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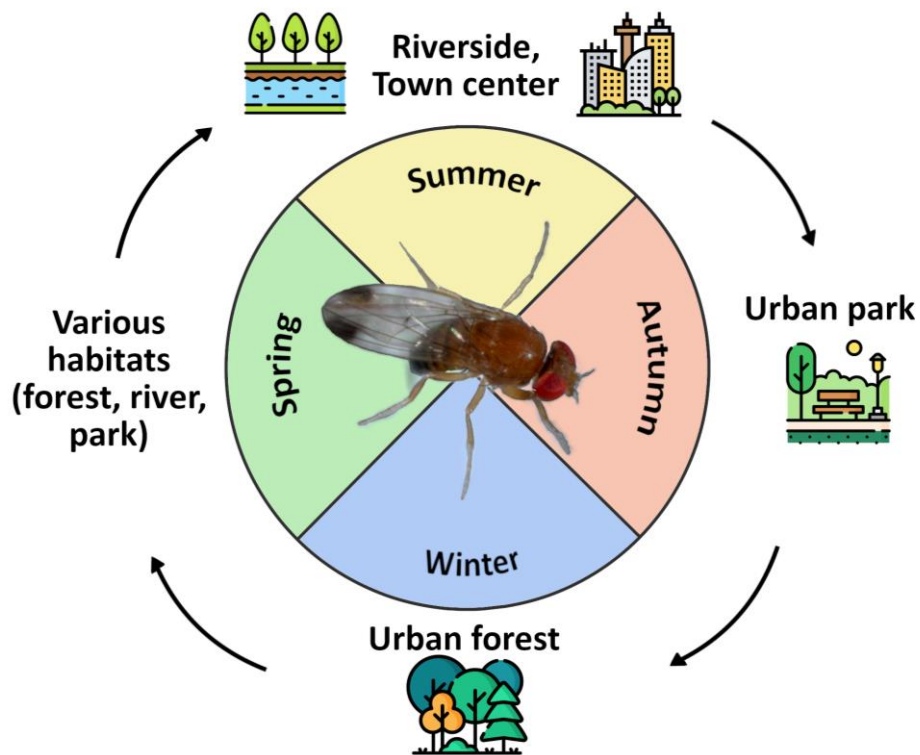
# Urban ecology of *Drosophila suzukii*

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15 **Abstract**

16 **Context**

17 Urban environments are vulnerable to the introduction of non-native species and sometimes  
18 contribute to their invasion success. Knowing how urban landscape features affect the  
19 population dynamics of exotic species is therefore essential to understand and manage these  
20 species.

21 **Objective**

22 The spotted wing drosophila, *Drosophila suzukii*, is a highly polyphagous fruit fly that has  
23 become a very problematic invasive species over the last decade. Because of its important  
24 damage on fruit production, *D. suzukii* populations have mainly been studied in agricultural  
25 areas, while their dynamics in urban landscape remain poorly explored. The objective of this  
26 study was to investigate the role of urban environment in the invasion success of *D. suzukii* by  
27 identifying local and landscape factors driving the abundance of the fly along seasons and  
28 urbanization gradients.

29 **Methods**

30 To achieve this, 526 insect traps were randomly set in four different habitats (urban forest,  
31 park, riverside and town centre) along an urbanization gradient in the city of Amiens (France),  
32 between September 2018 and August 2019. The influence of landscape and local  
33 environmental variables on Drosophilidae species diversity and composition was examined  
34 using GLM and multivariate analyses.

35 **Results**

36 We found that Drosophilidae species richness and abundance were negatively impacted by  
37 urbanization. The Drosophilidae community was dominated by *D. subobscura* and *D. suzukii*,  
38 but their relative abundance varied with seasons. *Drosophila suzukii* used urban forest during  
39 winter and also during heat waves in summer. The fly was still active in this habitat in winter

40 when the ground was covered with snow. The cover of brambles, shrubs, soil litter and dead  
41 wood debris were identified as valuable ecological indicators of the presence of *D. suzukii*

## 42 **Conclusion**

43 We highlight the role of the different components of urban environment in the ecology of *D.*  
44 *suzukii*, particularly with regard to its winter survival. These results could serve for designing  
45 management strategies in urban habitats in order to reduce the invasion success of *D. suzukii*.

46

47 **Keywords:** Urban landscape, biological invasion, spatial and temporal patterns, spotted-wing  
48 drosophila, exotic insect pest, insect diversity

49

50

## 51 **Introduction**

52

53           Urban environments offer very specific and harsh living conditions for organisms  
54 (Gilbert 1989; Fattorini 2011) and are often pointed as ‘a special case’ compared to other  
55 environments (Walbridge 1997). Most urban areas are highly artificialized in terms of  
56 building density, road traffic (Martin et al. 2018) and artificial night-time light (Owens and  
57 Lewis 2018); they are intimately close to human activities (Thomas et al. 2017) and generally  
58 warmer compared to adjacent rural areas (Oke 1973; Meineke et al. 2017). Artificial lights  
59 notably affect insect populations. These man-made environments harbor specific biodiversity  
60 (Raupp et al. 2010), and their importance in ecological studies has grown in the last two  
61 decades (McDonnell and Hahs 2008). Indeed, more than half of the world's human population  
62 lives in cities and the percentage of land used as urban areas has been growing at a quick rate  
63 (United Nations, 2018), at the expense of less artificial environments. Studies have shown that  
64 among the species living in urban areas, insects show a non-negligible diversity (Sattler et al.  
65 2010). This includes native species that can find in cities resources and/or shelter that become  
66 scarce in rural areas (Garcia et al. 2008; Unterweger et al. 2018), but also exotic and/or  
67 invasive species that also benefit from these favorable conditions (Garcia et al. 2012; Gaertner  
68 et al. 2017; Gentili et al. 2024) or rapidly adapt to urban constraints such light at night (Sato  
69 and Takahashi 2022). Urban areas can then become key places in the invasion success of  
70 certain species (Padayachee et al. 2017).

71           Among those invasive species, one has become very problematic during the last  
72 decade, the spotted wing drosophila, *Drosophila suzukii* (Matsumura 1931). This fruit fly is  
73 an invasive pest native to Southeast Asia. It was first spotted in 2008 in Europe (Cini et al.  
74 2014) and North America (Walsh et al. 2011), where it spread rapidly. It also spread to  
75 Central and South America where it was first spotted in 2013 and more recently in Africa

76 (2013 in Morocco and La Réunion, and 2019 in Kenya;  
77 <https://gd.eppo.int/taxon/DROSSU/distribution>). This highly polyphagous species infests a  
78 wide variety of wild fleshy-fruited plants (Kenis et al. 2016; Poyet et al. 2015), including  
79 invasive (Poyet et al. 2014) and toxic ones (Poyet et al. 2017), as well as cultivated species  
80 (Lee et al. 2011) causing important damages on agricultural production with considerable  
81 economic impact (Asplen et al. 2015; Yeh et al. 2020). Given the rapidity and the amplitude  
82 of its spread, understanding the causes of its invasion success is important to predict the future  
83 of its distribution.

84 As a consequence of their damage caused on crops, *D. suzukii* populations have been  
85 mainly studied in agricultural landscapes and in natural habitats in the vicinity of farms and  
86 fruit crops (Tonina et al. 2018; Santoiemma et al. 2018; Delbac et al. 2020; Ulmer et al.  
87 2022). Studies on the role played by cities and peri-urban areas in its invasion process are rare  
88 (Bombin and Reed 2016; Sato and Takahashi 2022). These works showed a significant  
89 correlation between land use and abundance (but not diversity) of drosophila species in  
90 Alabama and suggest that invasive drosophila such as *D. suzukii* could dominate the  
91 drosophila communities in urban environments. Lab studies also showed that environmental  
92 factors characteristic of cities (higher temperature and light at night) could trigger  
93 evolutionary and plastic responses of *D. suzukii* in terms of thermic tolerance and diurnal  
94 activity. Urban landscapes are vulnerable to the introduction of non-native species (Branco et  
95 al. 2019) and invasions are even more common in urban conditions than in rural conditions  
96 (Spence and Spence 1988). In Europe, and particularly in France, most of the first records of  
97 *D. suzukii* were made in urban areas such as parks (Calabria et al. 2012). Moreover, the  
98 dispersal of *D. suzukii* as well as other drosophila species follows commercial fruit trafficking  
99 routes (Cini et al. 2014; Lavrinienko et al. 2017; Estay et al. 2023) ending in urban areas.

100 Therefore, studying the ecology of *D. suzukii* in cities seems crucial in understanding how  
101 these environments shape the populations of the pest and affect its persistence.

102 Urban areas are not homogenous landscapes. Although cities are characterised by a  
103 prevalence of built surfaces, they remain mosaics of habitats with varying quality and  
104 constraints for insect populations. These habitats may offer both shelters with suitable  
105 conditions and trophic resources for insects (New 2015). Urban areas could be important for  
106 *D. suzukii* as they may provide frost-free shelters and become refuges during winter  
107 (Unterweger et al. 2018). Indeed, despite various studies on the subject, the way *D. suzukii*  
108 overwinters is still not fully understood (Panel et al. 2018). Insects commonly migrate to more  
109 protected areas to reduce the risk of freezing to death (Leather et al. 1995). As temperatures  
110 inferior to  $-7^{\circ}\text{C}$  are lethal for *D. suzukii* (Jakobs et al. 2015), cities, through the “heat island  
111 effect” (Oke 1973; Meineke et al. 2017), could represent a potential underestimated reservoir  
112 of the pest during the cold season. Nevertheless, the same urban heat islands may also  
113 represent a risk for the fly during the summer.

114 Variations in insect diversity and abundance in cities are often linearly structured  
115 along a main gradient of urbanization (Bennett and Gratton 2012; Bombin and Reed 2016;  
116 Tzortzakaki et al. 2019). On the one hand, mineral and impervious surfaces such as buildings,  
117 roads and other paved areas (parking lots, etc.) lack both food resource and shelter, and  
118 appear to be inhospitable for organisms. As a response, insect diversity generally increases  
119 from the town centre toward peri-urban areas (Geslin et al. 2016; Tzortzakaki et al. 2019;  
120 Fenoglio et al. 2021). On the other hand, parks, garden, hedgerows and grass strips may offer  
121 interesting features for insects feeding and reproducing (Beninde et al. 2015; Hall et al. 2017;  
122 Theodorou et al. 2020). Despite being often heavily anthropized and frequently disturbed,  
123 they generally offer a variety of fruit plants, shelters and man-made food (from human litter).  
124 Some ornamental plant species frequently found in city parks and green spaces bear fruits

125 earlier than most wild species (e.g. *Aucuba japonica*, *Elaeagnus* sp., *Symphoricarpos* sp.,  
126 Poyet et al. 2015). Private gardens can show a great variety of habitats and often contain  
127 cultivated fruits such as cherry, strawberry, raspberry, highly infested by *D. suzukii*. Even if  
128 they are smaller than parks, gardens are frequent and distributed throughout the cities, making  
129 them ideal stepping stones to connect larger patches of vegetation such as parks and green  
130 areas (Goddard et al. 2010). Urban forests are also hot spots of insect diversity in cities (New  
131 2015) and forests are commonly used by *D. suzukii* (Poyet et al. 2014) and promote fruit  
132 infestation by the fly (Ulmer et al., 2022). Most of the big cities are historically founded and  
133 expand along rivers because of their role as water supply and transport routes of goods by  
134 boat (Kondolf and Pinto 2017). Water bodies present within the cities, such as rivers or ponds,  
135 are often associated with increased atmospheric humidity and an air cooling effect (Murakawa  
136 et al. 1991; Hathway and Sharples 2012), both of which can be interesting for insects during  
137 the summer (Cregg and Dix, 2001; Kenneth, 1932). This may be particularly true for *D.*  
138 *suzukii*, which populations are moving closer to river streams in the hot season (Maceda-  
139 Veiga et al. 2021).

140         The goal of this study is to better understand the role of urban environment in the  
141 invasion success of *D. suzukii* and its place within the Drosophilidae communities of different  
142 urban habitats. Using a rather holistic approach combining Drosophilidae community, plant  
143 community, landscape ecology and meteorology, we aimed at identifying environmental  
144 biotic and abiotic factors driving the variations in the abundance of *D. suzukii* across seasons  
145 and habitats in urban areas.

146         More specifically, we sought to determine (1) what kind of urban habitats are favoring  
147 the persistence of *D. suzukii* during the year, and especially during the winter season, (2) what  
148 is the place (dominant core or satellite species; Deconninck et al. 2024) of *D. suzukii* within  
149 the Drosophilidae communities of urban habitats along seasons and (3) what are the effects of



150 environment constraints and resources availability on the distribution and life history traits of  
151 the species. To achieve this, insect trapping campaigns were conducted for an entire year in  
152 the city of Amiens, in the North of France. A total of 526 traps were placed at ten times in 4  
153 different urban environments along an urbanization gradient. These four selected  
154 environments, an urban forest, a recreational park, the banks of the Somme river, the town  
155 centre, were also chosen because they (i) were representative of the main contrasting features  
156 characterizing the urban landscape of the city of Amiens and (ii) represented different types of  
157 potential trophic sources (in terms of wild fruit composition, for example) or shelters  
158 (vegetated shelters versus anthropogenic shelters).

159

## 160 **Materials and methods**

161

### 162 *Study habitats and sampling design*

163

164 The study was conducted in Amiens (Somme, France, 49°53'40" N, 2°18'07" E), in a  
165 metropolitan area of around 160,000 inhabitants. The city of Amiens is moderately urbanized,  
166 with 42.6% of urbanized land cover and 13.7% of industrialized areas and road cover (Corine  
167 Land Cover database, 2018) leaving space for various forms of vegetated areas (parks, green  
168 spaces, wooded areas, agricultural areas). The city is also located along the channelled  
169 Somme River, highly ramified and meandering within the urban area. The insect trapping was  
170 conducted in four different habitats along an urbanization gradient (Figure 1): (i) An urban  
171 forest (FOREST), a wooded area with a dense tree cover dominated by *Acer pseudoplatanus*,  
172 *Fraxinus excelsior* and *Ulmus minor* colonized by the liana *Hedera helix*, in the border of the  
173 city (extending between Gutenberg road and Le chemin de Longpré, Amiens). (ii) The Saint-  
174 Pierre Park (PARK), a major artificialized green space composed of a mix of exotic

175 ornamental plant species and spontaneous or planted local species. The park is a mosaic of  
176 open wooded and grassland areas organized around playgrounds and walking path for  
177 families. It also contains concrete roads, buildings and several water bodies (pond, small  
178 channels). (iii) The banks of the Somme river (RIVER) meandering within the city and  
179 bordered by a hygrophilous vegetation. (iv) The centre of the city of Amiens (TOWN) is  
180 organized around the Cathedral and dominated by roads and buildings (>76% of the land  
181 cover, Figure 1). The four types of trap locations are characteristic of four urban landscapes  
182 dividing the city (a wood-dominated area, recreational green park, river-influenced area, and  
183 densely built centre) and their features are shown in Figure 1.

184         Between September 2018 and August 2019, nine trapping campaigns were organized  
185 to cover an entire year (dates of residence of traps in the field: 20<sup>th</sup>-27<sup>th</sup> September, 11<sup>th</sup>-18<sup>th</sup>  
186 October, 15<sup>th</sup>-22<sup>th</sup> November, 6<sup>th</sup>-13<sup>th</sup> December, 29<sup>th</sup> January- 5<sup>th</sup> February, 19<sup>th</sup>-26<sup>th</sup> Mars,  
187 6<sup>th</sup>-13<sup>th</sup> May, 1<sup>st</sup>-8<sup>th</sup> July, 22<sup>th</sup>-29<sup>th</sup> August). For each campaign, 15 traps were randomly  
188 placed in each habitat (giving 60 traps per campaign and 540 traps for the entire study). The  
189 60 traps were placed in the field on the same day and collected after seven days of residence.  
190 The locations of the traps were different in the different sampling periods. Fourteen traps out  
191 of the 540 were damaged during the whole sampling campaign (due to extreme wind events  
192 or human alterations) and were not considered in the analyses.

193         Additionally, we also sampled the drosophila species in fruit stores and in houses,  
194 where commercial fruit were present (i.e. mainly in the kitchen rooms of houses where fruit  
195 are stored between meals) using a total 139 traps and the same protocol as for other habitats.  
196 Nevertheless, given the extremely low abundance of *D. suzukii* in fruit shops and houses the  
197 results were shown in Supplementary Material (Supp. Mat. A).

198

199 *Drosophilidae species collection*

200

201 Insect traps were made using the lower half of a red plastic bottle (Badoit ®; Firlej and  
202 Vanoosthuyse 2017; Weydert et al. 2016), as red has been proved to be the optimal color for  
203 traps design (Renkema et al. 2014). The traps were 130 mm high and 85 mm in diameter. As  
204 traps with a side entry catch more individuals (Lee et al. 2013), five holes (Ø 5 mm; Hamby,  
205 et al. 2014) were drilled on the sides of traps at a distance of 70 mm from the bottom. The  
206 tops of the traps were covered with transparent plastic wrap to protect its content from rain  
207 and ease its collect. Before placing them on the field, the traps were filled with an attractive  
208 solution composed of apple cider vinegar (80 mL) and liquid cane sugar (20 mL) (Burrack et  
209 al. 2015; Lasa et al. 2020), with the addition of a drop of dish soap to break the surface  
210 tension (Lee et al. 2013). They were then hung at a height ranging from 1 m to 1.5 m.

211 After collecting the traps, their content was filtered and kept in a 70% ethanol solution.  
212 Using a Leica M205C stereomicroscope, the taxa of the Drosophilidae family were identified  
213 to the species level using Bächli, Viljoen, Escher, & Saura (2005) identification keys and the  
214 collection of standard specimen from the laboratory. *D. suzukii* individuals were sorted and  
215 kept in alcohol for further measurements.

216

#### 217 *Morphs description and wing size measurement of Drosophila suzukii*

218

219 *D. suzukii* individuals were counted, sexed, and divided into three morph categories  
220 (Panel et al. 2018). Individuals with a clear yellowish colour except for the last three dark  
221 tergites were classified as summer morphs. Individuals with mainly dark tergites but a clear  
222 pronotum were classified as intermediate morphs. Finally, individuals with dark tergites and  
223 pronotum were classified as winter morphs (Supp. Mat. B).

224 Wing dimensions are often used as an index of body size in *Drosophila* sp. (Misra and  
225 Reeve 1964; Sokoloff 1966; Huey 2000). For each trap, the wings of up to 5 males and 5  
226 females *D. suzukii* were randomly selected and measured. To do so, the right wing of the  
227 individual was removed and flattened between two microscope slides. Measurements were  
228 made with a Leica M205C stereomicroscope equipped with a Leica MC170 HD camera and  
229 the software Leica Application Suite, following the protocol used by Gilchrist et al. (2001) on  
230 *Drosophila subobscura*. Wing length was calculated by adding the length of two segments  
231 along vein IV, L1 (from the base of the fourth longitudinal vein to the posterior cross vein)  
232 and L2 (from the posterior cross vein to the distal end of the fourth longitudinal vein). The  
233 wing width W, was measured as the distance from the distal end of the fifth longitudinal vein  
234 on the trailing edge of the wing to the leading edge in a line perpendicular to the vein III. A  
235 wing area index was then calculated using the formula: Wing Area Index = (L1 + L2) x W.  
236 Intermediate wing measurements (L1, L2, W) were used to build the integrative Wing Area  
237 Index and were not further used given their inherent redundancy with the index.

238

#### 239 *Plant community characterization*

240

241 Around each trap, a vegetation survey was done within a 5 m-radius plot on the day of  
242 trap setting in the field. The cover of vascular plant species was estimated for each vegetation  
243 layer: herbaceous layer (<1 m), shrub layer (1-8 m), tree layer (>8 m). If fleshy fruits were  
244 present within a 10 m radius, the identity of their species was recorded. Plant species were  
245 identified following Lambinon (2004).

