

ORIGINAL ARTICLE

Diversity and abundance of drosophilid fruit flies and other insects in compost piles

Katarzyna Michalska¹ , Muhammad Arslan Ibrahim^{1*} , Mariusz Martyka¹,
Marcin Studnicki² , Grażyna Soika³ 

¹Department of Plant Protection, Institute of Horticultural Sciences, Warsaw University of Life Sciences, Warsaw, Poland

²Department of Biometry, Institute of Agriculture, Warsaw University of Life Sciences, Warsaw, Poland

³Department of Plant Protection, The National Institute of Horticultural Research, Skierniewice, Poland

Vol. 65, No. 4: 523–534, 2025

DOI: 10.24425/jppr.2025.155792

Received: December 25, 2024

Accepted: March 10, 2025

Online publication: November 06, 2025

*Corresponding address:

malikarslan462@yahoo.com

Responsible Editor:

Jacek Twardowski

Abstract

Compost piles serve as important habitats for various insect groups, including decomposers, predators, and parasitoids. While drosophilid fruit flies play a crucial role in organic matter recycling, the variation of their abundance and diversity in composters remains poorly understood. This study examines fruit fly assemblages across three compost localities in Poland: two orchards in Dąbrowice and Nowy Dwór-Parcela, and a vegetable-fruit farm in Skierniewice. Insects, collected using sweep netting and traps, varied in abundance. Dipteron flies were the most prevalent, representing 25 families, followed by beetles, bees, and wasps. Thrips and earwigs were the least represented. With 16 species from three genera, drosophilids were the predominant group, making up 95.6% of all specimens. These included seven cosmopolitan species, namely *Drosophila melanogaster*, *D. hydei*, *D. immigrans*, *D. buskii*, *D. repleta*, *D. simulans*, and *Scaptomyza pallida*, and three alien species, *D. suzukii*, *Chymomyza amoena*, and *D. triauraria*, the latter being a new Asian species recently reported in Poland and Europe. In addition to *D. suzukii*, another significant pest, *Carpophilus hemipterus*, was also recorded in the compost piles. Most species were fruit breeders or decaying plant material inhabitants, while others were mycetophagous (*D. testacea*, *D. transversa*, *D. phalerata*, *D. funebris*) or frugivorous-fungivorous (*D. subobscura*). Shannon-Wiener diversity indexes ranged between 1.1 and 1.4 across three localities, with the highest drosophilid diversity found at the Skierniewice farm. *Drosophila melanogaster* was the most numerous fruit fly at all the examined compost piles, while the relative abundance of other species depended on the composter site. These findings emphasize composters as underexplored hotspots for drosophilids, directing further study of their ecological niches and the potential presence of pest species.

Keywords: *Chymomyza amoena*, *Drosophila triauraria*, *Drosophila suzukii*, invasive insects, agroecosystem

Introduction

Biodiversity is crucial for the overall health of an ecosystem (Hough 2014). Insects contribute significantly to the biodiversity of terrestrial ecosystems, playing an essential role in maintaining ecosystem functions and stability (Weisser and Siemann 2008). Among Diptera, the Drosophilidae family is renowned for its exceptional ecological diversity, with 4,758 species worldwide (Bächli *et al.* 2004; Finet *et al.* 2021; Taxodros

2025). Their larvae live in various substrates, such as fermenting and decaying fruits, tree sap, mushrooms, litter, living flowers and leaves, and take part in the recycling of organic matter. Fruit flies feed mainly upon microorganisms, that is, yeast and bacteria responsible for fermentation processes, but also upon the decomposing material itself (Markow and O'Grady 2008). They can also act as predators, and consume bee larvae,

scale insects, and even spider and frog embryos (Ashburner 2005; Grimaldi and Richenbacher 2023). Some species are endemic, others cosmopolitan (Bächli *et al.* 2004; Markow and O'Grady 2006). Their widespread distribution and ease of sampling make them ideal indicators for monitoring anthropogenic disturbances (Mata *et al.* 2010).

The invasion of new environments by non-native species poses a significant threat to biodiversity, especially in natural and human-modified ecosystems (Wilcove *et al.* 1998; Pyšek *et al.* 2020). In Europe, invasive species like *Drosophila suzukii* Matsumura and *Chymomyza amoena* Loew are reshaping native Drosophilidae communities and disrupting the ecological balance of the local fauna (Deconninck *et al.* 2024). Another alien drosophilid species, *Drosophila triauraria* Bock and Wheeler 1972, has recently been reported in Poland and Europe (Michalska *et al.* 2025). The invasion of such alien species may cause native species to decline or even become locally extinct, as they may be outcompeted for food or breeding sites (David *et al.* 2017; Ribeiro *et al.* 2023). Across the vast Palearctic region, up to 1,730 species of drosophilids have been documented (Plotnikov *et al.* 2013). Over the past 45 years, significant efforts have been made to study drosophilid diversity in southeastern Europe. Research has been conducted at more than 60 geographic locations in Bosnia and Herzegovina, Croatia, Macedonia, Slovenia, Montenegro, and Serbia (Pajač-Živković *et al.* 2016).

Compost heaps, rich in rotting organic matter near orchards and wineries, serve as warm, nutrient-rich breeding habitats for diverse arthropod communities and attract numerous fly species, especially drosophilids (Goulson *et al.*, 1999; Ødegaard and Tømmerås, 2000; Bal *et al.*, 2017). Feeding on different fruit types may provide cold tolerance to *Drosophila* species (Henry *et al.*, 2020; Jiménez-Padilla *et al.*, 2020). These conditions also allow invasive species to establish and expand their populations, often dominating native fruit flies and disrupting local ecosystems (Deconninck *et al.* 2024; 2025).

Despite extensive research on drosophilid biodiversity and their interactions with fallen or decomposing fruits and vegetables in various regions worldwide, there is a noticeable lack of such studies from Poland. While regions like the neotropics and North America have been well-documented (Hochmüller *et al.* 2010; Emerich *et al.* 2012; Miller *et al.* 2017), with detailed investigations into both native and invasive drosophilid species, Poland's drosophilid fauna remains underexplored (Kovalenko *et al.* 2017, 2021). Drosophilid assemblages at composters are especially interesting in this respect, constituting "biodiversity islands" that may attract insects from different trophic levels.

This lack of data poses a challenge to fully understanding the country's local biodiversity, particularly in rotting fruits, which might support drosophilid populations or even facilitate the spread of invasive species like *D. suzukii* and *Ch. amoena*. Addressing this gap through focused research would prove crucial for the development of effective conservation strategies and management of potential agricultural pests, thus contributing to a more comprehensive understanding of drosophilid dynamics on a global scale.

The study aimed to evaluate the status, abundance and biodiversity of Drosophilidae species in compost piles from three localities in Poland: two orchards and one vegetable and fruit farm, where compost was piled up after the harvesting phase. Some other dipterans and insects from different orders captured in the traps and netting were also determined.

