UNIVERSIDADE ESTADUAL PAULISTA – UNESP

CÂMPUS DE JABOTICABAL

IN COTUTELLE WITH AVIGNON UNIVERSITY, IMBE

ECOSYSTEM SERVICES PROVIDED BY ARTHROPODS IN FOREST FRAGMENTS ADJACENT TO CULTIVATED AREAS

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Agronomist

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AUTHOR'S CURRICULUM DATA

SABRINA CESARIN DE OLIVEIRA was born on February 7, 1996, in Fortaleza, Ceará, Brazil. She earned her degree in Agronomy in 2019 from the Federal University of Ceará (UFC). During her undergraduate studies, she participated in the Tutorial Education Program (PET), working with the PET Agronomy group at UFC under the guidance of Prof. Dr. Rosilene Oliveira Mesquita, Prof. Dr. Ervino Bleicher, and Prof. Dr. Cândida Hermínia Campos de Magalhães Bertini. She was involved with the Laboratory of Applied Entomology (LEA), supervised by Prof. Dr. Patrik Luiz Pastori, and completed an internship at Embrapa Tropical Agroindustry, working with Prof. Dr. Fernando Antonio Souza de Aragão and Dr. Elaine Facco Celin. During this period, she actively participated in rearing pest insects such as *Plutella xylostella* (Linnaeus, 1758) (Lepidoptera: Plutellidae) and *Neoleucinodes elegantalis* (Guenée, 1854) (Lepidoptera: Crambidae), as well as parasitoids such as *Trichogramma pretiosum* Riley, 1879 (Hymenoptera: Trichogrammatidae) and *Tetrastichus howardi* (Olliff, 1893) (Hymenoptera: Eulophidae), in addition to assisting in the setup and evaluation of scientific experiments involving these insects. At the end of her undergraduate studies, she developed her final thesis on the resistance of melon genotypes to the leafminer *Liriomyza sativae* Blanchard, 1938 (Diptera: Agromyzidae). In August 2019, she began her master's degree in Agricultural Entomology at the School of Agricultural and Veterinary Sciences of São Paulo State University (Unesp), Jaboticabal campus, with a CNPq scholarship, in the Laboratory of Applied Ecology, under the supervision of Prof. Dr. Odair Aparecido Fernandes. Her dissertation addressed the natural mortality factors of *Diatraea saccharalis* (Fabricius, 1794) (Lepidoptera: Crambidae) in sugarcane fields adjacent to forest fragments. In August 2021, she started her PhD in the same program, also under the supervision of Prof. Dr. Odair Aparecido Fernandes, in a cotutelle arrangement with Avignon Université (France), where she carried out part of her activities under the co-supervision of Prof. Dr. Armin Bischoff.

“Even though the future seems far away, it is actually beginning right now.”

Mattie Stepanek

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ECOSYSTEM SERVICES PROVIDED BY ARTHROPODS IN FOREST FRAGMENTS ADJACENT TO CULTIVATED AREAS

ABSTRACT - Forest fragments embedded within agricultural landscapes play a critical role in maintaining insect biodiversity and ensuring the provision of essential ecosystem services. This thesis investigates how vegetation structure and landscape composition influence insect communities and their functional roles in both tropical and temperate agroecosystems, with a particular focus on pest regulation, pollination, and the stability of ecological interactions. The research was conducted in two contrasting regions: sugarcane fields adjacent to Atlantic Forest fragments in southeastern Brazil, and vineyards in southeastern France. By integrating studies from different environmental and agricultural contexts, this thesis provides a broader understanding of how semi-natural habitats contribute to biodiversity conservation and agroecosystem functioning. In the first part, we examined whether tree diversity in Atlantic Forest fragments promotes insect diversity and functional group abundance in both forest and adjacent sugarcane habitats. Using data from two sampling years, we found that higher tree species richness was associated with increased insect richness and greater frequencies of key functional groups such as predators and herbivores. Moreover, positive correlations between insect diversity in forests and sugarcane fields suggested inter-habitat spillover, reinforcing the role of forest fragments as sources of biodiversity and potential providers of ecosystem services. The second part focused on the order Hymenoptera, a taxonomically and functionally diverse group that includes parasitoids, predators, and pollinators. We assessed how seasonal variation affects their abundance and community composition across forest and sugarcane habitats. The results revealed distinct temporal dynamics, with forest fragments promoting more stable insect communities over time, whereas sugarcane fields exhibited higher seasonal fluctuations, likely resulting from agricultural practices and stronger changes in microclimatic conditions. Functional groups responded differently depending on the season and habitat, highlighting the ecological importance of forest fragments as refuges that buffer temporal instability in agricultural landscapes. In the third part, we expanded the analysis to a Mediterranean region and examined insect communities and predation rates in vineyards and adjacent woodlands in France. We evaluated how detailed vegetation characteristics, such as flower and herbaceous cover, affect insect abundance and functional composition. We found that floral resources and plant species richness were key drivers of beneficial insect abundance, particularly at vineyard borders, where spillover from forests was most evident. Sentinel prey experiments revealed higher predation rates in forest fragments, with positive effects extending into the vineyards, suggesting a contribution of semi-natural habitats to biological control. Overall, the thesis demonstrates that vegetation quality and spatial configuration significantly shape insect community dynamics and ecosystem service provision. Forest fragments enhance biodiversity and promote ecological interactions beyond their boundaries, although these effects tend to be spatially restricted and modulated by habitat structure and management practices. By integrating functional approaches and cross-regional comparisons, this work emphasizes the need for conservation and restoration strategies that maintain habitat quality and

functional connectivity in agricultural landscapes. The findings provide practical insights for designing sustainable agricultural landscapes that reconcile food production with biodiversity conservation.

