

Seasonal variability of *Drosophila* parasitoids in agricultural and semi-natural environments in Poland

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Abstract

The spotted wing drosophila (*Drosophila suzukii*) is an invasive pest causing significant damage to soft fruit crops in Europe. Native parasitoids may contribute to its biological control, yet information on their distribution and seasonal activity in Central Europe remains limited. This study aimed to investigate the species composition and seasonal dynamics of *Drosophila* parasitoids in agricultural and adjacent semi-natural habitats in Poland. Fieldwork was conducted during the early, middle, and late vegetation seasons in 2021–2022 using self-constructed traps baited with *Drosophila melanogaster* and *D. hydei* as hosts. Parasitoids emerging from collected traps were identified and quantified. Three hymenopteran parasitoid species were recorded: the larval parasitoid *Asobara tabida* and the pupal parasitoids *Trichopria drosophilae* and *Pachycrepoideus vindemmiae*. *P. vindemmiae* was the most abundant species, particularly in mid-season and in semi-natural areas. *T. drosophilae* dominated in the early season, while *A. tabida* was consistently less numerous. The overall parasitoid abundance was significantly higher in semi-natural habitats compared to agricultural sites. The structure of parasitoid assemblages changed with the season, with the highest species evenness in early and mid-season samples. These results highlight the influence of habitat type and seasonality on parasitoid occurrence and suggest that certain native species, especially *P. vindemmiae* and *T. drosophilae*, could contribute to the conservation biological control of *D. suzukii*. Promoting semi-natural refuges may enhance the presence and persistence of beneficial parasitoids in agricultural landscapes.

Key Words

Asobara tabida, natural enemies of pests, *Pachycrepoideus vindemmiae*, parasitoids, *Trichopria drosophilae*

Introduction

Small fruit flies (*Drosophila*) belong to the family Drosophilidae (Insecta: Diptera) and are mainly associated with overripe or rotting fruit. Some members of this genus play an essential role in scientific research regarding their life history, biology, phylogeny, ecology, and especially genetics. *Drosophila melanogaster* (Meigen) is one of the most popular model systems for genetic research (Markow and O’Grady 2007; Miller et al. 2017). However, a few species, e.g., spotted wing drosophila (*Drosophila suzukii* (Matsumura)), are important pests of fruit crops, as females can lay eggs in ripening fruit, which causes significant losses in soft fruit production

(Walsh et al. 2011; Asplen et al. 2015). *Drosophila suzukii* was detected almost simultaneously in Europe and North America in 2008 (Walsh et al. 2011; Cini et al. 2012; Rota-Stabelli et al. 2020), while its presence in South America and North Africa was reported several years later (Deprá et al. 2014; Andreazza et al. 2017). In regions where *D. suzukii* has invaded, its presence in farm areas can cause economic losses ranging from 20–50% in conventional soft fruit crops and up to 100% in organic systems (Walsh et al. 2011; Bellamy et al. 2013; Farnsworth et al. 2017). Raspberry yield losses in Minnesota, caused by spotted wing drosophila, were estimated at 20%, translating into annual revenue losses of USD 2.35 million (DiGiacomo et al. 2019). It can be even higher in

South America, estimated at USD 21.4 million for peach production and USD 7.8 million for figs in Brazil (Benito et al. 2016). In Chile, damages caused by this pest ranged from USD 5,000 to 17,550 per hectare for cherries and USD 4,000 for blueberries (Morales 2020). For the first time, *D. suzukii* was noted in Poland in 2014, marking the beginning of its spread in the region (Łabanowska and Piotrowski 2015).

To date, 1157 species of *Drosophila* are known worldwide, of which many are widespread or cosmopolitan (Miller 2017). The vast abundance of the small fruit flies caused them to serve as natural hosts to more than 50 species of parasitoid wasps (Carton et al. 1986). However, according to Lue et al. (2021), the species richness of the parasitoid wasps that attack *Drosophila* is widely underestimated, and only a fraction of parasitoids have been described. Parasitoid wasps represent a large group of obligate parasitic insects that specialize in attacking different developmental stages of their hosts. These include egg parasitoids, which target insect eggs; larval parasitoids – koinobionts; and pupal parasitoids – idiobionts (Haan et al. 1987; Fleury et al. 2009).