Materials and Methods

Study sites

The study was conducted at three locations in Łódzkie voivodeship: two orchards and one fruit and vegetable farm belonging to the Institute of Horticulture in Skieriewice. The fruit and vegetable farm in Skieriewice ($51^{\circ}57'47''N$ $20^{\circ}09'58''E$) was conventional and covered an area of 59 hectares. The compost heap, with the approximate dimensions of $20\text{ m (L)} \times 6\text{ m (W)} \times 4\text{ m (H)}$, was composed of relatively dry peat, soil, straw, and vegetable waste, including cucumbers, cabbage, tomatoes and rotting apples, and was surrounded by walnut, apple and oak trees as well as climbing clematis (Fig. 1A, B). The orchard at Dąbrowice ($51^{\circ}54'46''N$ $20^{\circ}06'54''E$) was also conventional, and extended over an area of 70 hectares, on which apple, pear, plum, apricot, sour and sweet cherry, bird cherry, blueberry, Kamchatka honeysuckle, grapes and cornel were grown. The compost pile, measuring approximately $2\text{ m (L)} \times 1.7\text{ m (W)} \times 0.4\text{ m (H)}$, was located in the middle of a small, deciduous, swampy forest at the edge of the orchard, in close proximity to a plot of highbush blueberries (Fig. 1C). The composter was rich in rotting apples, pears, plums and apricots, and surrounded by alder, bird cherry, elm, oak and birch trees as well as elderberry bushes (Fig. 1C). The 5-hectare orchard at Nowy Dwór-Pacela ($51^{\circ}52'12''N$ $20^{\circ}14'57''E$) was organic (Fig. 1D), and consisted of apple, plum, pear, peach, aronia, grape, Kamchatka honeysuckle and strawberry plots. The composter was located at the edge of the orchard near a thicket of elm and hazel trees, within dense vegetation, including nettles, goldenrod, wormwood and impatiens. It measured approximately $1.5\text{ m (L)} \times 1.5\text{ m (W)} \times 0.6\text{ m (H)}$. The composter was



Fig. 1. Compost piles studied: A, B – Skierniewice fruit and vegetable crop; C – Dąbrowice orchard; D – Nowy Dwór-Parcela orchard, September 2023

mainly filled with rotting plums, sweet cherries and blueberry drops, all covered by cut twigs and branches of deciduous trees (Fig. 1D). All the study sites were in close vicinity to each other. The Skierniewice farm was located 6.6 km from Dąbrowice and 11.7 km from the Nowy Dwór-Parcela orchard. The latter two orchards lay 10.3 km apart (Google-Maps 2025).

Sampling and identification

The sampling was conducted from September 1 to 13, 2023. Flies were captured using a sweep net and traps. An entomological net with a 24 cm diameter rim, a 37 cm long handle, and a 47 cm deep nylon cloth, modified from the design by Markow and O'Grady (2006), was used to catch flies on September 1st and 7th, 2023. Insects were captured by sweep netting in the morning from 9:30 am to 11:30 am. Sampling involved 18–20 net hits over the compost heaps. Four samples were taken at each location and date, and insects were transferred from the net to plastic string bags. Specimens were collected from the bags using an aspirator and then preserved in 70% ethanol. Two commercial drosophilid traps, Drososan (Koppert) and No Pest Fruit Fly Trap (Odstarszanie.pl), were employed for insect catching. Both traps used liquid baits that caused the flies and other insects to drown. Traps were installed around composters twice, on September 1 and 7. Each time, they were removed after a week and transported to the laboratory. Their positions were shuffled after a week. The insects were transferred from the traps to 70% ethanol, then counted and identified using a stereo binocular microscope connected to a cold light source. Drosophilid fruit fly species were identified following keys from Bächli *et al.* (2004), Markow and O'Grady (2006) and Werner *et al.* (2012).

and Jaenike (2017), while other Diptera, Coleoptera, Hymenoptera, Thysanoptera, and Dermaptera were determined to family level using keys by Marshall *et al.* (2016), Unwin (1985), Richards (1977), Cannings and Scudder (2005a, b), respectively. Furthermore, three nitidulid beetles were identified to the species level using taxonomic keys by Jelínek *et al.* (2010). The dissection and identification of drosophilid terminalia were conducted in potassium hydroxide (KOH) and absolute ethanol 1:1 following the EPPO (2013) procedure. Weather's record for the 1st two weeks of September 2023, from the local meteorological station in Skiernewice, showed that maximum daily temperatures fluctuated between 21.3°C and 31.9°C, while minimum daily temperatures ranged from 8.6°C to 15.0°C. The average daily temperatures varied within the range of 15.4°C to 21.7°C. Before the study, it was rainy but generally sunny and dry during the sampling phase. The relative humidity remained between 68% and 78% (IMWM-PIB, 2023).

Diversity estimation

To estimate the diversity of the drosophilid community in the composters, data obtained during two periods of insect trapping (Sept., 1–7 and Sept. 7–13, 2023) was pooled from each location. The analysis adopted the following calculation methods:

– The Shannon–Wiener diversity index (H) (Spearberg and Fedor 2003):

$$H = - \sum_{i=1}^S p_i \ln p_i,$$

where: p_i is the proportion (n/N) of individuals of a particular species (n) divided by the total number of individuals of all the species present in a record (N);

ln is the natural log; Σ is the sum of all the calculations; S is the total number of species in the community; and i is a particular species (ranging from 1 to S). The index considers both the number of species present (richness) and the evenness of their distribution. The higher the Shannon–Wiener index value, the greater the community diversity and vice versa.

– The Simpson index (1 – D) (Simpson 1949):

$$D' = 1 - D = 1 - \sum_{i=1}^S p_i^2,$$

where: p_i is the proportion (n/N) of individuals of a particular species (n) divided by the total number of individuals of all the species present in a record (N); Σ is the sum of the calculations; and S is the number of species in the community; and i is a particular species (ranging from 1 to S). The index ranges from 0 to 1, where 0 indicates no diversity, and 1 indicates infinite diversity. Higher values indicate greater diversity.

– Pielou's evenness index (J) (Zhang *et al.* 2012):

$$J = \frac{H'}{\ln(S)},$$

where: H' represents the observed value of the Shannon index, and S is the total number of species observed. This is a measure of how evenly species are distributed within a community. The index ranges from 0 to 1, where 0 indicates perfect unevenness (one species dominates), and 1 indicates ideal evenness (all species have equal abundance).

– Relative abundance of the i-th species (P_i) (Liu *et al.* 2021)

$$P_i = \frac{N_i}{N},$$

where: N_i is the number of individuals of the i -th species, and N is the total number of individuals.

The calculations of biodiversity parameters were performed using R 4.4.2 with the VEGAN package (Oksanen *et al.* 2024).

Results

Faunistic composition of drosophilids and other insects in three localities

A total of 18,915 insects, representing five orders and 38 families, were sampled through netting and trapping from the three compost locations (Table 1). Among them, 18,088 individuals were drosophilid fruit flies, which made up 95.6% of all specimens collected. The remaining 827 insects were other dipterans (3.67%), coleopterans (0.43%), hymenopterans (0.19%), thysanopterans (0.06%) and dermopterans (0.01%) (Table 1).

Using trapping and sweep netting, 16 species were collected from the family Drosophilidae (Table 2), including seven cosmopolitan and domestic species, namely *D. melanogaster* Meigen, *D. hydei* Sturtevant, *D. immigrans* Sturtevant, *D. buskii* Coquillett, *D. repleta* Wollaston, *D. simulans* Sturtevant and *Scaptomyza pallida* Zetterstedt, and three exotic species, i.e., *D. suzukii*, *Ch. amoena* and *D. triauraria*. The latter was recently identified molecularly and morphologically by the Michalska *et al.* (2025) (Table 2, Fig. 2A).

Traps captured more drosophilids than sweep netting, both in terms of individuals and species (15 species recorded in traps and nine in netting). Only one fruit fly species, *S. pallida*, was collected by sweep netting, but was not found in traps. The total number of drosophilids collected differed between the three localities (Table 2). The highest number of fruit flies, both trapped and sweep netted, were caught at the compost pile in the Dąbrowice orchard (61.17%), followed by Nowy Dwór-Parcela (31.54%) and Skieriewice (7.28%).