Keywords: Biodiversity, Habitat fragmentation, Multifunctional landscape, Spillover effects, Sustainable agriculture, Trophic interactions

SERVICES ÉCOSYSTÉMATIQUES FOURNIS PAR LES ARTHROPODES DANS LES FRAGMENTS FORESTIERS ADJACENTS AUX ZONES CULTIVÉES

RÉSUMÉ – Les fragments de forêt intégrés dans les paysages agricoles jouent un rôle fondamental dans le maintien de la biodiversité des insectes et dans la fourniture de services écosystémiques associés. Cette thèse vise à analyser de quelle manière les caractéristiques de la végétation et la composition du paysage influencent les communautés d'insectes et leurs rôles fonctionnels, dans des contextes agricoles tropicaux et tempérés, en portant une attention particulière à la régulation des ravageurs, à la pollinisation et à la stabilité des interactions écologiques. Les travaux ont été menés dans deux régions contrastées: des parcelles de canne à sucre adjacents à des fragments de forêt atlantique au sud-est du Brésil, et des vignobles situés dans le sud-est de la France. En intégrant des études dans des contextes environnementaux et agricoles différents, cette thèse apporte une compréhension approfondie sur la contribution des habitats semi-naturels à la conservation de la biodiversité et au fonctionnement des agroécosystèmes. La première partie s'intéresse à la relation entre la diversité des arbres rencontrés dans des fragments de forêt et la diversité ainsi que l'abondance des groups fonctionnels des insectes au sein des forêts mais aussi dans des parcelles agricoles adjacentes. Les données, récoltées pendant deux ans, montrent que la richesse spécifique d'arbres est positivement corrélée à la diversité d'insectes et à une fréquence accrue de groupes fonctionnels clés tels que les prédateurs et les phytophages. Des corrélations positives entre la diversité des insectes dans les forêts et dans les parcelles agricoles suggèrent un spillover à partir des forêts, mettant en évidence le rôle des fragments de forêt comme sources de biodiversité et fournisseurs potentiels de services écosystémiques. La deuxième partie porte sur l'ordre des Hyménoptères, un groupe présentant une diversité taxonomique et fonctionnelle remarquable, incluant des parasitoïdes, des prédateurs et des pollinisateurs. L'analyse de la variation saisonnière de leur abondance et de la composition des communautés révèle des dynamiques temporelles différenciées selon les habitats. Les fragments de forêt montrent des communautés plus stables au fil du temps, tandis que les parcelles de canne à sucre présentent des fluctuations plus marquées, probablement liées aux pratiques agricoles et aux variations microclimatiques plus importantes. Les réponses des groupes fonctionnels varient selon les saisons et les habitats, soulignant le rôle des fragments forestiers en tant que refuges atténuant l'instabilité écologique dans les paysages cultivés. Dans la troisième partie, l'analyse est élargie à une région méditerranéenne, à travers l'étude des communautés d'insectes et des taux de prédation dans les vignobles et les boisements adjacents. L'influence de différentes caractéristiques de la végétation, telles que la recouvrement en fleurs, le recouvrment herbacé et la richesse spécifique végétale, est évaluée. Les résultats montrent que les ressources florales et la diversité végétale sont des facteurs clés qui conduisent l'abondance des insectes auxiliaires, notamment en bordure de vigne, où l'effet de spillover depuis le milieu forestier est le plus marqué. La mise en place de proies sentinelles révèle des taux de prédation plus élevés dans les forêts, avec des effets positifs s'étendant vers les parcelles

viticoles, suggérant une contribution des habitats semi-naturels à la lutte biologique. Dans l'ensemble, cette thèse met en évidence l'importance de la qualité de la végétation et de la configuration spatiale du paysage dans la structuration des communautés d'insectes et la fourniture de services écosystémiques. Les fragments de forêt renforcent la biodiversité et favorisent les interactions écologiques au-delà de leurs limites, bien que ces effets restent spatialement limités et modulés par la structure des habitats et les pratiques culturales. En intégrant des approches fonctionnelles et comparatives entre régions, ce travail souligne la nécessité des stratégies de conservation et de restauration visant à préserver la qualité des habitats et la connectivité fonctionnelle dans les paysages agricoles. Les résultats obtenus fournissent des pistes concrètes pour la conception de systèmes agricoles durables conciliant production et conservation de la biodiversité.

Mots-clés : Biodiversité, Fragmentation des habitats, Paysage multifonctionnel, Spillover effect, Agriculture durable, Interactions trophiques

CHAPTER 1 – General considerations

In recent decades, agricultural intensification has been the main strategy to increase productivity and meet the growing global demand for food (Tilman et al., 1999). This process is characterized by large-scale crop fields and the intensive use of agrochemicals (Tilman et al., 2001). Although effective in increasing food production, these practices have led to negative environmental impacts, including biodiversity loss and the degradation of ecosystem services essential for long-term sustainability (Fahrig et al., 2015).

Biodiversity plays a fundamental role in maintaining ecological processes and ecosystem resilience (Garbach et al., 2014; Jankielsohn, 2018). Higher species richness enhances the diversity of ecological niches, allowing organisms to more efficiently use resources and interact with their environment in complementary or synergistic ways (Haan et al., 2021). Moreover, biodiversity is critical for the stability of ecosystem processes by ensuring that different species occupy similar functional niches but respond differently to environmental changes. The loss of one species can therefore be compensated by others with overlapping ecological functions (Elmqvist et al., 2003; Cadotte et al., 2011). However, land-use change and the simplification of agricultural landscapes have contributed to the loss and fragmentation of natural and semi-natural habitats, threatening biodiversity and compromising key ecosystem services (Haddad et al., 2015; Wilson et al., 2016).

