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Substrate-Dependent Parasitism of Synanthropic Diptera: Host Associations, Parasitism Rates, and Biological Control Potential

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Abstract: This study investigates the diversity, distribution, and ecological role of parasitoids associated with Diptera in different organic substrates and environments. The research focuses on parasitoid species obtained from substrates such as animal feces, viscera, and decomposing organic matter, which serve as breeding sites for dipteran hosts. The objective was to evaluate parasitoid occurrence, parasitism rates, and host–parasitoid relationships, highlighting their importance in biological control. A variety of parasitoid species belonging mainly to the families Pteromalidae, Braconidae, Figitidae, and Chalcididae were recorded. Parasitism rates varied significantly among substrates, ranging from low values in less favorable substrates to higher values in nutrient-rich environments, such as decomposing tissues. These results demonstrate that substrate composition strongly influences parasitoid activity and efficiency. The most representative species included *Brachymeria podagrica* (Fabricius, 1787) (Hymenoptera: Chalcididae) and *Pachycrepoideus vindemmiae* (Rondani, 1875) (Hymenoptera: Pteromalidae), which showed wide distribution and high adaptability across different substrates. The relationship between parasitoids and dipteran hosts revealed that host availability is a key factor determining parasitoid abundance and success. Substrates with higher densities of dipteran pupae supported increased parasitoid emergence. Morphological differences between parasitoids and their hosts, such as the presence of four wings in parasitoids and two wings in Diptera, further emphasize their distinct biological and ecological roles. These characteristics, combined with their parasitic behavior, reinforce their potential as natural enemies of pest flies. Overall, parasitoids play a fundamental role in regulating fly populations and represent effective, sustainable agents for biological control in both natural and managed ecosystems.

Keywords: Biological Control, Diptera, Organic Substrates, Parasitism, Parasitoids.

Review Paper

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1.0. INTRODUCTION

Dipteran insects are among the most important groups in terrestrial ecosystems due to their ecological, sanitary, and economic relevance, especially in tropical regions where environmental conditions favor their rapid development and high diversity. Many species of Diptera are directly associated with decomposing organic matter, animal excrement, and other nutrient-rich substrates, which provide ideal conditions for larval development and population growth. In addition, several dipteran species act as vectors of pathogens, including bacteria, viruses, protozoa, and helminths, representing significant risks to public and animal health (Marchiori *et al.,* 2000a; Marchiori, 2019a; Marchiori, 2019b; Marchiori, 2019c; Marchiori, 2022).

Their presence in rural and urban environments further increases their importance, as they are closely linked to human activities and livestock production systems. Consequently, understanding the biology, ecology, and distribution of Diptera is essential for developing effective management strategies and improving sanitary conditions in different environments (Marchiori *et al.,* 2000b; Marchiori *et al.,* 2007a; Marchiori *et al.,* 2010; Marchiori, 2019a).

Parasitoid insects associated with Diptera represent one of the most important functional groups in ecological regulation, acting as natural enemies that directly influence host population dynamics. These organisms develop in close association with their hosts, usually during immature stages, and their life cycle typically results in host mortality (Figure 1) (Marchiori, 2000d; Marchiori, 2021a; Marchiori, 2021b; Marchiori, 2021c; Marchiori, 2022).

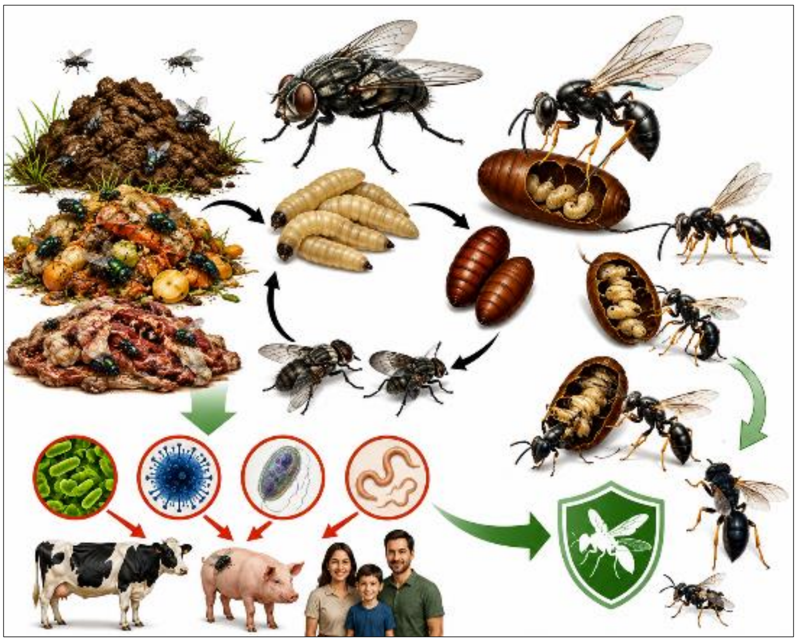

Figure 1: Integrated representation of Diptera and parasitoid interactions associated with decomposing organic substrates. The illustration shows Diptera adults with two wings colonizing nutrient-rich substrates, larval development, pupal formation, and parasitoids with four wings attacking host pupae. These interactions highlight the ecological role of parasitoids as natural enemies of Diptera and their potential contribution to the biological regulation of fly populations of sanitary, veterinary, and economic importance

Among parasitoids, Hymenoptera stands out as the most diverse and ecologically significant order, with numerous families specialized in exploiting dipteran hosts. The interaction between parasitoids and Diptera is highly structured and depends on biological, environmental, and behavioral factors that determine host selection and parasitism success. As a result, parasitoids play a fundamental role in controlling populations of synanthropic flies and other dipterans of sanitary and economic importance (Marchiori, 2009a; Marchiori, 2009b; Marchiori, 2019a). The diversity of parasitoids associated with Diptera is closely linked to the variety of substrates where hosts develop, as these environments influence both host availability and parasitoid activity. Substrates such as animal feces, decomposing organic matter, and animal tissues provide ideal conditions for dipteran development and consequently attract a wide range of parasitoid species. The composition of parasitoid communities may vary according to substrate type, reflecting differences in host species, microclimatic conditions, and resource availability (Marchiori, 2008a; Marchiori *et al.,* 2008b; Marchiori, 2019b).

In addition, environmental factors such as temperature, humidity, and habitat structure can significantly affect parasitism rates and species distribution. These variations highlight the importance of substrate-based studies in understanding parasitoid ecology and their role in biological control (Marchiori *et al.,* 2007a; Marchiori *et al.,* 2007b; Marchiori, 2021b; Marchiori, 2021c). Studies conducted in different environments have demonstrated that parasitoids of Diptera are widely distributed in rural, urban, and natural ecosystems, showing a high capacity for adaptation to diverse ecological conditions. In agricultural and livestock systems, these parasitoids are frequently associated with substrates such as cattle dung and poultry manure, where they contribute to reducing populations of pest species. In urban environments, parasitoids are also present in association with synanthropic flies, playing a role in mitigating sanitary risks (Marchiori *et al.,* 2000a; Marchiori *et al.,* 2007a; Marchiori, 2008a; Marchiori, 2010; Marchiori, 2014).

The variation in parasitoid abundance and diversity across environments is influenced by factors such as host density, habitat heterogeneity, and management practices. Therefore, the study of parasitoids in multiple habitats is essential for understanding their ecological importance and potential application in integrated pest management programs (Figure 2) (Marchiori *et al.,* 2007b; Marchiori *et al.,* 2008b; Marchiori, 2009a; Marchiori, 2009b).