246

#### 247 *Local, landscape and meteorological variables*

248

249 The environmental conditions of each trap locality were characterized using a set of  
250 local, landscape and meteorological variables. Within each 5 m-radius plots, the cover of tree  
251 layer, shrub layer, herbaceous layer, dead wood debris, leaf litter, waste container, river, road,  
252 building and trail was estimated (see the list of variables in Supp. Mat. C).

253 A geographic database was created using a Geographic Information System (GIS;  
254 ArcGIS Pro v.2.5, ESRI) to build maps of the landscape surrounding traps. The traps were  
255 positioned in the GIS and buffers of 100 m radius around each trap were created for  
256 subsequent analyses of landscape composition. This radius was chosen as a previous study  
257 showed that *D. suzukii* has a relatively low dispersal capacity, with a daily flight distance of  
258 less than 100 m (Vacas et al. 2019). Moreover, in a previous study, we showed that fruit  
259 infestation rates by *D. suzukii* responded to natural habitat cover in a 100 m radius around  
260 sampling sites (Ulmer et al., 2022). Landscape elements (wood, grass strip, grassland,  
261 hedgerow, crop, private garden, building, water, trail, road, bare soil) were extracted from the  
262 OSO database (Scientific Centre of Expertise OSO, 2018), updated by field observations and  
263 integrated to the GIS database. For each trap, the percentage of cumulated area of polygonal  
264 elements composing the landscape were then computed in the 100 m buffer.

265 The daily meteorological data between the first day of the year of trapping  
266 (01/01/2018 or 01/01/2019) and the day of trap collection were retrieved from the nearest  
267 meteorological station (<https://www.historique-meteo.net/france/>). The average distances  
268 from the traps to the nearest meteorological station were 18.70, 17.69, 17.39 and 17.28 km for  
269 forest, park, riversides and town centre, respectively. Daily minimum, mean, and maximum  
270 temperatures, as well as precipitation, were extracted for each day from January 1<sup>st</sup>. This  
271 allowed us to calculate the following variables from the beginning of the year to the day the  
272 traps were collected as well as during the 7 days of trapping: mean daily minimum  
273 temperatures, mean daily maximum temperatures, mean of daily mean temperatures, number

274 of frost days, cumulative temperature (degree-days). Degree-days were calculated using a  
275 lower threshold of 0°C between January 1<sup>st</sup> and the day of sampling (Baskerville and Emin  
276 1969). The baseline value of 0°C is a standard threshold commonly used in insect and plant  
277 studies (White et al. 2012; McNeil et al. 2020). This threshold is particularly adapted to study  
278 the temporal variations of fly populations (Iler et al. 2013) and was also chosen as we  
279 observed and captured *D. suzukii* individuals in activity at very low temperature (close to  
280 0°C) during winter days (Ulmer et al. 2022). Mean and cumulative rainfall between January  
281 1<sup>st</sup> and the day of sampling, as well as during the 7 days of trapping, were also calculated.

282

### 283 *Data analyses*

284

285 The influence of environmental factors (local biotic and abiotic conditions, landscape  
286 composition and meteorological variables; see the list in Supp. Mat. C) on the species  
287 richness of Drosophilidae community (SRdroso), the number of Drosophilidae individuals  
288 (ABUNdroso), the number of *D. suzukii* individuals (DSabund), the number of summer  
289 (DSEstivale) and dark (DSInt\_Hiver) morphs of *D. suzukii* and the mean wing size of female  
290 (WINGfem) and male (WINGmal) *D. suzukii* per trap was tested using general linear models  
291 (GLMs). The variables were checked for normality and transformed ( $\log_{10}+1$ ) when necessary  
292 prior to analyses (Quinn, & Keough, 2002). To avoid overfitting and for model simplification,  
293 only environmental variables the most significantly correlated with response variables (with  $R$   
294  $> 0.2$ , Pearson correlation) were considered in the models. A backward selection of  
295 explanatory variables and the Akaike information criterion (AIC) were used to select the most  
296 parsimonious model, *i.e.* the most significant model with the lowest AIC (Harrison et al.  
297 2018). The homoscedasticity of residuals from the models was checked using biplots and  
298 model predictions. The effect of habitat on  $\log_{10}+1$ -transformed Drosophilidae species

299 richness (number of species per trap) and species abundance (number of counted individuals  
300 per species per trap) was examined using mixed models (GLMMs) using habitat as  
301 explanatory factor (4 categories: forest, park, riverside, town centre). In these models, the  
302 sampling month was introduced as a random effect term to account for the effect of seasonal  
303 sampling. The differences in wing size (Wind Area Index) of *D. suzukii* individuals between  
304 morphs and between habitats were assessed using ANOVA. Post-hoc comparisons of means  
305 were performed using Tukey's honestly significant difference (HSD) test.

306         Multivariate analyses were used to examine the influence of environment on  
307 Drosophilidae species composition following the general recommendations of McCune and  
308 Grace (2002). First, a detrended correspondence analysis (DCA) (Hill and Gauch 1980) was  
309 ran on Drosophilidae species frequency matrix (482 traps x 25 Drosophilidae species) to  
310 decide (on the basis of the gradient lengths depicted by DCA axes) whether the linear or  
311 unimodal model was more appropriate in the subsequent multivariate analyses. Sampling  
312 plots with no Drosophilidae species in the trap were not considered in the species matrix (*i.e.*  
313 44 traps out of the 526 were removed from the analysis) and the Drosophilidae species matrix  
314 was  $\log_{10}+1$ -transformed prior to analyses so as to decrease the influence of extremely large  
315 numbers of individuals (Baar and ter Braak 1996). DCA results on species matrix showed  
316 short gradients ( $< 4$  S.D.), suggesting that an ordination technique based on the linear model,  
317 such as redundancy analysis (RDA), could be used (Jongman et al. 1995). On the basis of  
318 these results, a RDA of Drosophilidae species matrix (482 traps x 25 Drosophilidae species),  
319 constrained by environmental variables (482 plots x 31 environmental variables) was  
320 performed to examine the response of Drosophilidae species composition to environment. To  
321 avoid multicollinearity among the numerous meteorological variables, only cumulative  
322 temperature (TEMCUM), cumulative precipitation (CUMRAIN) and number of frost days  
323 (NFROST) measured at the year scale and during the week of sampling were considered in

324 the RDA. The first axis of the RDA was rotated by *D. suzukii* frequency in order to improve  
325 ease of interpretation of the constellation of plot and environmental gradients from the angle  
326 of the dominance of *D. suzukii* (Peck 2016). Finally, a second RDA was processed to assess  
327 the relationships between Drosophilidae species community (374 traps x 25 Drosophilidae  
328 species) and vascular plant species community (374 plots x 132 plant species from three  
329 vegetation strata), following the same procedure as above. In this last RDA, plots from the  
330 town centre with no spontaneous plant community and other plots with no plant species were  
331 not considered and plant species present in less than 2% of the sampling plots were removed  
332 from the matrix prior to analysis. To identify plant species indicator of the presence of *D.*  
333 *suzukii* along seasons, for each sampling date, Spearman correlations were calculated between  
334 the abundance of *D. suzukii* in traps and the cover of the plant species selected in the last  
335 RDA (*i.e.* plant species present in more than 2% of the sampling plots).

336 Univariate analyses were performed with IBM-SPSSv.24.0 (IBM, Armonk, NY, USA)  
337 and multivariate ones with PC-ORD v.7.03 (McCune and Mefford 2016).

338

## 339 **Results**

340

### 341 *Drosophilidae* species abundance and richness

342

343 A total of 91397 individuals belonging to 25 Drosophilidae species were collected in  
344 526 traps (Table 1). Drosophilidae community was largely dominated by two species,  
345 *Drosophila subobscura* (45.33% of the individuals, a mean of 78.77 individuals per trap) and  
346 *Drosophila suzukii* (38.35%, 66.61 individuals per trap). These species sometimes had a very



347 high local population abundance, with a maximum of 2422 individuals of *D. subobscura*  
348 counted in a single trap in forest in May and 1565 individuals of *D. suzukii* in a single trap in  
349 urban park in September. Only four other Drosophilidae species, *Drosophila immigrans*,  
350 *Drosophila kuntzei*, *Drosophila phalerata* and *Drosophila melanogaster*, reached values of  
351 relative abundance above 1% of the total individuals of the study.

352 The distribution patterns of Drosophilidae species were contrasted between habitats  
353 and seasons. *D. subobscura* and *D. suzukii*, were highly represented in urban forest with  
354 respective means of 166.14 and 117.16 individuals per trap (Figure 2 and Supp. Mat. D). *D.*  
355 *subobscura* was permanently present in forest and park (Supp. Mat. E) but showed population  
356 peaks in wooded habitat mainly in spring and autumn (Supp. Mat. F). *D. suzukii* mainly  
357 occurred in urban parks in autumn, took refuge in the forest during the cold season from  
358 November to March, and used riversides in spring and summer (Figure 3). Its peak of  
359 abundance was in September and an important increase of trapped individuals was noted in  
360 December (Supp. Mat. F), probably caused by an ephemeral warming during the sampling  
361 week (Supp. Mat. F). Urban forest was also the preferred habitat of *Drosophila kuntzei*,  
362 *Drosophila immigrans*, *Drosophila phalerata*. *Drosophila phalerata* left the forest for the  
363 riversides from September to November. *Drosophila melanogaster* was more represented  
364 along the riversides and in the town centre and *Drosophila hydei* in urban parks (Supp. Mat.  
365 E). Among the 139 traps placed in fruit stores and houses, we only collected 24 individuals of  
366 *D. suzukii*, which was only present in 7 traps (Supp. Mat. A). It corresponds to 1.6% of the fly  
367 abundance in stores and houses. Given this extremely low abundance of *D. suzukii* in fruit  
368 shops and houses (for comparison, 1565 individuals of *D. suzukii* were counted in a single  
369 trap located in urban park in September) the results were shown in Supp. Mat. A. Fruit shops  
370 and house rooms containing fruit were dominated by *Drosophila melanogaster* (67.83% of  
371 the trapped individuals) and *Drosophila hydei* (18.69%).

372 Drosophilidae species richness averaged  $4.06 \pm 0.13$  species per trap in the whole  
373 study (n=526 traps) and was significantly different between habitats ( $F = 72.496$ ;  $p < 0.001$   
374 between pairs of habitats) with a maximum in forest habitat and a minimum in the town  
375 centre (Figure 4a). A similar variation pattern was observed for Drosophilidae abundance  
376 (mean =  $173.76 \pm 13.20$  individuals per trap) with a decreasing number of Drosophilidae  
377 individual following the urbanization gradient, from the most natural to the most anthropized  
378 habitats ( $F = 39.062$ ;  $p < 0.001$  between habitats; Figure 4b). Numerous environmental  
379 variables influenced Drosophilidae species abundance and diversity (GLMs, Supp. Mat. H).  
380 Drosophilidae species richness increased with local cover of tree and shrub and decreased  
381 with local building density, water in the surrounding landscape and extremely low  
382 temperature during the sampling week. The total abundance of Drosophilidae individuals in  
383 traps increased with variables related to natural habitats, such as tree and shrub species  
384 richness, shrub cover and wood debris, and decreased with urbanization (BUILD, loROAD)  
385 and frost events. The abundance of *D. sukuzii* followed this trend, increasing with local shrub  
386 cover and wood debris and with wood cover at the landscape scale, while decreasing with  
387 road and building density (GLM, Supp. Mat. H). It should be noted that the number of fruit-  
388 bearing plant species (NFRUIT) surrounding traps promoted *D. sukuzii* populations. The  
389 presence of waste did not significantly influence *D. sukuzii* abundance in traps ( $R=0.022$ ,  
390  $p=0.616$ ). Cumulated rain during the sampling week reduced the number of *D. sukuzii*  
391 individual (variable RAINCUMw, Supp. Mat. H), while high temperatures (TEMTOP, Supp.  
392 Mat. H) were favourable to their abundance in the traps.

393

394 *Effect of environment on Drosophilidae community composition*

395

396 In the redundancy analysis (RDA) coupling environment and drosophilidae species  
397 matrices (Figure 5), the eigenvalues of the first two ordering axes explained 38.4% of the data  
398 variance (axis 1 = 22.5%, axis 2 = 15.9%, Monte Carlo test:  $p \leq 0.05$ ). In the ordination  
399 diagrams, the plots formed groups according to habitat (Figure 5b) and season (Figure 5c).  
400 Axis1 opposed samples from the town centre (empty circles) located toward the negative pole  
401 of the axis to the other samples (Figure 5b). The traps from the town centre were associated  
402 with high local road and building covers (variables loROAD and loBUILD, Figure 5a) and  
403 with the species *Drosophila melanogaster*, *Drosophila repleta*, *Drosophila busckii* and  
404 *Drosophila hydei*. Traps located in the most densely wooded areas (SRTree, SHRUB,  
405 LITTER, TREE) and surrounded by fruits (NFRUIT) were associated with *Drosophila suzukii*  
406 toward the positive pole of axis 1. Axis 2 separated traps sampled in the summer period with  
407 negative values on this axis (Figure 5c) from winter and spring samples with positive values.  
408 Most of drosophilidae species were mainly associated with summer samples (*Drosophila*  
409 *phalerata*, *Drosophila kuntzei*, *Drosophila funebris*, *Drosophila immigrans*, Figure 5a), while  
410 only a few species (*Drosophila tristis*, *Drosophila subobscura*) responded positively to frost  
411 and rain conditions (NFROTS, RAINCUMw), two meteorological characteristics typical of  
412 the winter season (see meteorological conditions recorded during the sampling periods, Supp.  
413 Mat. G).

414

#### 415 *Relationships between plant and Drosophilidae communities*

416

417 In the RDA examining the relationships between plant and Drosophilidae communities  
418 (Figure 6), axis1 captured 16.4% of the variance of the data set, while axis2 captured 10.1%  
419 of the variance (total for the first two ordering axes: 26.5%; Monte Carlo test:  $p \leq 0.05$ ). The

420 negative part of axis 1 was characterized by a group of Drosophilidae species (*Drosophila*  
421 *busckii*, *Scaptodrosophila rufifrons*, *Drosophila funebris*, *Drosophila immigrans*, *Drosophila*  
422 *simulans*, Figure 6a) associated with relatively open habitats (park and riverside, Figure 6c)  
423 characterized by grasses (*Lolium perenne*, *Festuca rubra*, *F. pratensis*), plants indicator of  
424 disturbed soil (*Polygonum aviculare*, *Plantago major*, growing on bare and trampled soil of  
425 paths), ornamental and planted trees (*Prunus laurocerasus*, *Malus sylvestris*) and wetland  
426 plant species (*Salix alba*, *Populus* sp., *Agrostis stolonifera*, Figure 6b). Isolated at the positive  
427 pole of axis 1 (Figure 6a), *Drosophila suzukii* was associated with open forest habitats  
428 colonized by the liana *Hedera helix* climbing on shrubs and trees (Hed.helS and Hed.helT in  
429 Figure 6b) and characterized by a dense shrub layer hosting numerous saplings (*Acer*  
430 *pseudoplatanus*, *Fraxinus excelsior*, *Prunus avium*, *Viburnum lantana*) and common forest  
431 herbs (*Geum urbanum*, *Carex sylvatica*). The second ordination axis isolated a large group of  
432 Drosophilidae species on its negative part (incl. *Drosophila hydei*, *Drosophila melanogaster*,  
433 *Drosophila subobscura*, *Drosophila bifasciata*, *Drosophila tristis*, Figure 6a) associated with  
434 grassland plant species (*Arrhenatherum eliatum*, *Poa trivialis*), some of them showing  
435 adaptation to mowing (rosette, stoloniferous and prostrated plants: *Taraxacum officinale*,  
436 *Plantago lanceolata*, *Bellis perennis*, *Trifolium repens*) or to soil disturbances (annual plants:  
437 *Poa annua*, *Stellaria media*), and with a group of nitrophilous plants (*Urtica dioica*, *Galium*  
438 *aparine*, *Anthriscus sylvestris*, *Heracleum spondylium*, Figure 6b). The Drosophilidae species  
439 grouped toward the positive pole of axis 2 (*Hirtodrosophila confusa*, *H. cameraria*,  
440 *Drosophila phalerata*, *Drosophila kuntzei*, *Chymomyza amoena*) were associated with closed  
441 forest habitats dominated by *Acer pseudoplatanus* in the tree layer, *Crataegus monogyna* and  
442 *Sambucus nigra* in the shrub layer and characterized by a herb layer colonized by brambles  
443 (*Rubus caesius*, *R. fruticosus*) under which a dense carpet of creeping *Hedera helix* (a shade  
444 tolerant species) was spreading.

445           The Spearman correlations between the abundance of *Drosophila suzukii* and the  
446 cover of plant species significantly varied between seasons (Supp. Mat. Ia). *Drosophila*  
447 *suzukii* was strongly and positively correlated with *Acer pseudoplatanus* trees (Ace.pseT)  
448 during the major part of the year and with *Acer pseudoplatanus* in shrub and herb layers only  
449 during the cold periods from October to March. *Drosophila suzukii* also took refuge in sites  
450 with a large canopy of the liana *Hedera helix* climbing on trees and shrubs (Hed.helT,  
451 Hed.helS) or spreading on the ground (Hed.helH) during the cold months from November to  
452 March and also in summer (Hed.helT and Hed.helS in August). Several other forest herbs  
453 forming evergreen tussocks or rosettes (*Carex sylvatica*, *Geum urbanum*) and shrubs with a  
454 branchy canopy (*Crataegus monogyna*, *Ribes rubrum*, *Sambucus nigra*, *Ulmus minor*)  
455 attracted the fly during the cold season. For some plant species, their cover was significantly  
456 correlated with the fly abundance only during their flowering period (vernal geophytes: *Arum*  
457 *maculatum*, *Ranunculus ficaria*) or their fruiting period (*Cornus sanguinea*, *Rubus*  
458 *fruticosus*). The bramble *Rubus caesius* attracted the fly both in the cold seasons and during  
459 its fruiting period.

460           Numerous plant species were negatively correlated with the abundance of *Drosophila*  
461 *suzukii* (Supp. Mat. Ib). *Drosophila suzukii* avoided plant species typical of open habitats such  
462 as grassland species (grasses: *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca rubra*,  
463 *Holcus lanatus*, *Lolium perenne*), species indicator of mowing and/or trampling (rosette or  
464 stoloniferous species: *Bellis perennis*, *Plantago lanceolata*, *Taraxacum officinale*, *Trifolium*  
465 *repens*), disturbed soils (therophytes: *Capsella bursa-pastoris*, *Cardamine hirsuta*, *Conyza*  
466 *canadensis*, *Lapsana communis*, *Mercurialis annua*, *Poa annua*, *Stellaria media*, *Veronica*  
467 *persica*), nutrient-rich soils (nitrophilous/ruderal species: *Anthriscus sylvestris*, *Artemisia*  
468 *vulgaris*, *Galium aparine*, *Heracleum sphondylium*, *Urtica dioica*) and hygrophilous species  
469 (*Agrostis stolonifera*, *Angelica sylvestris*, *Carex acutiformis*, *C. hirta*, *Populus* sp., *Salix* sp.).

470

471 *Seasonal variations in Drosophila suzukii morphs and wing size*

472

473         The proportions of summer, intermediate and winter morphs of *D. suzukii* showed  
474 continuous and gradual variations along the year (Figure 7). Summer morph appeared in May  
475 and disappeared after November with a peak in July and August. Winter morph was observed  
476 from October to May with a maximum in February. Several centimetres of snow were  
477 covering the ground during the sampling week of February and *D. suzukii* was still present in  
478 the traps; individuals were even observed walking in patches of sun light on tree trunks and  
479 flying around the traps in forest habitat.