Habitat fragmentation, a process by which large continuous areas of natural habitat are divided into small isolated fragments, is a prevalent phenomenon worldwide (Haddad et al., 2015). Fragmentation can lead to species loss and reduce the ability of fragments to sustain viable populations in the long term (Liu et al., 2019; Fletcher et al., 2023). Nevertheless, in agricultural landscapes, habitat fragments can function as important biodiversity refuges, maintaining populations of insects that contribute to the resilience and functionality of adjacent agricultural ecosystems (Mitchell et al., 2014; González et al., 2017). Insects provide essential ecosystem services, including pollination, pest control and decomposition (Schowalter et al., 2018). Their diversity and

functional roles are closely linked to the quality and configuration of surrounding habitats (Karp et al., 2018). However, our understanding of how semi-natural habitat characteristics influence insect communities and associated ecosystem services remains limited.

The presence of a diverse vegetation rich in resources for arthropods increases the complexity of insect communities, promoting beneficial ecological interactions, increasing stability and resilience of agro-ecosystems (Brockerhoff et al., 2017; Schuldt et al., 2019). Plants provide shelter and food resources for beneficial insects, such as pollen, foral and extraforal nectar, which support beneficial insects like pollinators, predators, and parasitoids. They can also sustain alternative prey populations that maintain predator communities (Gardarin et al., 2018). Many natural enemies of pests require distinct resources across life stages and thus require plant resources, such as nectar to complete their life cycles. Furthermore, the availability of such plant resources have positive effects on the survival and reproduction even on predators that do not change nutrition in their life cycle (Gardarin et al., 2018; Holm et al., 2021; Stowe et al., 2021). Thus, the preservation or restoration of semi-natural habitats near crop fields is key to maintaining ecological interactions that support sustainable agriculture (Bianchi et al., 2013; Gagic et al., 2018).

The Atlantic Forest biome in Brazil is an emblematic example of an ecosystem that has undergone intense fragmentation due to agricultural expansion and urbanization (Haddad et al., 2015). Originally one of the largest tropical forests, the Atlantic Forest occurs today in small scattered, often isolated fragments occupying only 28% of the pre-colonization area (Figure 1a) (Rezende et al., 2018). In most areas of Brazil, the Atlantic Forest Biome is limited to fragments surrounded by livestock farming and monocultures, such as sugarcane (Ferreira et al., 2015). Nevertheless, these fragments are crucial for the conservation of regional biodiversity, harboring a rich variety of plant and animal species, including arthropods that provide important ecological functions (Castro et al., 2010; Korasaki et al., 2013; Dos Santos et al 2018; Ribeiro et al., 2019). Thus, understanding how these fragments influence biodiversity and ecosystem

services in adjacent cultivated areas provides valuable insights required to improve agricultural policies and practices integrating biodiversity conservation.

In temperate and Mediterranean regions such as southeastern France, vineyards are usually embedded in heterogeneous landscapes and often include herbaceous vegetation between grapevine rows, that promote arthropod diversity and ecosystem services when properly managed (Blaise et al., 2021; Rocher et al., 2024). Although vineyards undergo periodic disturbances such as mowing and tillage (Winter et al., 2018; Fried et al., 2019), the management of inter-rows is generally less intense than that of annual crops like sugarcane (Filoso et al., 2015). Adjacent forest fragments may serve as important reservoirs for beneficial insects, complementing in-field resources and enhancing ecological functions (Figure 1b) (Chaperon et al., 2022; Zamberletti et al., 2021). However, the specific role of these semi-natural habitats and their vegetation characteristics in shaping vineyard insect communities remains poorly understood. Given the structural and compositional differences between tropical and temperate agroecosystems, comparative studies are needed to evaluate whether the ecological patterns are consistent. Integrating data from French vineyards and Brazilian sugarcane fields allows a broader understanding of how landscape composition and plant community composition affect insect biodiversity and the provision of ecosystem services.

In many studies evaluating insect biodiversity and ecosystem services in agricultural landscapes, vegetation is treated as a black box, with limited information about plant identity, resource availability, or vegetation structure. This often hampers a better understanding of how specific habitat characteristics influence insect communities. In this thesis, we aimed to go beyond this limitation. In Parts I and II, tree species were identified in forest fragments to explore the relationship between arboreal diversity and insect communities. In Part III, vegetation was characterized in greater detail, including estimates of flower, shrub, herbaceous and total cover, allowing for a more refined analysis of how vegetation structure influences insect abundance and predation. By incorporating plant community composition and structure into different parts of the thesis, we

provide a more comprehensive view of plant–insect interactions in fragmented agroecosystems.

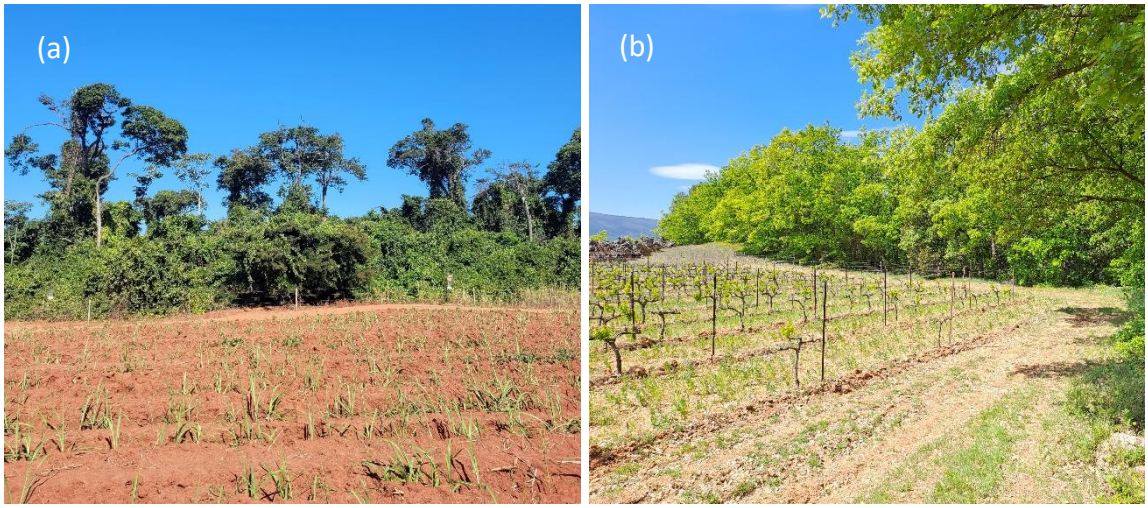

Figure 1. Forest fragment adjacent to a sugarcane field in Brazil (a) and adjacent to a vineyard in France (b).

