This might lead to

747   different competitiveness in forests and agriculture. Cold adaptation in *Drosophila* to colonise

748   temperate climates seems to be linked to longer development times (Santos et al. 2006,

749   Kinzner et al. 2018), and domestic species such as *D. melanogaster*, which originate in

750   warmer regions, have comparatively short development times (Markow and O'Grady 2005).

751   In laboratory experiments, it has been found that the presence of *D. melanogaster* on the

752   substrate significantly reduced adult *D. suzukii* emergence, reflecting a difference in minimum

753   development time (7 days for *D. melanogaster* and 11 days for *D. suzukii* at 25°C; (Dancau et

754   al. 2017, Shaw et al. 2018). Presumably, the presence of *D. suzukii* reduces native drosophilid

755   emergence as well. Coexistence of drosophilids across food-limited resource patches is

756   facilitated by aggregation over patches (eggs in clutches of more than one egg, as well as non-

757   random distributions of ovipositing females), which creates partial refuges and allows inferior

758   species to exist (Rosewell et al. 1990, Jaenike and James 1991, Sevenster and Alphen 1996,

759   Rohlfs and Hoffmeister 2003). In addition, parasitism facilitates the coexistence of

760   drosophilid species (Mitsui and Kimura 2000). However, as an invasive species, *D. suzukii* is

761   expected to be exposed to lower pressure from parasitoids (Torchin et al. 2003), resulting in

762   larger populations. Unlike other drosophilids, *D. suzukii* has been shown not to aggregate over

763   patches (Mitsui et al. 2006). Therefore, we suggest that it may exclude and outcompete other

764   drosophilids in the exploitation of resource patches, which is supported by our results: higher

765   abundance of *D. suzukii* was associated with lower abundance of other drosophilids.

766   ***Potential impact on host plants***

767   Piercing of the skin of undamaged fruit by *D. suzukii* provides an entry point for infestation

768   by pathogens, and inoculated microbes can act as a jump-start for decay. Microbes that infect

769   fruits have been hypothesised to make fruits unattractive to vertebrate frugivores that

770   potentially compete for fruit pulp (Janzen 1977, Ruxton et al. 2014). Just as humans respond

771   to infested fruit with rejection, birds have been shown to prefer intact fruit to infested fruit

772   (e.g. Manzur and Courtney 1984, Jordano 1987, Borowicz 1988, Buchholz and Levey 1990,

773   Cipollini and Stiles 1993, Traveset et al. 1995, but see Valburg 1992). Attacks by *D. suzukii*

774   alter the attractiveness of the fruit because it changes the chemical composition and visual

775   cues, such as colour, shape and reflective patterns. Since the choice of fruits by birds depends

776   on visual perception (Schaefer and Ruxton 2011), we assume that attacks on fruits by *D.*

777   *suzukii* could reduce the attractiveness for birds, resulting in reduced seed dispersal. This is

778   because many host plants of *D. suzukii* rely especially on frugivorous birds for dispersal

779   (Garcia et al. 2010). Negative effects on seeds are unexpected because attacks occur after seed

780   set.

781   In the field, when we observed symptoms of fruit decay after *D. suzukii* attacks, we noticed

782   that fruit decay progressed at very different rates among plant species, which may be due to

783   their different compounds and compositions. For example, the bright red fruits of *Lonicera*

784   *alpigena* were found to change into dry, brown fruit mummies (rotten fruits) within a short

785   time, while fruits of *Prunus padus* had hardly any symptoms of decay and hung intact on the

786   bushes for more than 40 days without decaying. On *Prunus padus*, a significant reduction in

787   the number of emerged *D. suzukii* adults and a significant delay in the larval-pupal

788   development time was detected compared with on *Prunus avium* (Alhmedi et al. 2019), where

789   oviposition by *D. suzukii* is known to trigger microbial development (Ayyanath et al. 2018).

790   Because larval development depends on the development of microbes (Sang 1956, Schwarz et

791   al. 2014, Hamby and Becher 2016), decay within a short time indicates a strong response of

792   microbial growth and development and better host suitability to *D. suzukii* offspring

793   development. Among the fruit traits we studied, we found that the pulp sugar content

794   determined the severity of the symptoms of decay after an attack by *D. suzukii*. The rapid

795   decomposition of simple carbohydrates leads to rapid microbial growth (Zhao et al. 2020),

796   explaining why more severe symptoms of decay were evident at higher sugar levels. Nutrient

797   levels deplete over time as microbes and larvae consume the resources, so rapid fruit decay

798   after an attack by *D. suzukii* means a loss of resources for other frugivores.

799

800   **Conclusion**

801   Almost half of the 39 studied forest plant species showed attack rates by *D. suzukii* of $> 50\%$,

802   with a high percentage showing severe symptoms of fruit decay after egg deposition. This

803   may lead to reduced fruit consumption by vertebrate seed dispersers. *Drosophila suzukii* is a

804   damaging agent for plants, and if the fly reproduces in large numbers, dispersal agents and

805   host plant may both suffer. Besides the direct effect of parasitism of forest fruits by *D. suzukii*,

806   leading to competition with other frugivorous species, the indirect effect of disrupting seed-

807   dispersal mutualisms can have far-reaching consequences for ecosystems. With ongoing

808   climate change, these potentially severe ecological impacts might be amplified, as higher

809   average and winter temperatures will most likely lead to shorter generation times and lower

810   winter mortality, which will eventually further increase the pressure on forest fruits and the

811   competitiveness of *D. suzukii* over native drosophilids.

812

813   Acknowledgements

References

817 Alhmedi A, Clymans R, Van Kerckvoorde V, Bylemans D, Beliën T (2019) Preference and
818   performance of *Drosophila suzukii* on *Prunus* species: A potential eco-friendly pest
819   management tool. Crop Protection 122: 35–41.
820   https://doi.org/10.1016/j.cropro.2019.04.018

821 Ali JG, Agrawal AA (2012) Specialist versus generalist insect herbivores and plant defense.
822   Trends in Plant Science 17: 293–302. https://doi.org/10.1016/j.tplants.2012.02.006

823 Anholt RRH (2020) Chemosensation and evolution of *Drosophila* host plant selection.
824   iScience 23: 100799. https://doi.org/10.1016/j.isci.2019.100799

825 Anholt RRH, O'Grady P, Wolfner MF, Harbison ST (2020) Evolution of reproductive
826   rehavior. Genetics 214: 49–73. https://doi.org/10.1534/genetics.119.302263

827 Antonacci R, Tritto P, Cappucci U, Fanti L, Piacentini L, Berloco M (2017) Drosophilidae
828   monitoring in Apulia (Italy) reveals *Drosophila suzukii* as one of the four most
829   abundant species. Bulletin of Insectology 70: 139–146.