Some non-target insects belonging to various orders and families were also caught by sweep netting and trapping (Table 1). Twenty-four dipteran families were collected, among which sphaerocerids and scatopsids were the most abundant. More than 200 sphaerocerid flies were caught by a sweep net at the compost pile in Skieriewice. A similarly high number of scatopsids were trapped at the compost pile in Nowy Dwór-Parcela. Flies from Anisopodidae, Sciaridae, Tachinidae, Lonchaeidae, Calliphoridae, and Phoridae families were caught in all localities but in much smaller numbers, from a few up to a dozen individuals, and mostly by trapping. Specimens from the remaining fly families were collected only sporadically by trapping and sweep netting (Table 1). The collected beetles belonged to five families. Three nitidulid species were identified: *Carpophilus hemipterus* (L) (Fig. 2D,E), *Glischrochilus quadrisignatus* (Say) (Fig. 2B) and *Epuarea unicolor* (Oliver) (Fig. 2C). These were the most numerous and trapped in all locations, with the highest number at the compost pile in Dąbrowice. Staphylinid beetles were trapped in much smaller numbers both in Dąbrowice and Nowy Dwór-Parcela. Only single individuals were collected from other coleopteran families: Monotomidae, Ptiliidae, and Carabidae. In this collection, hymenopterans were represented by five families, among which ants (Formicidae) were recorded in traps in Dąbrowice and Nowy Dwór-Parcela orchards, while braconid wasps were caught in all three locations and sampled by both sweep netting and trapping, in the highest number in the Dąbrowice orchard (Table 1). A few cynipids were also collected at composters in Dąbrowice and Skieriewice, and a single bee and a few wasps in the Nowy Dwór-Parcela orchard and Skieriewice farm. Furthermore, among the other

Table 1. Faunistic composition of insect orders collected in September 2023 by trapping and sweep netting at three compost localities in Łódzkie voivodeship: Skieriewice fruit and vegetable farm (S), Dąbrowice orchard (D) and Nowy Dwór-Parcela orchard (N)

Order	Family	Number of insects caught						
		netting			trapping			
		N	D	S	N	D	S	
Diptera	Drosophilidae	1110	1244	304	4595	9821	1014	18088
	Scatopsidae	0	0	4	258	12	11	285
	Sphaeroceridae	3	3	213	0	1	7	227
	Sciaridae	2	2	3	9	2	18	36
	Anisopodidae	0	0	0	13	14	1	28
	Tachinidae	0	0	1	19	0	4	24
	Lonchaeidae	0	0	0	3	0	16	19
	Calliphoridae	0	0	0	11	0	2	13
	Phoridae	0	0	0	5	4	2	11
	Chloropidae	3	0	1	6	0	3	13
	Milichiidae	0	0	0	1	0	6	7
	Psychodidae	0	1	0	0	1	5	7
	Ulidiidae	0	0	4	0	0	0	4
	Heleomyzidae	0	0	0	0	3	0	3
	Dolichopodidae	0	0	0	0	0	3	3
	Muscidae	0	0	0	0	1	2	3
	Dryomyzidae	0	1	0	0	2	0	3
	Mycetophilidae	0	0	0	1	1	0	2
	Ceratopogonidae	0	0	0	0	0	1	1
Coleoptera	Cecidomyiidae	0	0	0	1	0	0	1
	Scathophagidae	0	0	1	0	0	0	1
	Sepsidae	0	0	1	0	0	0	1
	Asteiidae	0	0	1	0	0	0	1
	Syrphidae	1	0	0	0	0	0	1
	Hybotidae	1	0	0	0	0	0	1
	Nitidulidae	0	0	0	8	54	6	68
	Staphylinidae	0	0	1	0	8	2	11
	Monotomidae	0	0	0	0	0	1	1
	Ptiliidae	0	0	0	0	0	1	1
Hymenoptera	Carabidae	0	0	0	1	0	0	1
	Formicidae	0	0	0	7	3	0	10
	Cynipidae	0	0	1	0	4	3	8
	Braconidae	2	4	1	0	6	1	14
	Vespidae	0	0	0	3	0	0	3
Thysanoptera	Apidae	0	0	0	0	0	1	1
	Thripidae	0	0	1	0	0	11	12
Dermoptera	Forficulidae	0	0	0	0	2	0	1
	Total	1122	1255	537	4941	9939	1121	18915

insects, thrips (Thripidae) were also trapped, but only at the compost pile in Skieriewice. The order Dermoptera was represented by only two Forficulidae specimens trapped in the Dąbrowice orchard (Table 1).

Species diversity and relative abundance of drosophilids

As shown in Table 3, the community of fruit flies trapped at the composter of the fruit and vegetable

Table 2. Faunistic composition of drosophilid fruit flies collected in September 2023 by trapping and sweep netting at three compost localities in Łódzkie voivodeship: Skieriewice fruit and vegetable farm (S), Dąbrowice orchard (D) and Nowy Dwór-Parcela orchard (N)

Species	Number of insects captured						Ecological characteristics	References		
	netting			trapping						
	N	D	S	N	D	S				
<i>Drosophila melanogaster</i> Meigen	872	963	54	2743	4137	370	cosmopolitan, domestic, predominantly decaying fruit breeder	Bächli <i>et al.</i> (2004); Zatwarnicki (2007)		
<i>D. hydei</i> Sturtevant	178	181	88	113	4075	113	cosmopolitan, domestic, predominantly decaying fruit breeder	Bächli <i>et al.</i> (2004); Kovalenko <i>et al.</i> (2017; 2021)		
<i>D. subobscura</i> Fallén	0	56	5	1099	1243	23	widespread palaearctic species, introduced to both Americas, frugivorous and fungivorous	Shorrocks (1977); Bächli <i>et al.</i> (2004); Zatwarnicki (2007)		
<i>D. immigrans</i> Sturtevant	56	33	34	509	127	190	cosmopolitan, domestic, in decaying plant material, predominantly fruit breeder	Bächli <i>et al.</i> (2004); Kovalenko <i>et al.</i> (2017; 2021)		
<i>D. busckii</i> Coquillett	0	0	117	10	32	316	cosmopolitan, domestic, in decaying plant material, milk, eggs, etc.	Bächli <i>et al.</i> (2004); Zatwarnicki (2007)		
<i>D. suzukii</i> Matsumura	1	3	0	71	158	0	invasive, native to Eastern and Southeastern Asia, oviposits into ripening fruit, less frequently into wounded or fermenting fruit	Cini <i>et al.</i> (2014); Łabanowska and Piotrowski (2015); Kienzle <i>et al.</i> (2020); Deconninck <i>et al.</i> (2024)		
<i>D. repleta</i> Wollaston	0	0	0	5	18	1	cosmopolitan, domestic, in decaying plant material and mushrooms	Bächli <i>et al.</i> (2004); Zatwarnicki (2007)		
<i>D. triauraria</i> Bock & Wheeler	0	0	0	24	2	0	invasive, native to Japan and Korea, fruit breeder	Minami (1979); Michalska <i>et al.</i> (2025)		
<i>D. phalerata</i> Meigen	0	0	0	8	9	0	widespread palaearctic species, fungus breeder	Bächli <i>et al.</i> (2004); Zatwarnicki (2007)		
<i>D. funebris</i> Fabricius	2	0	5	5	7	0	palaearctic species, global human commensal, facultative fungus breeder, attracted to decaying plant matter	Zatwarnicki (2007); Obbald (2023)		
<i>D. testacea</i> Van Roser	1	8	0	5	6	0	widespread palaearctic species, mushroom breeder	Bächli <i>et al.</i> (2004)		
<i>Chymomyza amoena</i> Loew	0	0	0	0	6	0	invasive, nearctic fruit breeder	Band <i>et al.</i> (2005); Zatwarnicki (2007); Deconninck <i>et al.</i> (2024)		
<i>D. transversa</i> Fallén	0	0	0	1	1	0	widespread holarctic species, mushroom feeder	Bächli <i>et al.</i> (2004); Zatwarnicki (2007)		
<i>D. simulans</i> Sturtevant	0	0	0	2	0	0	cosmopolitan, domestic, predominantly fruit breeder	Bächli <i>et al.</i> (2004); Kovalenko <i>et al.</i> (2017; 2021)		

