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Fallen fruit: a back-up resource during winter shaping fruit fly communities

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Keywords:	insect invasion, <i>Chymomyza amoena</i> , <i>Drosophila suzukii</i> , apple fruit, orchard, landscape composition, temperature, crop fruits, plant traits
Abstract:	<p>Most research on fruit insect pests focuses on the fruit maturity stages of interest for human consumption and generally neglects the post-harvest period. However, fallen fruit provide important feeding and breeding substrates for insects such as Drosophilidae and can be a potential trophic reservoir when usual host fruits become scarce.</p> <p>Recently, two invasive fruit fly species, <i>Drosophila suzukii</i> and <i>Chymomyza amoena</i>, have become established in Europe and are expected to alter existing Drosophilidae communities. In this study, carried out between September 2021 and April 2022 in northern France, we aimed to disentangle the relative roles of microclimatic, landscape and local factors driving the diversity of the Drosophilidae community in decaying fruit across seasons. Minimum site temperature during the week preceding sampling and the proportion of rotten fruit tissue had the strongest positive influence on Drosophilidae abundance and species richness. Drosophilidae abundance also increased with urbanization around the sampled trees. Decaying apples were important breeding sites for <i>C. amoena</i>, which dominated the community in autumn, but provided a suboptimal substrate for <i>D. suzukii</i>, which was only present in late summer.</p> <p>This study sheds light on the important role of unharvested fallen crop fruit in maintaining the diversity of an insect family that is generally overlooked in field studies. It also emphasises the importance of considering multiple scales and factors when studying the interactions between invasive species, native species and their shared trophic resources. Finally, our data highlight the importance of the Drosophilidae community in recycling agricultural waste.</p>

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1 **Fallen fruit: a back-up resource during winter shaping fruit fly** 2 **communities**

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13 14 **Running title**

15 Drosophilidae diversity in decaying apples

16 17 **Keywords**

18 insect invasion, *Chymomyza amoena*, *Drosophila suzukii*, apple fruit, orchard, landscape
19 composition, temperature, crop fruits, plant traits

20 21 **Abstract**

22
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24 consumption and generally neglects the post-harvest period. However, fallen fruit provide
25 important feeding and breeding substrates for insects such as Drosophilidae and can be a
26 potential trophic reservoir when usual host fruits become scarce.

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34 Drosophilidae abundance also increased with urbanization around the sampled trees. Decaying
35 apples were important breeding sites for *C. amoena*, which dominated the community in
36 autumn, but provided a suboptimal substrate for *D. suzukii*, which was only present in late
37 summer.

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39 diversity of an insect family that is generally overlooked in field studies. It also emphasises the
40 importance of considering multiple scales and factors when studying the interactions between
41 invasive species, native species and their shared trophic resources. Finally, our data highlight
42 the importance of the Drosophilidae community in recycling agricultural waste.

43

44 **Introduction**

45 In agricultural systems, herbivorous insects attract attention because of their pest status
46 and their damaging impacts on crop production and storage (Manosathiyadevan *et al.*, 2017).
47 Most research studying fruit pests focuses on the effects of insect attacks before or during fruit
48 ripening, when the economic consequences are greatest (Herrera, 1982; Alford, 2017).
49 However, what happens after the harvest period is often neglected including, for instance, the
50 role of insects in organic matter recycling in crop fields. Fallen fruit can play a significant role
51 as feeding and breeding substrates for arthropod communities (Alamiri, 2000; Rohlf &
52 Hoffmeister, 2004; Mészárosné Póss *et al.*, 2022). They could also represent a potential
53 reservoir for insect pests when cultivated fruits become scarce, providing a seasonal refuge and
54 potentially initiating future pest outbreaks (Liquido, 1991). Nevertheless, the temporal
55 dynamics of arthropod communities across the ‘lifespan’ of a decaying fruit have largely been
56 overlooked.

57 Drosophilidae species are of particular interest due to their significant role in the
58 recycling process of decaying fruit. The success of fruit infestation by Drosophilidae species is
59 influenced by numerous environmental factors. At the regional scale, climatic and
60 microclimatic conditions influence their presence. In particular, temperature and precipitation
61 patterns affect thermal limits and desiccation tolerance (Hoffman, 2009; Kellerman *et al.*, 2009;
62 Ulmer *et al.*, 2022). At finer scale, landscape composition, i.e., the cover of natural and
63 anthropic habitats surrounding a site, is a key driver of their diversity and abundance (Pope *et al.*,
64 2016; Furtado & Martins, 2018; Delbac *et al.*, 2020; Wen *et al.*, 2023). At local
65 microclimate scale, during cold seasons or cold parts of the day, decomposing fruit can provide
66 niches that are warmer than the surrounding environment, as microbial communities produce

67 heat during organic decomposition (Ryckeboer *et al.*, 2003). All these factors can independently
68 influence the infestation rates of different Drosophilidae species. Finally, the structure of
69 Drosophilidae communities is likely to be highly dynamic given that fruit can display profound
70 gradual changes over the period of decomposition, affecting the quality and quantity of
71 substrate they can provide for insects.

72 Drosophilidae community structure is also strongly influenced by biotic interactions.
73 Individual species may limit or facilitate infestation by other species, depending on their ability
74 or preference to oviposit and develop in a fruit at a given stage of decomposition and on their
75 competitive ability (Davis *et al.*, 1998; Hoffman, 2009). The number and identity of competitors
76 can influence the range and abundance of species (Davis *et al.*, 1998). Furthermore, invasive
77 species can disrupt the native community assemblage and cause cascading effects across trophic
78 networks, sometimes also facilitating native species infestations (Rodriguez, 2006; Poyet *et al.*,
79 2014). Worldwide, communities of frugivorous species have been impacted by invasive exotic
80 species. For instance, in Europe, the invasive members of the family *Drosophila suzukii*
81 Matsumara and *Chymomyza amoena* Loew are highly polyphagous and could profoundly alter
82 Drosophilidae community structures on fresh and decaying fruit (Band *et al.*, 2005; Poyet *et*
83 *al.*, 2014, 2015; Pajač Živković *et al.*, 2017).

84 On a short timescale, changes in the nutritional composition of fruit during the
85 decomposition process can affect fly foraging decisions and adult oviposition choices (Silva-
86 Soares *et al.*, 2017). Fruit with characteristically slower and longer decomposition allow study
87 of the temporal dynamics and environmental drivers of the Drosophilidae community
88 depending on them. Prolonged decomposition could include successive decomposition stages
89 characterised by different chemical composition and texture, sometimes spanning different
90 seasons and potentially offering successional niches to different Drosophilidae species. Apples
91 (*Malus domestica* Borkh) provide an excellent candidate fruit for such studies. Apples are a
92 major crop fruit in Europe and worldwide (FranceAgriMer, 2021; FAOSTAT, 2023). However,
93 a considerable proportion of many apple crops are damaged and commercially lost (Jeannequin
94 *et al.*, 2015). The large quantity of apples remained on the ground through damage or as
95 windfalls at the end of summer/beginning of autumn can provide an important potential trophic
96 resource for both vertebrates (Myczko *et al.*, 2013; Bouvier *et al.*, 2020; Castañeda *et al.*, 2022)
97 and a range of invertebrates (Papadopoulos *et al.*, 2001; Morimoto & Pietras, 2020), including
98 exotic species (Bal *et al.*, 2017). The apple decomposition process can extend throughout the
99 winter, both providing food for many organisms when other sources are scarce (Myczko *et al.*,
100 2013; Folwarczny *et al.*, 2022) and a microclimatically benign environment giving protection

101 from environmental extremes (Jiménez-Padilla *et al.*, 2020). Rotting apples contribute to
102 maintaining the diversity of decomposer insects in the ecosystem, amongst which frugivorous
103 Drosophilidae species (MacMillan *et al.*, 2016; Morimoto & Pietras, 2020) are of particular
104 interest because of (i) their significant role in the decomposition of decaying fruit and (ii) the
105 recent establishment in Europe of two major invasive Drosophilidae that can utilise these
106 decaying fruit.