830 Arnó J, Solà M, Riudavets J, Gabarra R (2016) Population dynamics, non-crop hosts, and
831   fruit susceptibility of *Drosophila suzukii* in Northeast Spain. Journal of Pest Science
832   89: 713–723. https://doi.org/10.1007/s10340-016-0774-3

833 Asplen MK, Anfora G, Biondi A, Choi D-S, Chu D, Daane KM, Gibert P, Gutierrez AP,
834   Hoelmer KA, Hutchison WD, Isaacs R, Jiang Z-L, Kárpáti Z, Kimura MT, Pascual M,
835   Philips CR, Plantamp C, Ponti L, Vétek G, Vogt H, Walton VM, Yu Y, Zappalà L,
836   Desneux N (2015) Invasion biology of spotted wing *Drosophila* (*Drosophila suzukii*):
837   a global perspective and future priorities. Journal of Pest Science 88: 469–494.
838   https://doi.org/10.1007/s10340-015-0681-z

839 Atallah J, Teixeira L, Salazar R, Zaragoza G, Kopp A (2014) The making of a pest: the
840   evolution of a fruit-penetrating ovipositor in *Drosophila suzukii* and related species.
841   Proceedings of the Royal Society B: Biological Sciences 281: 20132840–20132840.
842   https://doi.org/10.1098/rspb.2013.2840

843 Atkinson W, Shorrocks B (1977) Breeding site specificity in the domestic species of
844   *Drosophila*. Oecologia 29: 223–232. https://doi.org/10.1007/BF00345697

845 Ayyanath M-M, Zurowski CL, Scott IM, Lowery DT, Watson MC, O'Gorman DT,
846   MacKenzie KE, Úrbez-Torres JR (2018) Relationship between *Drosophila suzukii* and
847   postharvest disorders of sweet cherry. Phytobiomes Journal 2: 42–50.
848   https://doi.org/10.1094/PBIOMES-02-17-0007-R

849 Bächli G (2021) TaxoDros: The database on taxonomy of Drosophilidae. Available from:
850   https://www.taxodros.uzh.ch/search/class.php (27 March, 2021).

851 Bächli G, Vilela, Carlos R., Andersson Escher, Stefan, Saura, Anssi (2004) The Drosophilidae
852   (Diptera) of Fennoscandia and Denmark. Brill, Leiden ; Boston, 362 pp.

853 Bahder BW, Bahder LD, Hauser M, Beers E, Walsh DB (2016) Relative abundance and
854   phenology of *Drosophila* Fallén, 1815 (Diptera: Drosophilidae) species in south-

855   central Washington State. Pan-Pacific Entomologist 92: 92–99.
856   https://doi.org/10.3956/2016-92.2.92

857   Barth M, Hankinson TR, Zhuang H, Breidt F (2009) Microbiological spoilage of fruits and
858   vegetables. In: Sperber WH, Doyle MP (Eds), Compendium of the Microbiological
859   Spoilage of Foods and Beverages. Springer New York, New York, NY, 135–183.
860   https://doi.org/10.1007/978-1-4419-0826-1_6

861   Becher PG, Flick G, Rozpędowska E, Schmidt A, Hagman A, Lebreton S, Larsson MC,
862   Hansson BS, Piškur J, Witzgall P, Bengtsson M (2012) Yeast, not fruit volatiles
863   mediate *Drosophila melanogaster* attraction, oviposition and development. Thompson
864   K (Ed.). Functional Ecology 26: 822–828. https://doi.org/10.1111/j.1365-
865   2435.2012.02006.x

866   Bernays EA (2001) Neural limitations in phytophagous insects: Implications for diet breadth
867   and evolution of host affiliation. Annual Review of Entomology 46: 703–727.
868   https://doi.org/10.1146/annurev.ento.46.1.703

869   Bolda MP, Goodhue RE, Zalom FG (2010) Spotted wingd: potential economic impact of a
870   newly established pest. Agricultural and Resource Economics 13: 5–8.

871   Borowicz VA (1988) Do vertebrates reject decaying Fruit? An experimental test with *Cornus
872   amomum* fruits. Oikos 53: 74. https://doi.org/10.2307/3565665

873   Braun-Blanquet J (1932) Plant sociology. The study of plant communities. First ed. McGraw-
874   Hill Book Co., Inc., New York and London.

875   Briem F, Eben A, Gross J, Vogt H (2016) An invader supported by a parasite: Mistletoe
876   berries as a host for food and reproduction of spotted wing drosophila in early spring.
877   Journal of Pest Science 89: 749–759. https://doi.org/10.1007/s10340-016-0739-6

878   Briem F, Dominic A, Golla B, Hoffmann C, Englert C, Herz A, Vogt H (2018) Explorative
879   data analysis of *Drosophila suzukii* trap catches from a seven-year monitoring
880   program in southwest Germany. Insects 9: 125.
881   https://doi.org/10.3390/insects9040125

882   Brooks M E, Kristensen K, Benthem K J ,van, Magnusson A, Berg C W, Nielsen A, Skaug H
883   J, Mächler M, Bolker B M (2017) glmmTMB balances speed and flexibility among
884   packages for zero-inflated generalized linear mixed modeling. The R Journal 9: 378.
885   https://doi.org/10.32614/RJ-2017-066

886   Buchholz R, Levey DJ (1990) The evolutionary triad of microbes, fruits, and seed dispersers:
887   An experiment in fruit choice by cedar waxwings, Bombycilla cedrorum. Oikos 59:
888   200. https://doi.org/10.2307/3545535

889   Bueno E, Martin KR, Raguso RA, Mcmullen JG, Hesler SP, Loeb GM, Douglas AE (2020)
890   Response of wild spotted wing drosophila (*Drosophila suzukii*) to microbial volatiles.
891   Journal of Chemical Ecology 46: 688–698. https://doi.org/10.1007/s10886-019-
892   01139-4

893 Burla H, Bächli G (1991) A search for pattern in faunistical records of drosophilid species in
894   Switzerland. Journal of Zoological Systematics and Evolutionary Research 29: 176–
895   200. https://doi.org/10.1111/j.1439-0469.1991.tb01630.x

896 Burrack HJ, Fernandez GE, Spivey T, Kraus DA (2013) Variation in selection and utilization
897   of host crops in the field and laboratory by *Drosophila suzukii* Matsumara (Diptera:
898   Drosophilidae), an invasive frugivore. Pest Management Science 69: 1173–1180.
899   https://doi.org/10.1002/ps.3489

900 Carscadden KA, Emery NC, Arnillas CA, Cadotte MW, Afkhami ME, Gravel D, Livingstone
901   SW, Wiens JJ (2020) Niche breadth: causes and consequences for ecology, evolution,
902   and conservation. The Quarterly Review of Biology 95: 179–214.
903   https://doi.org/10.1086/710388

904 Chakraborty A, Mori B, Rehermann G, Hernández Garcia A, Lemmen-Lechelt J, Hagman A,
905   Khalil S, Håkansson S, Witzgall P, Becher PG (2022) Yeast and fruit fly mutual niche
906   construction and antagonism against mould. Functional Ecology: 1365-2435.14054.
907   https://doi.org/10.1111/1365-2435.14054

908 Cini A, Ioriatti C, Anfora G, others (2012) A review of the invasion of *Drosophila suzukii* in
909   Europe and a draft research agenda for integrated pest management. Bulletin of
910   Insectology 65: 149–160.