Table 2. Faunistic composition of drosophilid fruit flies collected in September 2023 by trapping and sweep netting at three compost localities in Łódzkie voivodeship: Skieriewice fruit and vegetable farm (S), Dąbrowice orchard (D) and Nowy Dwór-Parcela orchard (N) – continuation

Species	Number of insects captured						Ecological characteristics	References		
	netting			trapping						
	N	D	S	N	D	S				
<i>Hitrodrosohila sp.</i>	0	0	0	0	0	1		Zatwarnicki (2007)		
<i>Scaptomyza pallida</i> Zetterstedt	0	0	1	0	0	0	cosmopolitan, domestic, attracted to decaying plant matter (e.g. potato or beet), especially abundant in damp meadows and deciduous woods	Máca (1972); Bächli et al. (2004); Zatwarnicki (2007)		
Total	1110	1244	304	4595	9821	1014				

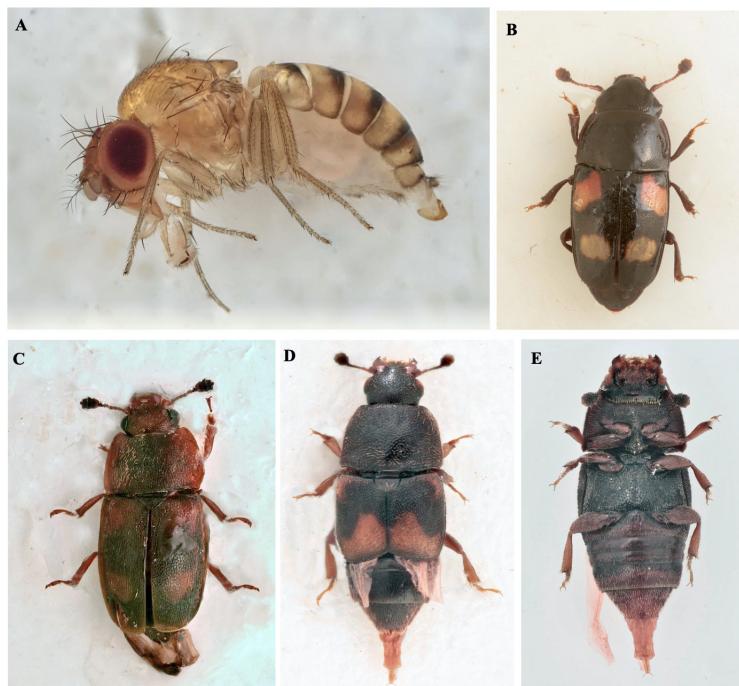


Fig. 2. Examples of insect species caught at composters: A – *Drosophila triauraria* (female with wings removed); B – *Glischrochilus quadrisignatus*; C – *Epuarea unicolor*; D, E – dorsal and ventral side of *Carpophilus hemipterus*

farm in Skieriewice was the most diverse, as indicated by a Shannon-Wiener index of 1.389, a Simpson's index of 0.722, and a Pielou's evenness index of 0.510. In the Nowy Dwór-Parcela orchard, all indexes had lower values. The lowest were recorded in the Dąbrowice orchard, indicating that the fruit fly community was the least diverse in this location.

Drosophila melanogaster was the most abundant species trapped across all three locations, while other fruit flies showed location-specific variations (Table 4). The relative abundance of *D. melanogaster* was nearly

60% in the orchard at Nowy Dwór-Parcela, 42% in the Dąbrowice orchard and 36% in the Skieriewice fruit and vegetable farm. In Skieriewice, *D. busckii* (31%) was the second most abundant drosophilid species, followed by *D. immigrans* and *D. hydei*. At the compost pile in the Dąbrowice orchard, *D. hydei* (41%) was the second most numerous species, followed by *D. subobscura* and *D. suzukii*. In the Nowy Dwór-Parcela orchard, *D. subobscura* (23.9%) and *D. immigrans* (11%) were the most abundant after *D. melanogaster*. *Drosophila simulans* was only found in Nowy Dwór-Parcela,

Table 3. Species diversity indexes for drosophilids caught in traps at three composter localities in Łódzkie voivodeship, 1–13 September 2023

Index	Locality		
	Dąbrowice	Nowy Dwór-Parcela	Skierniewice
Shannon	1.167	1.126	1.389
Simpson	0.634	0.573	0.722
Pielou's Evenness	0.272	0.319	0.510
Number of species	13	13	7

Table 4. Relative abundance (%) of fruit flies trapped at three composter localities in Łódzkie voivodeship, 1–13 September 2023

Species	Relative abundance [%] of drosophilids in different localities		
	Nowy Dwór-Parcela	Dąbrowice	Skierniewice
<i>D. melanogaster</i>	59.69	42.12	36.49
<i>D. hydei</i>	2.46	41.49	11.14
<i>D. subobscura</i>	23.92	12.66	2.27
<i>D. immigrans</i>	11.08	1.29	18.74
<i>D. busckii</i>	0.22	0.33	31.16
<i>D. suzukii</i>	1.55	1.61	0
<i>D. triauraria</i>	0.52	0.02	0
<i>D. repleta</i>	0.11	0.18	0.1
<i>D. phalerata</i>	0.17	0.09	0
<i>D. funebris</i>	0.11	0.07	0
<i>D. testacea</i>	0.11	0.06	0
<i>Ch. amoena</i>	0	0.06	0
<i>D. transversa</i>	0.02	0.01	0
<i>D. simulans</i>	0.04	0	0
<i>Hitrodrosophila</i> sps.	0	0	0.1

and its abundance was only 0.04%. Interestingly, in Nowy Dwór-Parcela, the alien species *D. triauraria* (0.46%) was in 7th place on the list of relative abundance of fruit fly species (just after the invasive *D. suzukii*), overtaking the invasive *Ch. amoena* and several native drosophilids found in this location (Table 4).

Discussion

In this study, drosophilid fruit flies accounted for 95.6% of all insects captured at composters using a sweep net or traps. Among other insects collected, flies, then beetles, bees and wasps were the most numerous, while thrips and earwigs were the least prevalent. Overall, 16 species of drosophilids were collected, including seven cosmopolitan and domestic species, i.e., *D. melanogaster*, *D. hydei*, *D. immigrans*, *D. busckii*, *D. repleta*, *D. simulans* and *S. pallida*, and three exotic species: *D. suzukii*, *Ch. amoena* and *D. triauraria*. The fruit fly

assemblage was the most diverse at the compost pile of the Skierniewice farm. Of all the trapped fruit fly species, *D. melanogaster* was dominant, with the highest relative abundance at all examined composters. Other cosmopolitan and domestic species, such as *D. hydei*, *D. busckii* and *D. immigrans*, as well as the frugivorous *D. subobscura*, were also numerous, though their relative abundance depended on the locality.