480         The abundance of summer and dark morphs of *D. suzukii* responded to different  
481 environmental variables in GLMs (Supp. Mat. H). The abundance of summer morph  
482 individuals increased with shrub cover, species richness in fleshy fruit-bearing plant and high  
483 temperature and decreased with local building density. Dark morph (=intermediate + winter  
484 morph) was promoted by wood and garden cover in the landscape, local shrub and wood  
485 debris cover, frost events and was negatively affected by local building density.

486         The Wing Area Indices of female and male *D. suzukii* both increased during the cold  
487 season and decreased in summer, showing a bell-shaped curve over the course of the year  
488 (Figure 8). The Wing Area Indices of males (mean =  $2.587 \pm 0.011$  mm<sup>2</sup>, n = 1332) were  
489 lower compared to that of females (mean =  $3.212 \pm 0.012$  mm<sup>2</sup>, n = 1505). The wing size was  
490 also significantly different between morph categories and increased from summer to  
491 intermediate and winter morphs (Supp. Mat. J) in females ( $F = 90.456$ ,  $p < 0.001$ ,  $ddl = 2$ ) and  
492 males ( $F = 104.159$ ,  $p < 0.001$ ,  $ddl = 2$ ). Very few environmental variables were found to  
493 explain these variations in GLMs (Supp. Mat. H). The wing size of both females and males

494 decreased with high temperature during the sampling week. Only tree species richness was  
495 positively associated with female wing size. This corroborated the variation patterns of Wing  
496 Area Indices between habitats: the wing size was significantly different between habitat types  
497 (Supp. Mat. K) in females ( $F = 10.739$ ,  $p < 0.001$ ,  $ddl = 3$ ) and males ( $F = 3.108$ ,  $p = 0.026$ ,  
498  $ddl = 3$ ). Both sexes exhibited lower Wing Area Index in the most urbanized habitat (town  
499 centre) compared to the most densely vegetated habitat (forest).

500

## 501 **Discussion**

502

503 The present study sheds light on the role of local and landscape factors shaping the  
504 diversity and composition of a Drosophilidae community invaded by *Drosophila suzukii* in  
505 urban environment. We found that (i) Drosophilidae species richness and abundance were  
506 negatively impacted by urbanization and the degree of habitat anthropization, (ii) two species,  
507 including *D. suzukii*, dominated the Drosophilidae community, (iii) Drosophilidae species  
508 differed in their response to urbanization and environmental variables, (iv) seasonal variations  
509 in meteorological variables were major factors driving community composition and richness,  
510 (v) *D. suzukii* moved between habitats and between plant species according to seasons and  
511 (vi) *D. suzukii* showed contrasted traits between cold and hot periods.

512

### 513 *Drivers of Drosophilidae species richness and abundance in urban environment*

514

515 Insect species richness and abundance are commonly described as the result of an  
516 equilibrium between the effects of local and landscape variables (Shackelford et al. 2013;

517 Picchi et al. 2016; Adams et al. 2020), local variables having generally a stronger effect on  
518 diversity during overwintering (Sarhou et al. 2014). In this study, we showed that  
519 Drosophilidae species richness and abundance abruptly declined along the urbanization  
520 gradient, from the most natural habitats to town centre. Thus, these two diversity metrics  
521 could be used as valuable indicators of habitat degradation associated with urbanization; and  
522 in particular Drosophilidae abundance, which is a measure easy to acquire.

523 Behind this urbanization gradient negatively impacting Drosophilidae species richness  
524 and abundance, a set of environmental variables were involved both at local and landscape  
525 scales. Drosophilidae species richness was negatively affected by the density of building in  
526 the very close vicinity of the trap, while it increased with shrub and tree covers. The  
527 predominance of impervious surfaces at the expense of vegetated ones reduces the  
528 opportunity for arthropods to find trophic resources, reproduction sites and shelters (Fenoglio  
529 et al. 2020). The atmospheric pollution associated with urbanization has also been  
530 demonstrated to cause significant genetic damage in the organisms of *Drosophila* (de Santana  
531 et al. 2018) and may be another component of the urban hostility for this taxonomic group.  
532 Drosophilidae abundance followed the same pattern as species richness, decreasing with local  
533 building and road density and increasing with shrub cover. Nevertheless, Drosophilidae  
534 abundance was also sensitive to plant species richness in shrub and tree layers. These two  
535 vegetation layers harbor several fleshy-fruited host plants (*Ribes rubrum*, *Rubus fruticosus*, *R.*  
536 *caesius*, *Sambucus nigra*, *Prunus* sp., etc.) and varied plant families whose diversity increases  
537 the diversity of potential feeding and breeding substrates for drosophila, *i.e.* the diversity of  
538 nectars and fruits, two major elements of drosophila diets (Poyet et al. 2015; Tochen et al.  
539 2016). Wood debris also promoted Drosophilidae abundance in our study. Dead trees and  
540 decaying branches host many fungus sporophores consumed by drosophila (Kearney 1983;  
541 Shorrocks & Charlesworth 1980). Wood debris can also serve as microhabitat as they hide a



542 labyrinthic network of holes and galleries commonly used by a wide range of insects  
543 (Sandström et al. 2019).

544         At the landscape scale, Drosophilidae abundance decreased with the proportion of  
545 building. The dominance of building in the landscape increases the physical isolation of  
546 patches of natural habitats in a hostile matrix in accordance with the theory of island  
547 biogeography (MacArthur and Wilson 1967) applied to urban terrestrial habitats (Bode &  
548 Maciejewski 2014; Fattorini et al. 2018). This mineral urban matrix composed of asphalt and  
549 concrete is devoid of food and shelter for most insect species that may impede their  
550 movement (Bode and Maciejewski 2014) and limit the connectivity between wooded patches  
551 (Beninde et al. 2015). The cover of water body also increased the proportion of hostile abiotic  
552 element in the landscape, contributing to the decrease in Drosophilidae abundance and  
553 richness in the study. The covers of both buildings/roads and water form abiotic patches in the  
554 landscape mosaic, the first being artificial structures made of concrete and the second a  
555 natural liquid area. These two landscape features share two common characteristics from an  
556 insect perception: they lack from food resources for flies and are even hostile elements due to  
557 the lethal risk of drowning for insects in water or being hit by car traffic on road. These two  
558 abiotic landscape elements had convergent negative effect on fly populations and diversity in  
559 our study.

560

### 561 *Community composition*

562

563         The Drosophilidae community was largely dominated by two species, the native *D.*  
564 *subobscura* and the invasive pest *D. suzukii*, in the present study. *D. suzukii* was the second  
565 dominant Drosophilidae species, whatever the habitat considered (Table 1). Thus, urban areas

566 and their mosaic of habitat clearly play a role of reservoir of *D. suzukii* and may become a  
567 potential source of infestation to nearby agricultural fields. This dominance of *D. subobscura*  
568 and *D. suzukii* in the Drosophilidae community is consistent with several other works  
569 conducted in France, in vineyards (Delbac et al. 2020) and in large and ancient forest (Poyet  
570 et al., 2014). In urbanized areas of Alabama, USA, *D. suzukii* was not noticed a dominant  
571 species, being the fifth most abundant Drosophila of the study (Bombin & Reed, 2016). *D.*  
572 *subobscura* was absent in that collection, given this species is exotic in USA. Based to the  
573 hierarchical continuum concept (Deconninck et al. 2024), our results show that *D. suzukii* can  
574 be considered as a core species structuring the adult Drosophilidae communities. Its  
575 dominance can be partly explained by the match between its high polyphagia and the high  
576 diversity of suitable fleshy fruits in the region (about half of them are used by the fly; Poyet et  
577 al. 2015). *D. suzukii* and *D. subobscura* are generally codominant species in wild fruit of  
578 natural habitats (Poyet et al. 2014). On the contrary, in suboptimal or decaying fruit, *D.*  
579 *suzukii* becomes a satellite species with a low effect on fruit fly community at the larval stage  
580 (Deconninck et al. 2024). An exotic species integrating a native community may have  
581 negative, neutral or positive influences on resident species. A question then arises: how these  
582 two dominant species successfully coexist over the course of a year? Niche partitioning in  
583 terms of resource requirements and temporal use could help explaining this durable  
584 coexistence (Finke and Snyder 2008). The first dominant species *D. subobscura* is known to  
585 have no impact on the oviposition activity of *D. suzukii* (*i.e.* a neutral effect, Ulmer et al.  
586 2021) and the two Drosophila are complementary species in the use of trophic resources  
587 (Poyet et al. 2014): *D. suzukii* pierces the skin of ripening fruits hanging on trees, and creates  
588 scars on them, enabling pathogens to enter the fruit and make it rot and fall prematurely. This  
589 benefits *D. subobscura* females that lay their eggs on rotting fruits fallen on the ground after  
590 their infestation by *D. suzukii* (Poyet et al. 2014). This facilitation process through temporal

591 partitioning of their larval trophic niche may explain the success of their coexistence  
592 (Atkinson 1979; Nunney 1990) and their shared dominance in the flying adult community in  
593 the aerial compartment of the ecosystem.

594 In the present study, landscape and local variables had strong effects on Drosophilidae  
595 community composition, but different effects on different taxa. This phenomenon of divergent  
596 responses of taxa to urbanization have already been reported in other groups of insects  
597 (Persson et al. 2020). The large majority of Drosophilidae species preferred urban forest and  
598 park habitats in the landscape and thus positively responded to the natural elements at local  
599 scale (litter cover, covers of the three vegetation layers, diversity of fruiting plants). Only  
600 *Drosophila melanogaster* was more abundant in the town centre, in fruit shops and houses  
601 and in other sites dominated by buildings and roads. The preference of *D. melanogaster* for  
602 urbanized environments had already been observed by Avondet et al. (2003) who mostly  
603 trapped the species in the business district and apartments. *D. melanogaster* is maybe the most  
604 commensal *Drosophila* of human; the disappearance of wild behaviour in favour of domestic  
605 behaviour in its worldwide population could date back more than 10 millennia (Lachaise and  
606 Silvain 2004). Although *D. suzukii* was highly associated with natural features and in  
607 particular wooded elements of the landscape, it remained the second most abundant species in  
608 the town centre. Given the recent nature of its invasion and association with human  
609 productions, habitats, tourism and traffic axes (Cini et al. 2014; Lavrinienko et al. 2017), this  
610 invasive species could also be on the way to domestication.

611

612 *Meteorological variables*

613

614 Meteorological patterns, that determine seasons along the year, were major factors  
615 driving variations in Drosophilidae community richness and composition in our study. The  
616 number of frost days and the minimum temperature reached during the week of sampling  
617 negatively affected the richness of Drosophilidae species trapped; frost days also affecting  
618 their abundance. This reduction of activity with decreasing temperature is well known in  
619 flying insects (Welti et al. 2022) and particularly in drosophila species whose population  
620 fluctuations (Ørsted et al. 2021) and oviposition frequency (Zerulla et al. 2017) are highly  
621 sensitive to thermal extremes. Variations in temperature and precipitation also explained the  
622 second gradient of Drosophilidae community composition in multivariate analyses. Most  
623 species were abundant during the hottest weeks (*Drosophila immigrans*, *D. phalerata*, *D.*  
624 *kuntzei*, *Chymomyza amoena*, etc.) and only a few species were associated with frost days and  
625 weekly precipitations (*Drosophila tristis*, *D. subobscura*, *D. bifasciata*). This seasonal  
626 organization of the activity of these two functional groups of Drosophilidae may increase their  
627 temporal complementarity in the use of resources and reduce competition (Nunney 1990).  
628 Indeed, a higher quantity of fresh food sources or oviposition sites (nectar, sap, fruit) is  
629 available in the warmest seasons up to early autumn but this food is to share between a high  
630 number of competing *Drosophila* species. The second group of species occurring mainly in  
631 winter and mid-seasons, including *D. subobscura* whose larvae are known to be poor  
632 competitors (Budnik and Brncic 1983) and feeding from rotting organic matter and  
633 mushrooms (Shorrocks and Bingley 1994), may escape pre-imago competition with the major  
634 pool of congeneric species. Given the high number of traps (>500) and their random  
635 distribution in each habitat each month, it was not possible to get continuous and individual  
636 microclimatic data for each trap, which is a limit of the study. These microclimatic data could  
637 have helped to better understand the thermal sheltering role of each habitat (Deconninck et al.

638 2024; Graae et al. 2012), and the reasons for changes in the distribution of flies between  
639 habitats over the seasons.

640

#### 641 *Drosophila suzukii* ecological cycle in urban environment

642

643 The description of chronological relationships between *Drosophila suzukii* populations  
644 and habitats, environmental variables and plant species for a whole year allowed us to  
645 reconstruct its ecological and seasonal cycle in urban area. A major observation was that *D.*  
646 *suzukii* was moving from a habitat to another between seasons to find resources for feeding or  
647 ovipositing and shelters for overwintering or escaping summer heats. In their study, Ulmer et  
648 al. (2022) showed that fruit infestation rates by *D. suzukii* responded to natural habitat cover  
649 in a 100 m radius around sampling sites. This corroborates our results indicating a positive  
650 effect of forest cover on *D. suzukii* abundance (Supp. Mat. H) within the same radius of 100  
651 m. This 100 m-distance of habitat influence also corresponds to the daily flight capacity of *D.*  
652 *suzukii*: flies are able to move daily between neighbouring habitats, driven by temperature,  
653 humidity and the presence of alternative hosts (Tait et al. 2020), limiting their movements to  
654 distances of less than 100 m (experimental measures from Vacas et al. (2019)). However,  
655 long-distance dispersal has also been reported (Tait et al. 2018; Vacas et al. (2019) and the  
656 spatial scale of habitat influence on drosophila species varies between studies and between  
657 habitat types. For example, Deconninck et al. (2024) showed an influence of building cover  
658 on Drosophilidae abundance within a radius of 50 m. Thus, 100 m distance/radius scale seems  
659 to be particularly appropriated for studying the effect of landscape elements on this fly in an  
660 urban environment.

661 In spring, *D. suzukii* was associated with a set of flowering plants present in urban  
662 forest and park. These spring blossoms may provide a food source for *D. suzukii* (Tochen et  
663 al. 2016) in habitats that are generally devoid of fruits at this period of the year (Poyet et al.,  
664 2015). Floral nectars are rich in sugars (Nicolson and Thornburg 2007) and contribute to *D.*  
665 *suzukii* survival in laboratory condition (Tochen et al. 2016) and probably in the field (Poyet  
666 et al., 2015; Wiman et al., 2016). From early spring to the end of summer, *D. suzukii*  
667 frequented riversides. Here, the fly may benefit from the cooling effect of water streams in  
668 urban areas (Murakawa et al. 1991) and the higher atmospheric humidity they produce, as the  
669 fly is very sensitive to dryness (Eben et al. 2018). Maceda-Veiga et al. (2021) also found a  
670 positive correlation between *D. suzukii* populations and the proximity of river streams in the  
671 hot season. In the summer period, *D. suzukii* continued to shelter under the canopy of *Acer*  
672 *pseudoplanus* shrubs and trees and the liana *Hedera helix*, probably to protect from heat  
673 waves, deleterious for its fertility (Green et al. 2019). Indeed, the understory vegetation of  
674 forest habitats of the region is known to reduce extreme hot temperatures of summer  
675 compared to forest outside (Graae et al. 2012; Zellweger et al. 2019). This buffering effect of  
676 high regional temperatures by forest ecosystems is well documented in France (Gril et al.  
677 2023) and in the Amiens region (Graae et al. 2012). Vegetation structure, dead wood debris  
678 and litter creates favorable microclimates in the understory vegetation benefiting many insect  
679 species (Scheffers et al. 2014; Kotze et al. 2022). In the summer and the first part of autumn,  
680 *D. suzukii* was associated with fruiting plants. Indeed, the peak of host fruit diversity is  
681 reached in October in Amiens region (Poyet et al., 2015). From November to March, *D.*  
682 *suzukii* took refuge in forest for overwintering and in particular in sites with a dense cover of  
683 brambles, shrubs and dead wood fragments on the ground. The fly was even trapped and  
684 observed in activity in this forest habitat in a week of February when the ground was covered  
685 by several centimetres of snow and the maximum temperatures recorded in the week did not

686 exceed 6°C and the minimum temperatures reached -5°C (mean week temperature = 1.3°C).  
687 Active *D. suzukii* were also observed under low temperature condition in the South of France  
688 (Ulmer et al., 2022) suggesting that its low thermal thresholds are probably overestimated.  
689 This resistance to very low temperatures could suggest an adaptation of populations;  
690 nevertheless, flies are already known to be able to recover from chill coma after 24h exposure  
691 to -1°C (Wallingford et al. 2016). Beyond this chronological organisation of *D. suzukii* along  
692 seasons, urbanization (through local density of road and building) remained the major factor  
693 negatively affecting the abundance of *D. suzukii* while the cover of wooded habitat was the  
694 main landscape-scale variable promoting its populations. These results corroborates those of  
695 other studies (Santoiemma et al. 2018; Ulmer et al. 2022). As for many other insect species,  
696 these isolated wooded elements probably act as stepping stone islands (Be et al. 2017) aiding  
697 the spread and persistence of the fly through the landscape.

698

#### 699 *Seasonal polyphenism of spotted-wing Drosophila*

700

701 Wing size and body pigmentation in insects are two traits commonly used to assess  
702 their fitness and explain their adaptation to varying environmental conditions (Crill et al.  
703 1996; Gilchrist and Huey 2004). Because of the correlation between life trait variables, wing  
704 size is often used as a proxy of body size and even sometimes body weight (Cavicchi et al.  
705 1985; Abbott et al. 2010). In the present study, wing size of *D. suzukii* was higher during cold  
706 periods. This result is congruent with the ecological generalizations of the rules of Bergmann  
707 and Rensch (Bergmann 1847; Rensch 1938) applied at the intra-specific level (Meiri, 2011).  
708 Differences in size are mediated by differences in development times, with the larger body  
709 developing for a proportionately longer time. In arthropods, and particularly among

710 *Drosophila* species, development time increases with lower temperature (Schlesener et al.  
711 2020), explaining the negative correlation between temperature and body size (Jalal et al.  
712 2015) and why larger individuals are found at higher latitudes, elevations or in colder  
713 climates, or even, as it is our case here, in the colder seasons. In our study, *D. suzukii* larvae  
714 developing in fruits in October or November and producing imago emerging a few weeks  
715 before winter, experienced lower temperature than summer larvae. Traits variation are  
716 generally related to variation in functionality, and thus wing plasticity may possibility have an  
717 adaptive value. In the study of Fraimout et al. (2018), developmental temperature was found  
718 to affect wing morphology and consequently flight performances (speed and acceleration) in  
719 *D. suzukii*, the fastest flies being found at the lowest temperature. Winter flies should be able  
720 to move rapidly from a site to another, should avoid spending too long time flying under cold  
721 conditions and finally should spare energy. In the present study, wing size of *D. suzukii* was  
722 larger in female individuals than in male individuals. The size difference observed between  
723 male and female is consistent with the sexual dimorphism usually reported in Diptera (Reis et  
724 al. 2021) and also known in *D. suzukii* (Tran et al. 2020). This could be explained by a  
725 fundamental difference in the way males and females manage their energy budget. Wing size  
726 may be the result of selection toward sex-specific fitness optima (Sztepanacz and Houle  
727 2021). In contrast, for one sex, several studies suggest that natural variation in wing size is  
728 caused by a combination of genetic and environmental factors. Indeed, an increase of wing  
729 size with lower temperatures has been observed on vinegar flies of both sexes (Hoffmann et  
730 al. 2003; Fraimout et al. 2018; Koch et al. 2020; Jardeleza et al. 2022). It has been suggested  
731 that this increase in wing size observed in *D. suzukii* winter morphs, in winter conditions,  
732 could be related to scarcer resources (mate, food) involving longer flight times (Jardeleza et  
733 al. 2022). Wing shape has also been shown to vary in *D. suzukii* depending on the species of  
734 its host plant during larval development, as demonstrated by Pajač Živković et al. (2018) who



735 observed narrower wings in flies grown in strawberries and wider wings in for flies grown in  
736 grapes. The different types of fruits available in the different seasons could therefore have  
737 also influenced the wing size of *D. suzukii* morphs. The same environmental factors (fruiting  
738 plant composition and temperature variations) could also explain the differences in wing size  
739 between habitats in relation with the urbanization gradient (Mat. Suppl. E). Indeed, wooded  
740 habitat are a major source of fruit suitable for the development of *D. suzukii* (Poyet et al.  
741 2015) while, at the opposite, urban environment conditions are well-known to negatively  
742 affect the fitness of insect species (Fenoglio et al. 2021).