911 Cipollini M (2000) Secondary metabolites of vertebrate-dispersed fruits: evidence for
912   adaptive functions. Revista Chilena de Historia Natural 73: 421–440.
913   https://doi.org/10.4067/S0716-078X2000000300006

914 Cipollini ML, Stiles EW (1993) Fruit rot, antifungal defense, and palatability of fleshy fruits
915   for frugivorous birds. Ecology 74: 751–762. https://doi.org/10.2307/1940803

916 Clark KE, Hartley SE, Johnson SN (2011) Does mother know best? The preference-
917   performance hypothesis and parent-offspring conflict in aboveground-belowground
918   herbivore life cycles. Ecological Entomology 36: 117–124.
919   https://doi.org/10.1111/j.1365-2311.2010.01248.x

920 Clarke AR, Powell KS, Weldon CW, Taylor PW (2011) The ecology of *Bactrocera tryoni*
921   (Diptera: Tephritidae): what do we know to assist pest management? Annals of
922   Applied Biology 158: 26–54. https://doi.org/10.1111/j.1744-7348.2010.00448.x

923 Cunningham JP, Zalucki MP (2014) Understanding heliothine (Lepidoptera: Heliothinae)
924   pests: What is a host plant? Journal of Economic Entomology 107: 881–896.
925   https://doi.org/10.1603/EC14036

926 Cunningham JP, Carlsson MA, Villa TF, Dekker T, Clarke AR (2016) Do fruit ripening
927   volatiles enable resource specialism in polyphagous fruit flies? Journal of Chemical
928   Ecology 42: 931–940. https://doi.org/10.1007/s10886-016-0752-5

929 DAISIE (Ed.) (2009) Handbook of alien species in Europe. Springer, Dordrecht, Netherlands,
930   399 pp.

931 Dancau T, Stemberger TLM, Clarke P, Gillespie DR (2017) Can competition be superior to
932   parasitism for biological control? The case of spotted wing drosophila (*Drosophila*

3

933   *suzukii*), *Drosophila melanogaster* and *Pachycrepoideus vindemmiae*. Biocontrol
934   Science and Technology 27: 3–16. https://doi.org/10.1080/09583157.2016.1241982

935   Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles J-M, Bradshaw CJA,
936   Courchamp F (2021) High and rising economic costs of biological invasions
937   worldwide. Nature 592: 571–576. https://doi.org/10.1038/s41586-021-03405-6

938   Dick JTA, Laverty C, Lennon JJ, Barrios-O'Neill D, Mensink PJ, Robert Britton J, Médoc V,
939   Boets P, Alexander ME, Taylor NG, Dunn AM, Hatcher MJ, Rosewarne PJ, Crookes
940   S, MacIsaac HJ, Xu M, Ricciardi A, Wasserman RJ, Ellender BR, Weyl OLF, Lucy
941   FE, Banks PB, Dodd JA, MacNeil C, Penk MR, Aldridge DC, Caffrey JM (2017)
942   Invader relative impact potential: a new metric to understand and predict the
943   ecological impacts of existing, emerging and future invasive alien species. Souza L
944   (Ed.). Journal of Applied Ecology 54: 1259–1267. https://doi.org/10.1111/1365-
945   2664.12849

946   Douglas AE (2009) The microbial dimension in insect nutritional ecology. Functional
947   Ecology 23: 38–47. https://doi.org/10.1111/j.1365-2435.2008.01442.x

948   Douglas AE (2015) Multiorganismal insects: diversity and function of resident
949   microorganisms. Annual Review of Entomology 60: 17–34.
950   https://doi.org/10.1146/annurev-ento-010814-020822

951   Dweck HK, Talross GJ, Wang W, Carlson JR (2021) Evolutionary shifts in taste coding in the
952   fruit pest *Drosophila suzukii*. eLife 10: e64317. https://doi.org/10.7554/eLife.64317

953   Eben A, Reifenrath M, Briem F, Pink S, Vogt H (2018) Response of *Drosophila suzukii*
954   (Diptera: Drosophilidae) to extreme heat and dryness: Heat wave effects on
955   *Drosophila suzukii*. Agricultural and Forest Entomology 20: 113–121.
956   https://doi.org/10.1111/afe.12235

957   eFloras (2021) eFloras. Available from: http://www.efloras.org/ (14 April, 2022).

958   Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. Annual Review of
959   Ecology, Evolution, and Systematics 41: 59–80. https://doi.org/10.1146/annurev-
960   ecolsys-102209-144650

961   Ehrlich PR, Raven PH (1964) Butterflies and plants: A study in coevolution. Evolution 18:
962   586. https://doi.org/10.2307/2406212

963   Ellenberg H, Klötzli F (1972) Waldgesellschaften und Waldstandorte der Schweiz.
964   Mitteilungen der Schweizerischen Anstalt für das forstliche Versuchswesen 48: 589–
965   930.

966   Elsensohn J, Loeb G (2018) Non-crop host sampling yields insights into small-scale
967   population dynamics of *Drosophila suzukii* (Matsumura). Insects 9: 5.
968   https://doi.org/10.3390/insects9010005

969   Entling W, Anslinger S, Jarausch B, Michl G, Hoffmann C (2019) Berry skin resistance
970   explains oviposition preferences of *Drosophila suzukii* at the level of grape cultivars
971   and single berries. Journal of Pest Science 92: 477–484.
972   https://doi.org/10.1007/s10340-018-1040-7

973   Eriksson O, Ehrlen J (1991) Phenological variation in fruit characteristics in vertebrate-
974   dispersed plants. Oecologia 86: 463–470. https://doi.org/10.1007/BF00318311

975   Fleury F, Gibert P, Ris N, Allemand R (2009) Chapter 1 Ecology and life history evolution of
976   frugivorous *Drosophila* parasitoids. In: Advances in Parasitology. Elsevier, 3–44.
977   https://doi.org/10.1016/S0065-308X(09)70001-6