107 The invasive *D. suzukii* is known to be able to attack healthy, ripening, fruit due to its
108 serrated ovipositor and it is recognised as a major threat globally to fruit crops including berries
109 and stone fruit (Walsh *et al.*, 2011). However, interactions between *D. suzukii* and apples have
110 been poorly documented, due to the low (if not imperceptible) level of damage it causes, leading
111 to very little commercial impact. However, decaying apples are likely to be attractive to adult
112 flies, as *D. suzukii* is attracted to apple juice (Feng *et al.*, 2018), products of apple degradation
113 (Feng *et al.*, 2018) and apple cider vinegar (Lasa *et al.*, 2020). Few studies have reported
114 infestations of apples by *D. suzukii* in orchards (Walsh *et al.*, 2011; Weydert & Mandrin, 2013;
115 Asplen *et al.*, 2015; Briem *et al.*, 2015; Bal *et al.*, 2017) and these infestations probably
116 primarily occurred on already damaged fruit with easily accessible flesh for oviposition (Lee *et al.*,
117 2011; Cai *et al.*, 2019). Under laboratory conditions, although poor larval performance was
118 generally recorded (Cai *et al.*, 2019; Stockton *et al.*, 2019; Jiménez-Padilla *et al.*, 2020), *D.*
119 *suzukii* has been successfully reared on various apple substrates, including cut apples (Jiménez-
120 Padilla *et al.*, 2020), fallen apples (Wallingford *et al.*, 2018), apple puree (Stockton *et al.*, 2019)
121 and artificial medium made from apple pulp (Englert & Herz, 2019) or apple juice (Sato *et al.*,
122 2021). Apples may therefore provide a back-up resource when other fruit are scarce.

123 The nearctic invasive species *C. amoena* is known to oviposit on already damaged or
124 parasitised fleshy fruit and nuts (Band *et al.*, 2005), but its contribution to fruit decomposition
125 has not been studied. It is not considered as a true pest (Band & Band, 1980; Pajač Živković *et al.*
126 *et al.*, 2017) at present and has received much less research attention than *D. suzukii*. Native to
127 North America, it has become widely established in Europe since its first detection in 1975 in
128 Czechia (Jong & van Zuijlen, 2003; Band *et al.*, 2005; Pajač Živković *et al.*, 2017). The species'
129 spread across Europe is likely to have been facilitated by association with regional transport of
130 fruits, probably apples, across the region (Burla & Bächli, 1992; Withers & Allemand, 1998;
131 Band *et al.*, 2006). Questions about its potential impact on the native Drosophilidae community
132 have been raised previously (Withers & Allemand, 1998), but no further investigations have
133 been made. The trophic resources used by *C. amoena* are varied, spanning multiple wild and
134 domestic fruit including apples (Band, 1991; Burla & Bächli, 1992; Band *et al.*, 1998, 2005,

135 2006). Oviposition mostly takes place in fruit scars, codling moth (*Cydia pomonella* Linnaeus)
136 tunnels or frass (Band, 1988; Band *et al.*, 2005) and is usually aggregated (Band, 1989).
137 *Chymomyza amoena* takes advantage of previous physical damage to fruit, including from
138 previous pest infestations (Band *et al.*, 1998, 2005). Both *C. amoena* and *D. suzukii* have been
139 reported co-occurring in apple orchards in Italy (Amiresmaeili *et al.*, 2019).

140 This study aimed to disentangle the relative roles of landscape and local factors in
141 controlling the diversity and composition of Drosophilidae communities using decaying apples,
142 including these two invasive species. We hypothesised that (i) the highly polyphagous *D.*
143 *suzukii* would preferentially utilise apples in the early stages of decomposition at the end of
144 summer, as it is a pioneer species preferentially infesting ripening fruit (Poyet *et al.*, 2014), and
145 (ii) *C. amoena* would use this fruit resource in autumn, as this fly is commonly found infesting
146 apples that has been first attacked by codling moth *Cydia pomonella* (Band *et al.*, 2005). We
147 also hypothesised that (iii), both native and exotic species would be positively associated with
148 the proximity of natural habitats (particularly woodland) which generally provide a refuge (and
149 thus reservoir) for *Drosophila* species (Basden, 1954), (iv) be affected by low temperature and
150 particularly frost days, and (v) be influenced by apple tree traits, such as the presence of large
151 canopy trees providing shelter or high apple production for feeding and oviposition. Worth
152 noticing that we focused on apples for the abovementioned reasons but other fruits could play
153 this bac-up resource role for Drosophilidae (e.g., pears, grapes, figs, persimmons, etc).

154

155

156 **Methods**

157

158 *Study area*

159

160 The study was conducted between September 2021 and April 2022 in the region of
161 Amiens (49°53'40" N, 2°18'07" E) in northern France. The region's climate is oceanic with a
162 mean annual temperature of 10.7°C and average rainfall of 691.9 mm (data from meteorological
163 station Dury-les-Amiens, StatIC network). The landscape of this region is largely characterised
164 by agricultural production and is a mosaic of open fields cultivated for cereals, rapeseed and
165 sugar beet, interspersed by apple orchards, grasslands and woodland patches. The apple
166 orchards are managed using various strategies including conventional and organic fruit

167 production. However, apple trees are also commonly present in domestic gardens, green spaces
168 in towns and villages, along roadsides and in pastures and woodlands.

169

170 *Apple collection and fruit and tree trait measurements*

171

172 Decaying apples were obtained from 19 sites randomly selected within a landscape
173 window of 30 × 45 km (see Table S1 for site characteristics and apple varieties). To capture the
174 temporal dynamics of communities, eight sampling sessions took place between September
175 2021 and April 2022 (21-22 September 2021, 19-20 October 2021, 16-17 November 2021, 14-
176 15 December 2021, 18-19 January 2022, 16 February 2022, 15 March 2022 and 12 April 2022).
177 Each month, at each site, six decaying apples were randomly collected from the ground below
178 the canopy of a single apple tree. After the last session in April, no decaying apples remained
179 on the ground at any of the sites. A total of 633 apples.

180 To evaluate the fruit resources available for the Drosophilidae, the following
181 quantitative and qualitative traits were measured for each apple collected: height (from the
182 flower scar to the fruit peduncle), diameter, mass, volume (mean radius³ × π × 4/3), proportion
183 of healthy skin of the fruit (based on colouration), proportion of rotting surface (based on visual
184 aspect), proportion of fruit surface with no skin (removed by physical wounds or animal
185 foraging), presence of mould (i.e., *Penicillium* and *Monilinia* fungal sporophores following the
186 identification keys of FREDON, 2002), and the number of holes associated with galleries
187 drilled by pests (including those from the codling moth *Cydia pomonella*). Since fruit sugar
188 levels are known to be associated with egg laying choices and/or larval development of some
189 *Drosophila* species (Lee *et al.*, 2008), Brix values (% sugar content) were measured both in the
190 healthy and rotting parts of each collected fruit using a refractometer (Bellingham+Stanley
191 sugar 0%-50%, serial number 019568 for low volume). The pH was also measured in both parts
192 of the apples using pH indicator paper (Special indicator paper, REF 902 05, pH 0.5-5.5
193 (MACHEREY-NAGEL) and pH indicator paper, pH 5.5-9.0 (Supelco).

194 The following vegetative and reproductive traits were recorded for each apple tree under
195 which fruit was collected in order to estimate their influence on community dynamics: tree
196 height, minimum and maximum canopy diameter, canopy area (π × max canopy radius × min
197 canopy radius) and trunk circumference (at 1.30 m height). The numbers of fruit hanging on
198 the tree and on the ground surface under the tree canopy in a 5 m radius around the trunk were
199 recorded. The relative proportions of healthy vs. damaged fruit on the ground were measured.

200 For each apple tree, the mean volume of an individual fruit (mean radius³ × π × 4/3) and the
201 total volume of fruit on the tree were calculated. The apple variety was also noted (Table 1).

202

203 *Emergence and identification of Drosophilidae flies*

204

205 Immediately after collection, apples were individually placed on wet cotton wool in
206 cylindrical plastic transparent containers (diameter = 118 mm, height = 135 mm, volume =
207 1,476 cm³), covered with a nylon mesh, and maintained in a temperature-controlled room at
208 20°C under a 16:8 L:D regime until all insects had emerged. Adult insects emerging were
209 collected daily and stored in 70% ethanol until identification. All collected fruit were
210 maintained in the emergence room for 100 days to check for any late emergence of imagos.
211 Emerged insects were subsequently sorted to select taxa representing Drosophilidae, which
212 were identified to species level using a Leica M205C stereomicroscope (equipped with a Leica
213 MC170 HD camera and Leica Application Suite software) following the keys provided by
214 Bächli *et al.* (2005) and a collection of standard specimens available in the laboratory.

215

216 *Environmental variables*

217

218 Local, landscape and meteorological variables were measured at each sampling site or
219 obtained from online databases to examine their relationships with the Drosophilidae
220 community emerging from the apples. The full list of variables, their units and their codes are
221 given in Suppl. Mat. (Table S1).

222 For each sampled tree, the altitude and the slope of the site were recorded. Within a 5
223 m-radius plot centred on the tree trunk, the cover and height of the tree layer, shrub layer and
224 herbaceous layer were estimated, as well as soil litter thickness. Leaf litter, dead wood debris
225 and the presence of a composting agent, such as apple pomace waste from cider factories, were
226 also noted. The proportions of local habitats surrounding the apple tree (wood, hedgerow,
227 orchard, grassland, crop, garden, building, road, river and pond) within 10 m and 50 m radii
228 were also noted. The management of the site herbaceous vegetation (mown vs. grazed
229 grasslands) and apple trees (yearly pruned vs. not or rarely pruned, pesticide treated vs. non-
230 treated) were noted.