Parasitoid wasps that target *Drosophila* flies are distributed across four families and at least 16 genera. Koinobionts of these parasitoids belong to the families Braconidae (*Asobara*, *Aphaereta*, *Phaenocarpa*, *Tanycarpa*, *Aspilota*, *Opius*) and Figitidae (*Leptopilina*, *Ganaspis*, *Kleidotoma*, *Dicerataspis*), while idiobionts to Diapriidae (*Trichopria*, *Spilomicrus*) and Pteromalidae (*Pachycrepoideus*, *Spalangia*, *Trichomalopsis*, *Toxomorpha*) (Carton et al. 1986). One of the well-studied groups of *Drosophila* parasitoids is koinobionts, which attack larvae that thrive in fermenting fruits from the genera *Leptopilina* and *Asobara*. Fleury et al. (2009) reviewed knowledge of this group, presenting the genetic bases of fitness trait variations, the physiology and genetics of resistance/virulence, and coevolutionary dynamics leading to local adaptation. The genus *Asobara* is represented by a species complex, among which *A. tabida* is widely distributed in Europe (Carton et al. 1986; Kraaijeveld et al. 1994; Kraaijeveld and Van Der Wel 1994). Among the genus *Leptopilina*, the well-studied are *L. heterotoma* (Thomson) and *L. boulandi* (Barbotin, Carton & Keiner-Pillault). However, *L. heterotoma* is the most generalist within this genus, with a wide Holarctic distribution, while *L. boulandi* is a specialist parasitizing frugivorous *Drosophila* spp., with a northern occurrence limit in South Europe (Fleury et al. 2009). All three species (*L. heterotoma*, *L. boulandi*, and *A. tabida*) share common hosts, *D. melanogaster* Meigen, *Drosophila simulans* Sturtevant, and *Drosophila subobscura* Collin.

Idiobionts attacking *Drosophila* pupae were found in two families: Diapriidae (*Trichopria* and *Spilomicrus*) and Pteromalidae (*Pachycrepoideus*, *Spalangia*, *Trichomalopsis* and *Toxomorpha*) (Carton et al. 1986; Forbes et al. 2018). Among them, *Pachycrepoideus vindemmiae* (Rondani) and *Trichopria drosophilae* (Perkins), are valuable in pest biocontrol strategies, especially those

attacking fruit (Rossi Stacconi et al. 2013; Wang et al. 2016b; Bezerra Da Silva et al. 2019; Rossi Stacconi et al. 2019; Wolf et al. 2020). *P. vindemmiae* and *T. drosophilae* are cosmopolitan and sympatric in many regions of the World. Less numerous pupal parasitoids inhabiting the *Drosophila*, *Spalangia simplex* Perkins (Hymenoptera: Pteromalidae) were noted in Mexico, while *Trichopria anastrephae* (Lima) (Hymenoptera: Diapriidae) were found in Brazil (Cruz et al. 2011; Vieira et al. 2020). Among these two the most common pupal parasitoids, *P. vindemmiae* is a generalist ectoparasitoid with a global distribution and a broad host range including several families of the order Diptera (Rossi Stacconi et al. 2013; Noyes 2019), and *T. drosophilae* is a generalist endoparasitoid distributed across Eurasia and America (Carton et al. 1986; Wang et al. 2016b; Lee et al. 2019).

Naturally occurring parasitoids play a significant role in regulating their host populations, helping to maintain ecological balance and prevent the excessive spread of these flies, which can be harmful to agricultural and natural ecosystems (Carton et al. 1986; Fleury et al. 2004; Miller et al. 2015; Daane et al. 2016; Guerrieri et al. 2016). *P. vindemmiae* and *T. drosophilae*, along with larval parasitoids previously identified as *Ganaspis brasiliensis* (Ihering) (Hymenoptera: Figitidae), are considered effective agents of biological control against *Drosophila suzukii*. While *P. vindemmiae* and *T. drosophilae* are primarily used in conservation and augmentative biological control strategies, *G. kimorum* is currently the focus of classical biological control programs (Gabarra et al. 2015; Rossi Stacconi et al. 2019; Rossi Stacconi 2022). Recently, what was formerly referred to as *G. brasiliensis* has been reclassified into three distinct species. Among these, two strains capable of parasitizing *D. suzukii* – G1 and G3 – have been formally described as *Ganaspis kimorum* Buffington and *Ganaspis lupini* Buffington, respectively. The remaining strain, G5, which does not attack *D. suzukii*, retains the name *G. brasiliensis* (Sosa-Calvo et al. 2024). This taxonomic clarification is crucial for accurately identifying effective biological control agents (BCAs) for *D. suzukii* management. There is another species, *Leptopilina japonica* (Novković & Kimura) (Hymenoptera: Figitidae), with high specificity to *D. suzukii*, which makes it a particularly promising BCA (Fleury et al. 2004; Girod et al. 2018). Adventive populations of this parasitoid, native to East Asia, have already been observed in Italy, the USA, and Canada, and its range is expanding across Europe and North America (Puppato et al. 2020; Daane et al. 2021; Abram et al. 2022; Martin et al. 2023; Garipey et al. 2024). Knowing the species composition of parasitoids in the invasive range of *D. suzukii* is crucial in order to evaluate potential use in biological and integrated control strategies. This study aims to delineate the species composition of *Drosophila* parasitoids in the agricultural and semi-natural environments surrounding soft fruit plantations in Poland. The data collected may evaluate whether naturally occurring species of parasitoid wasps can be used to control spotted wing drosophila, a new pest

in Poland (Łabanowska and Piotrowski 2015). Numerous studies conducted since 2012 in Europe, Africa, and the Americas have identified a few local parasitoid species attacking *D. suzukii*, such as *P. vindemmiæ* and *T. drosophilæ*. These studies recommend conservation biocontrol strategies (Haye et al. 2016; Wang et al. 2016a; Giorgini et al. 2019). However, similar ecological investigations have not yet been carried out in this region of Europe.