This thesis evaluates how forest fragments adjacent to crop fields affect insect communities, their potential contributions to ecosystem services, and the resulting effects on agroecosystem functioning. It is divided into three parts:

- Part I investigates whether insect diversity and the abundance of key functional groups are favored by tree diversity in Atlantic Forest fragments. It also examines whether insect communities in forest fragments are positively related to those in neighboring sugarcane fields, and how similar these communities are across habitats.

- Part II explores how these patterns vary seasonally, focusing on Hymenoptera due to their ecological relevance. This group includes many parasitoids, predators, and pollinators, which are key providers of ecosystem services such as biological control and pollination in agroecosystems. Their diversity and functional roles make them good indicators of ecological processes across habitats and seasons. It examines whether community composition, richness, and abundance vary across seasons and habitats, and whether there is an association in Hymenoptera abundance between fragments and sugarcane fields.

- Part III presents a comparative study conducted in southeastern France, exploring the relationships between woodlands and adjacent vineyards. It assesses whether forest plant composition influences insect community structure and predation services in both habitats, whether insects move across habitat boundaries, and whether predation rates in woodlands affect those in vineyards.

The inclusion of study sites in tropical (Brazil) and temperate (France) regions allows a broader perspective on the relationships between biodiversity and ecosystem services in contrasting environmental and agricultural contexts. Together, these three parts provide a comprehensive understanding of how forest fragments contribute to insect biodiversity and their potential ecosystem services. By integrating ecological knowledge from diverse landscapes, this thesis aims to inform sustainable agricultural practices that reconcile productivity with biodiversity conservation.

References

Bianchi FJJA, Booij CJH, Tscharntke T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity, and natural pest control. **Proceedings of the Royal Society B: Biological Sciences** 273:1715–1727.

Bianchi FJ, Schellhorn NA, Cunningham SA (2013) Habitat functionality for the ecosystem service of pest control: reproduction and feeding sites of pests and natural enemies. **Agricultural and Forest Entomology** 15:12–23.

Blaise C et al. (2021) The key role of inter-row vegetation and ants on predation in Mediterranean organic vineyards. **Agriculture, Ecosystems & Environment** 311:107327.

Brockerhoff EG et al. (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. **Biodiversity and Conservation** 26:3005–3035.

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. **Journal of Applied Ecology** 48:1079–1087.

Castro TMMG, Moraes GJ (2010) Diversity of phytoseiid mites (Acari: Mesostigmata: Phytoseiidae) in the Atlantic Forest of São Paulo. **Systematics and Biodiversity** 8:301–307.

Chaperon PN et al. (2022) Effects of adjacent habitat on nocturnal flying insects in vineyards and implications for bat foraging. **Agriculture, Ecosystems & Environment** 326:107780.

Elmqvist T et al. (2003) Response diversity, ecosystem change, and resilience. **Frontiers in Ecology and the Environment** 1:488–494.

Fahrig L et al. (2015) Farmlands with smaller crop fields have higher within-field biodiversity. **Agriculture, Ecosystems & Environment** 200:219–234.

Ferreira MP, Alves DS, Shimabukuro YE (2015) Forest dynamics and land-use transitions in the Brazilian Atlantic Forest: the case of sugarcane expansion. **Regional Environmental Change** 15: 365-377.

Fletcher Junior RJ, Smith TA, Kortessis N, Bruna EM, Holt RD (2023) Landscape experiments unlock relationships among habitat loss, fragmentation, and patch-size effects. **Ecology** 104:e4037.

Fried G, Cordeau S, Metay A, Kazakou E (2019) Relative importance of environmental factors and farming practices in shaping weed communities structure and composition in French vineyards. **Agriculture, Ecosystems & Environment** 275:1-13.

Gagic V, Paull C, Schellhorn NA (2018) Ecosystem service of biological pest control in Australia: the role of non-crop habitats within landscapes. **Austral Entomology** 57:194–206.

Garbach K, Milder JC, Montenegro M, Karp DS, DeClerck FAJ (2014) Biodiversity and ecosystem services in agroecosystems. **Encyclopedia of Agriculture and Food Systems** 2:21–40.

Gardarin A, Plantegenest M, Bischoff A, Valantin-Morison M (2018) Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. **Journal of Pest Science** 91:943–955.

González E, Salvo A, Valladares G (2017) Arthropod communities and biological control in soybean fields: forest cover at landscape scale is more influential than forest proximity. **Agriculture, Ecosystems & Environment** 239:359–367.

Holm LL, He X, Sigsgaard L (2021) Flower diet enhances *Adalia bipunctata* larval development significantly when prey is limited. **Entomologia Experimentalis et Applicata** 169:750–757.

Haddad NM et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. **Science Advances** 1:e1500052.

Haan NL, Iuliano BG, Gratton C, Landis DA (2021) Designing agricultural landscapes for arthropod-based ecosystem services in North America. **Advances in Ecological Research** 64:191–250.

Jankielsohn A (2018) The importance of insects in agricultural ecosystems. **Advances in Entomology** 6:62–73.

Karp DS et al. (2018) Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. **Proceedings of the National Academy of Sciences** 115:E7863-E7870.