231 The landscape composition around each sampled apple tree was characterised. A
232 geographic database was created using a Geographic Information System (GIS; ArcGIS Pro
233 v.2.5, ESRI). The sampled apple trees were positioned in the GIS and buffers of 10 m, 20 m,

234 50 m, 100 m, 250 m, 500 m, 750 m and 1000 m radii around each tree were created for
235 subsequent analyses of landscape composition. Landscape elements (woodland, grassland,
236 crop, building, road, water) were extracted from the OSO database (Centre d'Expertise
237 Scientifique OSO, 2021) and updated using aerial photographs and field observations (in
238 buffers < 100 m). The BD-Carto® database from French National Geography Institute was used
239 to refine mapping and georeferencing. For each sampled tree, the cumulative area of the
240 different habitats composing the landscape was then computed in each concentric buffer.

241 Macroclimatic conditions were characterised for each sampling site using regional
242 measurements. The daily meteorological data were retrieved from the three nearest
243 meteorological stations to each site (<https://www.historique-meteo.net/france/>), representing
244 large-scale climatic conditions. Daily minimum and maximum temperatures, rainfall and
245 snowfall were calculated for all sites using inverse-distance weighting (IDW) interpolation
246 (Willmott *et al.*, 1985) from the data from the three nearest weather stations (detailed in Table
247 S3 and S4). Daily temperatures were extracted for each day from January 1 2021 to the date of
248 sampling, allowing us to calculate the mean daily temperature range (daily maximum - daily
249 minimum) as well as the number of frost days since the beginning of the year. Accumulated
250 degree-days (Growth Degree Days, GDD) were calculated using a lower threshold of 0°C
251 between January 1 2021 and the date of sampling (Baskerville & Emin, 1969). The same
252 calculation was also performed from September 1 2021 to the date of sampling in order to better
253 match the ripening and collection period of the apples. The threshold value of 0°C is a standard
254 threshold commonly used in insect and plant studies (White *et al.*, 2012; McNeil *et al.*, 2020),
255 although it may not represent the precise threshold for all Drosophilidae. This threshold is
256 particularly appropriate for study of temporal synchrony between flies and plant resources (Iler
257 *et al.*, 2013). It was also selected as several *Drosophila* species are known to be active at very
258 low temperatures (<5°C) during winter days (January-February in Amiens and Bordeaux,
259 Ulmer *et al.*, 2022). Cumulative precipitation between January 1 2021 and the date of sampling
260 were also calculated from daily precipitation values.

261 Microclimatic temperatures were recorded at each sampling site, noting the temperature
262 of the ground surface on which the apples were laying and the air temperature within the apple
263 tree canopies. Hobo loggers (TIDBIT data logger V2 TEMP TBI-001, ONSET Company,
264 Bourne MA, USA) were used, recording every 60 min. Each sampling site was equipped with
265 two loggers (soil surface and within tree canopy). The first was placed on the ground surface
266 among decomposing apples ("bottom hobo"). The second was suspended 1.5 m above the
267 ground in the tree canopy, under the shade of a branch to avoid direct exposure to solar radiation

268 (“top hobo”) and oriented northward. The minimum, mean and maximum temperatures for
269 ground and air were extracted every day to compute the mean daily minimum, mean and
270 maximum temperatures, and used to assess the buffering ability of the soil relative to the local
271 air temperature. Accumulated degree-hours (Growth Degree Hours, GDH) were calculated
272 using a lower threshold of 0°C (Baskerville & Emin, 1969) during the week preceding the day
273 of each sampling.

274

275 *Statistical analyses*

276

277 General Linear Mixed Models (GLMMs) were used to test the influence of
278 environmental factors (apple traits, local conditions, landscape composition and meteorological
279 variables; see list in Table S1) on the temporal dynamics of species richness and abundance of
280 the Drosophilidae community emerging from the decomposing apples (n = 633 fruit). Part of
281 the analysis specifically focused on the number of *D. suzukii* and *C. amoena* individuals
282 emerging per fruit. “Site” was included as a random effect in the GLMMs to account for the
283 non-independence of apples sampled from the same site. Response variables were checked for
284 normality and transformed ($\log_{10}+1$) when necessary prior to analyses (Quinn & Keough,
285 2002). In the models, only the environmental variables that were significantly correlated with
286 the response variables, and with $R > 0.2$ (Pearson correlation), were considered in order to avoid
287 overfitting and excessive complexity. After backward selection of explanatory variables, the
288 Akaike information criterion (AIC) was used to select the most parsimonious model, i.e., the
289 most significant model with the lowest AIC (Harrison *et al.*, 2018). Model residuals were
290 checked for homoscedasticity using biplots of model predictions. Kruskal-Wallis tests were
291 used to test whether the numbers of species and individuals of Drosophilidae emerging from
292 apples varied between months. *Post-hoc* pairwise comparisons between months were
293 performed using Mann-Whitney U tests ($\alpha = 0.05$).

294 The influence of environmental conditions on Drosophilidae community composition
295 was examined using a redundancy analysis (RDA; Jongman *et al.*, 1995; McCune & Grace,
296 2002) of the Drosophilidae species matrix constrained by environmental variables. Before
297 performing the RDA, a detrended correspondence analysis (DCA) (Hill & Gauch, 1980) was
298 run on the species matrix to assess (on the basis of the gradient lengths depicted by DCA axes)
299 whether a linear or unimodal model was appropriate in the subsequent multivariate analyses.
300 DCA results on the species matrix showed short gradients (< 3 S.D.), supporting the use of an
301 ordination technique based on a linear model, such as RDA (Jongman *et al.*, 1995). The

302 Drosophilidae species matrix was built using the mean abundance of Drosophilidae species
303 calculated from the six apples collected per site for each month (91 samples x 7 Drosophilidae
304 species). The Drosophilidae species matrix was standardised with a general relativisation by
305 sites (McCune & Grace, 2002) and $\log_{10}+1$ -transformed prior to analyses to decrease the
306 influence of extreme variability in the numbers of individuals (Baar & ter Braak, 1996).
307 Drosophilidae species present in < 0.8% of the sampled apples (i.e., in < 6 apples amongst the
308 total of 633 apples collected) were removed from the matrix prior to analysis to avoid outlier
309 effects. To avoid multicollinearity among the numerous environmental variables measured at
310 the different spatial scales of the study (see list in Table S1), only the variables that correlated
311 with DCA axes and were ecologically non-redundant or statistically not inter-correlated were
312 retained, generating a final subset of 91 samples x 18 environmental variables.

313 Univariate analyses were performed using IBM-SPSS v.24.0 (IBM, Armonk, NY, USA)
314 and multivariate analyses using PC-ORD v.7.03 (McCune & Mefford, 2016).

315

316 **Results**

317

318 *Variations in quantity and quality of the apple resource*

319

320 Across all the sampling sites, apple resources declined progressively over the study
321 period (Fig. 1). Initially, 7,969 apples were present in September 2021, of which 7,040 were
322 hanging on the trees and 929 were laying on the ground. The numbers of apples progressively
323 declined until April, when no apples remained on the trees and only 65 on the ground.

324 The quality of the apples also changed across the study period, with a gradual decrease
325 in sugar content and increase in pH, especially in the rotten parts of the fruit (Fig. 2). Overall
326 mean sugar content decreased from $12.28\% \pm 0.28$ to $4.5\% \pm 1.03$ in the rotten parts of the fruit
327 between September and April, with the lowest concentration measured in February ($2.84\% \pm$
328 0.5). In the healthy parts of the fruit, sugar content decreased from $16.41\% \pm 0.85$ to $10.9\% \pm$
329 2.12 between September and March (apples collected in April were entirely rotten). Mean pH
330 of the rotten parts increased from 2.86 ± 0.07 to 3.36 ± 0.09 between September and April, with
331 the maximum value observed in February (4.66 ± 0.1). In the healthy parts, pH remained
332 relatively stable from September to February (between 3.35 and 3.60), but then increased to
333 reach 4.55 ± 0.51 in March.

334

335 *Microclimatic differences between soil and air over the study period*

336

337 Ground surface and canopy air temperature measurements confirmed that the soil acted
338 as a thermal buffer, especially during the coldest months. From February to April, differences
339 in mean monthly temperature between air and ground were observed (Fig. S1A). Notably, even
340 in months where the mean temperatures were similar, temperature variability was higher in the
341 air than on the ground (Fig. S1B), reaching both higher and lower temperatures daily than the
342 soil with differences of up to $\sim 10^{\circ}\text{C}$. At the site scale, temperature variation was even more
343 apparent when comparing the weekly variations between autumn, winter and spring (Figs. S1C,
344 S1D, S1E, respectively). In winter and spring, negative canopy air temperatures were
345 experienced, while the ground surface was protected from frost by the soil's buffering effect.