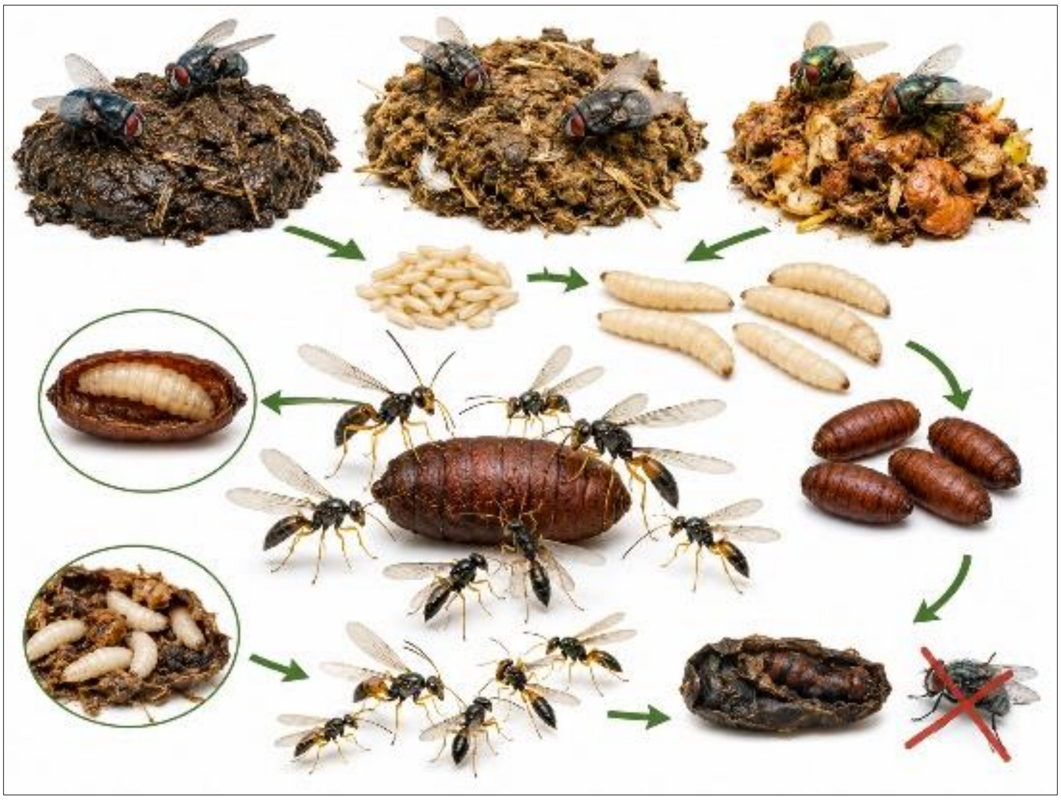

Figure 2: Schematic representation of Hymenoptera parasitoids associated with Diptera developing in decomposing organic substrates. The illustration shows adult Diptera with two wings, immature fly stages, pupae, and parasitoids with four wings interacting during host location, pupal parasitism, parasitoid development, and host mortality. This interaction highlights the ecological importance of parasitoids as natural regulators of synanthropic flies of sanitary and economic relevance

Host–parasitoid relationships involving Diptera are characterized by a high degree of specificity, although some parasitoid species are capable of exploiting multiple hosts across different substrates. This flexibility allows parasitoids to persist in environments where host availability fluctuates over time. The success of parasitism depends on several factors, including host size, developmental stage, and accessibility within the substrate. In addition, interspecific competition among parasitoids may influence community structure and parasitism efficiency. Understanding these interactions is essential for evaluating the ecological dynamics of parasitoid populations and their impact on dipteran communities in different environments (Marchiori *et al.,* 2004a; Marchiori *et al.,* 2006; Marchiori, 2014; Marchiori, 2019b; Marchiori, 2022).

The study of parasitoids associated with Diptera also has significant implications for biological control, as these organisms can naturally suppress populations of flies of medical, veterinary, and agricultural importance. Several parasitoid species have been identified as potential biological control agents due to their ability to locate hosts in complex substrates and adapt to different environmental conditions. Their use in integrated pest management programs can reduce the need for chemical control methods, minimizing environmental impacts and promoting sustainable practices. Furthermore, knowledge about parasitoid diversity and ecology contributes to the development of more effective strategies for managing dipteran populations in both rural and urban settings (Marchiori *et al.,* 2004a; Marchiori, 2004b; Marchiori *et al.,* 2010; Marchiori, 2014; Marchiori, 2019c; Marchiori, 2022).

Parasitoid assemblages associated with Diptera can vary significantly depending on environmental complexity and substrate diversity, which influence both host availability and parasitoid behavior. In heterogeneous environments, such as agroforestry systems and natural habitats, a higher diversity of parasitoids is often observed due to the increased availability of ecological niches. In contrast, simplified environments may support fewer species but sometimes higher abundances of specific parasitoids adapted to dominant hosts. This variation highlights the importance of landscape structure and habitat diversity in shaping parasitoid communities and their ecological functions. Consequently, studies that consider multiple environments are essential for understanding patterns of parasitoid distribution and diversity (Figure 3) (Marchiori *et al.,* 2003a; Marchiori, 2008a; Marchiori *et al.,* 2010; Marchiori, 2014; Marchiori, 2021a; Marchiori, 2021b).

Figure 3: Integrated representation of parasitoids of Diptera across rural, urban, and natural environments. The illustration shows decomposing substrates such as cattle dung, poultry manure, and organic waste serving as breeding sites for Diptera and as sources of larvae and pupae attacked by parasitoids. Parasitoids are represented with four wings, emphasizing their broad ecological distribution and their role as natural enemies contributing to the reduction of synanthropic fly populations

The type of substrate plays a decisive role in determining the composition of dipteran hosts and, consequently, the associated parasitoid fauna. Substrates such as bovine feces, poultry manure, and animal tissues differ in their physicochemical properties, influencing the development of Diptera and the attractiveness of these environments to parasitoids. These differences can affect host density, species composition, and the temporal availability of resources, all of which are critical factors for parasitoid establishment. Additionally, substrate characteristics may influence parasitoid searching behavior and oviposition success, thereby affecting parasitism rates. Understanding these relationships is fundamental for interpreting patterns of parasitoid occurrence in different substrates (Marchiori, 2003b; Marchiori *et al.,* 2007a; Marchiori *et al.,* 2007b; Marchiori, 2010).

Temporal variation is another important factor influencing parasitoid–Diptera interactions, as seasonal changes can affect both host availability and parasitoid activity. Climatic factors such as temperature and humidity directly impact the development rates of dipteran larvae and pupae, as well as parasitoid emergence and survival. In tropical regions, where climatic conditions may fluctuate throughout the year, these variations can lead to changes in species composition and parasitism levels over time. Long-term studies are therefore essential to capture these dynamics and provide a more comprehensive understanding of parasitoid ecology in different environmental contexts (Figure 4) (Marchiori *et al.,* 2000a; Marchiori *et al.,* 2000b; Marchiori *et al.,* 2010; Marchiori, 2014; Marchiori, 2019c; Marchiori, 2021a; Marchiori, 2022).