Materials and methods

A field collection of *Drosophila* parasitoids was conducted in Poland, spanning the central to eastern regions (Fig. 1) from 2021 to 2022, across the early, mid, and late vegetation seasons. Self-constructed plastic traps were used to sample parasitoids on soft fruit plantations (including blackcurrants, raspberries, blueberries, and cherries) and in semi-natural areas adjacent to these crops, such as forests or hedgerows (Table 1). The semi-natural areas were located 500 to 1000 meters from the plantations

and consisted of former agricultural lands or pastures now covered with naturally growing trees, including oaks, beeches, and birches. These areas form transitional zones between open fields and dense woodlands, providing valuable habitats for diverse species. The primary objective of this research was to investigate factors such as seasonal and habitat-related differences in parasitoid communities, rather than inter-annual variability. Consequently, while sampling was conducted over two years, the study emphasized capturing seasonal variability at all three moments of the vegetation seasons and between habitats, without focusing on year-to-year comparisons.

The traps were constructed using commercially available 500 ml transparent, round plastic containers made of polypropylene (PP) with lids, approximately 10 cm in diameter. Two holes, each 3 cm in diameter, were cut on opposite sides of the containers, covered with agrotexile, and securely attached using double-sided adhesive tape. A 2–3 cm layer of standard cornmeal–yeast–agar culture medium for *Drosophila* flies was placed in the container. The medium was prepared as follows (composition for 20