346

347 *Drosophilidae species abundance and richness*

348

349 From the 633 apples collected on the ground, a total of 6,283 individual flies
350 representing 14 Drosophilidae species emerged (Table 2, detailed by month in Table S2). The
351 Drosophilidae community was dominated by two species, *D. immigrans* (41.03% of
352 individuals) and *D. subobscura* (39.77%). Five other species contributed $> 1\%$ of total
353 individuals: *C. amoena* (7.93%), *D. melanogaster* (5.06%), *D. simulans* (2.72%), *D. suzukii*
354 (1.39%) and *D. tristis* (1.39%). The remaining species ($< 1\%$ of total) were *Scaptomyza palida*,
355 *D. ambigua*, *D. bifaciata*, *D. cameraria*, *D. obscura* and *D. kunzei*. Excepting *D. suzukii* and
356 *C. amoena*, all species were native.

357 The abundance patterns of Drosophilidae species were compared between months over
358 the study period (Fig. 3). The total number of individuals recorded per month rapidly and
359 consistently declined, from 3,635 emerging from apples collected in September to 84 from
360 apples collected in April. *Drosophila subobscura* was the only species that emerged from apples
361 collected throughout the sampling campaign. *Chymomyza amoena* emerged from apples
362 collected in all months except April. *Drosophila immigrans* emerged from apples collected
363 from September to December and *D. suzukii* only emerged from apples collected between
364 September and November.

365 Drosophilidae species richness per apple was 0.86 ± 1.24 species ($n = 633$ apples), but
366 differed significantly between months ($\chi^2 = 92.08$, $p < 0.001$; Fig. 4A) with a maximum of 2.02
367 ± 0.17 in September and a minimum of 0.38 ± 0.09 in March. Up to eight different species were
368 present in one apple in September. Drosophilidae abundance also decreased markedly over the

369 study period and also showed high variability, averaging 9.93 ± 36.66 emerging individuals per
370 apple overall, with a maximum in September of 33.66 ± 76.81 (Fig. 4B) and a minimum in
371 March of 2.43 ± 9.28 . Drosophilidae species richness and abundance were significantly
372 influenced by numerous variables (GLMMs, Table 3), increasing with apple size and the
373 percentage of rotten surface (MASSAV2, BROWNROTTEN2) in sites where the minimum
374 ground temperature was mild (i.e., highest local daily minimum temperature on the ground
375 during the week before sampling, MINTH7hb). The total abundance of Drosophilidae also
376 increased with variables related to direct human influence, such as the area represented by
377 buildings within a 50 m radius around the apple tree (BUILD50). The abundance of *C. amoena*
378 was positively correlated with apple size and percentage of rotten surface, as well as the
379 presence of codling moth holes (CARPOCAPSE2). The abundance of *D. suzukii* decreased with
380 the presence of *Penicillium* (PENICILI2) and with increasing apple tree canopy size
381 (CANOPY). Both *C. amonena* and *D. suzukii* abundances increased with higher local air
382 temperature during the week before sampling (MINTH7hh, MAXTH7hh) and with mowing of
383 the local vegetation (MOW).

384

385 *Influence of environment on Drosophilidae community composition*

386

387 Individual Drosophilidae species presence could be differentiated according to their
388 ecological niche in terms of substrate acidity and sugar content (Fig. 5). Two groups of species
389 were apparent: one, including *D. suzukii*, *D. melanogaster*, *D. simulans* and *D. immigrans*, was
390 associated with the sweetest and more acidic apples that were freshly fallen in early autumn;
391 the second, comprising *C. amoena*, *D. subobscura* and *D. tristis*, was mostly present in rotten
392 apples that had lower sugar content and increased pH.

393 In the redundancy analysis (RDA) coupling environmental factors and Drosophilidae
394 species matrices (Fig. 6), the eigenvalues of the first two ordination axes explained 54.8% of
395 the data variance. In the ordination diagrams, the plots formed groups associated with the
396 successive seasons (Fig. 6A). Along axis 1 (27.8%) groupings discriminated samples from
397 autumn (empty circles, positive part), associated with the warmest temperatures
398 (MAXMAX7Js; Fig. 6B), and winter and early spring samples (grey and black squares,
399 respectively, negative part). The negative part of axis 1 was associated with *D. subobscura*,
400 damaged apples (BIOORIGIN2), apple trees close to roads (ROAD10_%) and apple trees
401 surrounded by grasslands and shrubs (GRASS50_%, SHRUB50_%). Axis 2 (26.9%)
402 discriminated apple samples with *C. amoena*, collected under tall apple trees (HEIGHT),

403 growing in orchards (ORC10_%), and surrounded by woodland (WOOD50_%). The positive
404 part of axis 2 was associated with autumnal species (*D. immigrans*, *D. suzukii*, *D. melanogaster*)
405 present in the warmest periods (MAXMAX7Js), apples with the highest sugar content
406 (SUGAR2) and mass (MASSAV2), degree of rot (BROWNROTTEN2), and collected from a
407 human-influenced environment (BUILD50_%). In summary, the RDA showed that local and
408 seasonal thermal variation, habitat composition and fruit quality and quantity were the major
409 drivers of Drosophilidae species assemblages.

410

411 Discussion

412

413 Our study showed that four main categories of environmental drivers systematically influenced
414 the diversity and composition of the Drosophilidae community present in fallen apples (i) local
415 and seasonal thermal variation, (ii) habitat composition, and (iii) fruit quality and quantity.

416

417 *Climatic variation and the seasonal dynamics of the Drosophilidae community*

418

419 Local-scale variations in microclimate temperature appeared to influence Drosophilidae
420 diversity and species abundance more than regional-scale variations derived from
421 meteorological stations. Local and hourly microclimatic data are likely to provide a better
422 indicator of the impact of temperature extremes on the diversity and abundance of
423 Drosophilidae species, especially that of negative temperatures (freezing events). In temperate
424 regions, temperature is known to be a major driver of insect population dynamics and
425 geographic range (Sinclair *et al.*, 2003) because most insects are chill-susceptible and die due
426 to injuries caused by ice formation (Lee, 1991; Stephens *et al.*, 2015). Soil appeared to buffer
427 the ground surface temperatures experienced across seasons, especially during the coldest
428 months. In autumn, canopy shading may explain the smaller difference between air and ground
429 surface temperature. During winter and early spring, when the trees have lost their leaves, the
430 soil becomes the last compartment of the ecosystem capable of buffering the colder open air
431 temperatures and protecting on or near the ground surface from freezing temperatures.

432 The Drosophilidae community was structured by season, likely to be strongly influenced by the
433 different species' cold-tolerance strategies. Some species were present in apples collected
434 throughout the sampling, in particular *D. subobscura* and *C. amoena*, which are known to be
435 cold-tolerant (Band & Band, 1984; David *et al.*, 2003). Species known to be chill-susceptible

436 or freeze-intolerant were found only in apples collected in early autumn. These included *D.*
437 *suzukii* (Jakobs *et al.*, 2015; Winkler *et al.*, 2020), *D. immigrans* (Strachan *et al.*, 2011;
438 MacMillan *et al.*, 2015; Tamang *et al.*, 2017), *D. melanogaster* (Strachan *et al.*, 2011; Košťál
439 *et al.*, 2012; MacMillan *et al.*, 2015) and *D. simulans* (Strachan *et al.*, 2011; Lubawy *et al.*,
440 2022). Finally, *D. tristis* was found only in apples collected during the early months of autumn
441 and in March, probably indicating freeze-intolerance, although studies of this species' cold-
442 tolerance are lacking (Basden, 1954).

443 The cold tolerance strategies of different species are likely to structure seasonal
444 community composition, while partitioning may also take place when two species sharing the
445 same fruit have different fitness values (e.g., developmental time, number of eggs laid,
446 percentage of adult emergence, etc) when developing at the same temperature (Grimaldi, 1985).
447 For example, *D. melanogaster* lays more eggs than *D. simulans* at 15°C (McKenzie, 1978), and
448 their development times vary according to the season, with *D. melanogaster* developing more
449 rapidly in September than *D. simulans* (Behrman *et al.*, 2015). Laying more eggs and
450 developing more rapidly would favour *D. melanogaster* over *D. simulans*, as it results in
451 increased larval competitive ability (Grimaldi, 1985; Sevenster & Van Alphen, 1993). This
452 could explain why, in our study, the abundance of *D. melanogaster* was greater than that of *D.*
453 *simulans* in September but that the reverse was apparent in October after the temperature
454 dropped. Exploiting the resource first and having a short development time is another strategy
455 that would benefit a species (Nunney, 1990). This is the strategy adopted by *D. suzukii*, which
456 can utilise the fruit as it ripens, before any decomposition takes place (Walsh *et al.*, 2011;
457 Clemente *et al.*, 2018).