Figure 4: Schematic representation of how environmental factors influence parasitoid–Diptera interactions in decomposing substrates. The illustration shows differences in temperature, humidity, habitat structure, substrate condition, larval development, pupal availability, and parasitoid activity. Parasitoids are represented with four wings, highlighting their role as natural enemies of Diptera and their importance in biological control under variable environmental conditions

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The diversity of parasitoid species associated with Diptera also reflects evolutionary adaptations that allow these organisms to exploit specific hosts and substrates efficiently. Morphological, physiological, and behavioral traits contribute to the success of parasitoids in locating and parasitizing hosts in complex environments. Some species exhibit high host specificity, while others are more generalist, enabling them to persist in environments with fluctuating host populations. These adaptive strategies are essential for maintaining parasitoid populations and ensuring their role in regulating dipteran communities. Consequently, the study of parasitoid diversity provides valuable insights into ecological and evolutionary processes in terrestrial ecosystems (Marchiori *et al.,* 2000c; Marchiori *et al.,* 2004a; Marchiori, 2009b; Marchiori, 2021a; Marchiori, 2021b; Marchiori, 2021c).

In addition to their ecological importance, parasitoids of Diptera are valuable indicators of environmental quality, as their presence and diversity are closely linked to habitat conditions and resource availability. Changes in land use, agricultural practices, and environmental degradation can directly affect parasitoid communities by altering host populations and substrate availability. Therefore, monitoring parasitoid diversity can provide important information about ecosystem health and the impact of anthropogenic activities. This approach reinforces the relevance of parasitoid studies in both ecological research and environmental management (Marchiori, 2000d; Marchiori, 2008a; Marchiori, 2010; Marchiori, 2014).

Research on parasitoids associated with Diptera in different substrates has expanded significantly in recent years, contributing to a better understanding of their ecological roles and distribution patterns. Studies conducted in Brazil have highlighted the richness of parasitoid species associated with synanthropic flies, particularly in substrates such as animal feces and decomposing organic matter. These studies have also emphasized the importance of standardized methodologies for sampling and identifying parasitoids, allowing for more accurate comparisons across different environments and time periods. Such advances have strengthened the scientific basis for the application of parasitoids in biological control programs (Figure 5) (Marchiori and Linhares, 1999; Marchiori *et al.,* 2007a; Marchiori *et al.,* 2007b; Marchiori, 2008a; Marchiori *et al.,* 2008b).

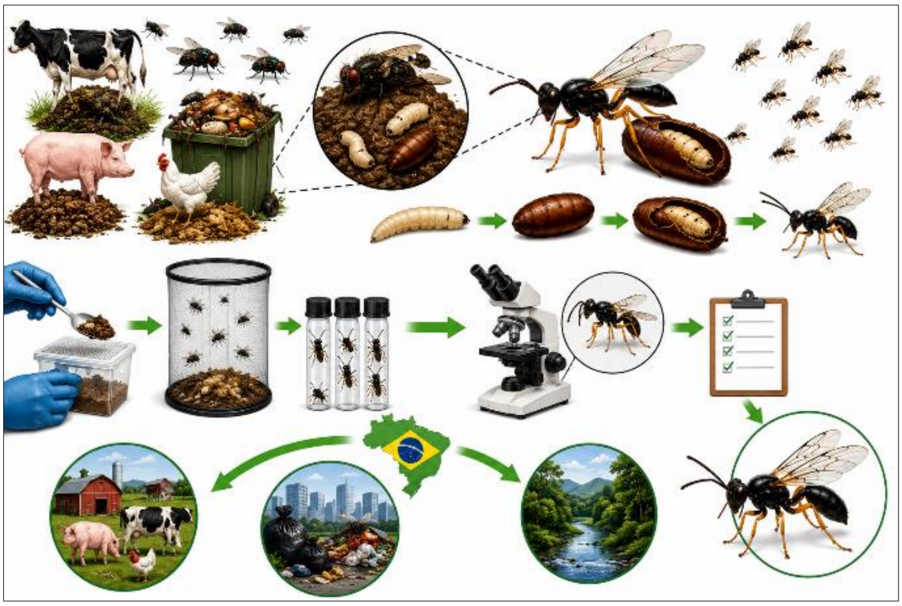

Figure 5: Integrated representation of research on parasitoids associated with Diptera in decomposing organic substrates. The illustration shows animal feces, poultry manure, organic waste, immature Diptera, pupae, and parasitoids with four wings, together with sampling, laboratory rearing, and identification procedures. The figure highlights the importance of standardized methods for studying parasitoid diversity, host associations, and their potential application in biological control programs in Brazil

Despite the advances in knowledge about parasitoids of Diptera, there are still gaps related to the influence of substrate type, environmental conditions, and host availability on parasitoid diversity and parasitism rates. Many studies have focused on specific environments or substrates, limiting the understanding of broader ecological patterns. Therefore, comprehensive studies that integrate different substrates and environments are necessary to provide a more complete picture of parasitoid ecology. Such approaches can contribute to improving biological control strategies and enhancing our understanding of host–parasitoid interactions in complex ecosystems (Marchiori *et al.,* 2001; Silva *et al.,* 2003; Marchiori *et al.,* 2006).

The objective of this study was to evaluate the diversity, abundance, and distribution of parasitoids (Hymenoptera) associated with Diptera collected in different substrates, including animal feces, animal tissues, and other organic materials, in various environments. Additionally, this study aimed to analyze host–parasitoid relationships and to determine the influence of substrate type and environmental conditions on parasitoid occurrence and parasitism rates.

2.0. MATERIALS AND METHODS

2.1. Method 1

Every two weeks, 10 fresh fecal pats from cattle and buffalo were marked immediately after deposition in *Brachiaria* pastures (*Brachiaria brizantha*), using white wooden stakes 30 cm high and 5 cm thick to ensure precise determination of the time between deposition and collection. The fecal samples remained in the field for 15 days. After this period, seven samples were collected and transported to the laboratory. Pupal extraction was performed using the flotation method. Along with the feces, approximately 5 cm of the underlying soil substrate was also collected. The pupae were recovered using a sieve, counted, and individually placed in gelatin capsules (size 00) until the emergence of flies and/or parasitoids (Figure 6).

Figure 6: Fresh fecal pats from cattle and buffalo used as substrates for Diptera development. These organic materials provide suitable conditions for oviposition and larval growth of flies. They also serve as important habitats for parasitoids, influencing host–parasitoid interactions and parasitism rates

2.2. Method 2

Ten fresh chicken fecal pats were marked immediately after deposition using white wooden stakes (30 cm in height and 5 cm in thickness) to allow precise determination of the time elapsed between deposition and collection. The pats remained in the field for fifteen days. Seven samples were collected and transported to the laboratory for pupae extraction using the flotation method. Along with the feces, approximately 5 cm of the underlying soil substrate beneath the deposition site was also collected. The pupae were separated using a sieve, counted, and individually placed into gelatin capsules (size 00) until the emergence of flies and/or parasitoids. The emerged flies and parasitoids were identified using a stereomicroscope and subsequently preserved in 70% ethanol (Figure 7).

Figure 7: Ten fresh chicken fecal pats (n = 10) were distributed in the field and marked with wooden stakes. Each pat was identified immediately after deposition to ensure accurate timing of exposure. This setup allowed subsequent sampling and evaluation of dipteran colonization and parasitoid activity

2.3. Method 3

Dipterans were collected using traps constructed from dark-colored cans measuring 19 cm in height and 9 cm in diameter, featuring two louver-like openings located in the lower third of a plastic container to allow insect entry. The upper part of the can was connected to a nylon funnel open at both ends, with its base oriented downward. This structure was enclosed with plastic bags so that, upon removal, the dipterans and parasitoids could be collected. Bovine kidneys and chicken viscera were used as bait and placed inside the plastic containers over a layer of soil. Four traps were deployed and suspended from trees at a height of approximately 1 meter above ground level, with a distance of 2 meters between them.