978   Fox J, Weisberg S (2018) Visualizing fit and lack of fit in complex regression models with
979   predictor effect plots and partial residuals. Journal of Statistical Software 87.
980   https://doi.org/10.18637/jss.v087.i09

981   Fox J, Weisberg S (2019) An R companion to applied regression. 3rd ed. Thousand Oaks CA.
982   Available from: https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

983   Garcia D, Zamora R, Amico GC (2010) Birds as suppliers of seed dispersal in temperate
984   ecosystems: Conservation guidelines from real-world landscapes: seed-dispersal by
985   frugivorous birds. Conservation Biology 24: 1070–1079.
986   https://doi.org/10.1111/j.1523-1739.2009.01440.x

987   Gilbert DG (1980) Dispersal of yeasts and bacteria by Drosophila in a temperate forest.
988   Oecologia 46: 135–137. https://doi.org/10.1007/BF00346979

989   Gleason JM, Roy PR, Everman ER, Gleason TC, Morgan TJ (2019) Phenology of *Drosophila*
990   species across a temperate growing season and implications for behavior. Desneux N
991   (Ed.). PLoS ONE 14: e0216601. https://doi.org/10.1371/journal.pone.0216601

992   Gower JC (1971) A general coefficient of similarity and some of its properties. Biometrics 27:
993   857. https://doi.org/10.2307/2528823

994   Grassi A, Gottardello A, Dalton DT, Tait G, Rendon D, Ioriatti C, Gibeaut D, Rossi Stacconi
995   MV, Walton VM (2018) Seasonal reproductive biology of *Drosophila suzukii*
996   (Diptera: Drosophilidae) in temperate climates. Environmental Entomology 47: 166–
997   174. https://doi.org/10.1093/ee/nvx195

998   Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-
999   performance relationships in phytophagous insects. Ecology Letters 13: 383–393.
1000   https://doi.org/10.1111/j.1461-0248.2009.01433.x

1001 Guruprasad BR, Hegde SN, Krishna MS (2010) Seasonal and altitudinal changes in
1002   population density of 20 species of *Drosophila* in Chamundi Hill. Journal of Insect
1003   Science 10: 1–12. https://doi.org/10.1673/031.010.12301

1004 Hamby KA, Becher PG (2016) Current knowledge of interactions between *Drosophila suzukii*
1005   and microbes, and their potential utility for pest management. Journal of Pest Science
1006   89: 621–630. https://doi.org/10.1007/s10340-016-0768-1

1007 Hamby KA, E. Bellamy D, Chiu JC, Lee JC, Walton VM, Wiman NG, York RM, Biondi A
1008   (2016) Biotic and abiotic factors impacting development, behavior, phenology, and
1009   reproductive biology of *Drosophila suzukii*. Journal of Pest Science 89: 605–619.
1010   https://doi.org/10.1007/s10340-016-0756-5

5

1011   Hansen AK, Moran NA (2014) The impact of microbial symbionts on host plant utilization by
1012   herbivorous insects. Molecular Ecology 23: 1473–1496.
1013   https://doi.org/10.1111/mec.12421

1014   Haro-Barchin E, Scheper J, Ganuza C, De Groot GA, Colombari F, van Kats R, Kleijn D
1015   (2018) Landscape-scale forest cover increases the abundance of *Drosophila suzukii*
1016   and parasitoid wasps. Basic and Applied Ecology 31: 33–43.
1017   https://doi.org/10.1016/j.baae.2018.07.003

1018   Hartig F (2022) DHARMa: residual diagnostics for hierarchical (multi-level / mixed)
1019   regression models. R package version 0.4.5. Available from: https://CRAN.R-
1020   project.org/package=DHARMa.

1021   Hauser M (2011) A historic account of the invasion of *Drosophila suzukii* (Matsumura)
1022   (Diptera: Drosophilidae) in the continental United States, with remarks on their
1023   identification. Pest Management Science 67: 1352–1357.
1024   https://doi.org/10.1002/ps.2265

1025   Herrera CM (1987) Vertebrate-dispersed plants of the Iberian Peninsula: A study of fruit
1026   characteristics. Ecological Monographs 57: 305–331. https://doi.org/10.2307/2937089

1027   Hirai Y, Goto SG, Yoshida T, Kimura MT (2000) Faunal and ecological surveys on
1028   drosophilid flies in Iriomotejima, a subtropical island of Japan. Entomological Science
1029   3: 273–284.

1030   Howe HF, Smallwood J (1982) Ecology of seed dispersal. Annual Review of Ecology and
1031   Systematics 1: 201–228.

1032   Howell K (2016) Spoilage: yeast spoilage of food and beverages. In: Encyclopedia of Food
1033   and Health. Elsevier, 113–117. https://doi.org/10.1016/B978-0-12-384947-2.00650-4

1034   Jaenike J (1990) Host specialization in phytophagous insects. Annual Revue of Ecology. and
1035   Systematics 21: 243–273.

1036   Jaenike J, James AC (1991) Aggregation and the coexistence of mycophagous *Drosophila*.
1037   The Journal of Animal Ecology 60: 913. https://doi.org/10.2307/5421

1038   Jaenike, John (1978) On optimal oviposition behavior in phytophagous insects. Theoretical
1039   population biology 14: 350–356. https://doi.org/10.1016/0040-5809(78)90012-6

1040   Janson EM, Stireman JO, Singer MS, Abbot P (2008) Phytophagous insect-microbe
1041   mutualism and adaptive evolutionary diversification. Evolution 62: 997–1012.
1042   https://doi.org/10.1111/j.1558-5646.2008.00348.x

1043   Janssen A, Driessen G, Haan MD, Roodbol N (1988) The impact of parasitoids on natural
1044   populations of temperate woodland *Drosophila*. Netherlands Journal of Zoology 38:
1045   61–73. https://doi.org/10.1163/156854288x00049

1046   Janzen DH (1977) Why fruits rot, seeds mold, and meat Spoils. The American Naturalist 111:
1047   691–713. https://doi.org/10.1086/283200

1048   Jeschke JM, Bacher S, Blackburn TM, Dick JTA, Essl F, Evans T, Gaertner M, Hulme PE,
1049   Kühn I, Mrugała A, Pergl J, Pyšek P, Rabitsch W, Ricciardi A, Richardson DM,

1050   Sendek A, Vilà M, Winter M, Kumschick S (2014) Defining the impact of non-native
1051   species. Conservation Biology 28: 1188–1194. https://doi.org/10.1111/cobi.12299

1052   Jordano P (1987) Avian fruit removal: effects of fruit variation, crop size, and insect damage.
1053   Ecology 68: 1711–1723.