As in other orchards or vineyards (Delbac *et al.* 2020; Zengin 2020; Başpinar *et al.* 2022), drosophilid fruit fly communities on compost piles in Dąbrowice and Nowy Dwór-Parcela orchards as well as the fruit and vegetable farm in Skierniewice were dominated by cosmopolitan and domestic species. This contrasts with fruit fly assemblages in natural biotopes, where synanthropic species appear only accidentally, through migration or wind transportation from human habitats (Gornostaev *et al.* 2023). *Drosophila melanogaster* was the most abundant cosmopolitan species at all three localities, although closely followed by *D. hydei* in Dąbrowice. Both species are predominantly

frugivorous (Bächli *et al.* 2004); they come from the tropics, but in a temperate climate they can overwinter well in buildings (Spencer 1941; Gleason *et al.* 2019). *Drosophila simulans*, another tropical, common fruit breeding species, closely related to *D. melanogaster* (Bächli *et al.* 2004; Capy and Gilbert 2004), occurred only in Nowy Dwór-Parcela and had a very low population density. This species usually dominates over *D. melanogaster* in orchards in the southern part of the Northern Hemisphere, but in the north, due to its greater sensitivity to cold, it is replaced by *D. melanogaster* (Gleason *et al.* 2019). *Drosophila immigrans*, another cosmopolitan species, feeds on fruit and other organic substances (Bächli *et al.* 2004); it hides in houses when winters are severe but can overwinter outside during mild winters (Spencer 1940). This fruit fly was relatively abundant both on the Skieriewice farm and in the orchards, especially Nowy Dwór-Parcela. The neighborhood of small forests in Dąbrowice and Nowy Dwór-Parcela might have favored the occurrence of fungus breeders, i.e., *D. testacea*, *D. transversa*, *D. phalerata*, and *D. funebris* (Bächli *et al.* 2004). Basidiomycetes, which mainly occur in forests, are a major food source for fungivorous drosophilids (Shorrocks 1977; Shorrocks and Charlesworth 1980; Delbac *et al.* 2020). These species were absent on the Skieriewice farm, which lacked such a semi-natural environment in its vicinity.

In this study, the composters differed markedly in the type of organic matter stored, which may have influenced species composition. Storage of vegetables such as tomato, cucumber, cabbage and onion in Skieriewice may have contributed to the occurrence of *D. busckii*, which often inhabits rotting vegetables, e.g., cruciferous vegetables, garlic, onion or tomato (Bächli *et al.* 2004; Szwejda 2023). By contrast, *D. subobscura*, which is a frugivorous and fungivorous species (Bächli *et al.* 2004), was abundant in the Dąbrowice and Nowy Dwór-Parcela orchards. This fruit fly is tolerant to cold and is commonly found in orchards in other European countries. As a specialist of fruit decomposition, it may dominate other species, e.g., *D. melanogaster* or *D. suzukii* (Delbac *et al.* 2020; Başpinar *et al.* 2022; Deconninck *et al.* 2024). As shown by Deconninck *et al.* (2024), the texture and biochemical properties of the fruit, such as pH and sugar content, can determine the preferences and abundance of fruit flies at a particular site. For example, *D. melanogaster* opts for sweet and relatively acidic fruits, while *Ch. amoena* or *D. subobscura* prefer to oviposit and develop in fruits with lower acidity and sugar content (Deconninck *et al.* 2024).

Three invasive, frugivorous species, *D. suzukii*, *Ch. amoena* and *D. triauraria*, were recorded in the Dąbrowice and Nowy Dwór-Parcela orchards. *Drosophila suzukii* is an important fruit pest, first recorded in Poland by Łabanowska and Piotrowski (2015).

Although it prefers ripe but undamaged fruit, it can also use rotting fruit after harvest (Kienzle *et al.* 2020). For comparison, *Ch. amoena* or *D. triauraria* are not pests, as they breed only in damaged fruit, but, like *D. suzukii*, they are polyphagous and can compete with *D. suzukii* over fallen fruit in the autumn (Mitsui *et al.* 2010; Deconninck *et al.* 2024). *Chymomyza amoena* is a Nearctic species native to North America, first recorded in Poland in 1974 (Nowakowski 1991; Deconninck *et al.* 2024), while *D. triauraria* is a newly reported alien species of Asian origin, most presumably introduced to Poland with plant material (Michalska *et al.* 2025). It belongs to the *auraria* species complex and *montium* group, which has never been recorded in Europe. The fruit fly was trapped during two seasons (2023 and 2024) at the Nowy Dwór-Parcela and Dąbrowice compost piles, which suggestss that its population is likely to be established in Poland in the future (Michalska *et al.* 2025). Current research shows that it can be more abundant than several native drosophilids, suggesting that it may threaten fruit flies' biodiversity in the future. This should be further investigated.

The richness and diversity of drosophilid communities are usually much lower in semi-natural environments or in crops than they are in the wild forests (Zengin 2020; Gornostaeve *et al.* 2023). This also appears to be confirmed by the present study. The number of drosophilid species was 13 at the compost piles of the Dąbrowice and Nowy Dwór-Parcela orchards and 11 in Skieriewice. The Shannon-Weaver index values ranged between 1.1 and 1.4. By contrast, in the Mordovia State Nature Reserve (European Russia), 34 species of drosophilids were noted, and the Shannon-Weaver index reached a value above three (Gornostaeve *et al.* 2023). It must be stressed, however, that diversity indexes can be influenced by many factors, including the study area, frequency of samplings and season (see e.g., Gornostaeve *et al.* 2024). Thus, further studies are required to fully estimate the diversity of fruit flies' assemblages at compost piles and the environmental factors influencing the variations in species diversity between composters.

In orchards or vegetable crops, apart from drosophilids, other insects from different trophic levels are usually present, flies being the most numerous taxon (Andreadis *et al.* 2015; Başpinar *et al.* 2022; Szwejda 2023). Similarly, in this study, dipterans were the most numerous in terms of species richness and quantity. Especially many Sphaeroceridae were caught on the Skieriewice fruit and vegetable farm. Flies belonging to this family are mostly coprophagous, but decomposing species are also common (Marchiori 2022). In turn, in Nowy Dwór-Parcela, scatopsids were the most abundant dipterans, immatures of which are known to be saprophagous and develop in various decaying

organic matter (Haenni and Vaillant 1994). Beetles from the Nitidulidae family are also worthy of attention, and were especially abundant in Dąbrowice. Overall, three species were identified, i.e., *C. hemipterus*, *G. quadrisignatus* and *E. unicolor*, which are known to be attracted by fermenting organic matter. Interestingly, while *E. unicolor* is a native species (Jankowiak *et al.* 2019; Avidal 2024), *C. hemipterus* comes from tropical and subtropical regions (Kałmuk and Pawłowski 2024) and *G. quadrisignatus* from North America (Kałmuk *et al.* 2024). Both alien nitidulids are cosmopolitan and already established in Poland. Furthermore, *C. hemipterus* is an important pest of stored, dried fruits and has been recorded outside warehouses (Kałmuk and Pawłowski 2024; Kałmuk *et al.* 2024). Our research also showed that potential predatory insects such as carabid and staphylinid beetles, wasps and ants, forficulids and parasitoids, including tachinid flies and barconid wasps, may be attracted to composters, where they may prey on other decomposer arthropods, thus increasing multitrophic relations and biodiversity in the studied crops.

In summary, these preliminary studies indicated the ecological significance of compost heaps as habitats of drosophilid fruit flies and many other insect taxa, including potential competitors, as well as predators and parasitoids of these flies. Although composting plays an important role in the recycling of organic waste in horticulture (Franke-Whittle *et al.* 2019; Boros *et al.* 2022), research on composts as refuges and niches for insects, particularly Drosophilidae, is still lacking. This study showed that in orchards, compost piles can be a source of potential pests like *D. suzukii* or *C. hemipterus*. This is new evidence that these pests can use decaying plant material, and therefore, new pest management strategies should be implemented in composter environments (Bal *et al.* 2017; Hooper and Grieshop 2020; Deconninck *et al.* 2024; 2025). Undoubtedly, research should be continued and expanded to include sampling during the growing season, at other localities and in different seasons. Composters should be given special attention, as they appear to be hotspots for drosophilids in which exotic and invasive pest species are likely to be found. Moreover, further research is needed to assess the long-term ecological consequences of the presence of invasive species for the abundance and diversity of native drosophilid species, both in semi-natural (e.g., field margins) and natural environments (e.g., forest reserves).