The collected insects were transported to the laboratory, euthanized using ethyl ether, and preserved in 70% ethanol for subsequent identification. For parasitoid recovery, the contents of the traps were transferred to plastic containers containing a layer of sand to serve as a substrate for larval pupation. After remaining in the field for 15 days, the sand was saved, and the pupae were extracted and individually placed into gelatin capsules (size 00) to allow the emergence of dipterans and/or parasitoids (Figure 8).

Figure 8: Bovine liver and chicken viscera were used as an attractant to lure flies, which are drawn by its odor and lay their eggs on the material. After oviposition, the eggs develop into larvae and later into pupae. During these stages, parasitoids can act by parasitizing these immature forms, contributing to the biological control of fly populations

Parasitism rates were calculated as the percentage of parasitized pupae in relation to the total number of pupae collected, using the formula: number of parasitized pupae divided by the total number of pupae multiplied by 100. In addition, the frequency of occurrence of parasitoid species and their respective hosts was determined. Data were analyzed considering the influence of substrate type and environment on parasitoid diversity and abundance. Comparative analyses were performed among substrates and collection sites to identify patterns in parasitoid distribution and host–parasitoid relationships.

2.4. Note

Figures include both photographic records and schematic illustrations. Wing venation was omitted or simplified in schematic figures for clarity and does not represent diagnostic morphological variation among parasitoid taxa (Table 1).

Table 1: Taxonomic table of the principal Diptera hosts and parasitoids cited in the study

Species	Authority	Order	Family	First citation in the text	Subsequent citation
Brachymeria podagrica	Fabricius, 1787	Hymenoptera	Chalcididae	*Brachymeria podagrica* (Fabricius, 1787) (Hymenoptera: Chalcididae)	*B. podagrica*
Chrysomya albiceps	Wiedemann, 1819	Diptera	Calliphoridae	*Chrysomya albiceps* (Wiedemann, 1819) (Diptera: Calliphoridae)	*C. albiceps*
Chrysomya megacephala	Fabricius, 1794	Diptera	Calliphoridae	*Chrysomya megacephala* (Fabricius, 1794) (Diptera: Calliphoridae)	*C. megacephala*

Species	Authority	Order	Family	First citation in the text	Subsequent citation
Drosophila suzukii	Matsumura, 1931	Diptera	Drosophilidae	*Drosophila suzukii* (Matsumura, 1931) (Diptera: Drosophilidae)	*D. suzukii*
Fannia pusio	Wiedemann, 1830	Diptera	Fanniidae	*Fannia pusio* (Wiedemann, 1830) (Diptera: Fanniidae)	*F. pusio*
Musca domestica	Linnaeus, 1758	Diptera	Muscidae	*Musca domestica* Linnaeus, 1758 (Diptera: Muscidae)	*M. domestica*
Ophyra aenescens	Wiedemann, 1830	Diptera	Muscidae	*Ophyra aenescens* (Wiedemann, 1830) (Diptera: Muscidae)	*O. aenescens*
Pachycrepoideus vindemmiae	Rondani, 1875	Hymenoptera	Pteromalidae	*Pachycrepoideus vindemmiae* (Rondani, 1875) (Hymenoptera: Pteromalidae)	*P. vindemmiae*
Paraganaspis egeria	Díaz, Gallardo & Walsh, 1996	Hymenoptera	Figitidae	*Paraganaspis egeria* Díaz, Gallardo & Walsh, 1996 (Hymenoptera: Figitidae)	*P. egeria*
Peckia chrysostoma	Wiedemann, 1830	Diptera	Sarcophagidae	*Peckia chrysostoma* (Wiedemann, 1830) (Diptera: Sarcophagidae)	*P. chrysostoma*
Spalangia drosophilae	Ashmead, 1885	Hymenoptera	Pteromalidae	*Spalangia drosophilae* Ashmead, 1885 (Hymenoptera: Pteromalidae)	*S. drosophilae*
Tricharaea occidua	Fabricius, 1794	Diptera	Sarcophagidae	*Tricharaea occidua* (Fabricius, 1794) (Diptera: Sarcophagidae)	*T. occidua*

3.0 RESULTS

A total of 3.473 dipteran pupae were collected from buffalo dung, of which 172 were parasitized, corresponding to a parasitism rate of 4.9%. The parasitoids identified included *Spalangia drosophilae* Ashmead, 1885 (Hymenoptera: Pteromalidae) and *Paraganaspis egeria* Díaz, Gallardo & Walsh, 1996 (Hymenoptera: Figitidae), being the most frequent species. The distribution of parasitoids indicated a clear association with dung substrates, where host availability was high. These results demonstrate that buffalo dung provides suitable conditions for parasitoid development and contributes to the maintenance of parasitoid populations (Figures 9-10).

Figure 9: Representation of parasitoids associated with Diptera pupae obtained from buffalo dung. The figure illustrates buffalo dung as a breeding substrate for Diptera, with larval development, pupal formation, and parasitism by the four-winged parasitoid *S. drosophilae* among the parasitoids identified. Sources: Photo#933556/ John Rosenfeld/Iowa State Universit/https://www.bugguide.net/node/view/933556

Figure 10: Schematic illustration of the parasitoid of *P. egeria* collected in bovine and buffalo dung in southern Goiás, Brazil. It is a species of parasitoid wasp belonging to the family Figitidae (subfamily Eucoilinae). It acts as a natural enemy, controlling populations of various fly species, including pests of medical and veterinary importance, by depositing its eggs in the larvae or pupae of its hosts

In cattle dung collected in Goiás, parasitism rates varied between regions, reaching 12.4% in the southern region and 6.4% in the central region. These differences indicate the influence of environmental conditions on parasitoid activity. The higher parasitism observed in the southern region suggests more favorable conditions for parasitoid development. Dipteran pupae in dung substrates supported a diverse parasitoid community, reinforcing the importance of this substrate for host–parasitoid interactions.

In a forest environment, dipteran pupae collected from substrates such as bovine kidney, human feces, and chicken viscera showed marked variation in parasitism. The highest parasitism rate was recorded in chicken viscera, reaching 51.7%, indicating highly favorable conditions for parasitoid development. The most frequent species were *Brachymeria podagrica* (Fabricius, 1787) (Hymenoptera: Chalcididae) and *Pachycrepoideus vindemmiae* (Rondani, 1875) (Hymenoptera: Pteromalidae), both emerging from pupae associated with decomposing substrates. Lower parasitism levels were observed in other substrates, demonstrating the influence of substrate type on parasitoid activity (Figure 11) (Bezerra *et al.,* 2019).

Figure 11: *Pachycrepoideus vindemmiae* attacking pupae of spotted-wing drosophila (SWD), *Drosophila suzukii* (Matsumura, 1931) (Diptera: Drosophilidae), in the laboratory (a) Female wasp inserting her ovipositor through the SWD's pupal case and performing internal evaluation of the host before oviposition. (b) A female wasp was host-feeding on the hemolymph of a SWD pupa following ovipositor withdrawal from the pupal case. Source: Doi:10.1371/journal.pone.0218301

In bovine kidney, dipteran pupae showed high parasitism levels, with parasitoids such as *P. vindemmiae* and *B. podagrica* frequently recorded. The availability of organic material in this substrate favored dipteran development and parasitoid emergence. The results indicate that animal tissues provide suitable conditions for parasitoid activity. Differences in parasitism among substrates highlight the importance of resource type in determining parasitoid success.

In Caldas Novas, Goiás, parasitism was observed in pupae collected from different substrates associated with synanthropic flies. The occurrence of parasitoids varied according to substrate type, with higher parasitism in substrates with greater organic content. Species such as *P. vindemmiae* were frequently recorded, demonstrating adaptability to urban and peri-urban environments. These results confirm that parasitoids are active under different environmental conditions and substrates. In urban environments, dipteran pupae collected from decomposing organic materials showed consistent parasitoid emergence. Parasitism levels varied according to substrate and host availability, but parasitoids were present in all sampled conditions. Species associated with synanthropic flies demonstrated adaptation to anthropogenic environments. These results indicate that parasitoids contribute to the regulation of dipteran populations even in urban ecosystems (Figure 12).