1054   Kambysellis MP, Heed WB (1971) Studies of oogenesis in natural populations of
1055   Drosophilidae. I. Relation of ovarian development and ecological habitats of the
1056   hawaiian species. The American Naturalist 105: 31–49.
1057   https://doi.org/10.1086/282700

1058   Kaneko A, Tokumitsu T (1969) *Drosophila* survey of Hokkaido, XXVII. : On drosophilid
1059   flies from seven localities of the Hidaka district in southern Hokkaido. Journal of the
1060   Faculty of Science, Hokkaido University. 6: 244–256.

1061   Kanton Zürich (2020) Vegetationskundliche Kartierung der Wälder im Kanton Zürich.
1062   Available from:
1063   http://maps.zh.ch/?scale=37682&srid=2056&topic=WaldVKZH&x=2697548.76&y=1
1064   261707.35 (31 March, 2021).

1065   Karageorgi M, Bräcker LB, Lebreton S, Minervino C, Cavey M, Siju KP, Grunwald Kadow
1066   IC, Gompel N, Prud'homme B (2017) Evolution of multiple sensory systems drives
1067   novel egg-laying behavior in the fruit pest *Drosophila suzukii*. Current Biology 27:
1068   847–853. https://doi.org/10.1016/j.cub.2017.01.055

1069   Keane R (2002) Exotic plant invasions and the enemy release hypothesis. Trends in Ecology
1070   & Evolution 17: 164–170. https://doi.org/10.1016/S0169-5347(02)02499-0

1071   Keesey IW, Knaden M, Hansson BS (2015) Olfactory specialization in *Drosophila suzukii*
1072   supports an ecological shift in host preference from rotten to fresh fruit. Journal of
1073   Chemical Ecology 41: 121–128. https://doi.org/10.1007/s10886-015-0544-3

1074   Kenis M, Tonina L, Eschen R, van der Sluis B, Sancassani M, Mori N, Haye T, Helsen H
1075   (2016) Non-crop plants used as hosts by *Drosophila suzukii* in Europe. Journal of Pest
1076   Science 89: 735–748. https://doi.org/10.1007/s10340-016-0755-6

1077   Kenis M, Auger-Rozenberg, Marie-Anne, Roques, Alain, Timms, Laura, Pe´re´, Christelle,
1078   Cock, Matthew J. W., Settele, Josef, Augustin, Sylvie, Lopez-Vaamonde, Carlos
1079   (2009) Ecological effects of invasive alien insects. Biological Invasions 11: 21–45.
1080   https://doi.org/DOI 10.1007/s10530-008-9318-y

1081   Kienzle R, Rohlfs M (2021) Mind the wound!—fruit injury ranks higher than, and interacts
1082   with, heterospecific cues for *Drosophila suzukii* oviposition. Insects 12: 424.
1083   https://doi.org/10.3390/insects12050424

1084   Kienzle R, Groß LB, Caughman S, Rohlfs M (2020) Resource use by individual *Drosophila*
1085   *suzukii* reveals a flexible preference for oviposition into healthy fruits. Scientific
1086   Reports 10: 3132. https://doi.org/10.1038/s41598-020-59595-y

1087   Kimura MT (1976) *Drosophila* Survey of Hokkaido, XXXII. : A Field Survey of Fungus
1088   Preferences of Drosophilid Flies in Sapporo (With 1 Text-figure and 8 Tables).
1089   Journal of the Faculty of Science, Hokkaido University. 20: 288–298.

1090   Kinzner M, Krapf P, Nindl M, Heussler C, Eisenkölbl S, Hoffmann AA, Seeber J, Arthofer
1091   W, Schlick-Steiner BC, Steiner FM (2018) Life-history traits and physiological limits
1092   of the alpine fly *Drosophila nigrosparsa* (Diptera: Drosophilidae): A comparative
1093   study. Ecology and Evolution 8: 2006–2020. https://doi.org/10.1002/ece3.3810

1094   Knapp L, Mazzi D, Finger R (2020) The economic impact of *Drosophila suzukii*: perceived
1095   costs and revenue losses of cherry, plum and grape growers. Pest Management
1096   Science: ps.6110. https://doi.org/10.1002/ps.6110

1097   Kremmer L, Thaon M, Borowiec N, David J, Poirié M, Gatti J-L, Ris N (2017) Field
1098   monitoring of *Drosophila suzukii* and associated communities in south eastern France
1099   as a pre-requisite for classical biological control. Insects 8: 124.
1100   https://doi.org/10.3390/insects8040124

1101   Kumschick S, Bacher S, Evans T, Marková Z, Pergl J, Pyšek P, Vaes-Petignat S, van der Veer
1102   G, Vilà M, Nentwig W (2015) Comparing impacts of alien plants and animals in
1103   Europe using a standard scoring system. Souza L (Ed.). Journal of Applied Ecology
1104   52: 552–561. https://doi.org/10.1111/1365-2664.12427

1105   Laliberté E, Legendre P (2010) A distance-based framework for measuring functional
1106   diversity from multiple traits. Ecology 91: 299–305. https://doi.org/10.1890/08-2244.1

1107   Laliberté E, Pierre Legendre, Bill Shipley (2014) FD: Measuring functional diversity from
1108   multiple traits, and other tools for functional ecology. R package version 1.0-12.
1109   Available from:
1110   https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.494.7392&rep=rep1&type
1111   =pdf.

1112   Lapin K, Bacher S, Cech T, Damjanić R, Essl F, Georges F-I, Hoch G, Kavčič A, Koltay A,
1113   Kostić S, Lukić I, Marinšek A, Nagy L, Agbaba SN, Oettel J, Orlović S, Poljaković-
1114   Pajnik L, Sallmannshofer M, Steinkellner M, Stojnic S, Westergren M, Zlatkovic M,
1115   Zolles A, de Groot M (2021) Comparing environmental impacts of alien plants,
1116   insects and pathogens in protected riparian forests. NeoBiota 69: 1–28.
1117   https://doi.org/10.3897/neobiota.69.71651

1118   Leblanc L, O'Grady PM, Rubinoff D, Montgomery SL (2009) New immigrant Drosophilidae
1119   in Hawaii, and a checklist of the established immigrant species. Proceedings of the
1120   Hawaiian Entomological Society. 41: 121–127.

1121   Lee JC, Bruck DJ, Curry H, Edwards D, Haviland DR, Van Steenwyk RA, Yorgey BM
1122   (2011) The susceptibility of small fruits and cherries to the spotted-wing drosophila,
1123   *Drosophila suzukii*. Pest Management Science 67: 1358–1367.
1124   https://doi.org/10.1002/ps.2225

1125   Lee JC, Dalton DT, Swoboda-Bhattarai KA, Bruck DJ, Burrack HJ, Strik BC, Woltz JM,
1126   Walton VM (2016) Characterization and manipulation of fruit susceptibility to
1127   *Drosophila suzukii*. Journal of Pest Science 89: 771–780.
1128   https://doi.org/10.1007/s10340-015-0692-9

1129   Lee TJ (1964) Taxonomy, and geographical distribution of Drosophilidae (Diptera) in Korea.
1130   Chungang University Theses Collection 9: 424–459.