458 Over the thermally-governed seasonal gradient extending from September to April, the
459 decaying apples were exploited by a succession of Drosophilidae species, which supports the
460 hypothesis of temporal partitioning of the use of this food resource. This strategy adopted by
461 organisms using a common resource has been reported in studies of *Drosophila* species (Hodge
462 *et al.*, 1996; Matavelli *et al.*, 2015) and in insects in general (Wettlaufer *et al.*, 2021; Vindstad
463 *et al.*, 2020). The sequential use of resources allows coexistence through minimising
464 competitive interactions, potentially avoiding exclusion. This temporal separation of the use of
465 decaying apples is not only determined by temperature changes differentially affecting
466 Drosophilidae species over time across seasons, but is also associated with the gradual
467 modification of fruit quality, which varies with its stage of decay, as shown in other guilds of
468 insects (Koskinen *et al.*, 2022). The hierarchical continuum model, primarily used in plant
469 communities (Collins *et al.*, 1993; Hanski 1982), may be applicable to Drosophilidae species

470 coexistence in decaying apples. Based on this concept, four strategies can be identified and
471 applied to species, termed ‘core’, ‘satellite’, ‘urban’ and ‘rural’ species, based on the responses
472 of their abundance (i.e., dominance) and distribution (i.e., frequency changes between months)
473 to the seasonal progression (Fig. 7). Only one species, *D. subobscura*, was typically dominant
474 and was present across the full seasonal sampling period (see Fig. 3 and Table S2) and, thus,
475 can be considered a ‘core’ species (*sensu* Collins *et al.*, 1993). This species plays a major role
476 in apple decomposition and its role in structuring the community by transforming the substrate
477 is fundamental. ‘Satellite’ species are found at low density and restricted to a smaller element
478 of the seasonal progression. This was the case for late-summer / early autumn species (*D.*
479 *suzukii*, *D. melanogaster*, *D. simulans*, *D. tristis*), that are probably opportunistic species
480 ovipositing and developing in fallen apples, using the freshest and sweetest wounded fruits (Lee
481 *et al.*, 2011; Cai *et al.*, 2019). *Drosophila immigrans* conformed to the description of an ‘urban’
482 species in the hierarchical continuum model, with a very high abundance peak (particularly in
483 September and October) restricted to the beginning of the seasonal progression. This strategy
484 indicates that *D. immigrans* is a strong performer in early autumn but is also very dependent on
485 the substrate quality (high sugar levels; Fig. 5). The invasive *C. amoena* was the only ‘rural’
486 species in the current, present throughout most of the seasonal progression from September to
487 March, but at low to moderate densities. Even though not dominant, its strategy of persisting
488 through the seasons could contribute to its invasion success. Its persistence in decaying apples
489 could indicate higher tolerance to acidic substrates (Fig. 5).

490

491 *Landscape and local factors driving community diversity and invasive populations*

492

493 Insect communities are affected by both local conditions and landscape composition (Mitchell
494 *et al.*, 2014). At the landscape scale, variables associated with direct human activities and semi-
495 natural habitats were significant drivers of the Drosophilidae community in our study.
496 Abundance and species richness increased with the cover of buildings in a 50 m radius (even
497 though this variable was not retained in the final GLMM of species richness). Anthropogenic
498 stress factors, such as urbanisation, reduce the overall abundance and richness of insect
499 communities (Vaz *et al.*, 2023) and may lead to ecological homogenisation (McKinney, 2006;
500 Knop, 2016; Eggleton, 2020) with specialist species being negatively impacted (Shuisong *et*
501 *al.*, 2013; Knop, 2016). However, some species benefit from urbanisation, including non-native
502 or invasive species (McKinney, 2006; Bertelsmeier, 2021), generalist species (Shuisong *et al.*,
503 2013), or human commensal species such as mosquitoes (Perrin *et al.*, 2022). Some members

504 of Drosophilidae could also benefit from urbanisation. *Drosophila immigrans*, *D.*
505 *melanogaster*, and *D. suzukii* were strongly correlated with the cover of buildings. The former
506 two species are known to be associated with human activities (David, 1979; Kojima & Kimura,
507 2003), especially *D. melanogaster*, which is considered as the most commensal *Drosophila*
508 species associated with humans (Lachaise & Silvain, 2004). In winter, all three of these species
509 may find overwintering refuges around human structures (Ulmer, 2022). Other species in this
510 study were affected by the presence of semi-natural habitats. *Drosophila subobscura* was found
511 in apples collected under trees close to roads. Road edges impact community structure, yet can
512 have positive effects on biodiversity (Rotholz & Mandelik, 2013). *Chymomyza amoena*
513 abundance was positively correlated to the presence of orchards with woodland within a 50 m
514 radius, consistent with previous studies (Band *et al.*, 2005).

515 At the local scale, Drosophilidae richness and abundance were mostly influenced by the
516 quantity and quality of the food resource, the management of the site's herbaceous vegetation
517 and the tree canopy. The larger the apples, the greater the richness and abundance present. This
518 could be explained by higher detectability of larger fruit, either visually or by olfaction, a
519 selection process similar to that of other frugivorous insects (Sallabanks, 1993), or by a
520 decreased larval competition in larger fruits. In association with a higher detectability, grass
521 mowing was associated with increased Drosophilidae abundance. Mowing could also
522 negatively impact the presence of some predators (Horton *et al.*, 2003; Dobbs & Potter, 2014),
523 contributing further to increased Drosophilidae abundance. The quality of the resource, that is,
524 the percentage of rotten surface, the presence of carpocapse or *Penicillium* and the presence of
525 damage of biotic origin, also influenced the Drosophilidae community. Apple skin is waxy and
526 robust and most Drosophilidae ovipositors may not be able to penetrate it (Atallah *et al.*, 2014).
527 Damage of biotic origin provides a point of entry for oviposition. This is especially the case for
528 *C. amoena*, which uses codling moth carpocapse tunnels to oviposit in walnuts and apples
529 (Band, 1988). Similarly, *D. melanogaster* needs naturally damaged grapes to oviposit but can
530 also benefit from *D. suzukii*'s oviposition sites (Rombaut *et al.*, 2017). In contrast, the presence
531 of *Penicillium* negatively affected *D. suzukii* abundance. *Penicillium commune* is found in *D.*
532 *suzukii* artificial diet (Gao *et al.*, 2017). It has been isolated from *D. suzukii* and had no effect
533 on host survival (Bing *et al.*, 2020). The odour profile of *Penicillium* spp. contains geosmin and
534 octenol, molecules associated with other fruit-associated plant pathogens, which could act as
535 an indicator of unsuitable substrate for oviposition for *D. suzukii* (Wallingford *et al.*, 2016).
536 Large trees were also negatively associated with *D. suzukii* presence, possibly as their canopy

537 shading is unsuitable for this species which may be more attracted by thermophilic and sites
538 exposed to full sun for oviposition as autumn approaches.

539

540 *Trophic niche partitioning and the role of Drosophilidae in fruit decomposition*

541

542 Trophic niche partitioning occurs when different species share the same nutritional resource but
543 use it differently, limiting competition (Roughgarden, 1976; Pocheville, 2015). In our study, up
544 to eight species were able to coexist in one fallen apple. This suggests temporal niche
545 partitioning. Temporal partitioning in relation to seasonal temperature variation was addressed
546 above. Another driver of temporal partitioning may relate to the fruit decay process and physical
547 and chemical changes over shorter timescales. When fruit is damaged, either by the fall from
548 the tree or by insect oviposition, microbial communities, mostly bacteria and yeasts,
549 immediately start to proliferate (Rombaut *et al.*, 2017), inducing changes in biochemical
550 composition (Nunney, 1990; Awmack & Leather, 2002; Matavelli *et al.*, 2015). In particular,
551 the protein:carbohydrate (P:C) ratio increases, allowing flies with different dietary requirements
552 for protein to use the resource sequentially (Matavelli *et al.*, 2015). For instance, the successive
553 stages of decay in figs are exploited sequentially by different Drosophilidae species as the sugar
554 and protein contents change (Lachaise *et al.*, 1982; Matavelli *et al.*, 2015). In early autumn,
555 apples are sweeter and more acidic than in winter and spring. Drosophilidae species appear to
556 be sensitive to sugar concentration and pH variation. Sugar and pH are known to impact
557 fecundity, survival and microbiota composition (Deshpande *et al.*, 2015; Fellous & Xuéreb,
558 2017). For example, *D. suzukii* prefers low sugar content substrate in which to oviposit and
559 shows lower survival and fecundity at higher sugar concentrations (Fellous & Xuéreb, 2017).
560 In adult *D. melanogaster*, acidic food increases palatability, food intake and survival
561 (Deshpande *et al.*, 2015). As decay continues, the fruit texture changes, and firmness of the
562 substrate can be of importance for oviposition (Kienzle & Rohlf, 2021; Sato *et al.*, 2021). For
563 example, *D. suzukii* oviposits in firm substrates (Kienzle & Rohlf, 2021; Sato *et al.*, 2021)
564 while *D. melanogaster* selects softer substrates (Sato *et al.*, 2021). Finally, spatial partitioning
565 may also have occurred between and within apples (see Suppl. Mat.).