Figure 12: Representation of *B. podagrica* as a pupal parasitoid associated with synanthropic Diptera. The figure illustrates adult parasitoids with four wings interacting with Diptera pupae in decomposing organic substrates, highlighting the role of this species as a natural enemy of flies of sanitary and veterinary importance. Sources: Photo#1675698/metrioptera/Iowa State

In poultry farms, a high number of dipteran pupae were collected from manure, with consistent parasitoid emergence observed. Parasitism was associated with high host density, favoring parasitoid development and reproduction. Several parasitoid species were recorded, demonstrating adaptation to manure substrates. The results indicate that poultry manure is an important substrate for parasitoid activity and contributes to the regulation of fly populations in confined systems. In agroforestry environments, dipteran pupae collected from different substrates supported a high diversity of parasitoid species. Parasitism rates varied according to substrate type, reflecting differences in host availability and environmental conditions. The heterogeneity of these environments contributed to increased parasitoid richness. These results demonstrate that agroforestry systems provide favorable conditions for maintaining diverse parasitoid communities.

In studies involving dipterans collected in cattle feces, parasitism varied according to substrate conditions and host density. Bovine feces supported a large number of dipteran pupae, favoring parasitoid occurrence. Several species were associated with this substrate, indicating strong ecological relationships. The variation in parasitism reflects environmental influences and resource availability, confirming the importance of dung as a key substrate for parasitoid development.

Across all studies, parasitism rates ranged from 4.9% in buffalo dung to 51.7% in decomposing organic substrates, demonstrating strong variation among environments and substrates. Species such as *B. podagrica*, *P. vindemmiae*, and *S. drosophilae* were consistently recorded across different conditions. These results indicate that parasitoid diversity and parasitism are strongly influenced by substrate type, host availability, and environmental conditions.

The diversity of parasitoids associated with Diptera varied according to substrate type and environmental conditions. Parasitoid species belonging mainly to the families Braconidae, Chalcididae, Figitidae, and Pteromalidae were recorded in different substrates, including animal feces, viscera, and decomposing organic matter. Parasitism rates showed considerable variation among substrates, ranging from 4.9% in buffalo dung to 51.7% in decomposing animal tissues. Substrates with higher organic content, such as chicken viscera and human feces, supported greater parasitoid activity, while lower parasitism rates were observed in more restrictive substrates such as bovine kidney (Figure 13).

Figure 13: Representation of Braconidae parasitoids associated with Diptera developing in decomposing organic substrates. The illustration shows adult braconid parasitoids with four wings searching for hosts, attacking immature Diptera stages, and contributing to the natural regulation of fly populations. This interaction highlights the ecological importance of Braconidae as natural enemies of Diptera of sanitary, veterinary, and economic relevance. Sources: Photo#45423/Matthew Ireland/Iowa State University

The most frequently recorded parasitoid species included *B. podagrica*, P. *vindemmiae*, and *S. drosophilae*, which were found across multiple substrates and environments, indicating a high ecological adaptability. In contrast, some species showed more specific associations with particular hosts or substrates. The relationship between parasitoids and their dipteran hosts demonstrated that host availability strongly influenced parasitoid occurrence and abundance. Substrates with higher densities of dipteran pupae supported greater parasitoid emergence, reinforcing the dependence of parasitoid populations on host resources. The main parasitoid species, their hosts, and parasitism rates are summarized in Table 2.

Table 2: Parasitoids of Diptera in different substrates. Diversity of parasitoids (Hymenoptera) associated with dipterans collected from animal-based organic substrates in rural, urban, and natural environments in Brazil. The table presents the main parasitoid species, their hosts, and the parasitism rates recorded in the analyzed studies

Author/Year	Substrate	Parasitoid species	Host group species	Parasitism (%)
Marchiori, 2010	Cattle feces	*Gnathopleura quadridentata*	Diptera	25.6
Marchiori, 2010	Chicken feces	*Spalangia endius*	Diptera	47.7
Marchiori, 2019a	Various substrates	*Spalangia drosophilae*	Diptera	17,4
Marchiori, 2019b	Various substrates	*Gnathopleura quadridentata*	*Sarcodexia lambens*	56.0
Marchiori, 2019c	Cattle liver	*Pachycrepoideus vindemmiae*	*Musca domestica*	74,2
Marchiori, 2009a	Buffalo feces	*Spalangia drosophilae*	Diptera	4.9
Marchiori, 2021a	Chicken viscera	*Brachymeria podagrica*	Diptera	51.7
Marchiori, *et al.,* 2007	Cattle kidney	*Pachycrepoideus vindemmiae*	Diptera	74.2
Marchiori *et al.,* 2008	Forest area	*Brachymeria podagrica*	*Musca domestica*	71.9
Marchiori, 2008c	Forest area	*Pachycrepoideus vindemmiae*	Diptera	28.1

A total of 734 dipteran pupae were collected from different substrates in a forest area in Brazil, from which 89 parasitoid specimens were obtained, resulting in an overall parasitism rate of 12.1%. The most abundant dipteran species was *Musca domestica* L. 1758 (Diptera: Muscidae) (37.3%), followed by *Peckia chrysostoma* (Wiedemann, 1830) (Diptera: Sarcophagidae) (31.3%) and *Oxysarcodexia thornax* (Walker, 1849) (Diptera: Sarcophagidae) (9.0%). Other species, such as *Fannia pusio* (Wiedemann, 1830) (Diptera: Fanniidae) (6.0%), *Ophyra aenescens* (Wiedemann, 1830) (Diptera: Muscidae) (6.3%), *Chrysomya megacephala* (Fabricius, 1794) (Diptera: Calliphoridae) (1.9%), and *Tricharaea occidua* (Fabricius, 1794) (Diptera: Sarcophagidae) (0.8%) were also recorded. Two parasitoid species were identified: *P. vindemmiae* with 28.1% and *B. podagrica* with 71.9%, indicating dominance of *B. podagrica*. 4,9% (Figure 14).

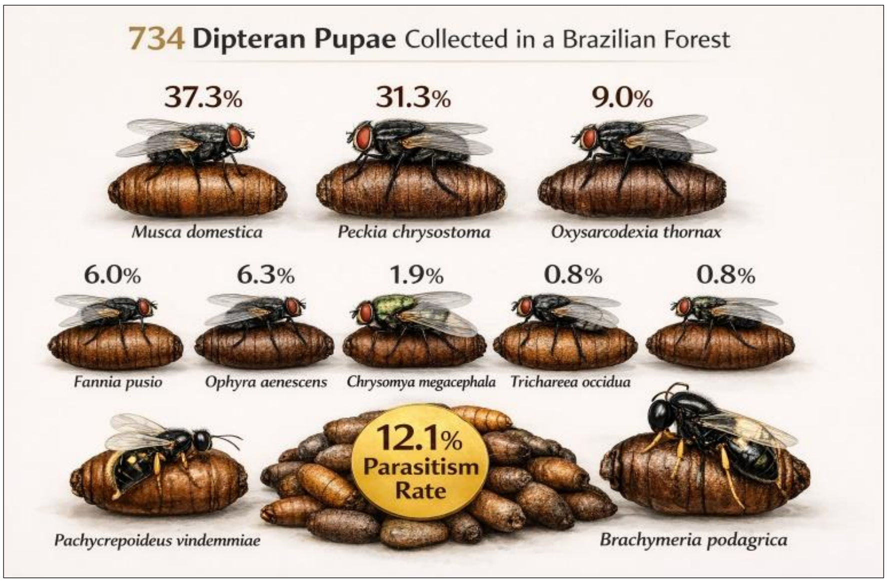

Figure 14: Relative abundance of dipteran species collected from organic substrates in a forest environment. followed by other less abundant taxa. These species represent the main hosts associated with parasitoid activity and biological control processes

Parasitism varied according to substrate, with the highest rate observed in chicken viscera (51.7%), followed by human feces (38.2%), fish (7.9%), and bovine kidney (2.2%). The highest number of hosts was recorded in human feces, where *M. domestica* reached 274 individuals, demonstrating a strong association with synanthropic environments. These results indicate that substrate type strongly influences both dipteran abundance and parasitoid occurrence.