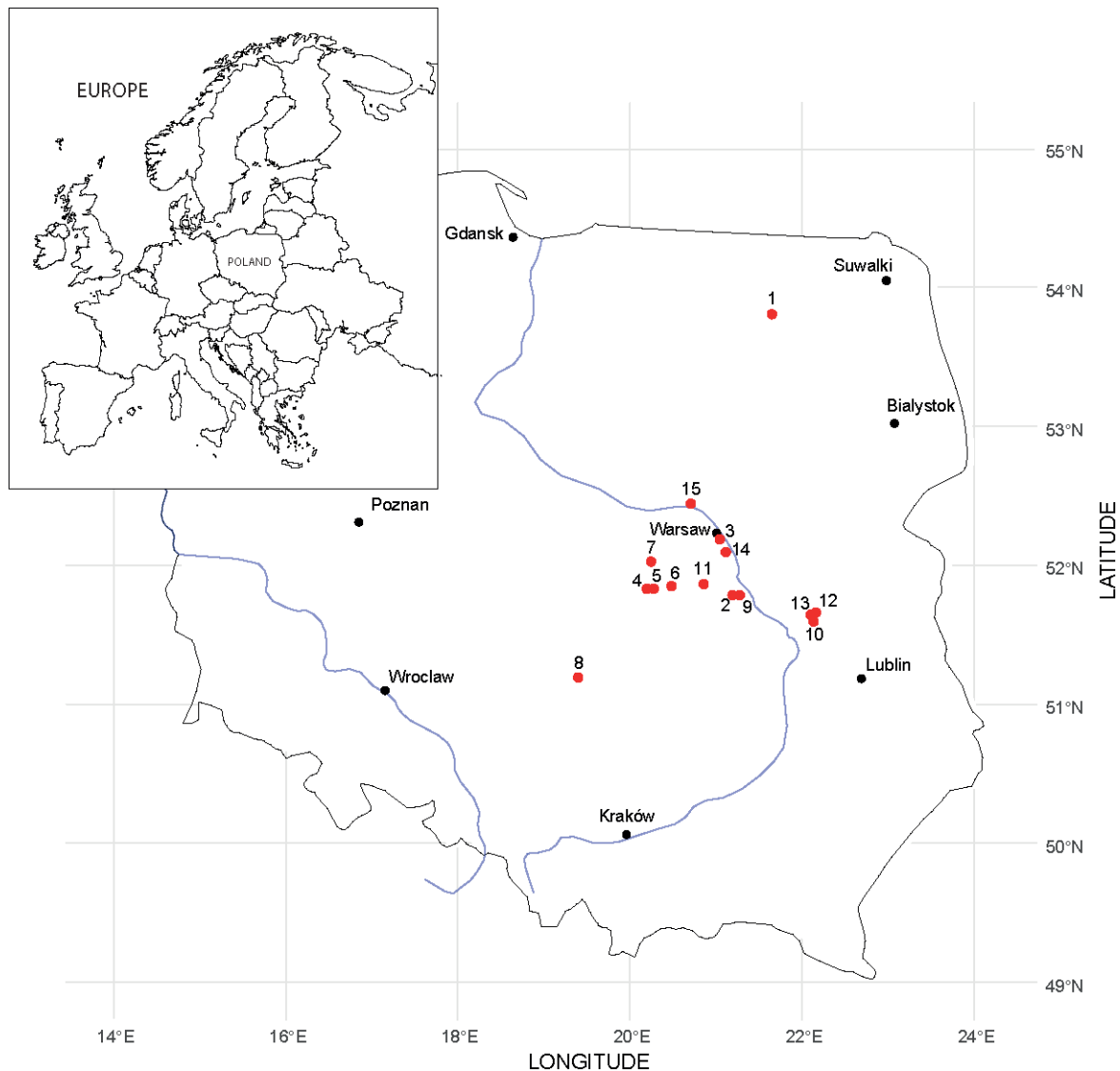


Figure 1. Map of sampling sites.

Table 1. Collection date, sites, and seasonal distribution of hymenopteran parasitoids associated with *Drosophila* flies.

Location	Geographical coordinates	Season	Type of habitat
Urwitałt	53°48'17.9"N, 21°38'56.1"E	spring-summer-autumn 2021	semi-natural area
Anielin	51°47'26.9"N, 21°17'00.6"E	spring-summer-autumn 2021	blackcurrant plantation semi-natural area
Warka	51°47'09.7"N, 21°11'13.2"E	spring-summer-autumn 2021	cherry orchard semi-natural area
Warszawa	52°09'32.9"N, 21°02'32.1"E	spring-summer-autumn 2021–2022	actinidia plantation semi-natural area
Kurzeszyn	51°49'48.0"N, 20°16'35.1"E	spring-summer-autumn 2021–2022	blackcurrant plantation semi-natural area
Rogówiec	51°49'48.0"N, 20°14'21.5"E	spring-summer-autumn 2021–2022	blueberry plantation semi-natural area
Niemirowice	51°50'56.2"N, 20°28'54.1"E	spring-summer-autumn 2021–2022	raspberry plantation semi-natural area
Puszcza Bolimowska	52°01'31.7"N, 20°14'38.3"E	autumn 2021	semi-natural area
Borowa	51°11'31.5"N, 19°23'50.8"E	autumn 2021	raspberry plantation (undercover) raspberry plantation semi-natural area
Uleź	51°35'39.9"N, 22°08'00.7"E	spring 2022	semi-natural area
Grójec	51°51'50.8"N, 20°51'21.1"E	spring 2022	blueberry plantation semi-natural area
Lendo Wielkie	51°39'32.2"N, 22°09'34.9"E	spring 2022	cherry orchard
Nowodwór	51°38'34.8"N, 22°05'53.5"E	spring 2022	apple orchard
Konstantin-Jeziorna	52°05'37.4"N, 21°06'46.8"E	spring 2022	semi-natural area
Warka	51°47'01.0"N, 21°11'33.7"E	spring 2022	strawberry plantation apple orchard
Modlin	52°26'33.1"N, 20°42'23.6"E	spring 2022	plum orchard semi-natural area

traps): 1040 ml of distilled water was brought to a boil. In a separate container, 12 g of agar was pre-dissolved in cold water and mixed with 120 g of cornmeal and 280 g of sucrose. This mixture was added to the boiling water and stirred continuously until fully homogenized. The pot was then removed from the heat. Next, 14 g of dry baker's yeast (previously dissolved in a small volume of warm water) and 14 g of fresh yeast (activated with sugar in a small amount of water) were added. After the mixture had cooled to approximately 60 °C, 10 ml of propionic acid was incorporated as an antifungal agent. The final medium was poured into the trap containers and allowed to solidify. Its surface was then covered with a 0.5 cm layer of sawdust and filled in with wood wool (Fig. 2). The sawdust layer mitigated the medium's drying, while the wood wool facilitated the movement of adult flies and parasitoid wasps during the egg-laying period. To avoid the introduction of the invasive and harmful pest *Drosophila suzukii* into agricultural areas, we used two non-flying *Drosophila* species, *D. melanogaster* and *D. hydei*, as hosts for parasitoids. These model species are widely used in laboratory studies due to their ease of rearing and well-known biology. Importantly, they do not pose any threat to fruit plantations, making them a safe and practical choice for field-based experiments involving parasitoid exposure.

Twenty individuals of each *Drosophila* species were introduced into containers and maintained in

the laboratory at 25 °C with a 16L:8D photoperiod for 7–10 days, until larvae and early-stage pupae developed. The traps containing the host material (Fig. 2) were then suspended approximately 1–1.5 meters above the ground, and the agrotexile covers were removed from the openings to allow parasitoids free access. In each habitat type – plantations and adjacent semi-natural areas – ten traps were deployed. Sampling was conducted three times during the growing season: early (spring, May), middle (summer, July), and late (autumn, September–October). The trap medium was inspected weekly and moistened when necessary to prevent desiccation.