566

567 *Conclusions and perspectives*

568

569 Ecological processes during the post-harvest period in agricultural systems is of particular
570 interest but has received limited research attention. Unharvested fruits can remain on the ground

571 for sometimes long periods of time, providing potential food resources and/or microclimatic
572 refuges. In our study, decomposing apples hosted up to eight species of Drosophilidae,
573 including two important invasive species, *D. suzukii* and *C. amoena*. The fly community
574 structure was strongly influenced by local and seasonal thermal variation, habitat composition,
575 and fruit quality and quantity. Decomposing fruits are a dynamic substrate allowing resource
576 niche partitioning, both temporal and spatial, with competition and facilitation processes
577 occurring. Our study raises questions relating to post-harvest pest management strategies.
578 Known serious pest species such as *D. suzukii* can use these post-harvest resources to increase
579 overwinter survival and accelerate subsequent proliferation after the cold season. As it is
580 already recommended to reduce other apple fruit pathogens and parasites (brown rot fungi
581 scab), actively removing these ‘waste’ fruits could, therefore reduce the pest’s abundance in the
582 subsequent spring. However, the native Drosophilidae community, which plays a key role in
583 the recycling process of organic matter, would clearly also be impacted if this management
584 strategy was applied. Similarly, while *C. amoena* is generally considered as a pest species, by
585 being present throughout the winter, it also contributes to reducing available resources in spring
586 for *D. suzukii* (see Wilson *et al.*, 2012). Finally, although this study focused on Drosophilidae,
587 other species will certainly benefit from these fallen fruits, including parasitoids and other
588 arthropods. Future studies should focus on the dynamics of these multitrophic relationships
589 across winter time in relation with these ephemeral resources.

590

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602

603 **Data availability:** The datasets generated during and/or analysed during the current study are
604 available from the corresponding author on reasonable request.

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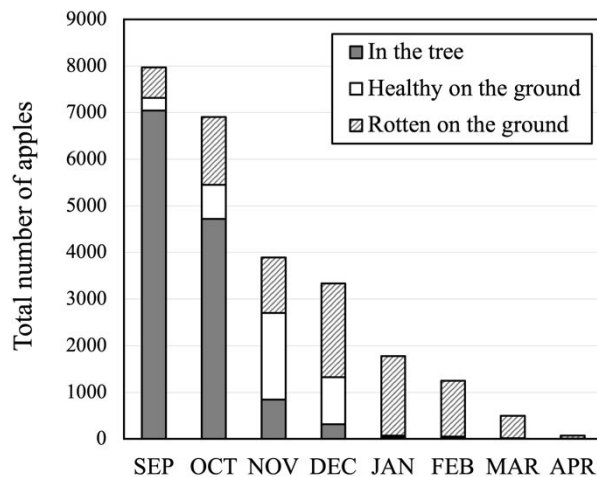
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Tables & Figures

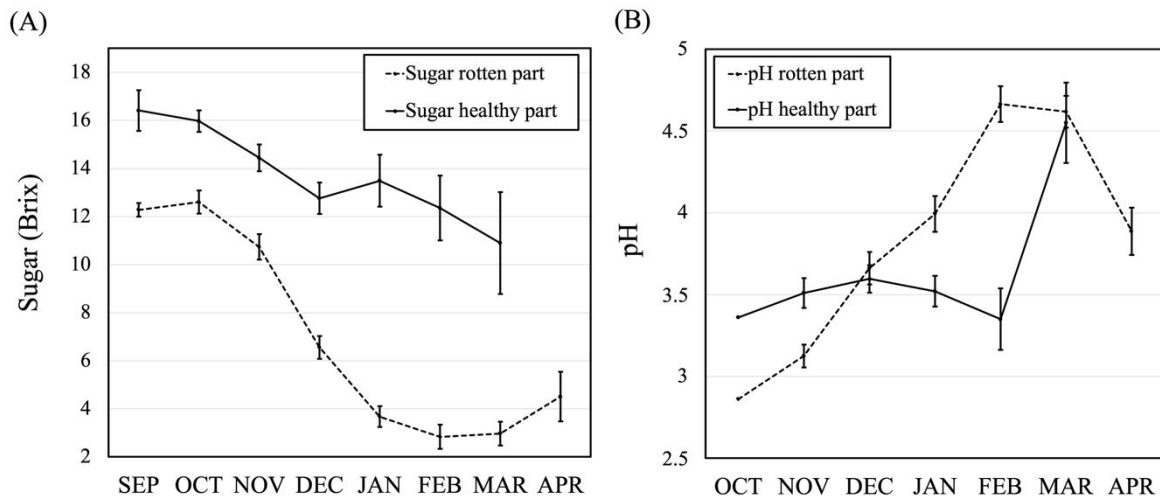


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Figure 1 Variation in apple abundance between September 2021 and April 2022, in relation to their position (in the trees vs. on the ground) and the status of the latter (healthy vs. rotten).

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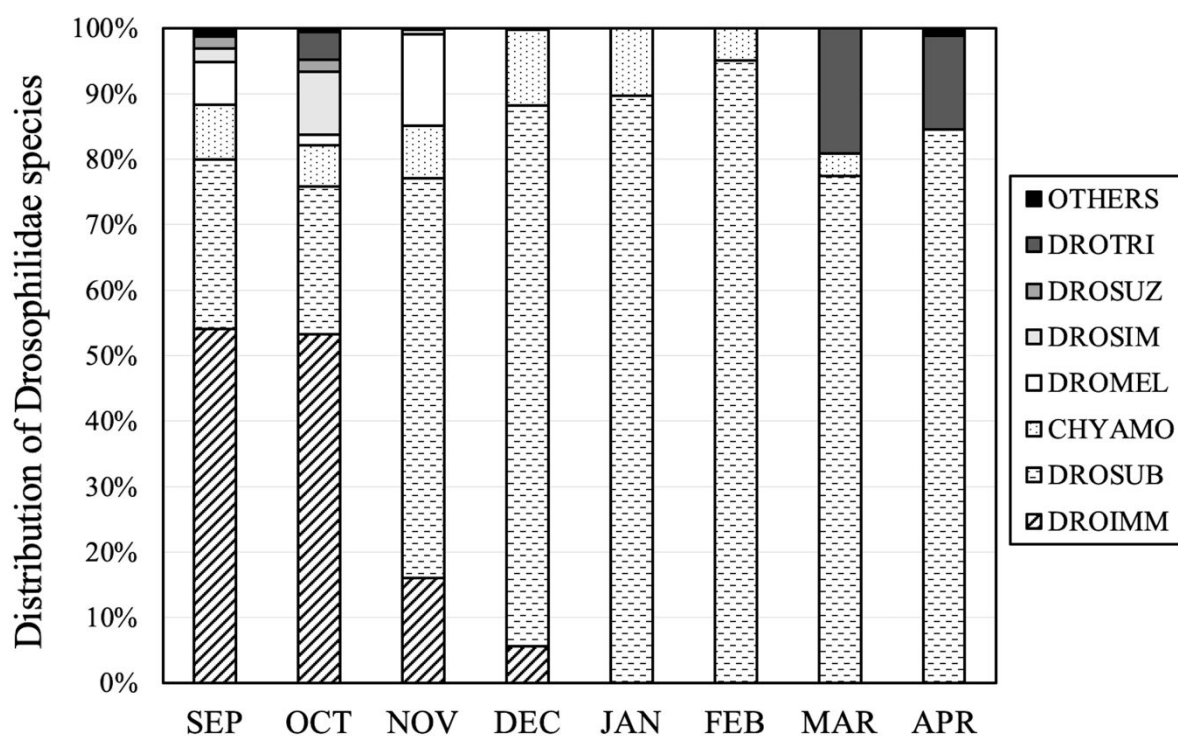
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Figure 2 Variation of mean (\pm SE) sugar content (A) and apple pH (B) between September 2021 and April 2022, with healthy (plain line) and rotten parts (dotted line) of the apples presented separately.