4.0. DISCUSSION

The predominance of dipteran species such as *C. megacephala, M. domestica* and *P. chrysostoma* in the evaluated substrates confirms the sanitary and ecological importance of these flies in decomposing organic matter. In the present dataset, *M. domestica* showed high abundance in human feces and other synanthropic substrates, reinforcing its close association with human-modified environments. This pattern agrees with studies carried out in rural and urban areas in Brazil, where synanthropic dipterans were consistently associated with substrates rich in organic matter. The high abundance of these hosts is directly reflected in parasitoid occurrence, since host density is one of the main factors determining parasitism levels and parasitoid establishment in different environments (Figure 15) (Marchiori *et al.,* 2003a; Marchiori *et al.,* 2003b; Marchiori, 2006; Marchiori *et al.,* 2007a; Marchiori *et al.,* 2007b; Marchiori *et al.,* 2007c).

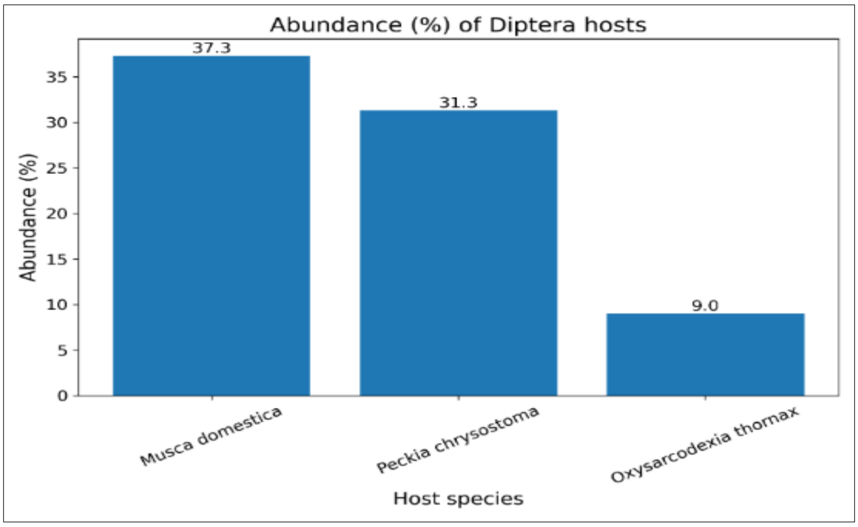

Figure 15: Relative abundance (%) of the main Diptera host species recorded in different substrates. *Musca domestica* and *P. chrysostoma* showed the highest abundance among hosts. Host availability plays a key role in determining parasitoid occurrence and parasitism rates

The variation in parasitism rates recorded among substrates, from 4.9% in buffalo dung to 51.7% in decomposing animal tissues, demonstrates that substrate composition strongly affects parasitoid performance. Substrates with high organic content and intense dipteran colonization, such as chicken viscera and human feces, supported greater parasitoid activity than more restricted substrates, such as bovine kidney. This pattern indicates that nutrient availability, decomposition stage, and host aggregation favor parasitoid development. Similar differences among substrates were reported in studies conducted with dung, urban substrates, and animal tissues, confirming that parasitism is highly dependent on local substrate conditions (Figure 16) (Marchiori and Linhares, 1999; Marchiori *et al.,* 2001; Marchiori *et al.,* 2002a; Marchiori *et al.,* 2002b; Silva *et al.,* 2003; Silva *et al.,* 2005; Marchiori *et al.,* 2010).

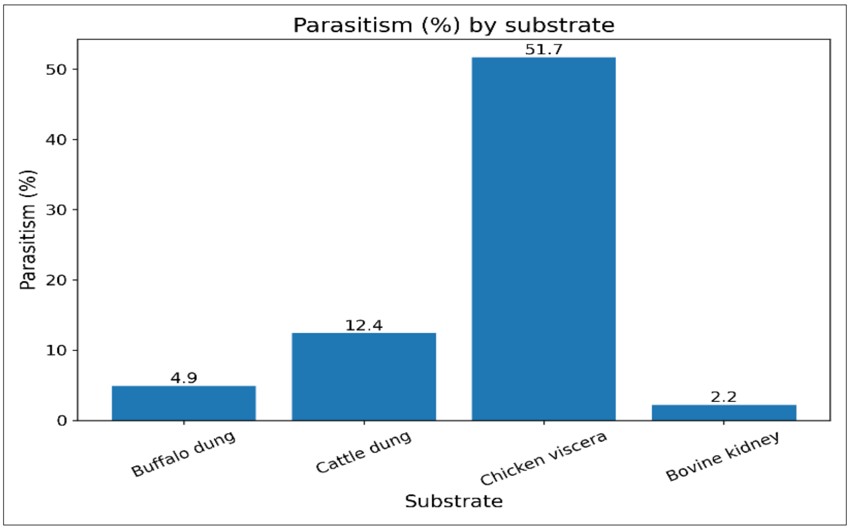

Figure 16: Parasitism rate (%) of Diptera pupae in different substrates. Higher parasitism was observed in substrates with greater organic content, especially chicken viscera. These results indicate that substrate type strongly influences parasitoid activity and success

The high frequency of *B. podagrica* and *P. vindemmiae* in different studies highlights the importance of these parasitoids in dipteran regulation. In the forest study, *B. podagrica* represented 71.9% of the parasitoids obtained, whereas *P. vindemmiae* accounted for 28.1%, showing clear dominance of these species in decomposing substrates. In urban and bovine-kidney substrates, *P. vindemmiae* was also frequent, indicating wide ecological tolerance and the capacity to exploit hosts in different environments. This repeated occurrence across studies suggests that these species are among the most important parasitoids associated with dipteran pupae in Brazil (Figure 17) (Marchiori *et al.,* 2000a; Marchiori *et al.,* 2000b; Marchiori, 2014; Marchiori, 2019a; Marchiori, 2019b; Marchiori, 2021a).