743 Darker cuticle pigmentation has been hypothesized to be involved in thermoregulation of  
744 ectotherms in cold environments, resulting in increased ultraviolet absorption and increased  
745 ability to warm up (Trullas et al. 2007). Shearer et al., (2016) showed that laboratory-  
746 simulated winter-like photoperiod and temperature conditions induced higher levels of  
747 melanization and larger wing size in *D. suzukii* and that these physiological characters were  
748 associated with an increase in cold-tolerance. As we found that wood areas represented  
749 possible refuges for *D. suzukii* in the winter, one could also hypothesize that darker winter  
750 morphs may benefit the flies in terms of camouflage in areas dominated by dead wood and  
751 decomposing leaves.

752

753 *Toward the use of ecological indicators to manage D. suzukii populations*

754

755         Knowing where and when *D. suzukii* is present in different habitats is essential for  
756 designing management strategies of the pest. In the field, several easy-to-measure variables  
757 related to ecosystem composition (identity and abundance of plant species), structure (cover  
758 of vegetation layers) or functioning (litter, dead wood debris) can be used as ecological

759 indicator of the presence of the fly. Microclimatic dataloggers placed both on the ground and  
760 in the tree canopy of urban forests and parks could also contribute our understanding of the  
761 small-scale spatial dynamics of *D. suzukii* populations in the vertical structure of the  
762 vegetation (Deconninck et al. 2024). Once the risk is evaluated in the field, a subsequent step  
763 in the strategy of *D. suzukii* control could consist, for example, in managing the expansion of  
764 over-dominant plants sheltering or feeding the fly at the appropriate moment of the year or  
765 favouring the presence of predators in microhabitats used by the fly (Ulmer et al. 2021).

766         Among the wide set of plant species recorded in the study, the liana *Hedera helix* (ivy)  
767 was one of the most strongly associated with *D. suzukii*. The fly sheltered in sites with dense  
768 canopy of *H. helix* during periods of the most extreme temperatures in both winter and  
769 summer. *H. helix* is also known to produce a large amount of nectar in autumn (Timberlake et  
770 al. 2021) that can help *D. suzukii* to prepare to the cold season (Poyet et al., 2015). Moreover,  
771 Grassi et al. (2018) also found that ivy berries can serve as an alternative but suboptimal non-  
772 crop host during the late dormant period for the fly. Thus, this plant may contribute to fulfil  
773 three major vital functions for the fly by providing shelter, food and breeding substrate. *H.*  
774 *helix* is considered as one of the most aggressive native plant species that may impact the  
775 plant richness of native woodlands by becoming ‘over-dominant’ (Marrs et al. 2013). Its  
776 abundance significantly increased in European forests over the last 50 years, as a consequence  
777 of temperature increase and a reduction in severe frost events accompanying climate change  
778 (Heinrichs and Schmidt 2015; Perring et al. 2020). As a consequence, this liana is likely to  
779 become more and more influential on the persistence of *D. suzukii* through time with climate  
780 change. A better management of *H. helix* expansion (often neglected) appears to be primordial  
781 in urban areas, in particular to reduce the number of overwintering microsites available to *D.*  
782 *suzukii*. Other plants attracted the fly during overwintering and hot periods and played a  
783 similar role as ivy did. It is the case of brambles (*Rubus* sp.) and young saplings and shrubs of

784 *Acer pseudoplatanus*. In general, a dense shrub layer, whatever its species composition, is a  
785 good indicator of the presence of *D. suzukii*.

786 Plant communities containing fleshy-fruited plants providing food and oviposition  
787 sites to *D. suzukii* in summer and early autumn are also key elements in the persistence of the  
788 fly in urban areas. Nevertheless, the fruits of these plants also feed a diversified community of  
789 birds (Pesotskaya et al. 2020) and mammals (Godó et al. 2022), and their elimination would  
790 threaten the biodiversity in invertebrates and is not recommended. One solution that could  
791 divert the pest away from infesting the fruits of wild plants would be to use a dead-end trap  
792 plant (Ulmer et al. 2020). These trap plants, attractive to *D. suzukii* gravid females searching  
793 oviposition sites while being lethal for its offspring, could be integrated in hedgerows of  
794 urban gardens and parks susceptible to *D. suzukii* invasion.

795 Abiotic elements of the ecosystem such as litter and dead wood debris are also  
796 ecological indicators strongly associated with the presence of *D. suzukii*. This decaying plant  
797 matter is a major component of ecosystem functioning and contributes to overall diversity by  
798 supporting fungi and insects that feed on it and/or live in it (Jabin et al. 2004). We suggest to  
799 maintain these dead wood debris to promote the diversity of local predators and competitors  
800 of *D. suzukii* in these sites as recommended by Ulmer et al. (2021). Nevertheless, nest boxes  
801 for insectivorous birds and bats, known to consume *D. suzukii* (Dekeukeleire et al. 2020),  
802 could also be installed in risk areas to prevent outbreak of the pest (Garfinkel and Johnson  
803 2015).

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## **Competing Interests**

The authors have no relevant financial or non-financial interests to disclose.

## **Author Contributions**

Romain Ulmer, Aude Couty, Patrice Eslin and Olivier Chabrerie contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors. The first draft of the manuscript was written by Romain Ulmer, Aude Couty, Patrice Eslin and Olivier Chabrerie and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

## TABLES

**Table 1** Abundance of Drosophilidae species in the study. N ind: total number of individuals trapped, Max: maximum number of individuals per trap, Min: minimum number of individuals per trap, Mean: mean number of individuals per trap, SE: standard error, %: percentage of individuals trapped.

Species	Code	Total study (526 traps)					
		N ind	Min	Max	Mean	SE	%
<i>Chymomyza amoena</i>	Chy.amo	4	0	2	0.008	0.005	0.004
<i>Drosophila bifasciata</i>	Dro.bif	123	0	15	0.234	0.061	0.135
<i>Drosophila busckii</i>	Dro.bus	325	0	21	0.618	0.095	0.356
<i>Drosophila funebris</i>	Dro.fun	128	0	7	0.243	0.039	0.140
<i>Drosophila helvetica</i>	Dro.hel	1	0	1	0.002	0.002	0.001
<i>Drosophila hydei</i>	Dro.hyd	720	0	45	1.369	0.162	0.788
<i>Drosophila immigrans</i>	Dro.imm	5083	0	627	9.663	1.791	5.561
<i>Drosophila kuntzei</i>	Dro.kun	4496	0	910	8.548	2.700	4.919
<i>Drosophila melanogaster</i>	Dro.mel	1325	0	96	2.519	0.352	1.450
<i>Drosophila obscura</i>	Dro.obs	1	0	1	0.002	0.002	0.001
<i>Drosophila phalerata</i>	Dro.pha	1794	0	327	3.411	0.848	1.963
<i>Drosophila repleta</i>	Dro.rep	67	0	6	0.127	0.025	0.073
<i>Drosophila simulans</i>	Dro.sim	94	0	9	0.179	0.038	0.103
<i>Drosophila subobscura</i>	Dro.sub	41433	0	2422	78.770	7.965	45.333
<i>Drosophila sukuzii</i>	Dro.suz	35053	0	1565	66.641	7.114	38.352
<i>Drosophila testacea</i>	Dro.tes	1	0	1	0.002	0.002	0.001
<i>Drosophila transversa</i>	Dro.tra	7	0	4	0.013	0.008	0.008
<i>Drosophila tristis</i>	Dro.tri	551	0	28	1.048	0.133	0.603
<i>Gitona distigma</i>	Git.dis	8	0	2	0.015	0.006	0.009
<i>Hirtodrosophila cameraria</i>	Hir.cam	7	0	2	0.013	0.006	0.008
<i>Hirtodrosophila confusa</i>	Hir.con	27	0	3	0.051	0.014	0.030
<i>Leucophenga maculata</i>	Leu.mac	8	0	2	0.015	0.006	0.009
<i>Phortica semivirgo</i>	Pho.sem	2	0	1	0.004	0.003	0.002
<i>Phortica variegata</i>	Pho.var	9	0	2	0.017	0.006	0.010
<i>Scaptodrosophila rufifrons</i>	Sca.ruf	130	0	13	0.247	0.045	0.142
<b>Total</b>		<b>91397</b>					

## FIGURES

**Fig. 1** Proportion of land covers around sampling traps (radius = 100 m) located in the four urban habitats studied in Amiens city: urban forest (FOREST), park (PARK), riverside (RIVER) and town centre (TOWN). Legend of land covers: BUILD: building, SOIL: bare soil, ROAD: road and car park, PATH: path, HSTRIP: herbaceous strip, WATER: water, HEDGE: hedgerow, GARDEN: private garden, CROP: crop (cereals), GRASS: grassland, WOOD: wooded area

**Fig. 2** Relative abundance of the 14 most abundant Drosophilidae species in the four urban habitats of Amiens city. Numeric values of total number of individuals trapped, maximum, minimum, mean number of individuals per trap and per habitat are given in Suppl. Mat **X**.

**Fig. 3** Seasonal distribution of *Drosophila suzukii* individuals among the different urban habitats (X-axis: months from September 2018 to August 2019; Y-axis: relative abundance of individuals between habitats for each month)

**Fig. 4** Mean Drosophilidae species richness (a) and abundance (b) per trap ( $\pm$ SE) in the four urban habitats sampled. Forest: n= 135, park: n = 134, riverside: n = 128, town centre: n = 129. Significant differences were found in Drosophilidae species richness ( $F = 72.496$ ;  $p < 0.001$  between pairs of habitat) and abundance ( $F = 39.062$ ;  $p < 0.001$ ) between habitats

**Fig. 5** Redundancy analysis (RDA) coupling environment and Drosophilidae species matrices. (a) Diagram of Drosophilidae species (lowercase letters) and environmental variables (capital letters), (b) Diagram of plots grouped by habitats and (c) grouped by seasons. Only the most significant environmental variables are shown (cutoff  $r^2$  value = 0.1)

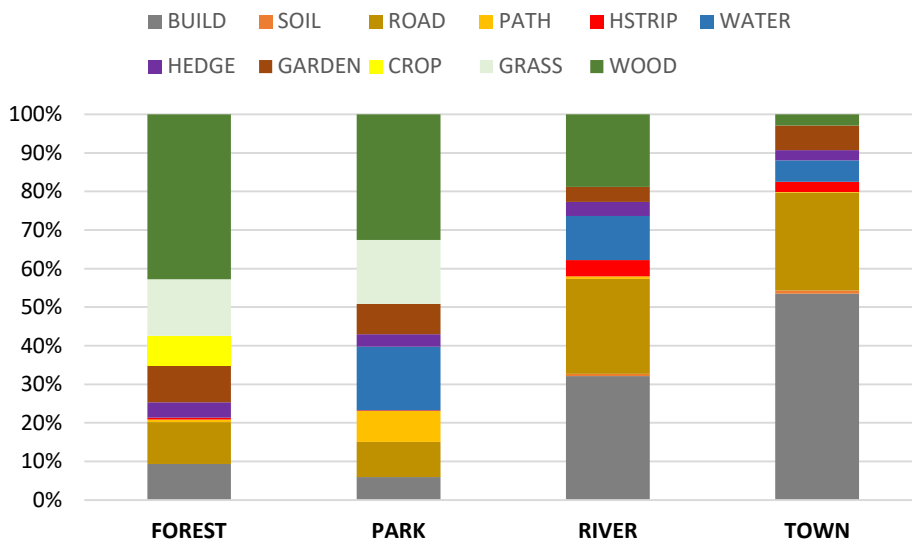


**Fig. 6** Redundancy analysis (RDA) coupling plant and Drosophilidae species matrices. (a) Diagram of Drosophilidae species, (b) Diagram of plant species. Only the most significant environmental variables are shown (cutoff  $r^2$  value = 0.1)

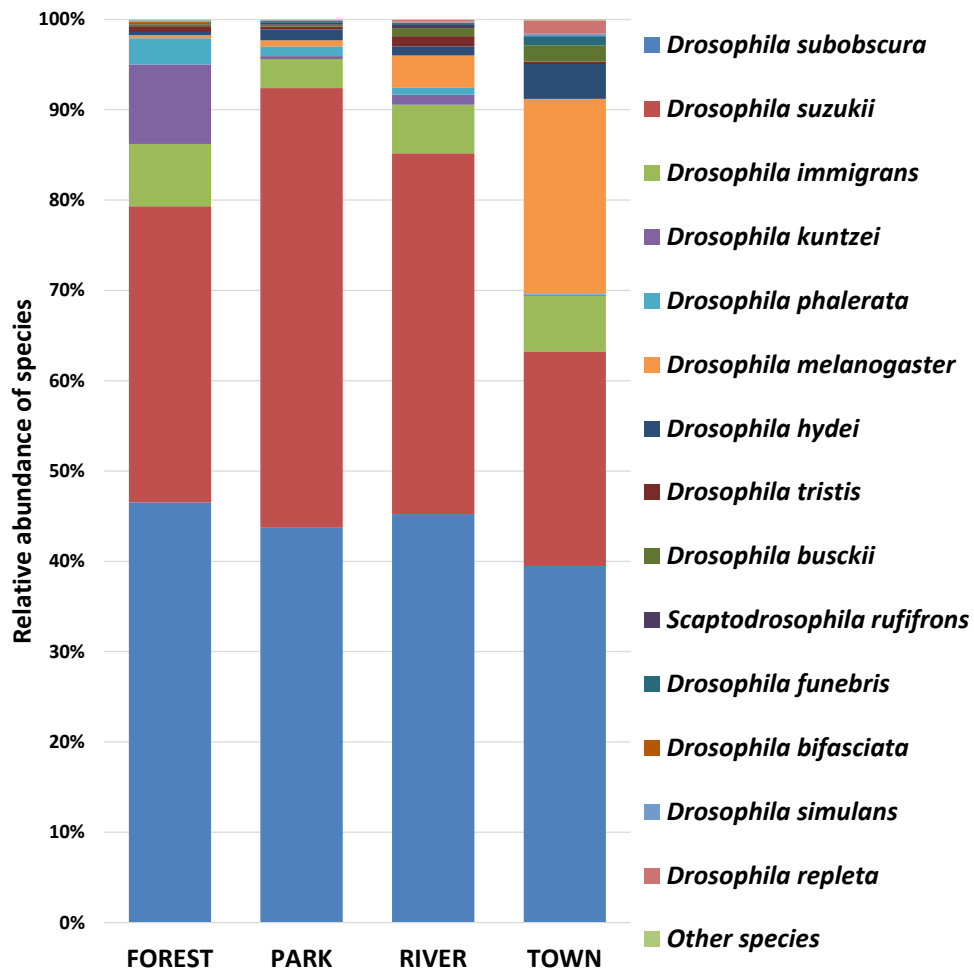
**Fig. 7** Proportions of *Drosophila suzukii* morphs over the course of the year

**Fig. 8** Mean wing sizes ( $\pm$  SE; wing area index in  $\text{mm}^2$ ) variation of female and male *Drosophila suzukii* over the course of the year. The number of traps used for wing trait measurements and the percentage of dark morph (D=intermediate + winter morphs) among measured individuals are indicated next to the corresponding dots on the graph. In each trap, between one and 5 individuals (depending on their availability in traps and conservation state) were measured for each sex. Total measured individuals: 1505 females in 377 traps and 1332 males in 322 traps

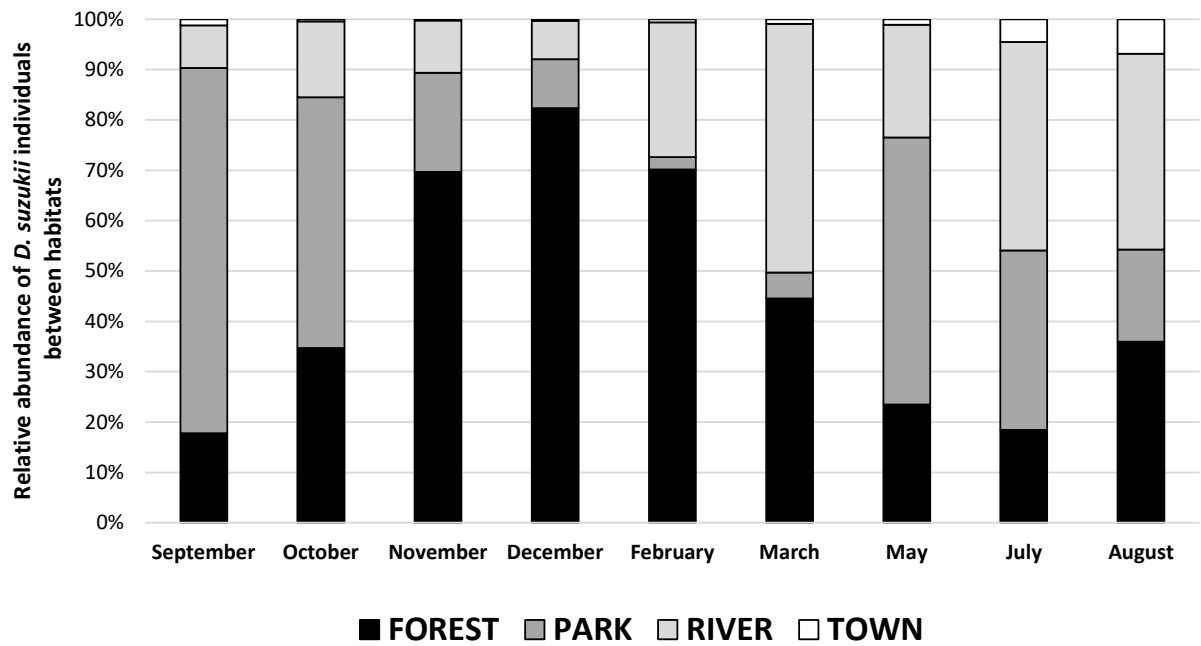
**Fig. 1** Proportion of land covers around sampling traps (radius = 100 m) located in the four urban habitats studied in Amiens city: urban forest (FOREST), park (PARK), riverside (RIVER) and town centre (TOWN). Legend of land covers: BUILD: building, SOIL: bare soil, ROAD: road and car park, PATH: path, HSTRIP: herbaceous strip, WATER: water, HEDGE: hedgerow, GARDEN: private garden, CROP: crop (cereals), GRASS: grassland, WOOD: wooded area



**Fig. 2** Relative abundance of the 14 most abundant Drosophilidae species in the four urban habitats of Amiens city. Numeric values of total number of individuals trapped, maximum, minimum, mean number of individuals per trap and per habitat are given in Suppl. Mat D.

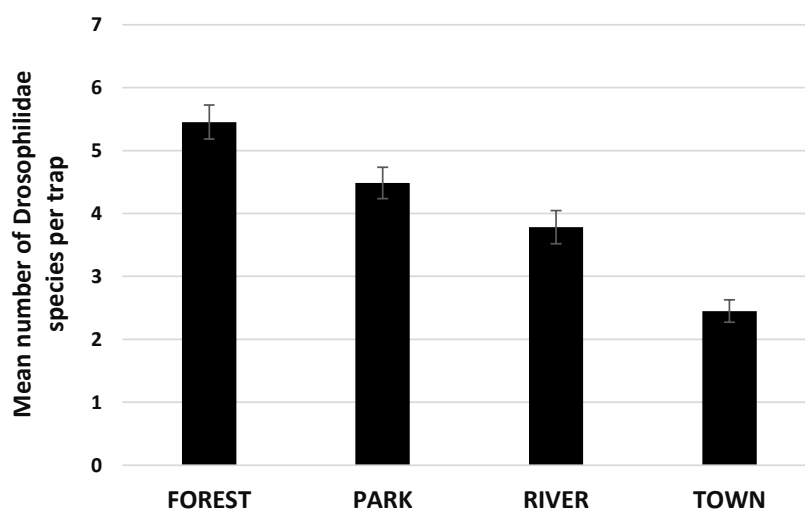


**Fig. 3** Seasonal distribution of *Drosophila suzukii* individuals among the different urban habitats (X-axis: months from September 2018 to August 2019; Y-axis: relative abundance of individuals between habitats for each month).