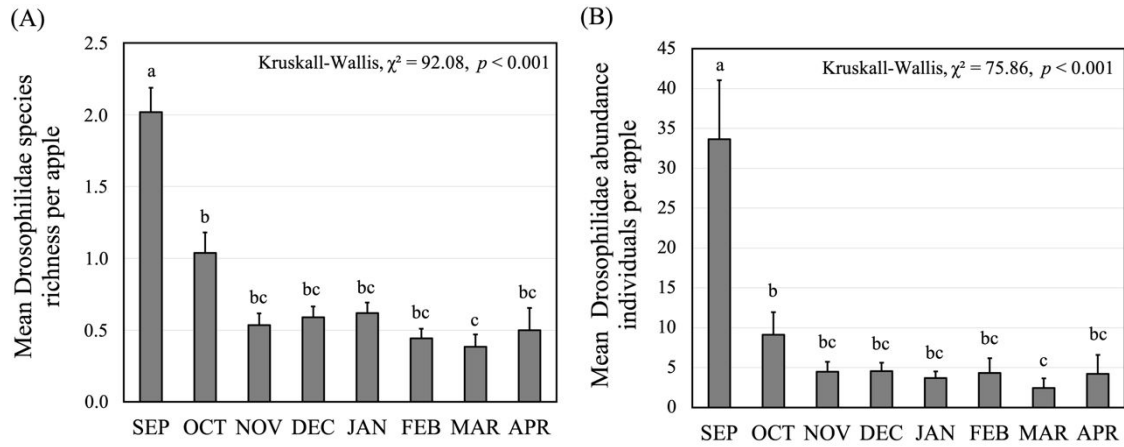
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Figure 3 Distribution of the most abundant Drosophilidae species emerging from apples collected during the study, from September 2021 to April 2022. DROTRI: *Drosophila tristis*, DROSUZ: *Drosophila suzukii*, DROSIM: *Drosophila simulans*, DROMEL: *Drosophila melanogaster*, CHYAMO: *Chymomyza amoena*, DROSUB: *Drosophila subobscura*, DROIMM: *Drosophila immigrans*, OTHERS: species representing less than 1% of the emerged flies.

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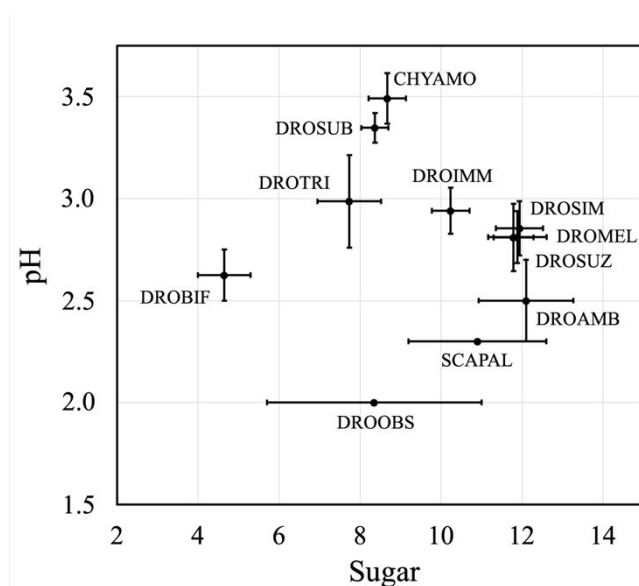
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Figure 4 Mean Drosophilidae species richness (A) and abundance (B) per apple (\pm SE) in the 19 sites sampled from September 2021 to April 2022.

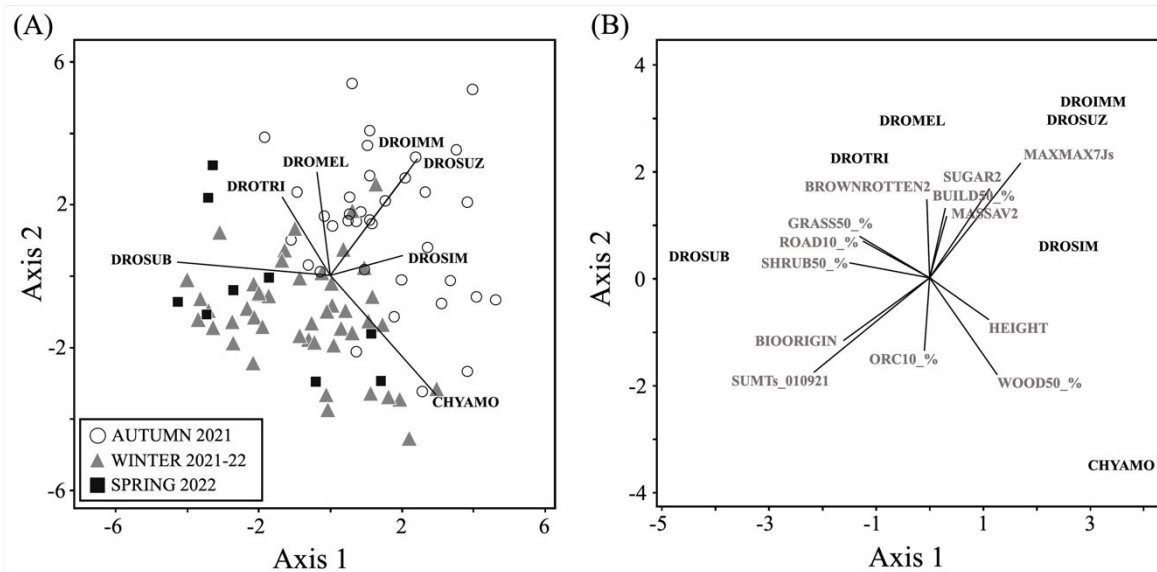
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Figure 5 Trophic preferences of Drosophilidae species based on mean (\pm SE) sugar content and apple pH. For each fly species, only apples in which the considered species was present were used to calculate the sugar and pH means presented in the figure. CHYAMO: *Chymomyza amoena*, DROAMB: *Drosophila ambigua*, DROBIF: *Drosophila bifasciata*, DROIMM: *Drosophila immigrans*, DROMEL: *Drosophila melanogaster*, DROOBS: *Drosophila obscura*, DROSIM: *Drosophila simulans*, DROSUB: *Drosophila subobscura*, DROSUZ: *Drosophila suzukii*, DROTRI: *Drosophila tristis*, SCAPAL: *Scaptomyza pallida*.

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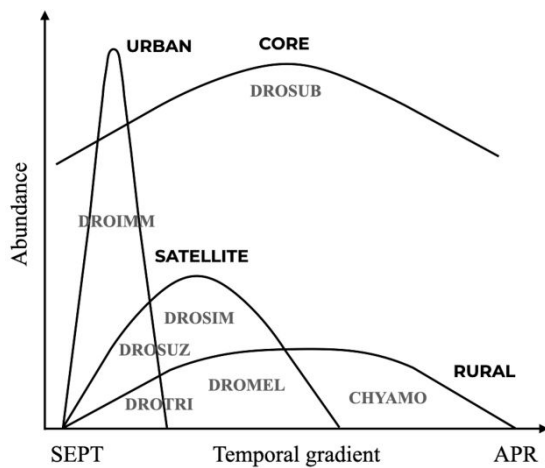
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Figure 6 Redundancy analysis (RDA) on (A) months and (B) environmental variables influencing the Drosophilidae community present in fallen apples. Only the most significant environmental variables are shown (cut-off r^2 value = 0.15). Months: AUTUMN: September and October; WINTER: November, December, January, and February; SPRING: March and April. Drosophilidae: CHYAMO: *Chymomyza amoena*, DROIMM: *Drosophila immigrans*, DROMEL: *Drosophila melanogaster*, DROSIM: *Drosophila simulans*, DROSUB: *Drosophila subobscura*, DROSUZ: *Drosophila suzukii*, DROTRI: *Drosophila tristis*. Environmental variables: BIOORIGIN2: Presence of damage from biotic origin (birds, mammals, molluscs, codling moth); BUILD50_#: Cover of building within 50 m; BROWNROTTEN2: Percentage of apple surface being brown because of rotting; HEIGHT: Height of the apple tree; GRASS50_#: Cover of grassland within 50 m; MASSAV2: Apple weight; MAXMAX7Js: Warmest temperature of the maximum temperatures during the 7 days before the apple sampling from meteorological stations); ORC10_#: Cover of apple orchard within 10 m; ROAD10_#: Cover of road within 10 m; SHRUB50_#: Cover of shrub within 50 m; SUGAR2: Mean sugar content in apple; SUMTs_01092021: Sum of positive temperatures from meteorological stations between 01/09/2021 and the sampling day; WOOD50_#: Cover of woodland within 50 m.