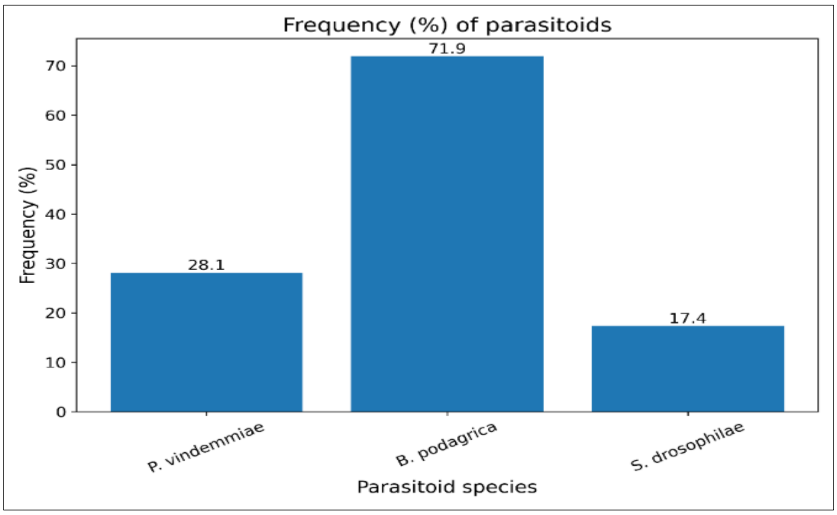

Figure 17: Frequency (%) of the main parasitoid species associated with Diptera. *B. podagrica* and *P. vindemmiae* were the most representative species across substrates. This pattern highlights their ecological importance as dominant parasitoids in different environments

Dung substrates, especially bovine and buffalo dung, consistently supported expressive host availability and parasitoid emergence in the present set of studies. In buffalo dung, 3,473 pupae yielded 172 parasitoids, while in cattle dung, parasitism reached 12.4% in southern Goiás and 6.4% in central Goiás. These values confirm that dung is one of the main substrates sustaining host–parasitoid interactions involving muscoid Diptera. In addition to host density, dung provides suitable humidity, microbial activity, and shelter for immature stages, which favor parasitoid development. This explains why dung-associated studies repeatedly show rich parasitoid assemblages and significant parasitism levels (Marchiori *et al.,* 2000c; Marchiori, 2000d; Marchiori *et al.,* 2010; Marchiori, 2014; Marchiori, 2019a; Marchiori, 2019b).

Urban environments, although more simplified than rural and forest systems, still maintain active parasitoid populations associated with synanthropic flies. In the urban-area study, 35 parasitoid specimens were obtained, with *P. vindemmiae* representing 74.2% of the total. This dominance indicates that some parasitoid species are well adapted to anthropogenic habitats and can persist where host populations remain available in decomposing organic residues. The persistence of parasitoids in urban environments is particularly relevant because these habitats favor dipterans of sanitary importance. Thus, even environments under strong human influence can sustain parasitoid activity and contribute to the natural regulation of synanthropic flies (Figure 18) (Marchiori *et al.,* 2001; Bonani *et al.,* 2006; Marchiori, 2021a; Marchiori, 2021b; Marchiori, 2021c; Jaume-Schinkela and Menguala, 2022; Marchiori, 2022).

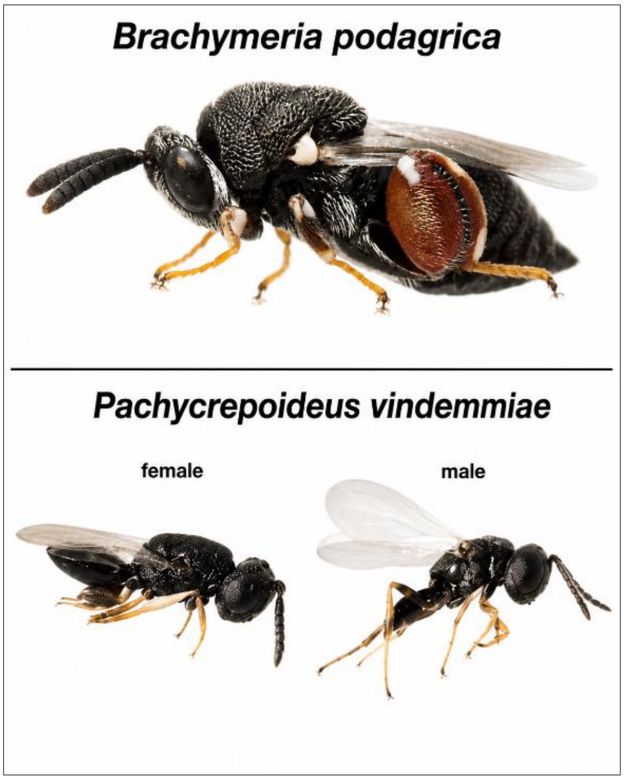

Figure 18: Morphological comparison of two pupal parasitoids associated with Diptera. The upper panel shows an adult of *B. podagrica*, emphasizing its robust body, enlarged hind femora, and characteristic reddish-brown markings. The lower panel presents lateral views of female and male *P. vindemmiae*, highlighting sexual differences in body form, abdomen, antennae, and wing position. Both species are pupal parasitoids of Diptera and may contribute to the natural regulation of fly populations developing in decomposing organic substrate

The results obtained in agroforestry and forest environments indicate that habitat heterogeneity contributes to higher parasitoid richness. In these systems, the coexistence of multiple substrates and microhabitats increases host diversity and expands the range of ecological niches available to parasitoids. The forest-area study showed high parasitism in specific substrates, especially chicken viscera, while agroforestry systems were characterized by greater diversity of species. These findings suggest that environmental complexity favors parasitoid coexistence, even when parasitism rates vary among substrates. Therefore, more heterogeneous environments appear to support richer and more structured parasitoid communities than simplified habitats (Figure 19) (Bonani *et al.,* 2006; Marchiori, 2021a; Marchiori, 2021b; Marchiori, 2021c; Jaume-Schinkela and Menguala, 2022).

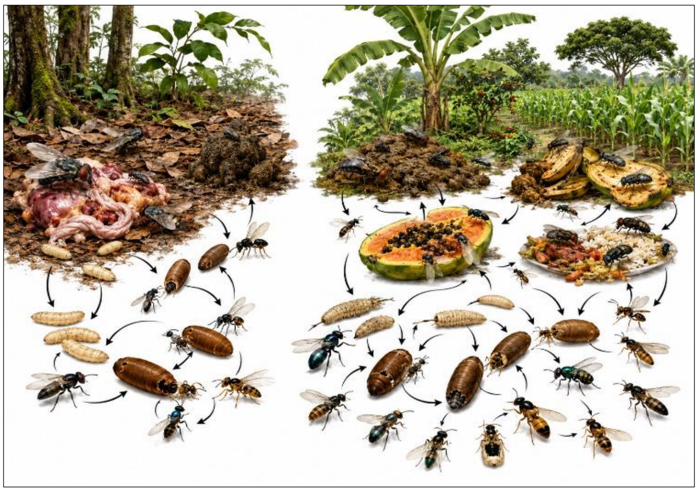

Figure 19: Integrated representation of parasitoid–Diptera interactions in forest and agroforestry environments. The illustration shows decomposing organic substrates acting as breeding sites for Diptera and as sources of immature hosts for parasitoids. Habitat heterogeneity, substrate diversity, and the coexistence of multiple microhabitats are represented as factors favoring greater parasitoid richness, host diversity, and more structured ecological interactions in complex environments

Host–parasitoid associations recorded in the present study indicate differences in ecological strategies among parasitoid species. Some species, such as *P. vindemmiae*, occur in several substrates and environments, indicating generalist behavior. Others appeared more closely associated with specific hosts or substrates, suggesting narrower ecological preferences. This combination of broad and restricted host use contributes to the organization of parasitoid communities and may reduce overlap among species exploiting the same host resource. The repeated occurrence of the same parasitoids across different studies suggests that host availability and substrate type jointly shape the balance between generalist and more selective parasitoid strategies (Figure 20) (Marchiori *et al.,* 2001; Marchiori *et al.,* 2004a; Marchiori, 2004b; Marchiori *et al.,* 2007a; Marchiori *et al.,* 2007b; Marchiori, 2019b; Marchiori, 2019c).