Acknowledgements

We wish to thank Jan Máca for the identification of *Scaptomyza pallida* and Marek W. Kozłowski for identification and photographs of *Carpophilus hemipterus*,

Glischrochilus quadrisignatus and *Epuarea unicolor*. We are also grateful to Stanisław Lesiak for his assistance in collecting fruit flies.

References

Andreadis S.S., Witzgall P., Becher P.G. 2015. Survey of arthropod assemblages responding to live yeasts in an organic apple orchard. *Frontiers in Ecology and Evolution* 3: 121. DOI: <https://doi.org/10.3389/fevo.2015.00121>

Ashburner M., Hawley R.S., Golic K.G. 2005. *Drosophila*. A Laboratory Handbook. Cold Spring Harbor, N.Y.: Cold Spring Harbor Laboratory Press.

Avidal 2024. Insektarium.Drosophilidae. [Available from: <https://insektarium.net/diptera-2/drosophilidae-wywilznowate/>] [Accessed 15 October 2024]

Bächli G., Vilela C.R., Andersson S., Saura A. 2004. The Drosophilidae (Diptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 39. Leiden: Brill. Vol. 39. Brill, Leiden, New York, 2004, 362 pp. ISBN 9-004-14074-3.

Bal H.K., Adams C., Grieshop M. 2017. Evaluation of off-season potential breeding sources for spotted wing drosophila (*Drosophila suzukii* Matsumura) in Michigan. *Journal of Economic Entomology* 110: 2466–2470. DOI: <https://doi.org/10.1093/jee/tox252>

Başpinar H., Akşit T., Kesici A., Deutsch F., Kiss B., Papp L. 2022. Seasonal abundance and diversity of family Drosophilidae (Diptera) and records of some other dipterans in fruit orchards in Aydin Province (Türkiye). *Türkiye Entomoloji Dergisi* 46 (3): 289–298. DOI: <https://doi.org/10.16970/entoted.1088263>

Boros L., Levavasseur F., Kebalo L.F., Bijon N., Morel K. 2022. Recycling local organic waste in peri-urban horticulture: a case-study in the Parisian region. *Acta Horticulturae* 1356: 1–10. DOI: <https://doi.org/10.17660/ActaHortic.2022.1356.37.hal-03765968v2>

Cannings R.A., Scudder G.G.E. 2005a. Families of Thysanoptera of British Columbia. In: Klinkenberg, Brian. (Editor) 2023. E-Fauna BC: Electronic Atlas of the Fauna of British Columbia. Department of Geography, University of British Columbia, Vancouver. [Available from: <https://linnet.geog.ubc.ca/biodiversity/efauna/FamiliesofThysanopteraofBritishColumbia.html>] [Accessed 01 October 2024].

Cannings R.A., Scudder G.G.E. 2005b. Families of Earwigs (Dermaptera) of British Columbia. In: Klinkenberg, Brian. (Editor) 2023. E-Fauna BC: Electronic Atlas of the Fauna of British Columbia. Department of Geography, University of British Columbia, Vancouver. [Available from: <https://linnet.geog.ubc.ca/biodiversity/efauna/FamiliesofDermapteraofBritishColumbia.html>] [Accessed 01 October 2024].

Capy P., Gibert P. 2004. *Drosophila melanogaster*, *Drosophila simulans*: so similar yet so different. *Genetica* 120 (1–3): 5–16. DOI: [10.1023/b:gene.0000017626.41548.97](https://doi.org/10.1023/b:gene.0000017626.41548.97). PMID: 15088643

Cini A., Anfora G., Escudero-Colomar L.A., Grassi A., Santosuoso U., Seljak G., Papini A. 2014. Tracking the invasion of the alien fruit pest *Drosophila suzukii* in Europe. *Journal of Pest Science* 87: 559–566. DOI: <https://doi.org/10.1007/s10340-014-0617-z>

David P., Thebault E., Anneville O., Duyck P.F., Chapuis E., Loeuille N. 2017. Impacts of invasive species on food webs: a review of empirical data. *Advances in Ecological Research* 56: 1–60. DOI: <https://doi.org/10.1016/bs.aecr.2016.10.001>

Deconninck G., Boulembert M., Eslin P., Couty A., Dubois F., Gallet-Morin E., Pincebourde S., Chabrerie O. 2024. Fallen fruit: A backup resource during winter shaping fruit fly communities. *Agricultural and Forest Entomology* 26 (2): 232–248. DOI: <https://doi.org/10.1111/afe.12610>

Deconninck G., Boulembert M., Eslin P., Couty A., Dubois F., Gallet-Moron Pincebourde S., Chabrerie O. 2025. Winter fleshy-fruited plants are the catalysts for spring populations of an invasive fruit fly. *Ecological Entomology* 50(2): 258–273. DOI: <https://doi.org/10.1111/een.13397>

Delbac L., Rusch A., Binet D., Thiéry D. 2020. Seasonal variation of Drosophilidae communities in viticultural landscapes. *Basic and Applied Ecology* 48: 83–91. DOI: <https://doi.org/10.1016/j.baae.2020.08.002>

Emerich P.P., Valadão H., Silva J.R.V.P., Tidon R. 2012. High abundance of neotropical drosophilids (Diptera: Drosophilidae) in four cultivated areas of central Brazil. *Neotropical Entomology* 41: 83–88. DOI: <https://doi.org/10.1007/s13744-011-0004-x>

EPPO. 2013. Diagnostic. PM 7/115 (1) *Drosophila suzukii*. EPPO Bulletin 43: 417–424. DOI: <https://doi.org/10.1111/epp.12059>

Finet C., Kassner V.A., Carvalho A.B., Chung H., Day J.P., Day S., Delaney E.K., De Ré F.C., Dufour H.D., Dupim E., Izumitani H.F., Gautério T.B., Justen J., Katoh T., Kopp A., Koshikawa S., Longdon B., Loreto E.L., Nunes M.D.S., Raja K.K.B., Rebeiz M., Ritchie M.G., Saakyan G., Sneddon T., Teramoto M., Tyukmaeva V., Vanderlinde T., Wey E.E., Werner T., Williams T.M., Robe L.J., Toda M.J., Marlétaz F. 2021. Drosophila: resources for drosophilid phylogeny and systematics. *Genome Biology and Evolution* 13: evab179. DOI: <https://doi.org/10.1093/gbe/evab179>

Franke-Whittle I.H., Juárez M.F.D., Insam H., Schweizer S., Naef A., Topp A.R., Kelderer M., Rühmer T., Baab G., Henfrey J., Manici L.M. 2019. Performance evaluation of locally available composts to reduce replant disease in apple orchards of central Europe. *Renewable Agriculture and Food Systems* 34 (6): 543–557. DOI: <https://doi.org/10.1017/S1742170518000091>

Gleason J.M., Roy P.R., Everman E.R., Gleason T.C., Morgan T.J. 2019. Phenology of *Drosophila* species across a temperate growing season and implications for behavior. *PLoS One* 14 (5): e0216601. DOI: <https://doi.org/10.1371/journal.pone.0216601>

Google-Maps 2025. Skieriewice, Dąbrowice, and Nowy Dwór-Pacela. [Available from: <https://www.google.com/maps/search/?api=1>] [Accessed 01 March 2025]

Gornostaev N.G., Ruchin A.B., Esin M.N., Lazebny O.E., Kulikov A.M. 2023. Vertical distribution of fruit flies (Diptera: Drosophilidae) in deciduous forests in the center of European Russia. *Insects* 14 (10): 822. DOI: <https://doi.org/10.3390/insects14100822>