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 of the Royal Society B: Biological Sciences 288: 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. Available from: 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. Gurevitch J (Ed.). 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: 387–408. https://doi.org/10.1146/annurev.ento.52.110405.091401

Little CM, Chapman TW, Hillier NK (2020) Plasticity is key to success of *Drosophila suzukii* (Diptera: Drosophilidae) Invasion. Godfrey K (Ed.). Journal of Insect Science 20: 5. https://doi.org/10.1093/jisesa/ieaa034

Little CM, Rizzato AR, Charbonneau L, Chapman T, Hillier NK (2019) Color preference of the spotted wing drosophila, *Drosophila suzukii*. Scientific Reports 9: 16051. https://doi.org/10.1038/s41598-019-52425-w

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. 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 119: 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: 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: 22.

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 of the Royal Society B: Biological Sciences 285: 20172733. https://doi.org/10.1098/rspb.2017.2733

1171 Manzur MI, Courtney SP (1984) Influence of insect damage in fruits of hawthorn on bird
1172   foraging and seed dispersal. Oikos 43: 265. https://doi.org/10.2307/3544142

1173 Markow TA (2019) Host use and host shifts in *Drosophila*. Current Opinion in Insect Science
1174   31: 139–145. https://doi.org/10.1016/j.cois.2019.01.006

1175 Markow TA, O'Grady P (2005) *Drosophila*: a guide to species identification and use.
1176   Academic Press.

1177 Markow TA, O'Grady P (2005) Evolutionary genetics of reproductive behavior in
1178   *Drosophila*: Connecting the Dots. Annual Review of Genetics 39: 263–291.
1179   https://doi.org/10.1146/annurev.genet.39.073003.112454

1180 Markow TA, O'Grady P (2008) Reproductive ecology of *Drosophila*. Functional Ecology 22:
1181   747–759. https://doi.org/10.1111/j.1365-2435.2008.01457.x

1182 Matsumura S (1931) 6000 illustrated insects of Japan-Empire. Toko Shoin, Tokyo, 1694 pp.

1183 Mcgill B, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from
1184   functional traits. Trends in Ecology & Evolution 21: 178–185.
1185   https://doi.org/10.1016/j.tree.2006.02.002

1186 Mitsui H, Kimura MT (2000) Coexistence of drosophilid flies: Aggregation, patch size
1187   diversity and parasitism: Coexistence of drosophilid flies. Ecological Research 15: 93–
1188   100. https://doi.org/10.1046/j.1440-1703.2000.00328.x

1189 Mitsui H, Kimura M (2000) Food preference of drosophilid flies in domestic and forest areas
1190   of central Japan. The Entomological Society of Japan 3: 285–289.

1191 Mitsui H, Takahashi KH, Kimura MT (2006) Spatial distributions and clutch sizes of
1192   *Drosophila* species ovipositing on cherry fruits of different stages. Population Ecology
1193   48: 233–237. https://doi.org/10.1007/s10144-006-0260-5

1194 Mitsui H., Beppu K., Kimura M.T. (2010) Seasonal life cycles and resource uses of flower-
1195   and fruit-feeding drosophilid flies (Diptera: Drosophilidae) in central Japan. The
1196   Entomological Society of Japan. 13: 60–67.

1197 Mollot G, Pantel JH, Romanuk TN (2017) The effects of invasive species on the decline in
1198   species richness. In: Advances in Ecological Research. Elsevier, 61–83.
1199   https://doi.org/10.1016/bs.aecr.2016.10.002

1200 Normark BB, Johnson NA (2011) Niche explosion. Genetica 139: 551–564.
1201   https://doi.org/10.1007/s10709-010-9513-5

1202 Novković B, Oikawa A, Murata Y, Mitsui H, Kimura MT (2012) Abundance and host
1203   associations of parasitoids attacking frugivorous drosophilids on Iriomote-jima, a
1204   subtropical island of Japan. European Journal of Entomology 109: 517–526.
1205   https://doi.org/10.14411/eje.2012.065

1206 Nunney L (1990) *Drosophila* on Oranges: Colonization, Competition, and Coexistence.
1207   Ecology 71: 1904–1915. https://doi.org/10.2307/1937598

1208 Oksanen J, Simpson GL, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R.
1209   Minchin, R.B. O'Hara, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs, Helene
1210   Wagner, Matt Barbour, Michael Bedward, Ben Bolker, Daniel Borcard, Gustavo
1211   Carvalho, Michael Chirico, Miquel De Caceres, Miquel De Caceres, Sebastien
1212   Durand, Heloisa Beatriz Antoniazi Evangelista, Rich FitzJohn, Michael Friendly,
1213   Michael Friendly, Brendan Furneaux, Geoffrey Hannigan, Mark O. Hill, Leo Lahti,
1214   Dan McGlinn, Marie-Helene Ouellette, Eduardo Ribeiro Cunha, Tyler Smith, Adrian
1215   Stier, Cajo J.F. Ter Braak, James Weedon (2020) vegan: community ecology Package.
1216   R package version 2.5-7. Available from: https://CRAN.R-project.org/package=vegan.

1217 Olazcuaga L, Rode NO, Foucaud J, Facon B, Ravigné V, Ausset A, Leménager N, Loiseau A,
1218   Gautier M, Estoup A, Hufbauer RA (2019) Oviposition preference and larval
1219   performance of *Drosphila suzukii* (Diptera: Drosophilidae), spotted-wing drosophila:
1220   effects of fruit identity and composition. Environmental Entomology: 15.

1221 Oosterbroek P (2006) The european families of the Diptera: Identification, Diagnosis,
1222   Biology. KNNV Publishing, 205 pp.