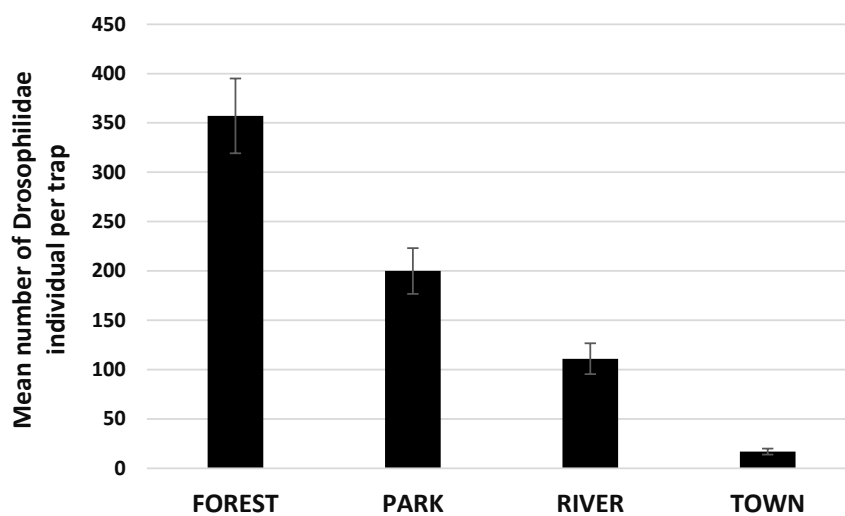


**Fig. 4** Mean Drosophilidae species richness (a) and abundance (b) per trap ( $\pm$ SE) in the four urban habitats sampled. Forest: n= 135, park: n = 134, riverside: n = 128, town centre: n = 129. Significant differences were found in Drosophilidae species richness ( $F = 72.496$ ;  $p < 0.001$  between pairs of habitat) and abundance ( $F = 39.062$ ;  $p < 0.001$ ) between habitats

(a)



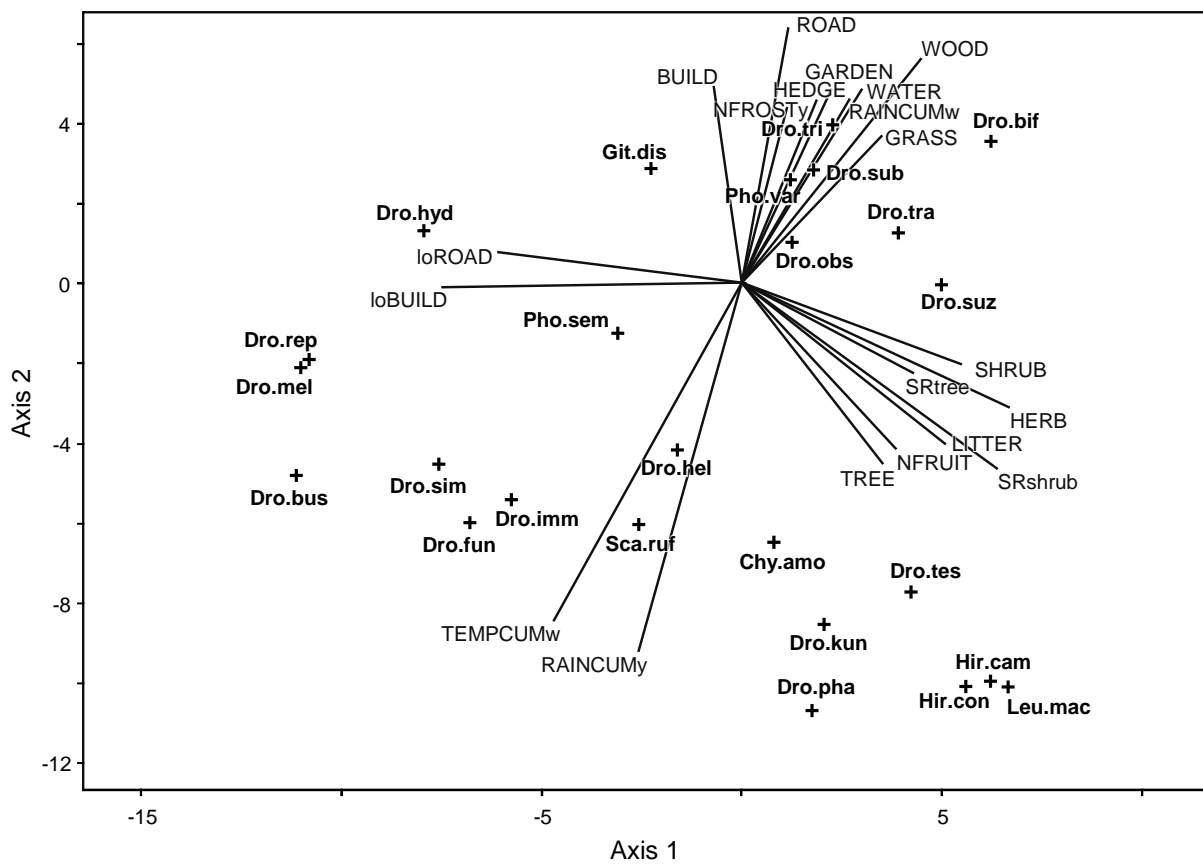
(b)



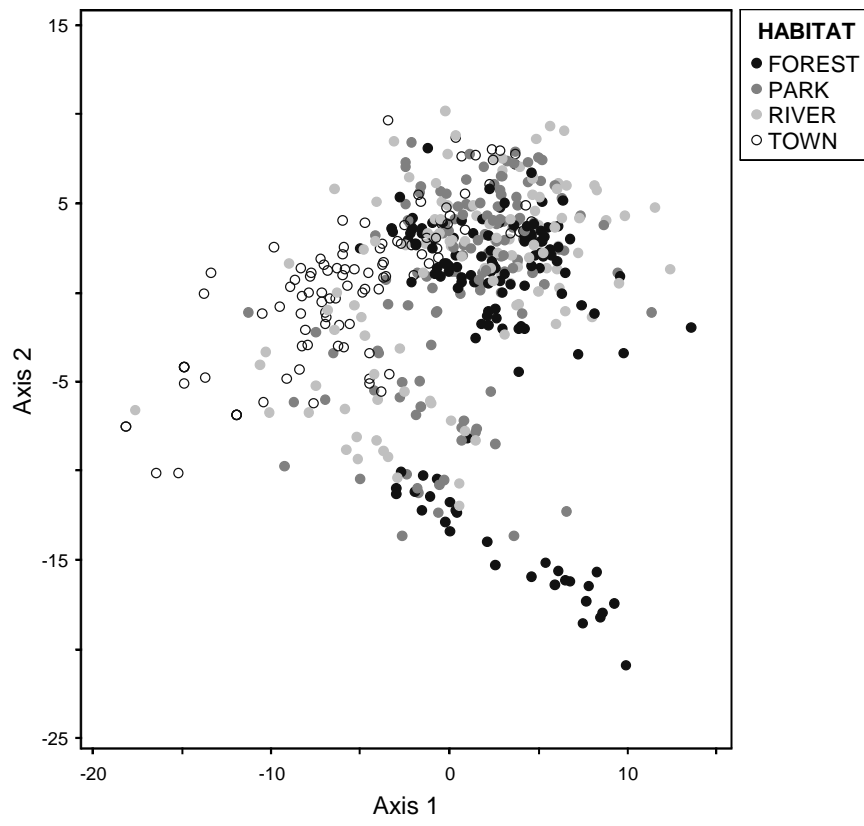


**Fig. 5** Redundancy analysis (RDA) coupling environment and Drosophilidae species matrices. (a) Diagram of Drosophilidae species (lowercase letters) and environmental variables (capital letters), (b) Diagram of plots grouped by habitats and (c) grouped by seasons. Only the most significant environmental variables are shown (cutoff  $r^2$  value = 0.1). Codes and full names for Drosophilidae species are given in Table 1

(a)

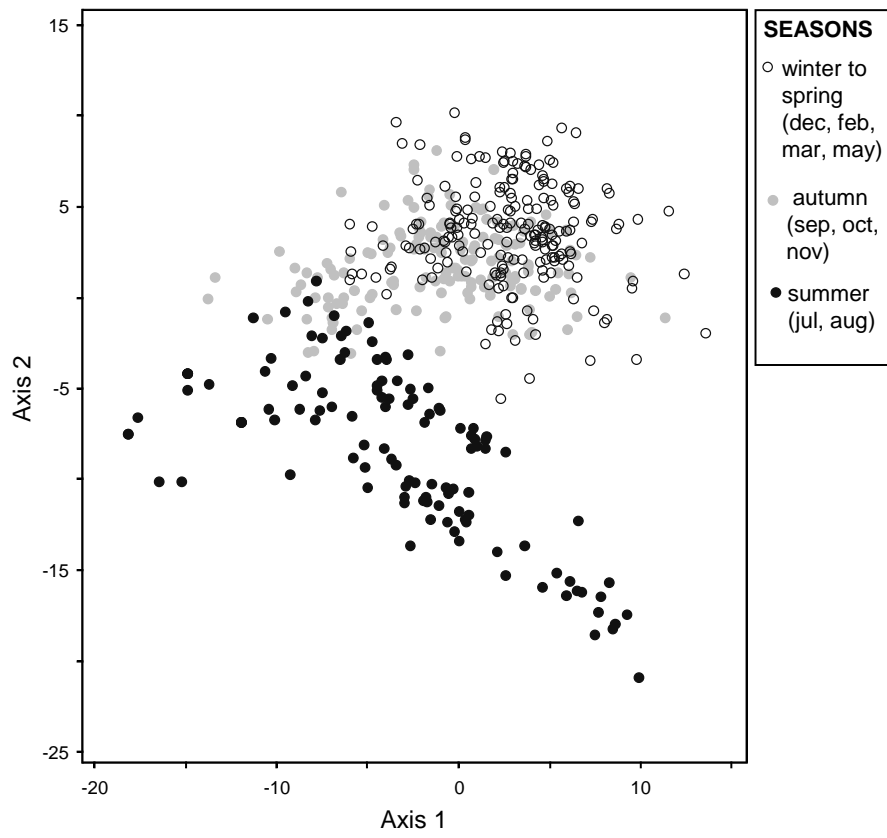


(b)



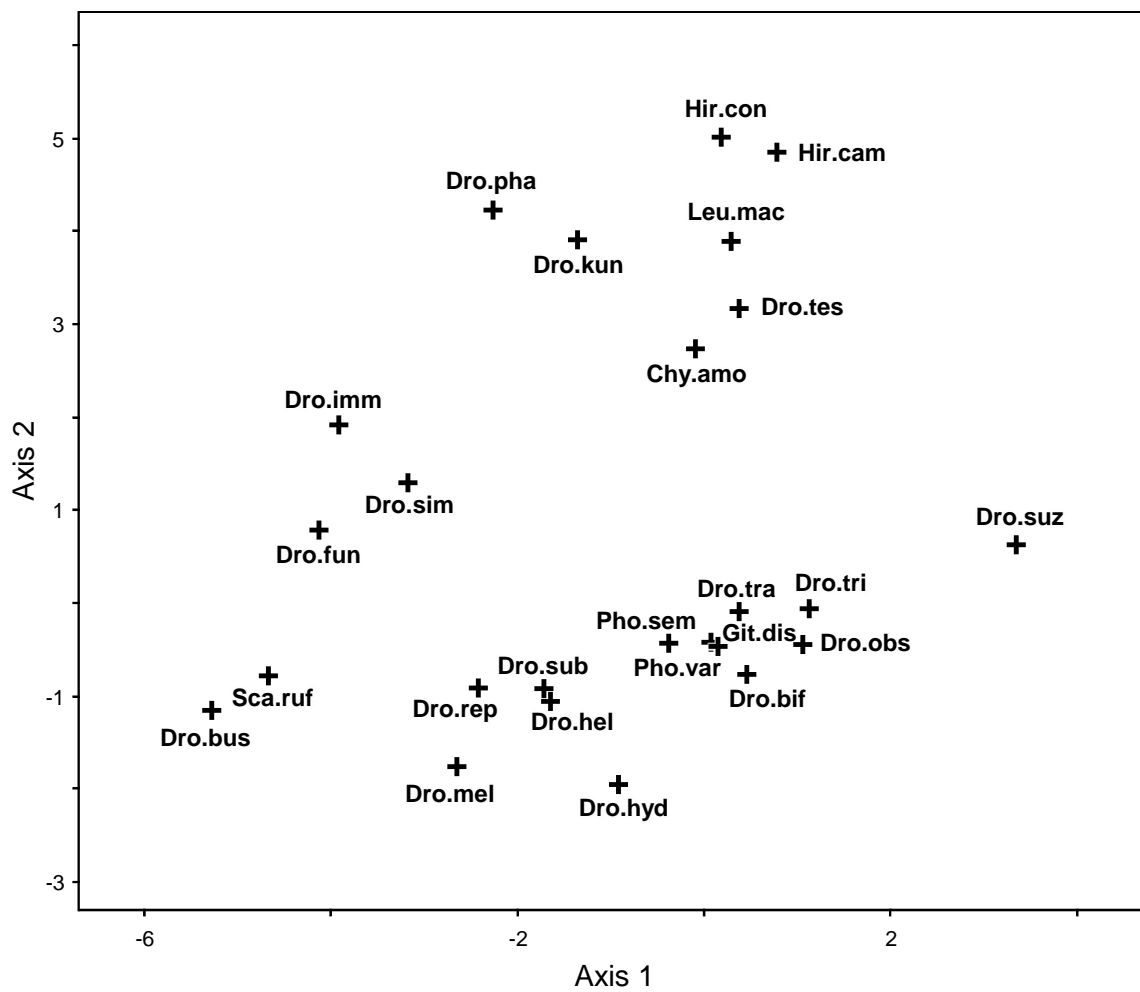


(c)



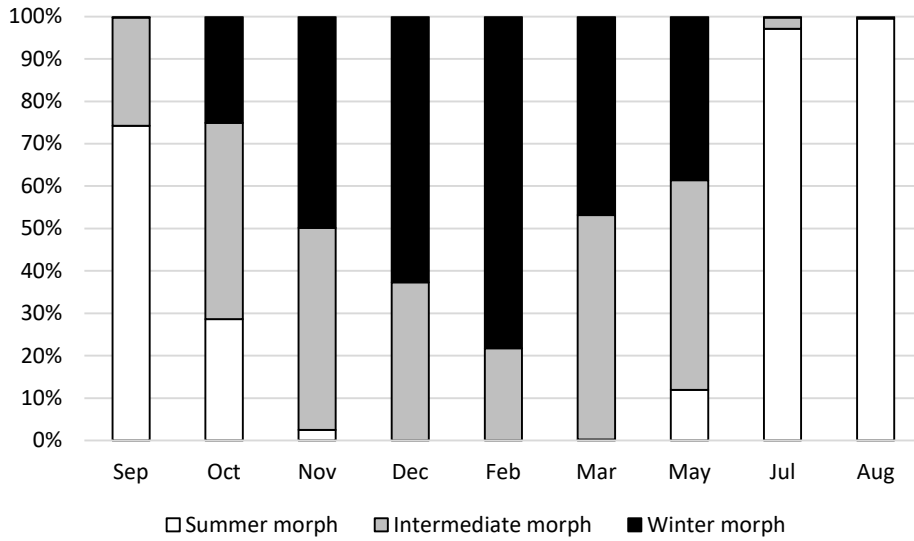
**Fig. 6** Redundancy analysis (RDA) coupling plant and Drosophilidae species matrices. (a) Diagram of Drosophilidae species, (b) Diagram of plant species. Only the most significant environmental variables are shown (cutoff  $r^2$  value = 0.1). Codes and full names for Drosophilidae species are given in Table 1

(a)

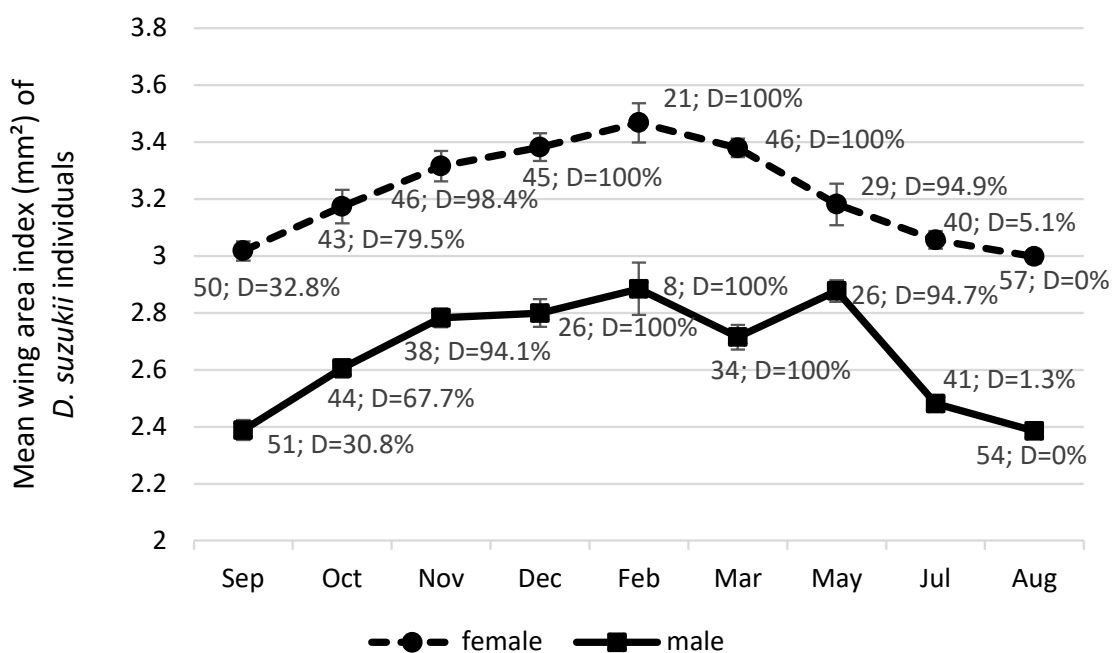




**Fig. 7** Proportions of *Drosophila suzukii* morphs over the course of the year



**Fig. 8** Mean wing sizes ( $\pm$  SE; wing area index in  $\text{mm}^2$ ) variation of female and male *Drosophila suzukii* over the course of the year. The number of traps used for wing trait measurements and the percentage of dark morph (D=intermediate + winter morphs) among measured individuals are indicated next to the corresponding dots on the graph. In each trap, between one and 5 individuals (depending on their availability in traps and conservation state) were measured for each sex. Total measured individuals: 1505 females in 377 traps and 1332 males in 322 traps



## SUPPLEMENTARY INFORMATION

**Supp. Mat. A:** Distribution of Drosophilidae species in the fruit stores and houses of Amiens city. N ind: total number of individuals trapped, Max: maximum number of individuals per trap, Min: minimum number of individuals per trap, Mean: mean number of individuals per trap, SE: standard error, Frequency: number of traps with presence of the species / total number of traps, %: percentage of individuals trapped.

**Supp. Mat. B:** Picture of male individuals showing the 3 morphs considered in the analysis. (a) summer morph, (b) intermediate morph and (c) winter morph.