Korasaki V, Lopes J, Gardner Brown G, Louzada J (2013) Using dung beetles to evaluate the effects of urbanization on Atlantic Forest biodiversity. **Insect Science** 20:393–406.

Liu J et al. (2019) Forest fragmentation in China and its effect on biodiversity. **Biological Reviews** 94:1636–1657.

Mitchell MGE, Bennett EM, Gonzalez A (2014) Forest fragments modulate the provision of multiple ecosystem services. **Journal of Applied Ecology** 51:909-918.

Rezende CL et al. (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. **Perspectives in Ecology and Conservation** 16:208-214

Ribeiro DG, Silvestre R, Garcete-Barrett BR (2019) Diversity of wasps (Hymenoptera: Aculeata: Vespidae) along an altitudinal gradient of Atlantic Forest in Itatiaia National Park, Brazil. **Revista Brasileira de Entomologia** 63:22–29.

Rocher L, Melloul E, Blight O, Bischoff A (2024) Effect of spontaneous vegetation on beneficial arthropods in Mediterranean vineyards. **Agriculture, Ecosystems & Environment** 359:108740.

Santos LAO, Bischoff A, Fernandes OA (2018) The effect of forest fragments on abundance, diversity and species composition of predatory ants in sugarcane fields. **Basic and Applied Ecology** 33:58–65.

Schowalter TD, Noriega JA, Tscharntke T (2018). Insect effects on ecosystem services—Introduction. **Basic and Applied Ecology** 26:1-7.

Schuldt A et al. (2019) Multiple plant diversity components drive consumer communities across ecosystems. **Nature Communications** 10:1460.

Stowe HE, Michaud JP, Kim TN (2021) Floral resources enhance fecundity, but not flight activity, in a specialized aphid predator, *Hippodamia convergens* (Coleoptera: Coccinellidae). **Frontiers in Ecology and Evolution** 9:748870.

Tilman D (1999) Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. **Proceedings of the National Academy of Sciences** 96:5995–6000.

Tilman D et al. (2001) Forecasting agriculturally driven global environmental change. **Science** 292:281–284.

Winter S et al. (2018) Effects of vegetation management intensity on biodiversity and ecosystem services in vineyards: a meta-analysis. **Journal of Applied Ecology**, 55, 2484-2495.

Wilson MC et al. (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. **Landscape Ecology** 31:219–227.

Zamberletti P et al. (2021) More pests but less pesticide applications: Ambivalent effect of landscape complexity on conservationbiological control. **PLoS Computational Biology** 17: p.e1009559.

Malaise trap in forest fragment (Jaboticabal, Brazil)

CHAPTER 2 – The role of tropical forest fragment vegetation in maintaining arthropod diversity and spillover to adjacent sugarcane fields[1]

ABSTRACT - The degradation of forests in tropical agricultural landscapes has reduced biodiversity and may negatively affect ecosystem services. However, the role of forest fragments in the provision of ecosystem for agroecosystems, such as biological control, is still not well understood. This study analyses the relationship between tree diversity and arthropod communities in forest fragments and adjacent sugarcane fields around Jaboticabal (São Paulo, Brazil) to evaluate the benefits of preserving Atlantic Forest fragments. We tested the hypotheses: (1) arthropod diversity and the abundance of key functional groups are favored by tree diversity, (2) diversity and abundance of these functional groups in sugarcane fields depend on adjacent forests, and (3) the insect community composition of forest fragments and sugarcane fields is similar due to spillover effects. Arthropods were sampled in ten forest fragments over two years (2020 and 2022) using traps (Malaise, yellow pan) and direct tree sampling. We identified arthropods to morphospecies (2020) and family level (2022) and associated families to functional groups. We found that the quality of forest fragments, particularly tree species richness, was positively related to forest arthropod richness and frequency (occupied samples) of functional groups involved in ecosystem services such as predators but also of phytophagous insects. There was also a strong positive correlation between insect family richness and functional groups of forest fragments and adjacent sugarcane fields, indicating potential spillover and spatial connectivity between habitats. Although insect community composition was significantly different between forest fragments and sugarcane fields, NMDS ordination revealed partial overlap of family communities, suggesting many shared taxa in both habitats. This study highlights the importance of forest fragments in preserving insect biodiversity and related ecosystem services in tropical agricultural landscapes and advocates for the conservation and restoration of these habitats. However, the benefits in terms of crop damagae reduction and yields remain to be confirmed.

Keywords: Agroecology, biodiversity, biocontrol, ecosystem services, natural enemies, woodlands

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1. Introduction

Human land use has caused the loss and fragmentation of natural and semi-natural habitats affecting the stability of ecosystems (Newbold et al., 2015; Jacobson et al., 2019). Fragmentation is the division of such habitats into more os less distant native remnants, characterized by the emergence of ecological discontinuities within the ecosystem (Fahrig et al., 2003). Fragmentation is often the result of partial transformation to arable land (Heisswolf et al., 2009; Wilson et al., 2016). The replacement of semi-natural habitats by simplified agricultural systems negatively affects ecosystems including the loss of biodiversity and related services (Asbjornsen et al., 2014; Wilson et al., 2016). To maintain or improve ecosystem services in agricultural landscapes, it is necessary to conserve and/or restore biodiversity (Garbach et al., 2014). However, efficient conservation and restoration require the understanding of interactions and mechanisms driving biodiversity and abundance of taxonomic or functional groups providing such services (Gutierrez-Arellano and Mulligan, 2018).