Gornostaev N.G., Lyupina Y.V., Lazebny O.E., Kulikov A.M. 2024. Seasonal Dynamics of Fruit Flies (Diptera: Drosophilidae) in Natural Parks of Moscow City, Russia. *Insects* 15(6), 398. DOI: <https://doi.org/10.3390/insects15060398>

Goulson D., Hughes W.O.H., Chapman J.W. 1999. Fly populations associated with landfill and composting sites used for household refuse disposal. *Bulletin of Entomological Research* 89(06): 493 - 498. DOI: <https://doi.org/10.1017/S0007485399000644>

Grimaldi D.A., Richenbacher C. 2023. Exceptional species diversity of Drosophilidae (Diptera) in a Neotropical Forest. *American Museum Novitates* 3997: 1–28. DOI: <https://doi.org/10.1206/3997.1>

Haenni J.P., Vaillant F. 1994. Description of dendrolimnobiontic larvae of Scatopsidae (Diptera) with a review of our knowledge of the preimaginal stages of the family. *Mitteilungen der Schweizerischen Entomologischen Gesellschaft* 67: 43–59. DOI: <https://doi.org/10.5555/19960503658>

Henry Y., Overgaard J., Colinet H. 2020. Dietary nutrient balance shapes phenotypic traits of *Drosophila melanogaster* in interaction with gut microbiota. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 241: 110626. DOI: <https://doi.org/10.1016/j.cbpa.2019.110626>

Hochmüller C.J., Lopes-da-Silva M., Valente V.L., Schmitz H.J. 2010. The drosophilid fauna (Diptera, Drosophilidae) of the transition between the Pampa and Atlantic Forest Biomes in the state of Rio Grande do Sul, southern Brazil: first records. *Papéis Avulsos de Zoologia* 50: 286–295. DOI: <https://doi.org/10.1590/S0031-10492010001900001>

Hooper H., Grieshop M.J. 2021. Composting susceptible fruit wastes reduces *Drosophila suzukii* (Diptera: Drosophilidae) reproductive habitat. *Pest Management Science* 77 (1): 202–207. DOI: <https://doi.org/10.1002/ps.6008>

Hough R.L. 2014. Biodiversity and human health: evidence for causality? *Biodiversity and Conservation* 23: 267–288. DOI: <https://doi.org/10.1007/s10531-013-0614-1>

IMWM-PIB 2023. Institute of Meteorology and Water Management – National Research Institute, Poland/Measurement of meteorological data/(2023). [Available from: <https://dane.imgw.pl/datastore>; https://danepubliczne.imgw.pl/data/dane_pomiarowo_observacyjne/] [Accessed August 2025 13]

Jankowiak R., Bilański P., Ostafińska A., Linnakoski R. 2019. Ophiostomatales associated with wounds on hardwood trees in Poland. *Plant Pathology* 68 (7): 1407–1424. DOI: <https://doi.org/10.1111/ppa.13061>

Jelínek J., Carlton C., Cline A.R., Leschen R.A.B. 2010. Chapter 10.26. Nitidulidae Latreille, 1802. In: Leschen, R.A.B., Beutel, R.G., Lawrence, J.F. (eds.), *Handbook of Zoology, Arthropoda: Insecta, Coleoptera, Beetles, Vol. 2: Morphology and Systematics*. De Gruyter, Berlin, New York, p. 390e407.

Jiménez-Padilla Y., Ferguson L.V., Sinclair B.J. 2020. Comparing apples and oranges (and blueberries and grapes): Fruit type affects development and cold susceptibility of immature *Drosophila suzukii* (Diptera: Drosophilidae). *Canadian Entomologist* 152: 532–545. DOI: <https://doi.org/10.4039/tce.2020.36>

Kałmuk J., Daniel Kubisz D., Pawłowski J. 2024. *Glischrochilus quadrifasciatus* (Say, 1835). In: *Gatunki Obce w faunie Polski. Publikacja internetowa Instytutu Ochrony Przyrody PAN*, (Kałmuk J., Kubisz D., Pawłowski J., eds.) [Available from: <https://www.iop.krakow.pl/gatunkiobce/default0003.html?nazwa=opis&id=57&je=pl>] [Accessed 17 November 2024] (in Polish)

Kałmuk J., Pawłowski J. 2024. *Carpophilus hemipterus* (Linnaeus, 1758). In: „*Gatunki Obce w faunie Polski. Publikacja internetowa Instytutu Ochrony Przyrody PAN*” (Kałmuk J., Kubisz D., Pawłowski J., eds.) [Available from: <https://www.iop.krakow.pl/ias/gatunki/746>] [Accessed 17 November 2024].

Kienzle R., Groß L.B., Caughman S., Rohlf M. 2020. Resource use by individual *Drosophila suzukii* reveals a flexible preference for oviposition into healthy fruits. *Scientific Report* 10: 3132. DOI: <https://doi.org/10.1038/s41598-020-59595-y>

Kovalenko P., Protsenko O., Shulga V., Serga S.V., Ślęzak-Parnikoza A., Wojciechowski K., Parnikoza I., Kozeretska I. 2017. Species diversity of Drosophilidae from Poland and Ukraine. The 12th International Conference of Young Naturalists. From biotechnology to nature protection. The interdisciplinary meeting of young naturalists, 22–24 November 2017, Zielona Góra, Poland, Poland. Book of Abstracts, 66 pp.

Kovalenko P., Serga S.V., Protsenko O., Gora N.V., Ślęzak-Parnikoza A., Zinchenko M.Yu., Wojciechowski K., Kozeretska I. A. 2021. Drosophilidae of Ukraine and Poland. The 7th International Conference “*Drosophila* in Experimental genetics and biology. p. 33–36. 9.09–10.09. 2021, Odesa, Ukraine.

Łabanowska B.H., Piotrowski W. 2015. The spotted wing drosophila, *Drosophila suzukii* Matsumura (1931) – monitoring and first records in Poland. *Journal of Horticultural Research* 23: 49–57. DOI: <https://doi.org/10.2478/johr-2015-0020>

Liu J., Yan X., Song X., Zhang J., Wu D., Gao M. 2021. Distribution characteristics of insect diversity in long-term fixed monitoring plots in Northeast China. *PLoS ONE* 16 (8): e0250689. DOI: <https://doi.org/10.1371/journal.pone.0250689>

Máca J. 1972. Czechoslovak species of the genus *Scaptomyza* Hardy (Diptera: Drosophilidae) and their bionomics. *Acta Entomologica Bohemoslovaca* 69: 119–132.

Marchiori C.H. 2022. Importance of Sphaeroceridae family as accelerators of the putrefaction process, nutrient recycling and in its association with the cadaveric decomposition process (Insecta: Diptera). *Biology and Pharmacy* 4 (02): 28–42. DOI: <https://doi.org/10.53022/oarjbp.2022.4.2.0039>

Markow T.A., O'Grady P. 2006. *Drosophila* A Guide to Species Identification and Use. Elsevier 66: 157–158. Academic Press Inc (November 1, 2005).