After approximately two weeks, the traps were collected, the holes were resealed with agrotexile, and the traps were stored in an MLR-350 (Sanyo, Osaka, Japan) culture chamber for the subsequent six weeks at 25 °C, maintaining a 16L:8D photoperiod. Adult parasitoid wasps that emerged from the traps were collected alive using an aspirator and quantified. Representative individuals from each sampling site were preserved in 96% ethyl alcohol for species identification based on morphological features, using taxonomic keys and scientific publications (Carton et al. 1986; Forshage and Nordlander 2008; Modic et al. 2019; Abram et al. 2020). The abundance of parasitoid wasp species was then compared across habitats and throughout the growing season.



Figure 2. Trap for monitoring and mass trapping of parasitoids.

Statistical analysis

The data collected from the traps were analyzed to compare the abundance of parasitoids across the growing season and between crop areas and adjacent semi-natural habitats. A comparison between the two study years was not performed because the data from one of the years lacked sufficient variability for a meaningful statistical analysis. A modified Morisita’s similarity coefficient (Mo) (Horn 1966) was used to compare the structure of the parasitoid assemblages. The index values were analyzed using the unweighted pair-group method with arithmetic mean (UPGMA) clustering (Krebs 1999), and a cluster dendrogram was constructed. These analyses were performed with MVSP Package, version 3.22 (Kovach 2010).

Statistical analysis of the number of parasitoids emerging from traps was conducted using Statistica™ v. 13.1 (Dell Inc., Round Rock, TX, USA). As the data did not meet the assumptions of normality or homoscedasticity required by ANOVA, the Kruskal-Wallis non-parametric ANOVA test was employed. Dunn’s post-hoc test was applied to identify significant differences between groups. A significance level of $p < 0.05$ was used for all tests.

Additionally, a biplot from principal component analysis (PCA) was generated to examine the relationships between environment type, season, and mean parasitoid abundance.

Results

The traps have attracted several female parasitoids, which have successfully oviposited. Consequently, three hymenopteran parasitoid species of *Drosophila* flies were

captured: *A. tabida*, a larval parasitoid, and two pupal parasitoids, *T. drosophilae*, and *P. vindemmiae*. The Modified Morisita’s similarity index revealed a high similarity (0.992) in parasitoid species composition between agricultural and semi-natural habitats. In semi-natural areas, the percentage shares of the two dominant species, *P. vindemmiae* and *T. drosophilae*, were nearly equal. Conversely, in fruit plantations, *T. drosophilae* showed greater dominance compared to *P. vindemmiae*. The percentage share of *A. tabida* was notably higher in agricultural areas (Fig. 3A). Seasonal variations in the assemblage structure of *Drosophila* parasitoids were observed. *T. drosophilae* dominated during the early season. In the middle season, its share became comparable to that of *P. vindemmiae*, while *A. tabida* maintained a consistent share. Sampling across the early and middle seasons showed a high similarity based on the Modified Morisita’s index (0.978). However, the late season formed a distinct subclade (0.779), with *P. vindemmiae* dominating at nearly 70%, while the proportions of the other two species were relatively equal within the parasitoid assemblage structure (Fig. 3B).

No significant differences were observed in the number of *A. tabida* and *T. drosophilae* individuals across seasons and habitat types (Table 2). *A. tabida* was less frequently recovered from the traps, while *T. drosophilae* displayed mean values ranging from 4.5 to 28.1 individuals per

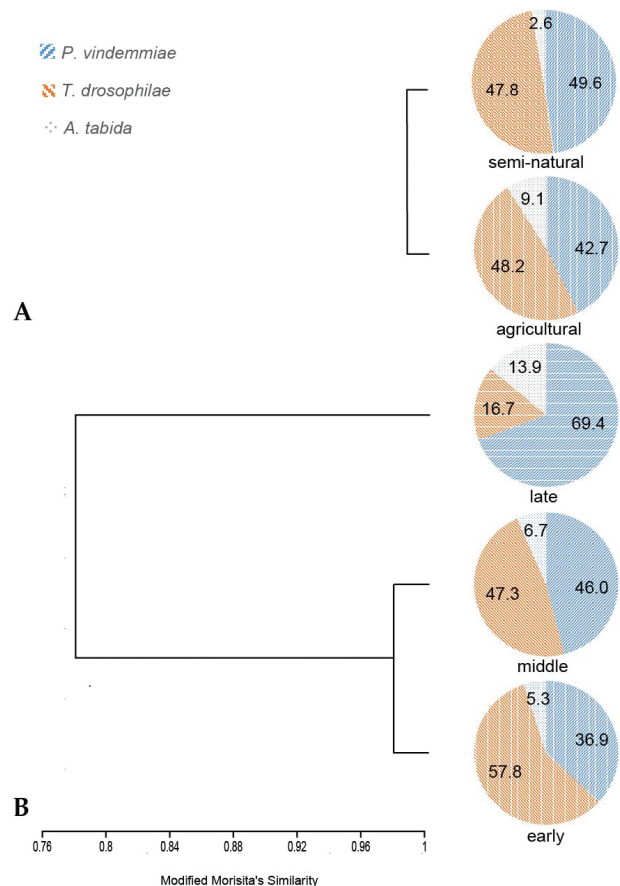


Figure 3. Assemblage structure of hymenopteran parasitoids: **A.** Comparison between agricultural and semi-natural habitats; **B.** Variation across different periods of the vegetation seasons.