**Supp. Mat. C:** List of the variables used in the study.

**Suppl. Mat. D** Distribution of Drosophilidae species in the four urban habitats of Amiens city. N ind: total number of individuals trapped, Max: maximum number of individuals per trap, Min: minimum number of individuals per trap, Mean: mean number of individuals per trap, SE: standard error, %: percentage of individuals trapped.

**Suppl. Mat. E** Seasonal distribution of the proportion of individuals of the most abundant Drosophilidae species among the different urban habitats (X-axes: months from September 2018 to August 2019; Y-axes: relative abundance of individuals in percentage between habitats for each month).

**Suppl. Mat. F** Variation of the number of individuals of the most abundant Drosophilidae species in the different urban habitats over the course of the year (X-axes: months from September 2018 to August 2019; Y-axes: cumulated number of individuals in the four habitats for each month).

**Supp. Mat. G:** meteorological characteristics of the sampling periods. Cumulative temperature (red line): sum of daily mean temperatures ( $>0^{\circ}\text{C}$ ) of the sampling week (degree-days). Cumulative precipitation (blue histograms): total rainfall for the week of sampling (mm).

**Supp. Mat. H** Effect of environmental variables on the species richness of Drosophilidae community, the number of Drosophilidae individuals (Drosophila abundance), the number of *D. suzukii* individuals (*D. suzukii* abundance), the number of summer and dark morphs of *D. suzukii* and the wing area index (wing size) of female and male *D. suzukii* per trap analysed by GLM. n = number of traps used in analyses.

**Supp. Mat. I** Plant species the most correlated with the abundance of *Drosophila suzukii* over the year (Spearman correlation coefficients, non-significant results are not shown, \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ). Only species present in at least 2% of the sampling plots were selected and samples from town centre were removed. Layer (vegetation layer): T: tree layer, S: shrub layer, H: herb layer.

**Supp. Mat. J:** Differences in wing sizes ( $\pm$  SE, wing area index in  $\text{mm}^2$ ) between morph categories (summer, intermediate and winter morphs) of *Drosophila suzukii* females (a) and males (b). The number of individuals used for wing trait measurements is indicated in italic above the histograms. The wing size was significantly different between morph categories in females ( $F = 90.456$ ,  $p < 0.001$ ,  $\text{ddl} = 2$ ) and males ( $F = 104.159$ ,  $p < 0.001$ ,  $\text{ddl} = 2$ ).

**Supp. Mat. K:** Differences in wing sizes (wing area index in  $\text{mm}^2$ , mean  $\pm$  SE) between urban habitats (forest, park, riverside, town centre) of *Drosophila suzukii* females (a) and males (b). The number of fly individuals used for wing size measurements is indicated in italic above histograms. The wing size was significantly different between habitats in females

( $F = 10.739$ ,  $p < 0.001$ ,  $ddl = 3$ ) and males ( $F = 3.108$ ,  $p = 0.026$ ,  $ddl = 3$ ). Letters above histograms indicate significant differences between habitats.

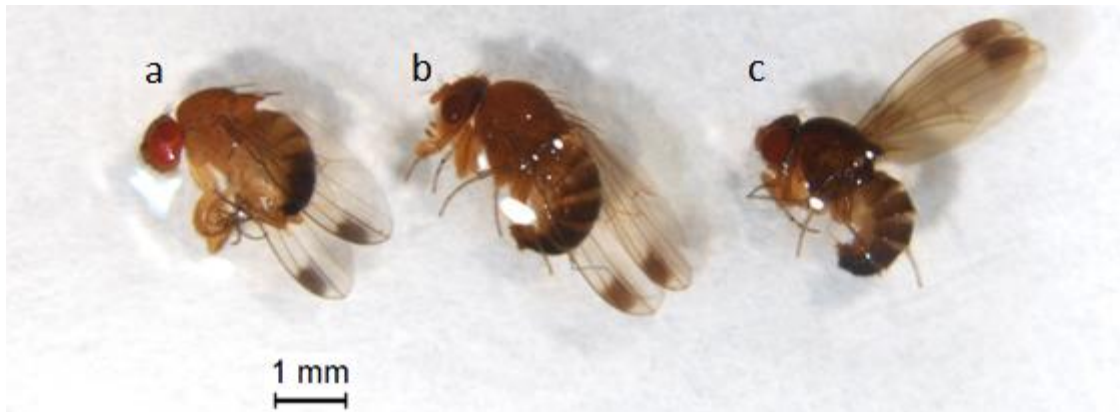


**Supp. Mat. A:** Distribution of Drosophilidae species in the fruit stores and houses of Amiens city (north of France). N ind: total number of individuals trapped, Max: maximum number of individuals per trap, Min: minimum number of individuals per trap, Mean: mean number of individuals per trap, SE: standard error, Frequency: number of traps with presence of the species / total number of traps, %: percentage of individuals trapped.

Species	Code	Fruit stores and houses (139 traps)						
		N ind	Min	Max	Mean	SE	Frequency	%
<i>Chymomyza amoena</i>	Chy.amo	0	0	0	0.000	0.000	0.000	0.00
<i>Drosophila bifasciata</i>	Dro.bif	0	0	0	0.000	0.000	0.000	0.00
<i>Drosophila busckii</i>	Dro.bus	33	0	16	0.237	0.123	0.079	2.25
<i>Drosophila funebris</i>	Dro.fun	8	0	2	0.058	0.027	0.036	0.55
<i>Drosophila helvetica</i>	Dro.hel	0	0	0	0.000	0.000	0.000	0.00
<i>Drosophila hydei</i>	Dro.hyd	274	0	77	1.971	0.737	0.223	18.68
<i>Drosophila immigrans</i>	Dro.imm	40	0	6	0.288	0.078	0.129	2.73
<i>Drosophila kuntzei</i>	Dro.kun	4	0	2	0.029	0.020	0.014	0.27
<i>Drosophila melanogaster</i>	Dro.mel	995	0	171	7.158	2.009	0.360	67.83
<i>Drosophila obscura</i>	Dro.obs	0	0	0	0.000	0.000	0.000	0.00
<i>Drosophila phalerata</i>	Dro.pha	4	0	2	0.029	0.018	0.022	0.27
<i>Drosophila repleta</i>	Dro.rep	32	0	7	0.230	0.082	0.086	2.18
<i>Drosophila simulans</i>	Dro.sim	7	0	4	0.050	0.036	0.014	0.48
<i>Drosophila subobscura</i>	Dro.sub	45	0	19	0.324	0.151	0.108	3.07
<b><i>Drosophila suzukii</i></b>	<b>Dro.suz</b>	<b>24</b>	<b>0</b>	<b>11</b>	<b>0.173</b>	<b>0.093</b>	<b>0.050</b>	<b>1.64</b>
<i>Drosophila testacea</i>	Dro.tes	0	0	0	0.000	0.000	0.000	0.00
<i>Drosophila transversa</i>	Dro.tra	0	0	0	0.000	0.000	0.000	0.00
<i>Drosophila tristis</i>	Dro.tri	1	0	1	0.007	0.007	0.007	0.07
<i>Gitona distigma</i>	Git.dis	0	0	0	0.000	0.000	0.000	0.00
<i>Hirtodrosophila cameraria</i>	Hir.cam	0	0	0	0.000	0.000	0.000	0.00
<i>Hirtodrosophila confusa</i>	Hir.con	0	0	0	0.000	0.000	0.000	0.00
<i>Leucophenga maculata</i>	Leu.mac	0	0	0	0.000	0.000	0.000	0.00
<i>Phortica semivirgo</i>	Pho.sem	0	0	0	0.000	0.000	0.000	0.00
<i>Phortica variegata</i>	Pho.var	0	0	0	0.000	0.000	0.000	0.00
<i>Scaptodrosophila rufifrons</i>	Sca.ruf	0	0	0	0.000	0.000	0.000	0.00
Total		1467						100.000

**Supp. Mat. B:** Picture of male individuals showing the 3 morphs considered in the analysis.

(a) summer morph, (b) intermediate morph and (c) winter morph.



**Supp. Mat. C:** List of the variables used in the study.

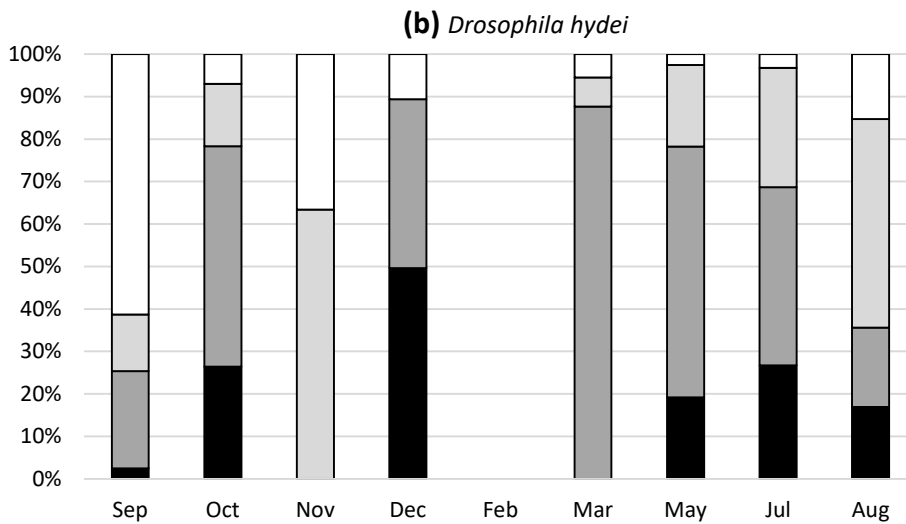
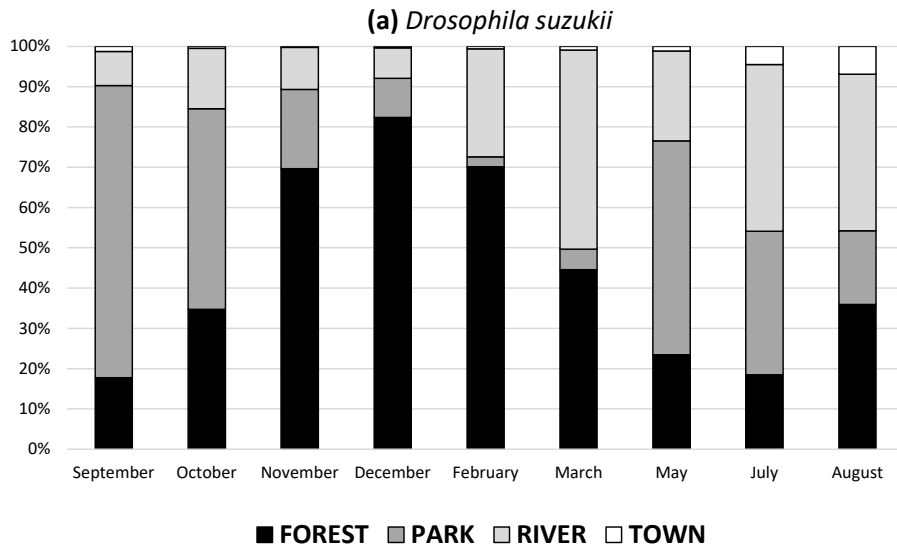
Category	Variable description	Unit	Code
Insects (in traps)	Abundance of <i>Drosophila suzukii</i>	individuals	DSabund
	Species richness of Drosophilidae	species	SRdroso
	Abundance of Drosophilidae	individuals	ABUNdroso
	Abundance of <i>D. suzukii</i> male	individuals	Dsmale
	Abundance of <i>D. suzukii</i> female	individuals	Dsfemale
	Abundance of <i>D. suzukii</i> summer morph	individuals	DSEstivale
	Abundance of <i>D. suzukii</i> intermediate morph	individuals	DSIntermed
	Abundance of <i>D. suzukii</i> winter morph	individuals	DSHiver
	Abundance of <i>D. suzukii</i> dark morph (intermediate + winter)	individuals	DSInt_Hiver
	Abundance of other non-drosophilidae arthropods	individuals	ABUNarth
Life traits of <i>D. suzukii</i>	Average wing surface area of <i>D. suzukii</i> female	mm <sup>2</sup>	WINGfem
	Average wing surface area of <i>D. suzukii</i> male	mm <sup>2</sup>	WINGmal
Local environment (5m-radius around traps)	Cover of tree layer (height>8m)	%	TREE
	Plant species richness in tree layer	species	SRtree
	Cover of shrub layer (height between 1m and 8m)	%	SHRUB
	Plant species richness in shrub layer	species	SRshrub
	Cover of herb layer (height<1m)	%	HERB
	Plant species richness in herb layer	species	SRherb
	Cover of dead wood debris	%	DWOOD
	Cover of leaf litter	%	LITTER
	Cover of waste	%	WASTE
	Cover of river	%	loRIVER
	Cover of road	%	loROAD
	Cover of building	%	loBUILD
	Cover of trail	%	loPATH
Number of fruiting plant species around the trap (radius = 10m)	species	NFRUIT	
Landscape (100m-radius around traps)	Cover of herbaceous strip	%	HSTRIP
	Cover of building	%	BUILD
	Cover of forest	%	WOOD
	Cover of crop	%	CROP
	Cover of trail	%	PATH
	Cover of water	%	WATER
	Cover of hedgerow	%	HEDGE
	Cover of private garden	%	GARDEN
	Cover of grassland	%	GRASS
	Cover of bare soil	%	SOIL
	Cover of road and paved surface	%	ROAD
Meteorology of the year (between the 1st January and the day of trap collection)	Cumulative temperatures >= 0, degree-days (year)	°C	TEMPCUMy
	Cumulative precipitation (year)	mm	RAINCUMy
	Mean of maximum temperatures (year)	°C	TEMPMAXy
	Mean of minimum temperatures (year)	°C	TEMPMINy
	Mean of mean temperatures (year)	°C	TEMPMEAy
	Highest temperature (year)	°C	TEMPTOPy
	Lowest temperature (year)	°C	TEMPLOWy
	Number of frost days (year)	/	NFROSTy
Meteorology of the sampling week	Cumulative temperatures >= 0, degree-days (week)	°C	TEMPCUMw
	Cumulative precipitation (week)	mm	RAINCUMw
	Mean of maximum temperatures (week)	°C	TEMPMAXw
	Mean of minimum temperatures (week)	°C	TEMPMINw
	Mean of mean temperatures (week)	°C	TEMPMEAw
	Highest temperature (week)	°C	TEMPTOPw
	Lowest temperature (week)	°C	TEMPLOWw
	Number of frost days (week)	/	NFROSTw

**Suppl. Mat. D** Distribution of Drosophilidae species in the four urban habitats of Amiens city. N ind: total number of individuals trapped, Max: maximum number of individuals per trap, Min: minimum number of individuals per trap, Mean: mean number of individuals per trap, SE: standard error, %: percentage of individuals trapped.

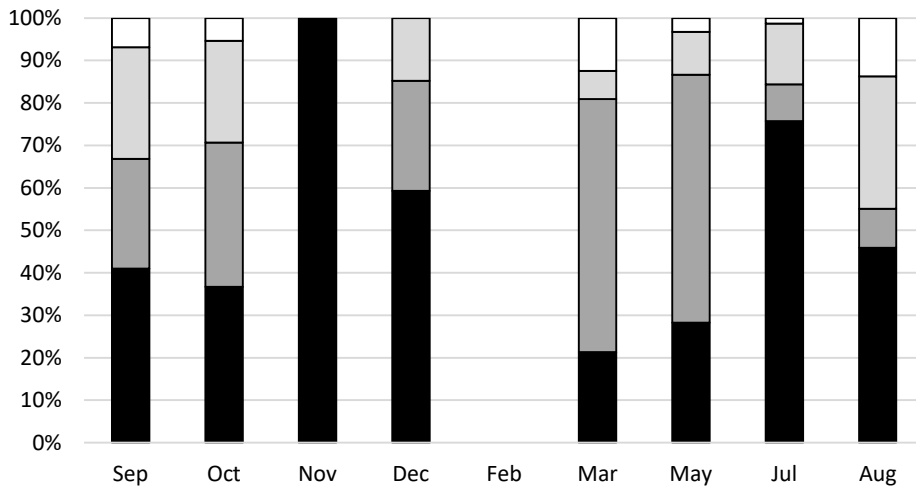
Species	Code	FOREST (135 traps)					PARK (134 traps)				
		N ind	Max	Mean	SE	%	N ind	Max	Mean	SE	%
<i>Chymomyza amoena</i>	Chy.amo	3	2	0.022	0.017	0.01	1	1	0.007	0.007	0.00
<i>Drosophila bifasciata</i>	Dro.bif	72	13	0.533	0.179	0.15	39	15	0.291	0.142	0.15
<i>Drosophila busckii</i>	Dro.bus	100	11	0.741	0.177	0.21	58	12	0.433	0.128	0.22
<i>Drosophila funebris</i>	Dro.fun	54	6	0.400	0.092	0.11	22	5	0.164	0.058	0.08
<i>Drosophila helvetica</i>	Dro.hel	0	0	0.000	0.000	0.00	1	1	0.007	0.007	0.00
<i>Drosophila hydei</i>	Dro.hyd	162	45	1.200	0.355	0.34	329	28	2.455	0.451	1.23
<i>Drosophila immigrans</i>	Dro.imm	3326	627	24.637	6.592	6.90	859	77	6.410	1.092	3.21
<i>Drosophila kuntzei</i>	Dro.kun	4248	910	31.467	10.286	8.81	88	26	0.657	0.244	0.33
<i>Drosophila melanogaster</i>	Dro.mel	168	17	1.244	0.251	0.35	180	14	1.343	0.217	0.67
<i>Drosophila obscura</i>	Dro.obs	0	0	0.000	0.000	0.00	1	1	0.007	0.007	0.00
<i>Drosophila phalerata</i>	Dro.pha	1393	327	10.319	3.177	2.89	288	45	2.149	0.565	1.07
<i>Drosophila repleta</i>	Dro.rep	2	1	0.015	0.010	0.00	7	3	0.052	0.027	0.03
<i>Drosophila simulans</i>	Dro.sim	58	9	0.430	0.121	0.12	18	6	0.134	0.065	0.07
<i>Drosophila subobscura</i>	Dro.sub	22429	2422	166.141	25.753	46.52	11716	871	87.433	11.817	43.73
<i>Drosophila sukuzii</i>	Dro.suz	15817	1035	117.163	15.774	32.80	13044	1565	97.343	20.359	48.68
<i>Drosophila testacea</i>	Dro.tes	1	1	0.007	0.007	0.00	0	0	0.000	0.000	0.00
<i>Drosophila transversa</i>	Dro.tra	7	4	0.052	0.032	0.01	0	0	0.000	0.000	0.00
<i>Drosophila tristis</i>	Dro.tri	310	28	2.296	0.394	0.64	77	11	0.575	0.141	0.29
<i>Gitona distigma</i>	Git.dis	0	0	0.000	0.000	0.00	4	1	0.030	0.015	0.01
<i>Hirtodrosophila cameraria</i>	Hir.cam	7	2	0.052	0.022	0.01	0	0	0.000	0.000	0.00
<i>Hirtodrosophila confusa</i>	Hir.con	20	3	0.148	0.048	0.04	4	3	0.030	0.024	0.01
<i>Leucophenga maculata</i>	Leu.mac	8	2	0.059	0.023	0.02	0	0	0.000	0.000	0.00
<i>Phortica semivirgo</i>	Pho.sem	1	1	0.007	0.007	0.00	1	1	0.007	0.007	0.00
<i>Phortica variegata</i>	Pho.var	3	1	0.022	0.013	0.01	3	1	0.022	0.013	0.01
<i>Scaptodrosophila rufifrons</i>	Sca.ruf	28	5	0.207	0.062	0.06	54	8	0.403	0.102	0.20
Total		48217					26794				