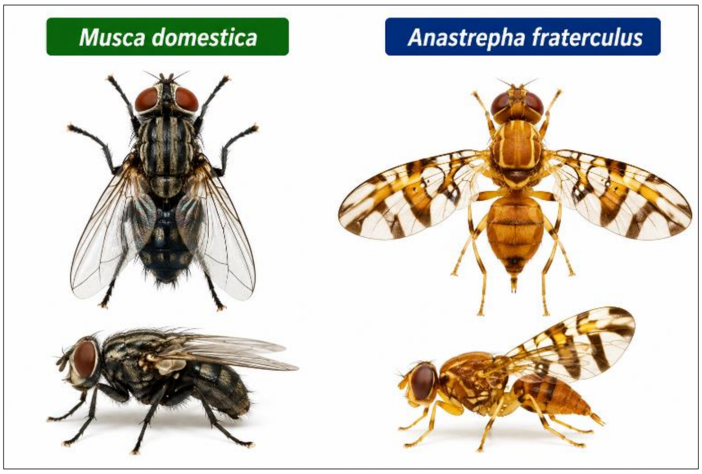

Figure 20: Comparative morphology of two dipteran hosts. Dorsal and lateral views of *Musca domestica* (Linnaeus, 1758) (Diptera: Muscidae) and *Anastrepha fraterculus* (Wiedemann, 1830) (Diptera: Tephritidae). Both species possess a single functional pair of wings, a characteristic feature of Diptera. The figure highlights the darker body and longitudinal thoracic stripes of *M. domestica* and the yellowish-brown body and distinctly patterned wings of *A. fraterculus*

Temporal variation in parasitoid occurrence can be inferred from differences among studies conducted in different years, seasons, and sampling conditions. Although this study integrates multiple field datasets, the variation in abundance and parasitism percentages indicates that parasitoid activity changes according to host availability and substrate exposure over time. Studies involving dung, manure, and animal tissues show that some parasitoid species are consistently present, whereas others vary across sampling periods. This pattern indicates that parasitoid populations are dynamic and respond to temporal changes in resource availability, especially in ephemeral substrates (Figure 21) (Marchiori, 2010; Marchiori, 2014; Marchiori, 2019a; Marchiori, 2019b; Marchiori, 2021c; Marchiori, 2023).

Figure 21: Temporal variation in parasitoid–Diptera interactions associated with ephemeral decomposing substrates. The illustration represents changes in substrate condition, Diptera abundance, immature host availability, pupal formation, and parasitoid occurrence over time. Parasitoids are represented with four wings, emphasizing their role as natural enemies of Diptera in dung, manure, and animal tissue substrate

The broad distribution of parasitoids across rural, urban, agroforestry, and forest environments reinforces their role as key natural enemies of Diptera. Their presence in all evaluated conditions demonstrates that these insects are not restricted to a single habitat type but are part of a broader ecological network associated with decomposing substrates and synanthropic flies. This ecological amplitude allows parasitoids to remain active across contrasting environmental conditions, contributing to host regulation in multiple systems. The consistency of parasitoid occurrence across studies reinforces their importance as biological regulators in Brazilian ecosystems (Figure 22) (Marchiori *et al.,* 2004a; Marchiori, 2004b; Marchiori, 2008a; Marchiori *et al.,* 2008b; Marchiori, 2009a; Marchiori, 2009b; Marchiori, 2021a).

Figure 22: Integrated representation of parasitoid–Diptera interactions across rural, urban, agroforestry, and forest environments. The illustration shows decomposing organic substrates serving as breeding sites for Diptera and as sources of larvae and pupae attacked by parasitoids. The broad occurrence of parasitoids in contrasting habitats highlights their ecological amplitude and their importance as natural enemies contributing to the regulation of synanthropic fly populations in different Brazilian ecosystems

Taken together, the results demonstrate that parasitoid diversity and parasitism rates are strongly influenced by substrate type, host abundance, and environmental complexity. Low values, such as 4.9% in buffalo dung, and high values, such as 51.7% in decomposing tissues, show that parasitoid performance varies markedly depending on ecological conditions (Figure 23) (Marchiori *et al.,* 2002a; Marchiori *et al.,* 2002b; Silva *et al.,* 2005; Marchiori *et al.,* 2006; Marchiori *et al.,* 2007a).

Figure 23: Integrated representation of how substrate type, host abundance, and environmental complexity influence parasitoid–Diptera interactions. The illustration shows buffalo dung, decomposing fruit, and animal tissues as contrasting substrates that support different levels of Diptera larvae, pupae, and parasitoid activity. The greater concentration of parasitoids in decomposing tissues represents higher parasitism under favorable ecological conditions, whereas buffalo dung represents lower parasitism despite the presence of available hosts

At the same time, the recurrent presence of species such as *B. podagrica*, *P. vindemmiae*, and *S. drosophilae* indicates that a relatively small group of parasitoids plays a central role across multiple substrates. This synthesis confirms that parasitoid communities associated with Diptera are structured by consistent ecological gradients and represent an important component of natural regulation in decomposing substrates (Figure 24) (Marchiori *et al.,* 2000c; Marchiori *et al.,* 2003a; Marchiori *et al.,* 2003b; Marchiori *et al.,* 2007b).

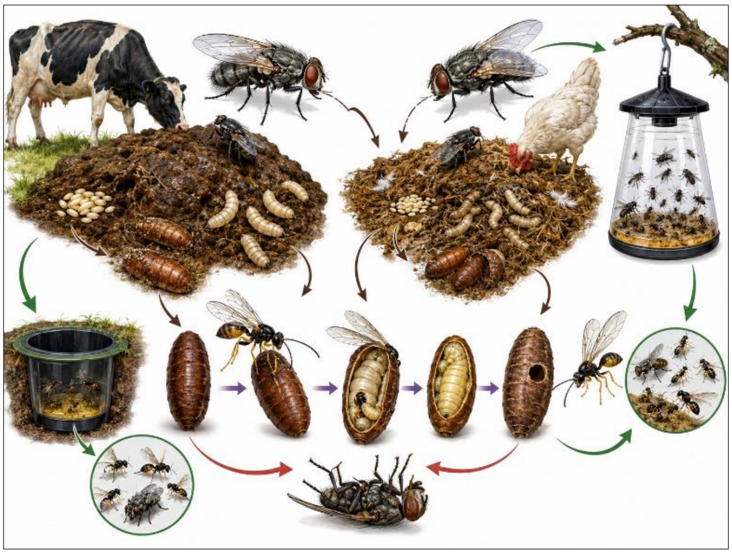

Figure 24: Integrated representation of parasitoid–Diptera interactions across different substrates, including cattle feces, poultry manure, and trapping systems. The figure combines host breeding sites with parasitoid life cycle stages, illustrating host location, parasitism of pupae, development, and emergence leading to host mortality, highlighting their role in biological control

5.0. CONCLUSION

The present study highlights the diversity and ecological importance of parasitoids associated with Diptera in different organic substrates and environments. Variations in parasitism rates demonstrate that substrate type plays a key role in influencing parasitoid occurrence, development, and efficiency. The predominance of species such as *B. podagrica* and *P. vindemmiae* across multiple substrates indicates their high adaptability and relevance as natural enemies of synanthropic flies. In addition, the clear relationship between host availability and parasitoid abundance reinforces the dependence of parasitoid populations on dipteran hosts. Morphological and biological differences between parasitoids and their hosts, such as the presence of four wings in parasitoids and two wings in Diptera, further emphasize their distinct ecological roles. These characteristics, combined with their parasitic behavior, contribute significantly to the regulation of fly populations. Overall, parasitoids represent effective and sustainable biological control agents, playing a crucial role in reducing pest fly populations and contributing to environmental balance in both natural and managed ecosystems.

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