Table 2. Descriptive statistics of the observed parasitoids in types of environments and seasons.

	Season/type of habitat	N	Mean	Median	Dunn-test	Min	Max	SD
<i>A. tabida</i>	early/semi-natural	14	3.0	0.0	a*	0	19	6.2
	early/agricultural	16	0.9	0.0	a	0	15	3.8
	middle/semi-natural	10	5.6	0.0	a	0	39	12.9
	middle/agricultural	10	0.0	0.0	a	0	0	0.0
	late/semi-natural	11	3.1	0.0	a	0	23	7.4
	late/agricultural	12	0.6	0.0	a	0	7	2.0
<i>P. vindemmiae</i>	early/semi-natural	14	19.6	11.0	ab	0	76	24.7
	early/agricultural	16	9.0	5.5	ab	0	30	9.5
	middle/semi-natural	10	26.8	24.0	a	3	65	19.3
	middle/agricultural	10	12.2	9.5	ab	0	36	10.7
	late/semi-natural	11	7.1	5.0	ab	0	25	9.1
	late/agricultural	12	10.5	2.0	b	0	80	22.5
<i>T. drosophilae</i>	early/semi-natural	14	26.5	2.0	a	0	123	39.6
	early/agricultural	16	17.9	1.5	a	0	110	29.4
	middle/semi-natural	10	28.1	0.0	a	0	105	45.9
	middle/agricultural	10	12.0	0.0	a	0	42	16.8
	late/semi-natural	11	4.5	0.0	a	0	40	12.1
	late/agricultural	12	0.0	0.0	a	0	0	0.0

trap. Notably, no *T. drosophilae* were recorded in traps deployed in the late season in fruit plantations. The mean number of *P. vindemmiae* ranged from 7.0 to 26.8 individuals, with significant differences observed in the median number of captured specimens. The highest values were recorded during the middle season in semi-natural areas, while the lowest were found in traps placed during the late season on fruit plantations (Table 2, Suppl. material 1).

A Principal Component Analysis (PCA) biplot, explaining 95% of the total variability, illustrated the relationship between habitat types and the mean number of parasitoids. PC1 accounted for 81% of the variability, indicating it captured the dominant patterns in the dataset. The highest mean values for *T. drosophila*, *A. tabida*, and *P. vindemmiae* were observed during the early and middle seasons in semi-natural habitats, while the lowest mean values for parasitoids occurred in the late season in agricultural sites (Fig. 4).

Discussion and conclusion

Live traps allowed the capture of parasitoids from three Hymenoptera families residing in a natural environment and specializing in parasitizing hosts within the *Drosophila* genus. The individuals that emerged were used to assess parasitoid species composition and abundance, as well as to collect live specimens for subsequent investigations. Unlike previous studies by Rossi Stacconi et al. (2013) and Knoll et al. (2017), which employed smaller containers such as Petri dishes or plastic cups (~160 ml), our traps incorporated a layer of sawdust and wood wool. This additionally prevented desiccation, allowed adult fly movement and egg deposition, and maintained the rearing medium for field use over two weeks. As hosts in the traps, we used laboratory populations of two *Drosophila* species: *D. hydei* and *D. melanogaster*, but not *D. suzukii*, which is

a serious pest of soft fruit crops. By excluding *D. suzukii* from trap construction, we avoided the risk of introducing this pest into the study area. Nevertheless, *D. melanogaster* has been effectively used to attract parasitoids, as demonstrated by Rossi Stacconi et al. (2013) and Knoll et al. (2017). Using larvae and pupae of *D. melanogaster*, these authors collected all parasitoid species also recorded in our study, it were: *A. tabida*, *T. drosophilae*, and *P. vindemmiae*. Based on a review of available sources, including databases such as the Global Biodiversity Information Facility (GBIF 2024), there are no previous reports of the presence of *A. tabida*, *P. vindemmiae*, and *T. drosophilae* in Poland. This study, representing the first confirmation of their occurrence in the country, makes a significant contribution to the documentation of parasitoid fauna associated with *D. suzukii*. It is important to note, however, that the absence of these species in available databases (GBIF 2024) does not exclude the possibility of their prior occurrence; they may simply have gone unrecorded. Our findings are consistent with Knoll et al. (2017), who also reported *T. drosophilae* and *P. vindemmiae* in Switzerland, but Knoll et al. recorded eight hymenopteran species across four families parasitizing spotted wing drosophila. Gabarra et al. (2015) similarly reported *P. vindemmiae* and *T. drosophilae* among species associated with *Drosophila suzukii* in Spain. Mazzetto et al. (2016) noted the presence of *P. vindemmiae* and *L. heterotoma* as key parasitoids in Italy, highlighting variability in parasitoid communities across regions. Miller et al. (2015) recovered three species (*P. vindemmiae*, *L. heterotoma*, and *L. boulandi*) in Italy and Oregon, USA, while Rossi Stacconi et al. (2013) identified *P. vindemmiae* as the sole parasitoid in Italy. In contrast, our study adds *A. tabida*, a species widespread across Europe, particularly in southern regions (Kraaijeveld and Godfray 1999; Shaw et al. 2023), to the list of parasitoids associated with *Drosophila* hosts in Poland.