Arthropods, in particular insects, are key organisms providing many ecosystem services such as pollination, biological control of pest and organic matter decomposition (Millennium Ecosystem Assessment – MEA, 2005; Ramos et al., 2020). However, arthropod populations and the services they provide can be negatively affected by habitat degradation (Gagic et al., 2018; Schowalter et al., 2018). Several studies have documented the decline in abundance, species diversity, and quality of ecosystem services in disturbed environments, in particular the decline in pollinator and seed-dispersing ant abundance (Winfree et al., 2009; Mata et al., 2013; Leal et al., 2014). This decline is related to the degradation of plant communities, such as species loss and spread of exotic plants, that directly affect insect populations (Diniz et al., 2010). Conversely, increased plant diversity increases the availability and variety of resources, which in turn promotes greater insect abundance, diversity and the provision of ecosystem services (Brockerhoff et al., 2017). Therefore, ecosystem services provided by arthropods are increasingly considered in land management decisions including practices that protect biodiversity (Losey and Vaughan, 2006).

Maintaining or enhancing ecosystem services in agricultural landscapes may be facilitated by preserving non-crop areas, particularly semi-natural vegetation zones near crop fields sustaining beneficial insect populations (Parry et al., 2015; Pywell et al., 2015; Gagic et al., 2018). This facilitation can be explained by movements of insects between habitats (habitat spillover), and among them several groups represent important ecological functions and services (Rand et al., 2006; Blitzer et al., 2012). Forest fragments are examples of natural or semi-natural habitats that influence the provision of multiple ecosystem services in adjacent fields (Mitchell et al., 2014; Decocq et al., 2016). Several studies have shown that arthropods involved in biological control of tropical crops are favored by adjacent natural forests (Klein et al. 2006; Sousa et al. 2011; Santos et al. 2018) but they did not take into account habitat quality. Areas with high plant species diversity are key drivers of insect diversity and abundance (Rowe et al., 2013; Zhang et al., 2016), contributing to the overall ecological quality of the habitat. The biodiversity and ecosystem services provided by forest fragments depend on their ecological quality, including resource availability, vegetation structure and connectivity (Haddad et al., 2015; Hertzog et al., 2019). A more comprehensive understanding of the specific habitat and vegetation characteristics that promote insect biodiversity and the abundance of beneficial arthropods is crucial to preserve or improve related ecosystem services (Bartual et al., 2019).

The Brazilian Atlantic Forest, in particular the semi-deciduous forest vegetation of Southeastern Brazil, has been largely fragmented, resulting in a sugarcane dominated agricultural landscape with a low proportion of remnant forest fragments (Ribeiro et al., 2009; Haddad et al., 2015). Recent estimates indicate that only 28% of the original Atlantic Forest cover remains of which an unknown part is highly disturbed by previous cutting or burning (Rezende et al., 2018). The size of these fragments is usually small (< 50 ha) and they are often isolated. However, these forest fragments may still represent an important reservoir of beneficial arthropods and potentially contribute to the provision of ecosystem services in adjacent crop fields through spillover effects (Castro and Moraes, 2010). A deeper knowledge of interactions between forest quality and arthropod communities in forest and the spillover to adjacent agroecosystems is

needed to support beneficial arthropod populations and their associated ecosystem services.

Thus, this study aims at improving the knowledge of the arthropod communities in fragments of the Atlantic Forest and their influence on communities of adjacent sugarcane fields. We further relate arthropod occurrence and community composition to characteristics of forest fragment vegetation. We tested the following hypotheses: (1) insect diversity and the abundance of key functional groups are favored by tree diversity; (2) richness and/or abundance of insect functional groups in sugarcane fields depend on richness and/or abundance of the same functional groups in adjacent forests; and (3) the insect family composition of forest fragments and sugarcane fields is similar due to spillover effects.

2. Material and methods

2.1. Study sites and design

The study was conducted in fragments of the Atlantic rain forest (Mata Atlantica) and adjacent sugarcane fields in the municipality of Jaboticabal, São Paulo state, Brazil (21° 15′ 19″ S, 48° 19′ 21″ W). The study area is characterized by the dominance of sugarcane fields with a small percentage of remnant gallery and plateau forests. The climate is mesothermic with dry winters and a rainy summer season, an annual rainfall of 1300 mm and a mean temperature of 22°C. The western, more continental parts of the Atlantic rain forest are semi-deciduous and represent a transition zone to the drier savanna systems (Brazilian Cerrado). Atlantic rain forest was the prevailing vegetation of the study area before European colonization.

Arthropods were sampled in April 2020 and August 2022, using direct and indirect (trapping) collection methods. The 2020 samples served as a preliminary baseline to support and refine our 2022 sampling design. In 2020, ten forest

fragments (Figure 1) were selected according to the following selection criteria: >50m width and length, no commercial tree plantation in the fragments and minimum distance of 1 km from each other. Five fragments were situated on shallow slopes (plateau fragments) whereas the other five were gallery forest remnants close to rivers and creeks (river valley or gallery fragments). Plateau fragments typically exhibited a greater cover of shrub and liana species compared to river valley fragments. River valley fragments are protected as Permanent Preservation Areas (PPAs), in particular to preserve water quality of tap water catchment areas (Santos et al., 2018). Three fragments had to be replaced in 2022 due to access problems and wildfire. In each forest fragment, we collected data in a randomly selected 50m x 20m plot, 5m from the edge.

Arthropods were also sampled in sugarcane fields adjacent to forest fragments (5m from the field edge). Sugarcane is usually harvested after the dry season from September on and resprouts from rhizomes in the rainy season after November. Herbicide treatments are common, but no insecticides were applied during the study period.