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Figure 7 Distribution of the most abundant Drosophilidae species collected during the study, from September 2021 to April 2022. Adaptation from the hierarchical continuum concept described by Collins (1993). DROTRI: *Drosophila tristis*, DROSUZ: *Drosophila suzukii*, DROSIM: *Drosophila simulans*, DROMEL: *Drosophila melanogaster*, CHYAMO: *Chymomyza amoena*, DROSUB: *Drosophila subobscura*, DROIMM: *Drosophila immigrans*.

1061 **Table 1** Site, apple tree and apple characteristics. Site: site code, Coordinate: geographic
 1062 coordinates of the apple tree (coordinate system: WGS 84), Altitude: mean altitude of the apple
 1063 tree, Variety: variety of the apple tree, Sum collected apples: total of apples collected, Mean
 1064 sugar content: mean sugar content in healthy part of apples sampled \pm standard error, Mean pH:
 1065 mean pH in healthy part of apples sampled \pm standard error.
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Site	Coordinate	Altitude (m)	Variety	Total collected apples	Mean sugar content (Brix)	Mean pH
PrV	49.823692 N ; 2.385196 E	59.836	Marie Mesnard	14	17.283 \pm 0.393	3.783 \pm 0.101
PrC	49.822715 N ; 2.392622 E	38.947	Golden	20	15.9 \pm 0.1	2.9 \pm 0.4
JL	49.897864 N ; 2.319218 E	24.346	Falstaff	42	12.925 \pm 1.649	2.875 \pm 0.125
BsPR	49.765967 N ; 2.002825 E	92.223	Colapuy	28	13.533 \pm 0.769	3.433 \pm 0.067
BsPM	49.771729 N ; 1.994607 E	96.904	Cardinal rouge	42	16.4 \pm 0	3.5 \pm 0
Bg	49.742929 N ; 2.021757 E	120.06	Colapuy	42	13.45 \pm 0.15	2.6 \pm 0.1
NaV	49.791208 N ; 2.094462 E	139.983	Belle Fille	44	17.3 \pm 1.8	3.7 \pm 0
T	49.802371 N ; 2.136424 E	110.422	Racine	48	17.7 \pm 0.866	4.25 \pm 0.144
N	49.839968 N ; 2.165911 E	78.762	Reine des reinettes	17	13.8 \pm 1.795	4.333 \pm 0.167
CF	49.823927 N ; 2.149882 E	123.489	Médaille d'Or	48	14.8 \pm 1.401	3.633 \pm 0.067
CS	49.859573 N ; 2.170174 E	115.905	Reinette étoilée	18	15.45 \pm 0.55	3.4 \pm 0.1
A	49.879944 N ; 2.318306 E	59.741	Reine des reinettes	36	11.25 \pm 1.25	3.1 \pm 0.4
Pc	49.637533 N ; 2.427752 E	136.781	Rateau	34	11 \pm 0	3.3 \pm 0
H	49.987074 N ; 2.055347 E	28.451	Kermerrien	24	21.325 \pm 0.99	3.4 \pm 0.117
Bl	49.993649 N ; 2.121355 E	64.168	Noël des Champs	38	16.15 \pm 0.85	4 \pm 0
W	49.92154 N ; 1.947491 E	55.99	Groseille	12	16.8 \pm 0.4	2.5 \pm 0
C	49.922992 N ; 2.08597 E	109.09	Boskoop	42	14.7 \pm 0	2.5 \pm 0
LIA	49.922801 N ; 2.26735 E	35.414	Natural seedling (close to Golden)	48	17 \pm 1.966	2.333 \pm 0.167
F	49.883266 N ; 2.170291 E	105.483	Doux Blanc	36	17.15 \pm 0.55	4.4 \pm 0.1
Total				633		

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1071 **Table 2** Distribution of the Drosophilidae species in the study. N ind: total number of
 1072 individuals emerged from apples, Min: minimum number of individuals per apple, Max:
 1073 maximum number of individuals per apple, Mean: mean number of individuals per apple, SE:
 1074 standard error, %: percentage of individuals of the species among all individuals that emerged
 1075 from apples, AFreq: frequency of apples infested by the species among all apples sampled.
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Species	Code	Total study (633 apples)						
		N ind	Min	Max	Mean	SE	%	AFreq
<i>Chymomyza amoena</i>	CHYAMO	498	0	34	0.787	0.121	7.926	0.197
<i>Drosophila ambigua</i>	DROAMB	6	0	2	0.009	0.046	0.095	0.008
<i>Drosophila bifasciata</i>	DROBIF	2	0	1	0.003	0.04	0.032	0.003
<i>Drosophila hydei</i>	DROHYD	24	0	21	0.038	0.172	0.382	0.003
<i>Drosophila immigrans</i>	DROIMM	2578	0	375	4.073	0.561	41.031	0.1
<i>Drosophila kuntzei</i>	DROKUN	1	0	1	0.002	0.04	0.016	0.002
<i>Drosophila melanogaster</i>	DROMEL	318	0	136	0.502	0.329	5.061	0.047
<i>Drosophila obscura</i>	DROOBS	2	0	1	0.003	0.04	0.032	0.003
<i>Drosophila simulans</i>	DROSIM	171	0	61	0.27	0.242	2.722	0.033
<i>Drosophila subobscura</i>	DROSUB	2499	0	115	3.948	0.206	39.774	0.384
<i>Drosophila suzukii</i>	DROSUZ	87	0	16	0.137	0.112	1.385	0.043
<i>Drosophila tristis</i>	DROTRI	87	0	16	0.137	0.122	1.385	0.032
<i>Hirtodrosophila cameraria</i>	HIRCAM	2	0	2	0.003	0.056	0.032	0.002
<i>Scaptomyza pallida</i>	SCAPAL	8	0	3	0.013	0.056	0.127	0.008
Total		6283						

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1087 **Table 3** Effect of environmental variables on the species abundance and richness of the full
 1088 *Drosophilidae* community, *Chymomyza amoena* abundance and *Drosophila suzukii* abundance,
 1089 analysed by GLMMs. BROWNROTTEN2: % of rotten part on apple surface, MASSAV2:
 1090 apple mass, BUILD50: % of buildings in a radius of 50 m, MINTH7Jhb: soil minimum
 1091 temperature in the preceding 7 days, VOL2: apple volume, MAXTH7Jhh: air maximum
 1092 temperature in the preceding 7 days, MOW: mowing of herbaceous vegetation,
 1093 CARPOCAPSE2: presence of codling moth borehole, CANOPY: radius of the apple tree
 1094 canopy, MINTH7Jhh: air minimum temperature in the preceding 7 days, and PENICILI2:
 1095 presence of *Penicillium* sporophore on apple
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Dependent variables	Explanatory variables	Model parameters						
		F	Estimates	SE	d.f.	t	p	AIC
<i>Drosophilidae</i> abundance (log ₁₀ , n = 633 apples)	Model constant	16.665	-0.2332	0.0571	47.00	-4.082	0.000	892.16
	BROWNROTTEN2	66.609	0.0041	0.0005	593.02	8.161	0.000	
	MASSAV2	44.404	0.0044	0.0007	323.61	6.664	0.000	
	BUILD50	14.610	0.0180	0.0047	17.01	3.822	0.001	
	MINTH7Jhb	49.331	0.0333	0.0047	505.88	7.024	0.000	
<i>Drosophilidae</i> species richness (log ₁₀ , n = 633 apples)	Model constant	0.128	-0.0091	0.0256	53.80	-0.358	0.722	-273.05
	BROWNROTTEN2	65.421	0.0016	0.0002	627.49	8.088	0.000	
	MASSAV2	20.649	0.0012	0.0003	517.87	4.544	0.000	
	MINTH7Jhb	73.374	0.0165	0.0019	607.50	8.566	0.000	
<i>Chymomyza amoena</i> abundance (log ₁₀ , n = 633 apples)	Model constant	0.285	-0.1329	0.0452	194.53	-2.940	0.004	87.55
	BROWNROTTEN2	9.838	0.0008	0.0003	620.92	3.137	0.002	
	VOL2	8.476	0.0009	0.0003	375.85	2.911	0.004	
	MAXTH7Jhh	13.832	0.0078	0.0021	610.42	3.719	0.000	
	MOW	4.293	0.1210	0.0584	585.35	2.072	0.039	
	CARPOCAPSE2	5.209	0.0769	0.0337	626.98	2.282	0.023	
<i>Drosophila suzukii</i> abundance (log ₁₀ , n = 633 apples)	Model constant	22.827	0.0637	0.0183	18.61	3.479	0.003	-998.57
	CANOPY	10.782	-0.0002	0.0001	19.18	-3.284	0.004	
	MINTH7Jhh	38.693	0.0069	0.0011	617.17	6.220	0.000	
	MOW	24.130	0.1217	0.0248	609.07	4.912	0.000	
	PENICILI2	3.871	-0.0406	0.0206	625.35	-1.968	0.050	

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