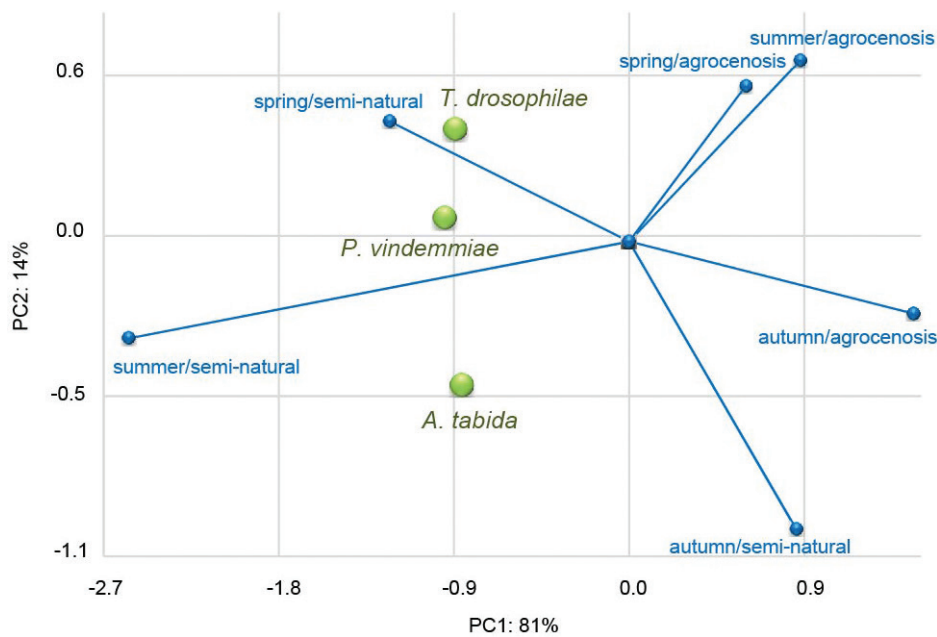


Figure 4. Biplot of the first two components of the PCA model, illustrating the relationship between the mean number of parasitoids, environment type, and season.

The abundance of insects in the environment is modified by biotic and abiotic factors, among which one of the most important are climatic components (Hance et al. 2007; Rossi Stacconi et al. 2017; Amiresmaeili et al. 2018; Wang et al. 2018; Colombari et al. 2020). Seasonal changes in these factors during the vegetation period significantly affected the number of *Drosophila* parasitoids. Our data showed that the most significant number of parasitoids emerged from the traps during the middle of the vegetation season, which could be induced by the relatively high activity of parasitoids caused by favorable thermal conditions. Differences in the assemblage structure of parasitoid species that emerged from traps may be attributed to different environmental conditions and interactions with the host and other parasitoids (Miller et al. 2015; Mazzetto et al. 2016; Knoll et al. 2017). Indeed, Knoll et al. (2017) suggest that the high abundance of *P. vindemmiae* may reduce the population size of *A. tabida* through internal parasitism. In our study, *A. tabida* was less abundant, possibly due to interactions with *P. vindemmiae* or the defense mechanisms of host larvae, such as encapsulating parasitoid eggs (Knoll et al. 2017). Research conducted on plantations in different regions of Switzerland demonstrated that *P. vindemmiae* was recorded to parasitize fly pupae inhabited as larvae by *A. tabida* (Knoll et al. 2017). This internal parasitism highlights the complex intraspecific interactions within parasitoid communities.

Anthropogenic factors, such as plant cultivation and crop protection practices, are also significant in influencing the occurrence of parasitoids. These factors could directly affect insect biodiversity and abundance (Schlesener et al. 2019; Morais et al. 2022). Our study demonstrated this phenomenon, where more parasitoids were found in semi-natural than agricultural areas. In habitats associated

with intensive agriculture, a much lower abundance of hymenopteran parasitoids was recorded, probably due to excessive use of insecticides, especially neonicotinoids, and artificial fertilization. Therefore, moving towards the extensification of agricultural practices is necessary to maintain the diversity and abundance of beneficial organisms. As a result of organic production, its diversity may significantly increase, which will ensure the productivity of agricultural ecosystems through biological control and pollination of crops (Schlesener et al. 2019; Morais et al. 2022).