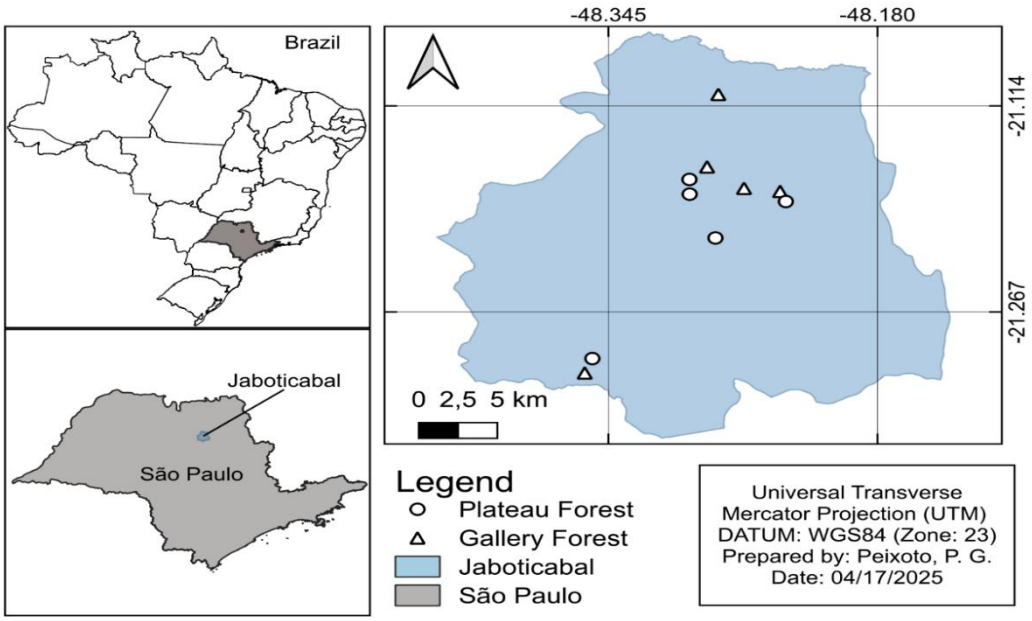

Figure 1. Study area and geographical position of the ten studied forest fragments.

2.2. Tree species and habitat quality index

At the end of the rainy season in 2020, we set up a preliminary study focusing on arthropod biodiversity of forest fragments. We defined woody plants of more than 5cm diameter at breast height as trees and identified them to species. Sampling was limited to 20 trees associated to five subplots of 1m² in each plot (closest tree to each corner). We used a simple habitat quality index to characterize forest fragments suggested by Felfili et al. (2011). The index uses tree cover as positive criterion and climber and grasses cover as negative criteria. Forest disturbance by tree cutting or fire increases the cover of climbers (lianas, vines) and grasses relative to tree cover. The cover was estimated as the vertical projection of aboveground plant organs using a scale from 0 to 1 with 0.1 intervals. The quality index was calculated as the sum of the three parameters with liana and grass cover fitted as negative and tree cover as positive values. In August 2022, a more detailed method was used to obtain more information on plant and arthropod community characteristics. All trees of the 1000m² plots were identified and insects were sampled from all trees in the dry season.

2.3. Athropod sampling

On each tree, we carefully cut a randomly selected branch at 2-5m height with a long reach pruning shears and manually captured all arthropods. If insects flew away or fell to the ground during cutting, another branch was collected to reduce losses by escape. Sampled arthropods were transferred to 70% diluted ethanol prior to identification. In 2020, insects and spiders were identified to morphospecies level. In 2022, we identified sampled insects individualst o family level in order to obtain more information on taxonomic and functional groups (Báldi, 2003) but we did not include spiders. We assigned all insects sampled in 2022 to the following functional groups using knowledge on life-history feeding features of the majority of species in each family: parasitoids, predators, omnivores, and phytophagous arthropods (Fernandez and Sharkey, 2006; Brown

et al., 2009; Brown et al., 2010). Families that could not be clearly assigned to a functional group were considered omnivorous and finally removed from analyses of functional groups. For insects that change feeding between larval and adult stages, we used the larval feeding behavior, as larvae generally have higher resource demands and are the primary consumers in the life cycle (Kaleka et al., 2019).

In August 2022, we additionally used trapping to sample flying insects. A Malaise-type trap was positioned in each forest fragment plot. The catching recipient of the traps was filled with 400ml of 70% alcohol solution, and the insects were collected after 48h. In sugarcane fields, we placed two yellow pan traps (42x28x8cm) 15m apart and 5m from the field edge. Each pan trap was filled with 2L of water and 10 drops of detergent before exposure for a duration of 48 hours. Likewise, the insects were preserved in 70% diluted ethanol, identified at family level and classified into functional groups.

2.4. Data analysis

We ran generalized linear mixed models (GLMM) to analyse the effects of habitat quality (2020 habitat quality index, 2022 tree richness) on arthropod richness (2020 morphospecies, 2022 insect family), family frequency and functional group frequency. Frequency was calculated as the number of occupied branches per fragment (only 2022). We fitted fragment type (plateau or gallery) as a random effect to account for variation among different fragments resulting in the following model structure: diversity measure ~ habitat quality + (1|fragment type). Poisson distribution with log-link was used when data were not overdispersed, and negative binomial error distribution in the case of overdispersion. Using the same model structure, we also tested the relationship between 2020 habitat quality index and 2022 tree species richness. We further calculated the marginal and conditional R^2 using the r.squaredGLMM function of the MuMIn package to analyse model fit.

Similar models were run to analyse the influence of insect family richness (total and within functional groups) in forest fragments on the same variables in adjacent sugarcane fields following the model structure: sugarcane family richness ~ forest family richness + (1|fragment type). Additionally, insect family composition of forest fragments and sugarcane fields was compared using non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity in presence-absence data. The NMDS was run using the metaMDS function from the vegan package with a maximum of 100 random starts (trymax = 100) to avoid local minima. The NMDS ordination was visualized with convex hulls representing each habitat–forest type combination, and point colors and shapes were used to differentiate forest types and habitat types. We tested differences between the sugarcane and forest fragment habitat using permutational multivariate analysis of variance (PERMANOVA). Statistical tests were run using the adonis2 functions of the vegan package with 999 permutations and Jaccard distance as the dissimilarity metric. All analyses were performed using R 3.6.2 software (R Core Team, 2024).