Species	Code	RIVER (128 traps)					TOWN (129 traps)				
		N ind	Max	Mean	SE	%	N ind	Max	Mean	SE	%
<i>Chymomyza amoena</i>	Chy.amo	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Drosophila bifasciata</i>	Dro.bif	12	8	0.094	0.064	0.08	0	0	0.000	0.000	0.00
<i>Drosophila busckii</i>	Dro.bus	128	21	1.000	0.300	0.90	39	6	0.302	0.095	1.79
<i>Drosophila funebris</i>	Dro.fun	30	7	0.234	0.090	0.21	22	6	0.171	0.063	1.01
<i>Drosophila helvetica</i>	Dro.hel	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Drosophila hydei</i>	Dro.hyd	145	18	1.133	0.227	1.02	84	9	0.651	0.134	3.87
<i>Drosophila immigrans</i>	Dro.imm	764	129	5.969	1.464	5.38	134	18	1.039	0.231	6.17
<i>Drosophila kuntzei</i>	Dro.kun	157	37	1.227	0.443	1.10	3	2	0.023	0.017	0.14
<i>Drosophila melanogaster</i>	Dro.mel	509	96	3.977	1.004	3.58	468	91	3.628	0.953	21.54
<i>Drosophila obscura</i>	Dro.obs	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Drosophila phalerata</i>	Dro.pha	110	23	0.859	0.295	0.77	3	2	0.023	0.017	0.14
<i>Drosophila repleta</i>	Dro.rep	26	6	0.203	0.069	0.18	32	5	0.248	0.070	1.47
<i>Drosophila simulans</i>	Dro.sim	12	3	0.094	0.038	0.08	6	4	0.047	0.033	0.28
<i>Drosophila subobscura</i>	Dro.sub	6430	506	50.234	8.493	45.24	858	157	6.651	1.679	39.48
<i>Drosophila sukuzii</i>	Dro.suz	5676	699	44.344	7.931	39.94	516	131	4.000	1.189	23.75
<i>Drosophila testacea</i>	Dro.tes	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Drosophila transversa</i>	Dro.tra	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Drosophila tristis</i>	Dro.tri	158	21	1.234	0.288	1.11	6	2	0.047	0.022	0.28
<i>Gitona distigma</i>	Git.dis	2	2	0.016	0.016	0.01	2	1	0.016	0.011	0.09
<i>Hirtodrosophila cameraria</i>	Hir.cam	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Hirtodrosophila confusa</i>	Hir.con	3	2	0.023	0.017	0.02	0	0	0.000	0.000	0.00
<i>Leucophenga maculata</i>	Leu.mac	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Phortica semivirgo</i>	Pho.sem	0	0	0.000	0.000	0.00	0	0	0.000	0.000	0.00
<i>Phortica variegata</i>	Pho.var	3	2	0.023	0.017	0.02	0	0	0.000	0.000	0.00
<i>Scaptodrosophila rufifrons</i>	Sca.ruf	48	13	0.375	0.134	0.34	0	0	0.000	0.000	0.00
Total		14213					2173				

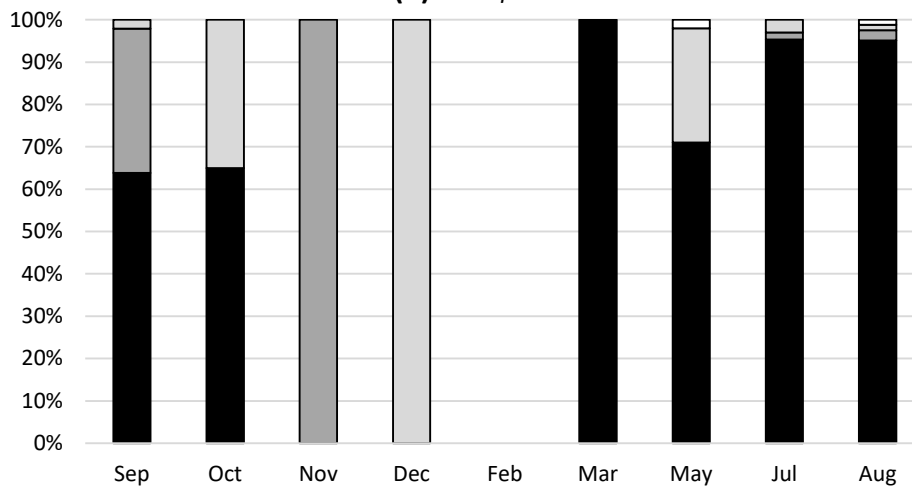
**Suppl. Mat. E** Seasonal distribution of the proportion of individuals of the most abundant *Drosophilidae* species among the different urban habitats (X-axes: months from September 2018 to August 2019; Y-axes: relative abundance of individuals in percentage between habitats for each month).



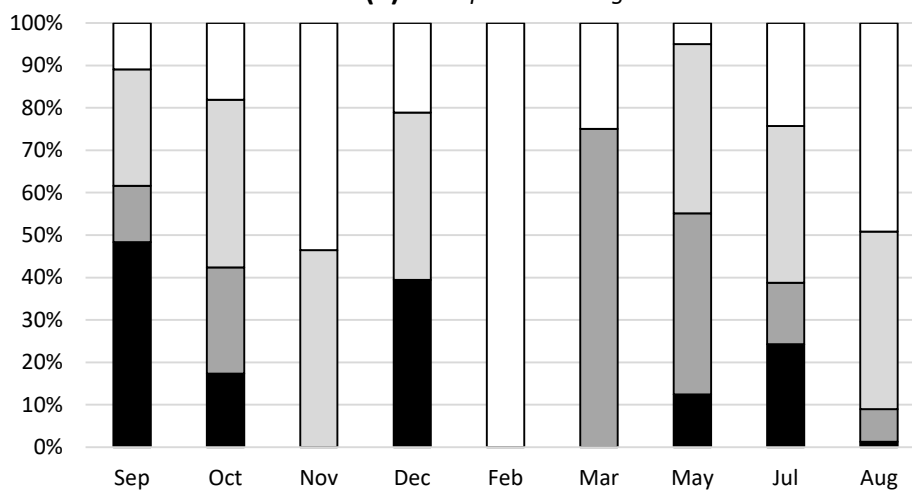
**(c) *Drosophila immigrans***



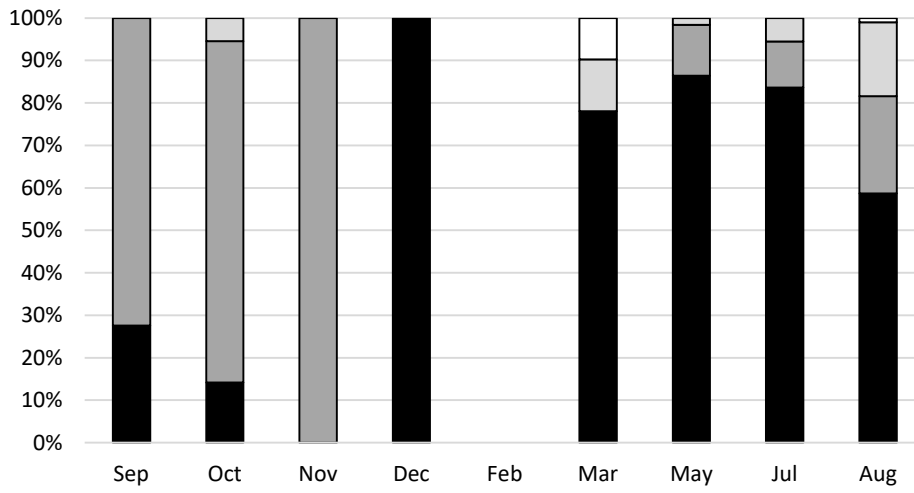
**(d) *Drosophila kuntzei***



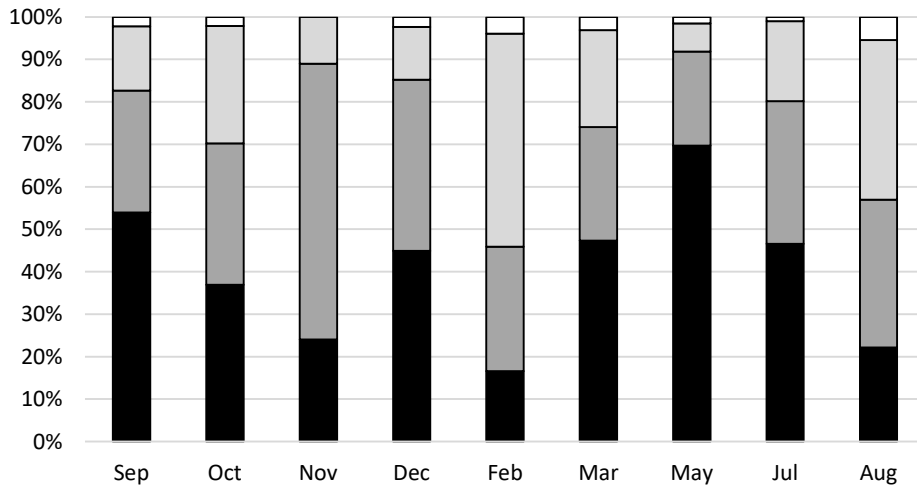
**(e) *Drosophila melanogaster***



**(f)** *Drosophila phalerata*

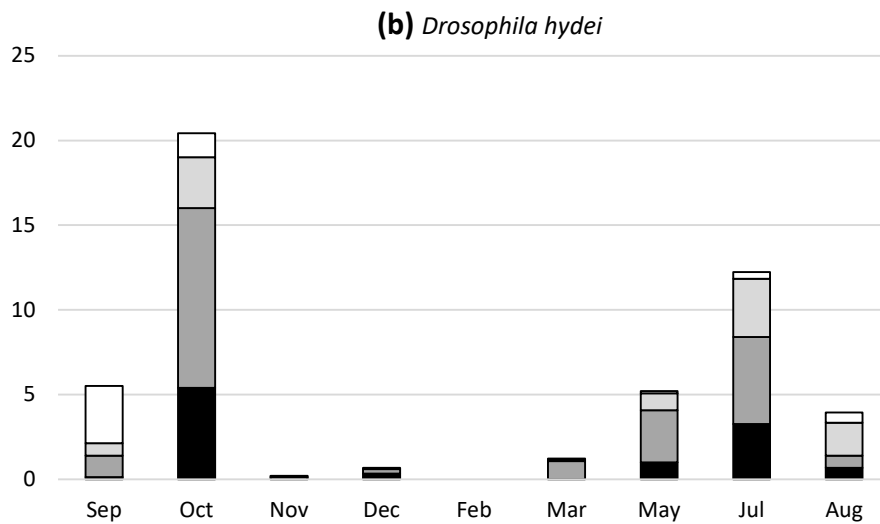
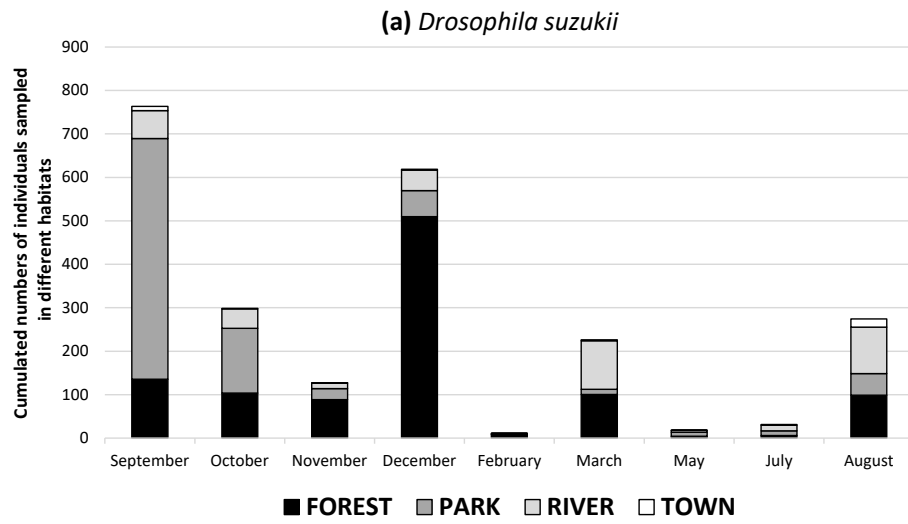


**(g)** *Drosophila subobscura*

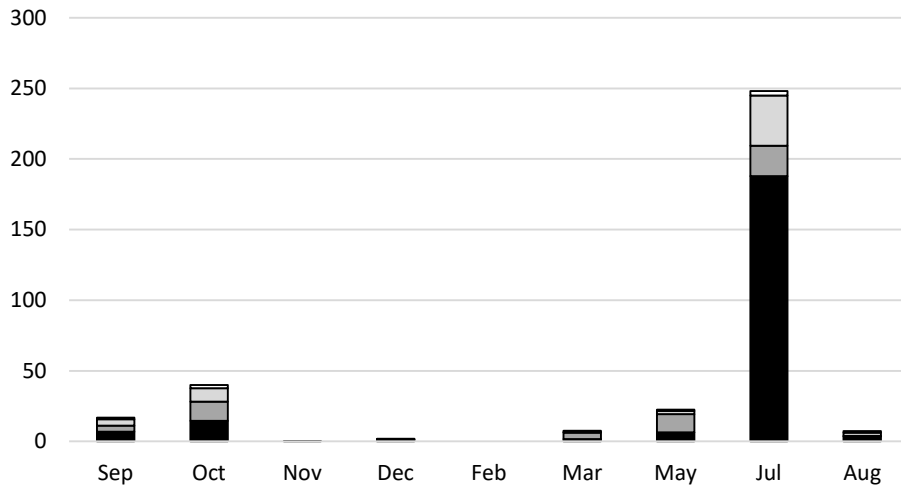




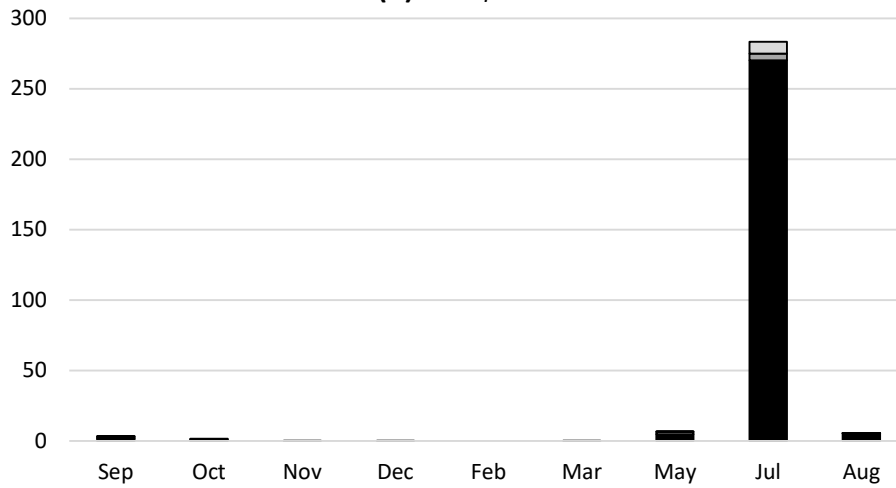
**Suppl. Mat. F** Variation of the number of individuals of the most abundant Drosophilidae species in the different urban habitats over the course of the year (X-axes: months from September 2018 to August 2019; Y-axes: cumulated number of individuals in the four habitats for each month).



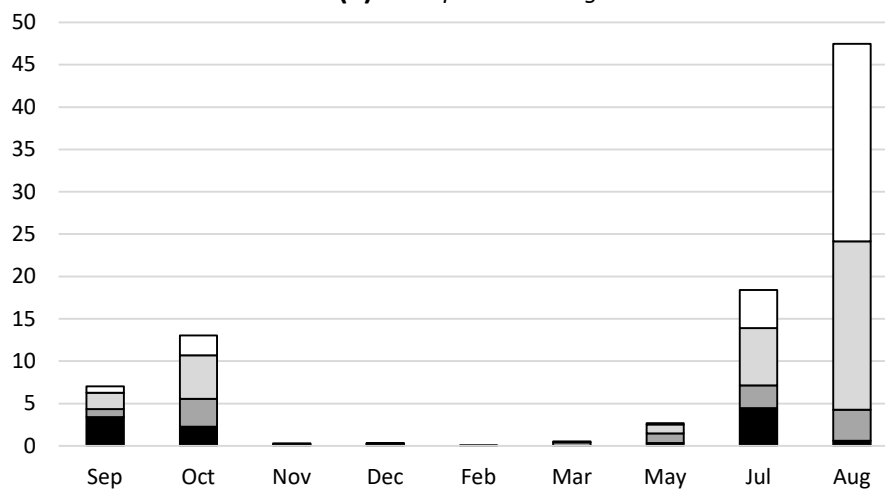
**(c)** *Drosophila immigrans*



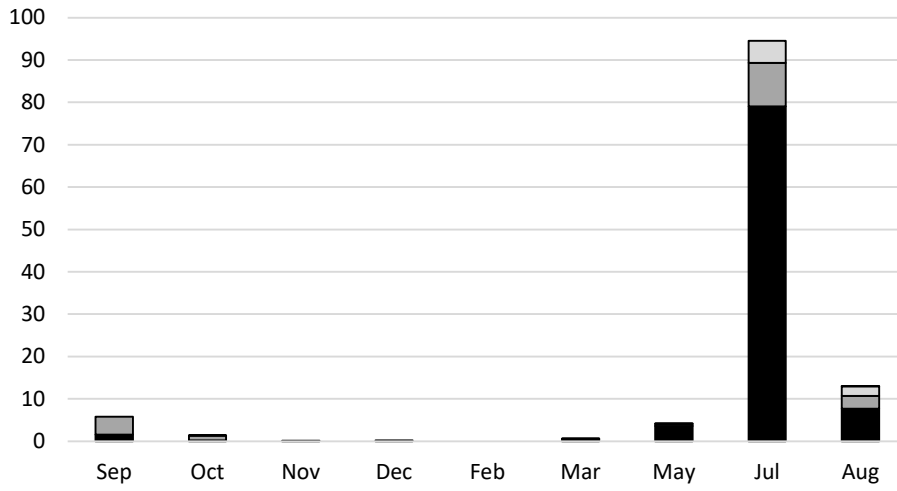
**(d)** *Drosophila kuntzei*



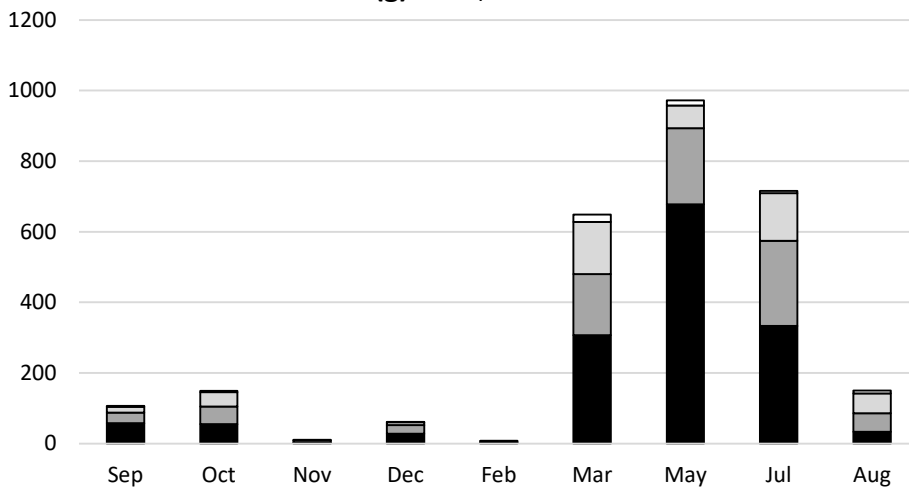
**(e)** *Drosophila melanogaster*



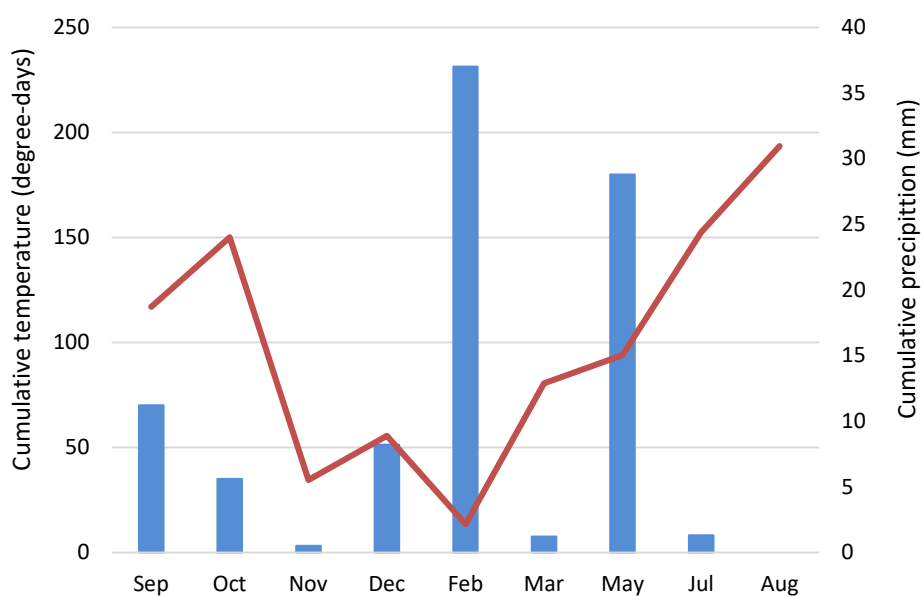
**(f)** *Drosophila phalerata*



**(g)** *Drosophila subobscura*



**Supp. Mat. G:** meteorological characteristics of the sampling periods. Cumulative temperature (red line): sum of daily mean temperatures ( $>0^{\circ}\text{C}$ ) of the sampling week (degree-days). Cumulative precipitation (blue histograms): total rainfall for the week of sampling (mm).