The most commonly occurring species in our studies, *P. vindemmiae*, was most abundant in summer, during the middle of vegetation season. This parasitoid can survive and reproduce in a broader range of temperatures than *T. drosophilae* (Rossi Stacconi et al. 2013; Wang et al. 2016b; Kaçar et al. 2017). As a result, *P. vindemmiae* may be better adapted to regions with more variable temperatures, while *T. drosophilae* is too mild climates. These differences in thermal tolerance suggest that releasing both species at different times of the year or in different climatic regions may enhance the overall effectiveness of *Drosophila* population suppression.

Interactions between native Hymenoptera and the invasive spotted wing drosophila can exhibit variable dynamics, highlighting to need for caution when implementing new biological control strategies. Experiments by Chabert et al. (2012) focusing on the European larval parasitoid *A. tabida* population revealed a significant reluctance to parasitize spotted wing drosophila, with only three attacks observed out of 160 host larvae. This low parasitism efficiency raises concerns about host specificity. The study suggests that differences in parasitism efficiency between Asian and European *A. tabida* populations tested under the same conditions might be attributed to the local European populations not yet fully

adapting to this exotic host. Consequently, it seems unlikely that a parasitoid species would succeed more in natural environments than in controlled laboratory conditions (Chabert et al. 2012). Such insights underscore the need for a nuanced approach in assessing the efficacy of biological control measures against spotted wing drosophila, considering the intricate dynamics between the invasive species and native hymenopteran parasitoids. Moreover, as Knoll et al. (2017) emphasized, the broader ecological impact of biological control should be carefully assessed, considering their potential to affect multiple species across different trophic levels.

Research on assessing naturally occurring parasitoid wasps holds the potential to bring numerous benefits in controlling *Drosophila* populations. Understanding the interactions between parasitoids and their hosts is crucial for comprehending population dynamics, *Drosophila*'s defense strategies, and parasitoids' adaptations. By investigating defense mechanisms and parasitoid adaptation to their hosts, we can better understand the factors influencing the evolution of these organisms and which strategies might be effective in controlling populations of harmful insects. The findings from these studies could have practical applications in agriculture, particularly in pest management. They may lead to the development of more precise and environmentally friendly biological control methods, offering an alternative to traditional chemical pesticides. These approaches would not only be more sustainable but also contribute to preserving biodiversity and maintaining ecological balance.

The use of *T. drosophilae* as a biological control agent against the spotted wing drosophila and its superiority over *P. vindemniae* in managing this pest was demonstrated by Wang et al. (2018). According to these authors, the narrow host range of *T. drosophilae* within the Drosophilidae family, particularly its preference for the spotted wing drosophila, contributes to its efficacy. Additionally, its cosmopolitan distribution across South Korea, China, Spain, Italy, France, and North America (Mexico and the USA) enhances its applicability in reducing the population of this pest (Gabarra et al. 2015; Wang et al. 2016a; Zhu et al. 2017). Field studies conducted in commercial berry fields assessing the introduction of local parasitoids for the spotted wing drosophila control revealed *T. drosophilae* as a cost-effective option. Results indicated a fourfold increase in parasitism by *T. drosophilae* at release sites compared to control sites without parasitoid release. Notably, there was an approximate 50% reduction in *D. suzukii* populations (Gonzalez-Cabrera et al. 2019), emphasizing the potential of *T. drosophilae* for integrated pest management strategies. A similar field experiment was previously conducted in Italy by Rossi Stacconi et al. (2018, 2019), further confirming the promise of *T. drosophilae* as a biological control agent under field conditions. A field experiment involving augmentative releases of *T. drosophilae* in Italy (Rossi Stacconi et al. 2019) demonstrated a ~34% reduction in fruit infestation by *D. suzukii* and significantly increased parasitism

in release areas compared to controls. Additionally, earlier studies (Rossi Stacconi et al. 2018) showed that *T. drosophilae* disperses effectively up to 40 m from release points and significantly reduces pest emergence within at least a 10 m radius. Consequently, biological control strategies are gaining prominence, primarily relying on natural enemies such as hymenopterans, nematodes, or fungi (Woltz et al. 2015). Among these, parasitoid wasps, targeting both larval and pupal stages of flies, emerge as the most researched and promising biocontrol agent for spotted wing drosophila control (Chabert et al. 2012; Lee et al. 2019). In light of these findings, research into the interactions between parasitoid wasps and *Drosophila* provides valuable insights into their ecological relationships and the evolutionary defense mechanisms that fruit flies have developed under parasitic pressure. Employing parasitoid wasps – particularly those already established or naturalized in a given region – as a biological control method may offer a promising approach to managing *Drosophila* populations. However, this strategy requires a comprehensive understanding of host-parasitoid dynamics and careful assessment of potential ecological impacts.

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Competing interests

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Supplementary material 1

Number of parasitoids trapped

Authors: Wioleta Koźbiał, Elżbieta Wójcik-Gront, Mariusz Lewandowski

Data type: docx

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