Markow T.A., O'Grady P. 2008. Reproductive ecology of *Drosophila*. *Functional Ecology* 28: 747–759. DOI: <https://doi.org/10.1111/j.1365-2435.2008.01457.x>

Marshall A.S., Kirk-Spriggs H.A., Muller S.B., Paiero M.S., Yau T., Jackson D.M. 2016. Key to Diptera families-adults. Manual of Afrotropical Diptera 2106(1): 1–81. Publisher: SANBI Graphics & Editing, Editors: Ashley H. Kirk-Spriggs, Bradley J. Sinclair

Mata R.A., McGeoch M., Tidon R. 2010. Drosophilids (Insecta, Diptera) as tools for conservation biology. *Natureza & Conservação* 8: 60–65. DOI: <https://doi.org/10.4322/natcon.00801009>

Michalska K., Máca J., Ibrahim M.A., Mácová A., Hrček J., Svoboda S., Kozłowski M.W., Wakuliński W., Soika G. 2025. Is the *Drosophila montium* species group knocking on the doors of Europe? The case of the Asian fruit fly, *Drosophila triauraria* Bock & Wheeler, 1972. *BioInvasions Records* 14 (2): 281–288. DOI: <https://doi.org/10.3391/bir.2025.14.2.02>

Miller M.E., Marshall S.A., Grimaldi D.A. 2017. A review of the species of *Drosophila* (Diptera: Drosophilidae) and genera of Drosophilidae of northeastern North America. *Canadian Journal of Arthropod Identification* (31). DOI: [doi:10.3752/cjai.2017.31](https://doi.org/10.3752/cjai.2017.31)

Minami N. 1979. Niche analysis of three closely related species of the genus *Drosophila* (With 4 Text-figures and 3 Tables). *Journal of Faculty of Science, Hokkaido University. Series VI, Zoology* 22 (1): 33–41.

Mitsui H., Beppu K., Kimura M.T. 2010. Seasonal life cycles and resource uses of flower- and fruit-feeding drosophilid flies (Diptera: Drosophilidae) in central Japan. *Entomological Science* 13: 60–67. DOI: <https://doi.org/10.1111/j.1479-8298.2010.00372.x>

Nowakowski J.T. 1991. Braulidae to Curtonotidae. p. 224–228. In: „Wykaz zwierząt Polski” (Razowski, J., ed.). Vol. I. Ossolineum, Wrocław – Warszawa – Kraków, Poland (in Polish)

Obbard D.J. 2023. The genome sequence of the fruit fly, *Drosophila funebris* (Fabricius, 1789). *Wellcome Open Research* 8: 437 DOI: <https://doi.org/10.12688/wellcomeopenres.20035.1>

Ødegaard F., Tømmerås B.Å. 2000. Compost heaps – refuges and stepping-stones for alien arthropod species in northern Europe. *Diversity and Distributions* 6 (1): 45–59.

Oksanen J., Simpson G., Blanchet F., Kindt R., Legendre P., Minchin P., O'Hara R., Solymos P., Stevens M., Szoecs E., Wagner H., Barbour M., Bedward M., Bolker B., Borcard D., Borman T., Carvalho G., Chirico M., De Caceres M., Durand S., Evangelista H., FitzJohn R., Friendly M., Furneaux B., Hannigan G., Hill M., Lahti L., McGlinn D., Ouellette M., Ribeiro Cunha E., Smith T., Stier A., Ter Braak C., Weedon J. 2024. vegan: Community Ecology Package. R package version 2.7-0 [Available from: <https://github.com/vegandevs/vegan>, <https://vegandevs.github.io/vegan/>] [Accessed 18 November 2024].

Pajač-Živković I., Barić B., Lemić D., Blažević I., Šubić M., Seljak G., Mešić A. 2016. The Drosophilid fauna (Diptera, Drosophilidae) of IPM vineyards in Croatia. *Agriculturae Conspectus Scientificus* 81 (4): 231–234.

Plotnikov I.S., Sidorenko V.S., Krivokhatsky V.A. 2013. Zoogeographic analysis of the Palaearctic fauna of Drosophilid flies (Diptera, Drosophilidae) with description of clusterization software for provincial faunas. *Entomological Review* 93: 831–843. DOI: [10.1134/S0013873813070051](https://doi.org/10.1134/S0013873813070051)

Pyšek P., Hulme P.E., Simberloff D., Bacher S., Blackburn T.M., Carlton J.T., Dawson W., Essl F., Foxcroft L.C., Genovesi P., Jeschke J.M., Kühn I., Liebhold A.M., Mandrak N.E., Meyerson L.A., Pauchard A., Pergl J., Roy H.E., Seebens H., Kleunen M., Vilà M., Wingfield M.J., Richardson D.M. 2020. Scientists' warning on invasive alien species. *Biological Reviews* 95: 1511–1534. DOI: <https://doi.org/10.1111/brv.12627>

Ribeiro L.B., Proença C.E.B., Tidon R. 2023. Host preferences shown by Drosophilids (Diptera) in a commercial fruit and vegetable distribution center follow the wild neotropical pattern. *Insects* 14: 375. DOI: <https://doi.org/10.3390/insects14040375>

Richards O.W. 1977. Hymenoptera. Introduction and key to families. London: Royal Entomological Society.

Shorrocks B. 1977. An ecological classification of European *Drosophila* species. *Oecologia* 26: 335–345.

Shorrocks B., Charlesworth P. 1980. The distribution and abundance of the British fungal breeding *Drosophila*. *Ecological Entomology* 5 (1): 61–78.

Simpson E.H. 1949. Measurement of diversity. *Nature* 168: 668. DOI: <https://dx.doi.org/10.1038/163688a0>

Spellerberg I.F., Fedor P.J. 2003. A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the 'Shannon–Wiener' Index. *Global Ecology and Biogeography* 12: 177–179. DOI: <https://doi.org/10.1046/j.1466-822X.2003.00015.x>

Spencer 1941. Ecological factors and *Drosophila* speciation. *Ohio Journal of Science* 41:190–200.

Spencer W. 1940. On the biology of *Drosophila immigrans* Sturtevant with special reference to the genetic structure of populations. *Ohio Journal of Science* 40 (6): 345–361.

Szwejda H.J. 2023. Diptera pests occurring on vegetable crops in Poland. *Journal of Horticultural Research* 31 (1): 155–174. DOI: <https://doi.org/10.2478/johr-2023-0030>

Taxodros 2025. The database on Taxonomy of Drosophilidae; TaxoDros: Classification. [Online] [Available from: <https://www.taxodros.uzh.ch/search/class.php>] [Accessed 26 February 2025].

Unwin D.M. 1985. Key to the Families of British Beetles. Mad River PressInc.

Weisser W.W., Siemann E. 2008. The various effects of insects on ecosystem functioning. p. 3–24. In: "Insects and Ecosystem Function". Berlin, Heidelberg: Springer Berlin Heidelberg.

Werner T., Jaenike J. 2017. Drosophilids of the Midwest and Northeast. [Available from: <https://hdl.handle.net/1802/34909>] [Accessed 17 June 2024].

Wilcove D.S., Rothstein D., Dubow J., Phillips A., Losos E. 1998. Quantifying threats to imperilled species in the United States. *BioScience* 48: 607–615. DOI: <https://doi.org/10.2307/1313420>

Zatwarnicki T. 2007. Wywilznowate (Drosophilidae). In "Fauna of Poland. Characteristics and checklist of species" (Bogdanowicz W., Chudzicka E., Pilipiuk I., Skibinska E., eds.), Vol. 2.: 130–131, 216–217. Muzeum i Institut Zoologii PAN, Warszawa. (in Polish)

Zengin E. 2020. Occurrence of invasive species and seasonal dynamics of fruit flies (Diptera: Drosophilidae) species in Uşak province, Turkey. *Revista de la Sociedad Entomológica Argentina* 79 (1): 21–30, 2020 Sociedad Entomológica Argentina, Argentina. [Available from: <https://www.redalyc.org/articulo.oa?id=322061697004>] [Accessed 17 November 2024].

Zhang H., John R., Peng Z., Yuan J., Chu C., Du G., Zhou S. 2012. The relationship between species richness and evenness in plant communities along a successional gradient: a study from sub-alpine meadows of the Eastern Qinghai-Tibetan Plateau, China. *PloS One* 7(11): e49024. DOI: <https://doi.org/10.1371/journal.pone.0049024>