**Supp. Mat. H** Effect of environmental variables on the species richness of Drosophilidae community, the number of Drosophilidae individuals (Drosophila abundance), the number of *D. suzukii* individuals (*D. suzukii* abundance), the number of summer and dark morphs of *D. suzukii* and the wing area index (wing size) of female and male *D. suzukii* per trap analysed by GLM. n = number of traps used in analyses.

**Explanatory variables:** **WATER:** Cover of water (radius=100m); **loBUILD:** Cover of building (radius=5m); **TREE:** Cover of tree layer (radius=5m); **SHRUB:** Cover of shrub layer (radius=5m); **TEMPLOWw:** Lowest temperature in the sampling week; **NFROSTw:** Number of frost days during the sampling week; **BUILD:** Cover of building (radius=100m); **DWOOD:** Cover of dead wood debris (radius=5m); **loROAD:** Cover of road (radius=5m); **SRtree:** Plant species richness in tree layer (radius=5m); **SRshrub:** Plant species richness in shrub layer (radius=5m); **WOOD:** Cover of forest (radius=100m); **NFRUIT:** Number of fruiting plant species around the trap (radius = 10m); **TEMPTOPy:** Highest temperature between the 1st January and the day of trap collection; **RAINCUMw:** Cumulative precipitation during the sampling week; **TEMPTOPw:** Highest temperature in the sampling week; **GARDEN:** Cover of private garden (radius=100m); **NFROSTy:** Number of frost days between the 1st January and the day of trap collection. More details about measured variables are given in the full list of variables (see Supp. Mat. C)

Dependent variables	Explanatory variables	Model parameters					
		B	Standard residual	Wald $\chi^2$	d.f.	p	AIC
Drosophila species richness (log <sub>10</sub> , n = 526)	Model constant	0.4895	0.0302	262.18	1	<0.001	-333.09
	WATER	-0.0032	0.0009	12.46	1	<0.001	
	loBUILD	-0.0021	0.0004	22.57	1	<0.001	
	TREE	0.0013	0.0003	25.21	1	<0.001	
	SHRUB	0.0022	0.0004	37.39	1	<0.001	
	TEMPLOWw	0.0181	0.0022	67.29	1	<0.001	
	NFROSTw	-0.0428	0.0088	23.74	1	<0.001	
Drosophila abundance (log <sub>10</sub> , n = 526)	Model constant	1.7886	0.0740	583.77	1	<0.001	811.67
	BUILD	-0.0046	0.0014	10.07	1	0.002	
	WATER	-0.0088	0.0027	10.63	1	0.001	
	DWOOD	0.0057	0.0027	4.48	1	0.034	
	loROAD	-0.0037	0.0016	5.66	1	0.017	
	loBUILD	-0.0086	0.0016	29.01	1	<0.001	
	SRtree	0.1012	0.0256	15.62	1	<0.001	
	SHRUB	0.0050	0.0013	14.57	1	<0.001	
	SRshrub	0.0385	0.0168	5.27	1	0.022	
	NFROSTw	-0.2781	0.0143	377.42	1	<0.001	
<i>D. sukuzii</i> abundance (log <sub>10</sub> , n = 526)	Model constant	-0.4149	0.1554	7.13	1	0.008	936.47
	WOOD	0.0137	0.0014	90.69	1	<0.001	
	DWOOD	0.0085	0.0029	8.59	1	0.003	
	loBUILD	-0.0067	0.0017	16.22	1	<0.001	
	loROAD	-0.0038	0.0017	4.68	1	0.030	
	SHRUB	0.0046	0.0013	12.85	1	<0.001	
	NFRUIT	0.0569	0.0260	4.79	1	0.029	
	TEMPTOPy	0.0314	0.0043	53.99	1	<0.001	
	RAINCUMw	-0.0080	0.0029	7.49	1	0.006	
	TEMPTOPw	0.0161	0.0047	11.90	1	0.001	
Summer morph abundance (log <sub>10</sub> , n = 526)	Model constant	-0.8741	0.0843	107.41	1	<0.001	800.17
	loBUILD	-0.0056	0.0012	20.47	1	<0.001	
	SHRUB	0.0028	0.0011	7.10	1	0.008	
	NFRUIT	0.1443	0.0226	40.88	1	<0.001	
	TEMPTOPy	0.0120	0.0032	13.87	1	<0.001	
	TEMPTOPw	0.0495	0.0037	180.32	1	<0.001	
Dark morph abundance (log <sub>10</sub> , n = 526)	Model constant	-1.2132	0.1115	118.46	1	<0.001	852.01
	WOOD	0.0149	0.0013	132.55	1	<0.001	
	GARDEN	0.0124	0.0036	12.06	1	0.001	
	DWOOD	0.0055	0.0027	4.24	1	0.040	
	loBUILD	-0.0059	0.0013	20.31	1	<0.001	
	SHRUB	0.0036	0.0012	9.87	1	0.002	
	NFROSTy	0.0831	0.0057	213.86	1	<0.001	
Wing size of females <i>D. sukuzii</i> (n=380)	Model constant	3.4860	0.0503	4794.38	1	<0.001	159.11
	SRtree	0.0442	0.0133	11.10	1	0.001	
	TEMPTOPw	-0.0177	0.0020	76.68	1	<0.001	
Wing size of males <i>D. sukuzii</i> (n=328)	Model constant	3.0837	0.0400	5941.04	1	<0.001	-27.29
	TEMPTOPw	-0.0229	0.0018	166.08	1	<0.001	

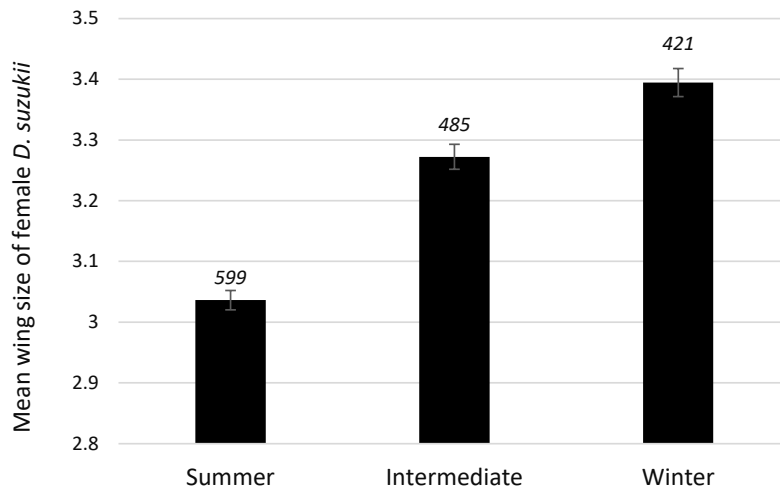
**Supp. Mat. I** Plant species the most correlated with the abundance of *Drosophila suzukii* over the year (Spearman correlation coefficients, non-significant results are not shown, \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ). Only species present in at least 2% of the sampling plots were selected and samples from the town centre were removed. Layer (vegetation layer): T: tree layer, S: shrub layer, H: herb layer.

	Layer	Code	SEP (n=39)		OCT (n=41)		NOV (n=43)		DEC (n=43)		FEB (n=33)		MAR (n=42)		MAY (n=44)		JUL (n=44)		AUG (n=45)		Total (n=374)	
			R	p	R	p	R	p	R	p	R	p	R	p	R	p	R	p	R	p	R	p
<b>(a) Species positively correlated with <i>D. suzukii</i></b>																						
<i>Acer pseudoplatanus</i>	T	Ace.pseT					0.544 ***		0.706 ***		0.726 ***		0.679 ***		0.302 *		-0.305 *		0.439 **		0.184 ***	
<i>Fraxinus excelsior</i>	T	Fra.excT													0.357 *							
<i>Hedera helix</i>	T	Hed.helT					0.608 ***		0.769 ***		0.649 ***		0.513 ***						0.361 *		0.315 ***	
<i>Salix sp.</i>	T	Sal.spT	0.374 *		0.316 *																0.167 ***	
<i>Ulmus minor</i>	T	Ulm.minT							0.369 **												0.178 ***	
<i>Acer pseudoplatanus</i>	S	Ace.pseS			0.325 *		0.389 ***		0.455 **		0.401 *		0.609 ***				-0.370 *		0.488 ***		0.237 ***	
<i>Cornus sanguinea</i>	S	Cor.sanS	0.507 ***																		0.134 **	
<i>Corylus avellana</i>	S	Cor.aveS											0.320 *									
<i>Crataegus monogyna</i>	S	Cra.monS					0.379 *		0.348 *						0.319 *						0.117 *	
<i>Fraxinus excelsior</i>	S	Fra.excS	0.341 *																			
<i>Hedera helix</i>	S	Hed.helS					0.516 ***		0.734 ***		0.718 ***		0.569 ***						0.332 *		0.229 ***	
<i>Prunus avium</i>	S	Pru.aviS							0.323 *												0.109 *	
<i>Rubus fruticosus</i>	S	Rub.fruS															0.423 **					
<i>Sambucus nigra</i>	S	Sam.nigS							0.494 ***		0.654 ***											
<i>Ulmus minor</i>	S	Ulm.minS							0.515 ***				0.387 *								0.164 ***	
<i>Acer pseudoplatanus</i>	H	Ace.pseH			0.375 *		0.571 ***		0.636 ***				0.448 **		0.378 *				0.356 *			
<i>Arum maculatum</i>	H	Aru.macH													0.393 **							
<i>Carex sylvatica</i>	H	Car.sylH							0.387 **		0.484 **		0.565 ***		0.333 *				0.337 *			
<i>Cornus sanguinea</i>	H	Cor.sanH			0.427 **										0.353 *							
<i>Corylus avellana</i>	H	Cor.aveH					0.339 *															
<i>Equisetum arvense</i>	H	Equ.arvH													0.345 *							
<i>Fraxinus excelsior</i>	H	Fra.excH					0.351 *															
<i>Geum urbanum</i>	H	Geu.urbH					0.376 *		0.533 ***		0.522 **		0.479 ***		0.456 **							
<i>Hedera helix</i>	H	Hed.helH					0.626 ***		0.702 ***		0.553 ***		0.649 ***		0.419 **						0.124 *	
<i>Ranunculus ficaria</i>	H	Ran.ficH											0.355 *								-0.126 *	
<i>Ribes rubrum</i>	H	Rib.rubH					0.316 *				0.367 *											
<i>Rubus caesius</i>	H	Rub.caeH							0.630 ***		0.525 **		0.508 ***		0.353 *				0.377 *		0.121 *	
<i>Sambucus nigra</i>	H	Sam.nigH													0.427 **							
<i>Ulmus minor</i>	H	Ulm.minH													0.341 *							
<i>Veronica hederifolia</i>	H	Ver.hedH										0.343 *		0.439 **								
<b>(b) Species negatively correlated with <i>D. suzukii</i></b>																						
<i>Platanus acerifolia</i>	T	Pla.aceT																			-0.124 *	
<i>Populus sp.</i>	T	Pop.spT											-0.369 *								-0.144 **	
<i>Salix sp.</i>	S	Sal.spS											-0.345 *									
<i>Agrostis stolonifera</i>	H	Agr.stoH									-0.457 **										-0.125 *	
<i>Angelica sylvestris</i>	H	Ang.sylH													-0.359 *						-0.138 **	
<i>Anthriscus sylvestris</i>	H	Ant.sylH																			-0.114 *	
<i>Arrhenatherum eliatum</i>	H	Arr.eliH							-0.458 **				-0.400 **								-0.222 ***	
<i>Artemisia vulgaris</i>	H	Art.vulH											-0.336 *									
<i>Bellis perennis</i>	H	Bel.perH							-0.462 **												-0.228 ***	
<i>Bryonia dioica</i>	H	Bry.dioH																			-0.132 **	
<i>Capsella bursa-pastoris</i>	H	Cap.burH																			-0.178 ***	
<i>Cardamine hirsuta</i>	H	Car.hirH										-0.402 *									-0.207 ***	
<i>Carex acutiformis</i>	H	Car.acuH							-0.378 *													
<i>Carex hirta</i>	H	Car.hirtH	-0.336 *																			
<i>Chelidonium majus</i>	H	Che.majH													-0.307 *						-0.114 *	
<i>Cirsium arvense</i>	H	Cir.arvH					-0.368 *															
<i>Conyza canadensis</i>	H	Con.canH																	-0.306 *		-0.115 *	
<i>Cotoneaster sp.</i>	H	Cot.spH							-0.423 **												-0.171 ***	
<i>Dactylis glomerata</i>	H	Dac.gloH									-0.402 *		-0.431 **								-0.117 *	
<i>Festuca rubra</i>	H	Fes.rubH													-0.333 *						-0.186 ***	
<i>Galium aparine</i>	H	Gal.apaH																			-0.215 ***	
<i>Geranium molle</i>	H	Ger.molH																			-0.157 **	
<i>Glechoma hederacea</i>	H	Gle.hedH							-0.364 *				-0.322 *								-0.180 ***	
<i>Heracleum spondylium</i>	H	Her.spoH																			-0.143 **	
<i>Holcus lanatus</i>	H	Hol.lanH													-0.311 *						-0.106 *	
<i>Lapsana communis</i>	H	Lap.comH				-0.311 *															-0.107 *	
<i>Lolium perenne</i>	H	Lol.perH																			-0.226 ***	
<i>Malva sylvestris</i>	H	Mal.sylH					-0.322 *															
<i>Mercurialis annua</i>	H	Mer.annH													-0.356 *						-0.161 **	
<i>Plantago lanceolata</i>	H	Pla.lanH	-0.351 *				-0.347 *														-0.146 **	
<i>Poa annua</i>	H	Poa.annH					-0.313 *		-0.355 *				-0.354 *								-0.266 ***	
<i>Poa trivialis</i>	H	Poa.triH																			-0.164 ***	
<i>Ranunculus repens</i>	H	Ran.repH																			-0.138 **	
<i>Solanum dulcamara</i>	H	Sol.dulH													-0.307 *							
<i>Sonchus oleraceus</i>	H	Son.oleH																			-0.121 *	
<i>Stellaria media</i>	H	Ste.medH																			-0.140 **	
<i>Taraxacum officinale</i>	H	Tar.offH	-0.325 *		-0.316 *				-0.481 ***						-0.558 ***						-0.241 ***	
<i>Trifolium repens</i>	H	Tri.repH					-0.326 *								-0.395 **							
<i>Urtica dioica</i>	H	Urt.dioH							-0.366 *				-0.311 *		-0.368 *							
<i>Veronica persica</i>	H	Ver.perH																			-0.126 *	

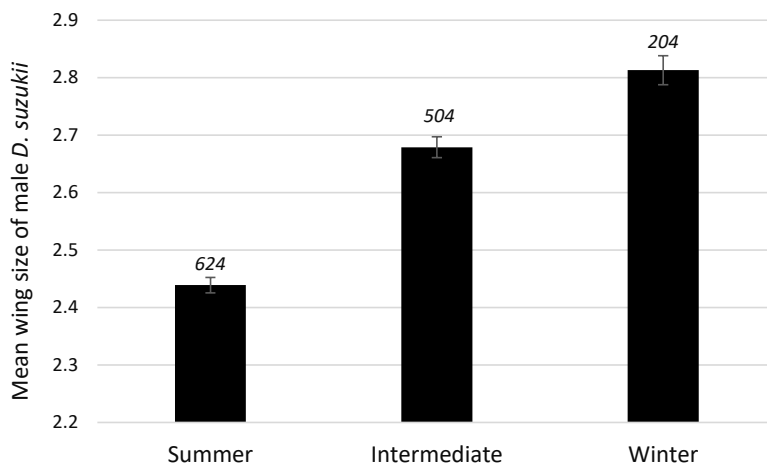


**Supp. Mat. J:** Differences in wing sizes ( $\pm$  SE, wing area index in mm<sup>2</sup>) between morph categories (summer, intermediate and winter morphs) of *Drosophila suzukii* females (a) and males (b). The number of individuals used for wing trait measurements is indicated in italic above the histograms. The wing size was significantly different between morph categories in females ( $F = 90.456$ ,  $p < 0.001$ ,  $ddl = 2$ ) and males ( $F = 104.159$ ,  $p < 0.001$ ,  $ddl = 2$ ).

(a)

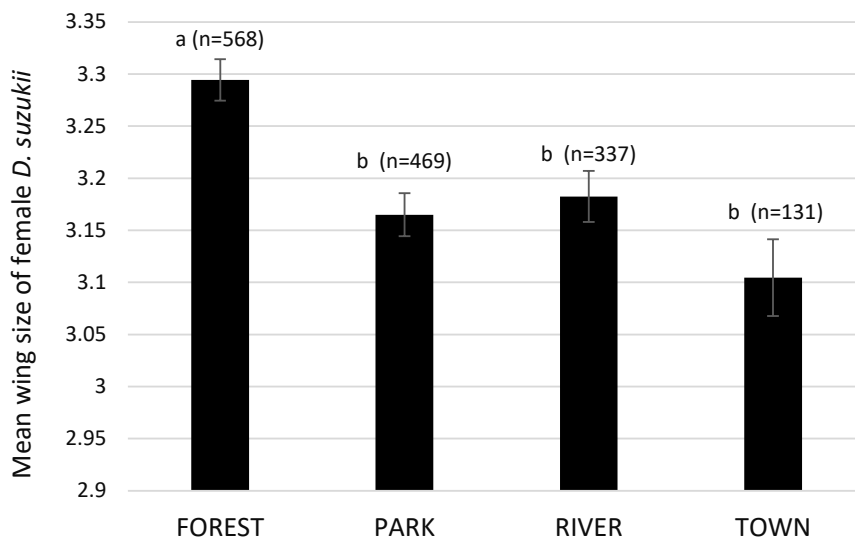


(b)



**Supp. Mat. K:** Differences in wing sizes (wing area index in mm<sup>2</sup>, mean  $\pm$  SE) between urban habitats (forest, park, riverside, town centre) of *Drosophila suzukii* females (a) and males (b). The number of fly individuals used for wing size measurements is indicated in italic above histograms. The wing size was significantly different between habitats in females (F = 10.739, p < 0.001, ddl = 3) and males (F = 3.108, p = 0.026, ddl = 3). Letters above histograms indicate significant differences between habitats.

(a)



(b)