1223 Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson
1224   MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a
1225   framework for understanding the ecological effects of invaders. Biological Invasions
1226   1: 3–19. https://doi.org/10.1023/A:1010034312781

1227 Pelton E, Gratton C, Isaacs R, Van Timmeren S, Blanton A, Guédot C (2016) Earlier activity
1228   of *Drosophila suzukii* in high woodland landscapes but relative abundance is
1229   unaffected. Journal of Pest Science 89: 725–733. https://doi.org/10.1007/s10340-016-
1230   0733-z

1231 Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs
1232   associated with alien-invasive species in the United States. Ecological Economics 52:
1233   273–288. https://doi.org/10.1016/j.ecolecon.2004.10.002

1234 Podani J (1999) Extending Gower's general coefficient of similarity to ordinal characters.
1235   Taxon 48: 331–340. https://doi.org/10.2307/1224438

1236 Poyet M, Le Roux V, Gibert P, Meirland A, Prévost G, Eslin P, Chabrerie O (2015) The wide
1237   potential trophic niche of the asiatic fruit fly *Drosophila suzukii*: The key of its
1238   invasion success in temperate Europe? Desneux N (Ed.). PLoS ONE 10: e0142785.
1239   https://doi.org/10.1371/journal.pone.0142785

1240 Prasanna V, Prabha TN, Tharanathan RN (2007) Fruit ripening phenomena–an overview.
1241   Critical Reviews in Food Science and Nutrition 47: 1–19.
1242   https://doi.org/10.1080/10408390600976841

1243 Pyšek P, Richardson DM (2010) Invasive species, environmental change and management,
1244   and health. Annual Review of Environment and Resources 35: 25–55.
1245   https://doi.org/10.1146/annurev-environ-033009-095548

1246 Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F,
1247   Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson
1248   LA, Pauchard A, Pergl J, Roy HE, Seebens H, Kleunen M, Vilà M, Wingfield MJ,

11

1249   Richardson DM (2020) Scientists' warning on invasive alien species. Biological
1250   Reviews 95: 1511–1534. https://doi.org/10.1111/brv.12627

1251 R Core Team (2020) R: A language and environment for statistical computing, version 4.0.2.
1252   R Foundation for Statistical Computing, Vienna, Austria. Available from:
1253   https://www.R-project.org/.

1254 Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL (2013) Progress toward understanding
1255   the ecological impacts of nonnative species. Ecological Monographs 83: 263–282.
1256   https://doi.org/10.1890/13-0183.1

1257 Roche DP, Stoleson SH, Lituma CM (2021) Invasion of eastern deciduous forests by the
1258   spotted wing drosophila: impacts and knowledge gaps. Wildlife Society Bulletin 45:
1259   711–718. https://doi.org/10.1002/wsb.1234

1260 Rodriguez-Cabal MA, Stuble KL, Nuñez MA, Sanders NJ (2009) Quantitative analysis of the
1261   effects of the exotic Argentine ant on seed-dispersal mutualisms. Biology Letters 5:
1262   499–502. https://doi.org/10.1098/rsbl.2009.0297

1263 Rohlfs M, Hoffmeister TS (2003) An evolutionary explanation of the aggregation model of
1264   species coexistence. Proceedings of the Royal Society of London. Series B: Biological
1265   Sciences 270. https://doi.org/10.1098/rsbl.2003.0002

1266 Rohlfs M, Hoffmeister TS (2005) Maternal effects increase survival probability in *Drosophila*
1267   *subobscura* larvae. Entomologia Experimentalis et Applicata 117: 51–58.
1268   https://doi.org/10.1111/j.1570-7458.2005.00334.x

1269 Rohlfs M, Obmann, Björn, Petersen, Ralf (2005) Competition with filamentous fungi and its
1270   implication for a gregarious lifestyle in insects living on ephemeral resources.
1271   Ecological Entomology: 8. https://doi.org/10.1111/j.0307-6946.2005.00722.x

1272 Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats:
1273   The fauna of collards (*Brassica oleracea*). Ecological Monographs 43: 95–124.
1274   https://doi.org/10.2307/1942161

1275 Rosewell J, Shorrocks B, Edwards K (1990) Competition on a divided and ephemeral
1276   resource: testing the assumptions. I. Aggregation. The Journal of Animal Ecology 59:
1277   977. https://doi.org/10.2307/5026

1278 Ruxton GD, Wilkinson DM, Schaefer HM, Sherratt TN (2014) Why fruit rots: theoretical
1279   support for Janzen's theory of microbe–macrobe competition. Proceedings of the
1280   Royal Society B: Biological Sciences 281: 20133320.
1281   https://doi.org/10.1098/rspb.2013.3320

1282 Sallabanks R, Courtney SP (1992) Frugivory, seed predation, and insect-vertebrate
1283   interactions. Annual Revue Entomology 37: 377–400.

1284 Sang JH (1956) The quantitative nutritional requirements of *Drosophila melanogaster*. J Exp
1285   Biology 33: 45–72. https://doi.org/10.1242/jeb.33.1.45

1286 Santoiemma G, Trivellato F, Caloi V, Mori N, Marini L (2018) Habitat preference of
1287   Drosophila suzukii across heterogeneous landscapes. Journal of Pest Science.
1288   https://doi.org/10.1007/s10340-018-1052-3

1289 dos Santos LA, Mendes MF, Krüger AP, Blauth ML, Gottschalk MS, Garcia FRM (2017)
1290   Global potential distribution of *Drosophila suzukii* (Diptera, Drosophilidae). Wicker-
1291   Thomas C (Ed.). PLoS ONE 12: e0174318.
1292   https://doi.org/10.1371/journal.pone.0174318

1293 Santos M, Brites D, Laayouni H (2006) Thermal evolution of pre-adult life history traits,
1294   geometric size and shape, and developmental stability in *Drosophila subobscura*.
1295   Journal of Evolutionary Biology 19: 2006–2021. https://doi.org/10.1111/j.1420-
1296   9101.2006.01139.x

1297 Sato, Airi, Tanaka, Kentaro M., Yew, Joanne Y., Takahashi, Aya (2021) *Drosophila suzukii*
1298   avoidance of microbes in oviposition choice. Royal Society Open Sci. 8.
1299   https://doi.org/10.1098/rsos.201601

1300 Schaefer HM, Ruxton GD (2011) Plant-animal communication. Oxford University Press.
1301   https://doi.org/10.1093/acprof:osobl/9780199563609.001.0001

1302 Schwarz S, Durisko Z, Dukas R (2014) Food selection in larval fruit flies: dynamics and
1303   effects on larval development. Naturwissenschaften 101: 61–68.
1304   https://doi.org/10.1007/s00114-013-1129-z

1305 Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P,
1306   Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-
1307   Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H,
1308   Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J,
1309   Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R,
1310   Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P,
1311   Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species
1312   worldwide. Nature Communications 8: 14435. https://doi.org/10.1038/ncomms14435

1313 Sevenster JG, Alphen JJMV (1996) Aggregation and coexistence. II. A neotropical
1314   *Drosophila* community. The Journal of Animal Ecology 65: 308.
1315   https://doi.org/10.2307/5877

1316 Shackleton RT, Shackleton CM, Kull CA (2019) The role of invasive alien species in shaping
1317   local livelihoods and human well-being: A review. Journal of Environmental
1318   Management 229: 145–157. https://doi.org/10.1016/j.jenvman.2018.05.007

1319 Shaw B, Brain P, Wijnen H, Fountain MT (2018) Reducing *Drosophila suzukii* through
1320   competition. Pest Management Science 74: 1466–1471.
1321   https://doi.org/10.1002/ps.4836

1322 Shea K (2002) Community ecology theory as a framework for biological invasions. Trends in
1323   Ecology & Evolution 17: 170–176. https://doi.org/10.1016/S0169-5347(02)02495-3

1324 Shorrocks B (1977) An ecological classification of European *Drosophila* species. Oecologia
1325   26: 335–345. https://doi.org/10.1007/BF00345533

1326 Silva R, Clarke AR (2020) The "sequential cues hypothesis": a conceptual model to explain
1327   host location and ranking by polyphagous herbivores. Insect Science 27: 1136–1147.
1328   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. 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. Kleijn D (Ed.). 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. Poyser, Calton Scotland, 268 pp.

Stamps JA, Yang LH, Morales VM, Boundy-Mills KL (2012) *Drosophila* regulate yeast density and increase yeast community similarity in a natural substrate. Kytöviita M-M (Ed.). PLoS ONE 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. MS. Carl-von-Ossietzki-Universität Available from: http://oops.uni-oldenburg.de/254/2/stifru03.pdf (12 March, 2022).

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: 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: 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: 1213–1224. https://doi.org/10.1007/s10340-018-0985-x

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. The Canadian Entomologist 151: 34–48. https://doi.org/10.4039/tce.2018.47

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: 221–232. https://doi.org/10.1093/ee/nvx178

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: 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: 283–295. https://doi.org/10.1007/BF02347097

1370   Tonina L, Giomi F, Sancassani M, Ajelli M, Mori N, Giongo L (2020) Texture features
1371   explain the susceptibility of grapevine cultivars to *Drosophila suzukii* (Diptera:
1372   Drosophilidae) infestation in ripening and drying grapes. Scientific Reports 10: 10245.
1373   https://doi.org/10.1038/s41598-020-66567-9

1374   Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species
1375   and their missing parasites. Nature 421: 628–630. https://doi.org/10.1038/nature01346

1376   Traveset A, Richardson D (2006) Biological invasions as disruptors of plant reproductive
1377   mutualisms. Trends in Ecology & Evolution 21: 208–216.
1378   https://doi.org/10.1016/j.tree.2006.01.006

1379   Traveset A, Willson MF, Gaither JC (1995) Avoidance by birds of insect-infested fruits of
1380   *Vaccinium ovalifolium*. Oikos 73: 381. https://doi.org/10.2307/3545962

1381   Trienens M, Keller NP, Rohlfs M (2010) Fruit, flies and filamentous fungi - experimental
1382   analysis of animal-microbe competition using *Drosophila melanogaster* and
1383   *Aspergillus* mould as a model system. Oikos 119: 1765–1775.
1384   https://doi.org/10.1111/j.1600-0706.2010.18088.x

1385   TRY (2021) TRY plant trait database. Available from: https://www.try-
1386   db.org/TryWeb/Home.php (April 14, 2022).

1387   Underwood N, Inouye BD, Hambäck PA (2014) A conceptual framework for associational
1388   effects: When do neighbors matter and how would we know? The Quarterly Review
1389   of Biology 89: 1–19. https://doi.org/10.1086/674991

1390   Valburg LK (1992) Eating infested fruits: Interactions in a plant-disperser-pest triad. Oikos
1391   65: 25. https://doi.org/10.2307/3544883

1392   Valladares G, Lawton JH (1991) Host-plant selection in the holly leaf-miner: Does mother
1393   know best? The Journal of Animal Ecology 60: 227. https://doi.org/10.2307/5456

1394   Verschut TA, Becher PG, Anderson P, Hambäck PA (2016) Disentangling associational
1395   effects: both resource density and resource frequency affect search behaviour in
1396   complex environments. Blanckenhorn W (Ed.). Functional Ecology 30: 1826–1833.
1397   https://doi.org/10.1111/1365-2435.12670

1398   Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P, Gollasch S, Nentwig W, Olenin S,
1399   Roques A, Roy D, Hulme PE (2010) How well do we understand the impacts of alien
1400   species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in
1401   Ecology and the Environment 8: 135–144. https://doi.org/10.1890/080083

1402   Wallingford AK, Rice KB, Leskey TC, Loeb GM (2018) Overwintering behavior of
1403   *Drosophila suzukii*, and potential springtime diets for egg maturation. Environmental
1404   Entomology 47: 1266–1273. https://doi.org/10.1093/ee/nvy115

1405   Wang Y, Ma Y, Zhou D-S, Gao S-X, Zhao X-C, Tang Q-B, Wang C-Z, van Loon JJA (2017)
1406   Higher plasticity in feeding preference of a generalist than a specialist: experiments
1407   with two closely related *Helicoverpa* species. Scientific Reports 7: 17876.
1408   https://doi.org/10.1038/s41598-017-18244-7

1409   Wertheim B, Marchais J, Vet LEM, Dicke M (2002) Allee effect in larval resource
1410   exploitation in *Drosophila* : an interaction among density of adults, larvae, and micro-
1411   organisms: Allee effect in larval resource exploitation. Ecological Entomology 27:
1412   608–617. https://doi.org/10.1046/j.1365-2311.2002.00449.x

1413   West SA, Paul Cunningham J (2002) A general model for host plant selection in
1414   phytophagous insects. Journal of Theoretical Biology 214: 499–513.
1415   https://doi.org/10.1006/jtbi.2001.2475

1416   White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in
1417   invasion biology. Diversity and Distributions 12: 443–455.
1418   https://doi.org/10.1111/j.1366-9516.2006.00265.x

1419   Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to
1420   imperiled species in the United States. BioScience 48: 607–615.
1421   https://doi.org/10.2307/1313420

1422   Wiman NG, Walton VM, Dalton DT, Anfora G, Burrack HJ, Chiu JC, Daane KM, Grassi A,
1423   Miller B, Tochen S, Wang X, Ioriatti C (2014) Integrating temperature-dependent life
1424   table data into a matrix projection model for *Drosophila suzukii* population estimation.
1425   Bourtzis K (Ed.). PLoS ONE 9: e106909.
1426   https://doi.org/10.1371/journal.pone.0106909

1427   Wright GA (2015) Olfaction: smells like fly food. Current Biology 25: R144–R146.
1428   https://doi.org/10.1016/j.cub.2014.12.052

1429   Yamamoto A (1984) Heat and cold resistances of sixteen *Drosophila* species from Japan in
1430   relation to their field ecology. Zoological Society of Japan 1: 641–652.

1431   Zhao P, Ndayambaje JP, Liu X, Xia X (2020) Microbial spoilage of fruits: A review on
1432   causes and prevention methods. Food Reviews International: 1–22.
1433   https://doi.org/doi:10.1080/87559129.2020.1858

1434

1435