3. Results

In the ten forest fragments of our study, we found 115 tree species of 35 plant families. *Croton floribundus* (Euphorbiaceae), *Astronium graveolens* (Anacardiaceae) and *Acacia polyphylla* (Fabaceae) were the most frequent tree species (Supplementary Table 1). Tree density was on average 79.1 (29 to 125) per 1000m² plot (only measured in 2022).

In 2020, we collected 200 arthropod morphospecies including 148 insect morphospecies (Supplementary Table 2). In 2022, we found 33 insect families in direct collections, of which six families were predatory, seven parasitoids and 15 phytophagous (Supplementary Table 3). Trapping of 2022 provided 121 insect families of which twenty families were predators, 26 parasitoids, and 40 families of phytophagous. Seventy families occurred in both habitats, 36 only in forest fragments and 15 only in sugarcane fields (Supplementary Table 4).

The influence of forest fragment quality measured as habitat quality index was significant for overall arthropod morphospecies richness (estimate = 0.384, $\chi^2(1) = 13.659$, $P < 0.001$, marginal/conditional $R^2 = 0.59$; Figure 2a), but not for insect morphospecies richness (estimate = 0.267, $\chi^2(1) = 2.490$, $p = 0.115$, marginal/conditional $R^2 = 0.23$; Figure 2b) in 2020.

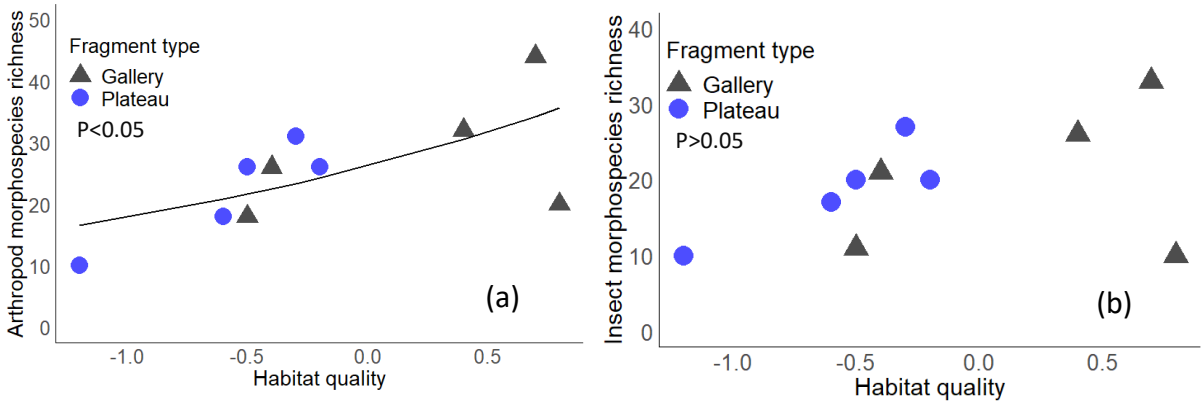

Figure 2. Relationship between habitat quality index and 2020 invertebrate morphospecies richness in gallery and plateau forest fragments. Total arthropod morphospecies richness (a) and insect morphospecies richness (b).

The habitat quality index of 2020 was positively correlated with tree species richness of 2022 in seven fragments analyzed in both years (estimate = 0.040, $\chi^2(1) = 8.2824$, $P = 0.004$, marginal $R^2 = 0.53$, conditional $R^2 = 0.79$) indicating that the index was a reliable estimate of tree diversity (Figure 3).

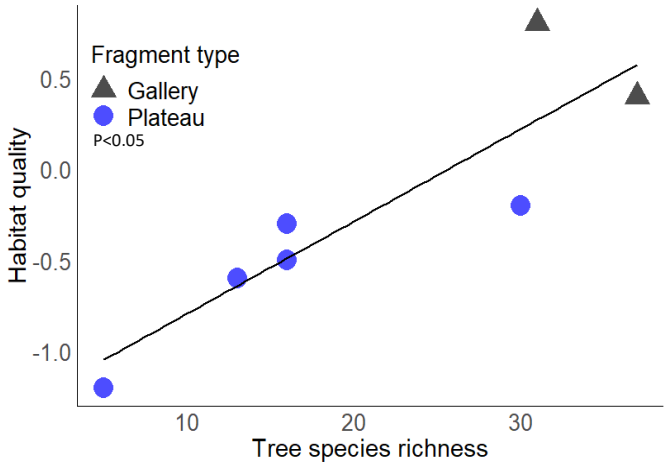

Figure 3. Relationship between habitat quality index estimated in 2020 and tree species richness in 2022.

The family richness of insects (Figure 4a), as well as the frequency of phytophagous (Figure 4b) and predatory insects (Figure 4c) were positively related to tree species richness whereas the relationship with parasitoids (Figure 4d) was not significant (Table 1).

Table 1. Generalized linear mixed model (GLMM) testing the effects of tree species richness on insect family richness and the frequency of phytophagous insects, predators and parasitoids in 1000m^2 in forest fragment plots (2022). P-values in bold are significant at P<0.05.

	Estimate	Chi^2	P	Marginal R^2	Conditional R^2
All families (richness)	0.035±0.012	$\chi^2(1) = 9.010$	**0.003**	0.549	0.549
Phytophagous (frequency)	0.062±0.011	$\chi^2(1) = 30.05$	**<0.001**	0.837	0.837
Predators (frequency)	0.067±0.030	$\chi^2(1) = 4.989$	**0.026**	0.438	0.438
Parasitoids (frequency)	0.012±0.034	$\chi^2(1) = 0.124$	0.725	0.047	0.047

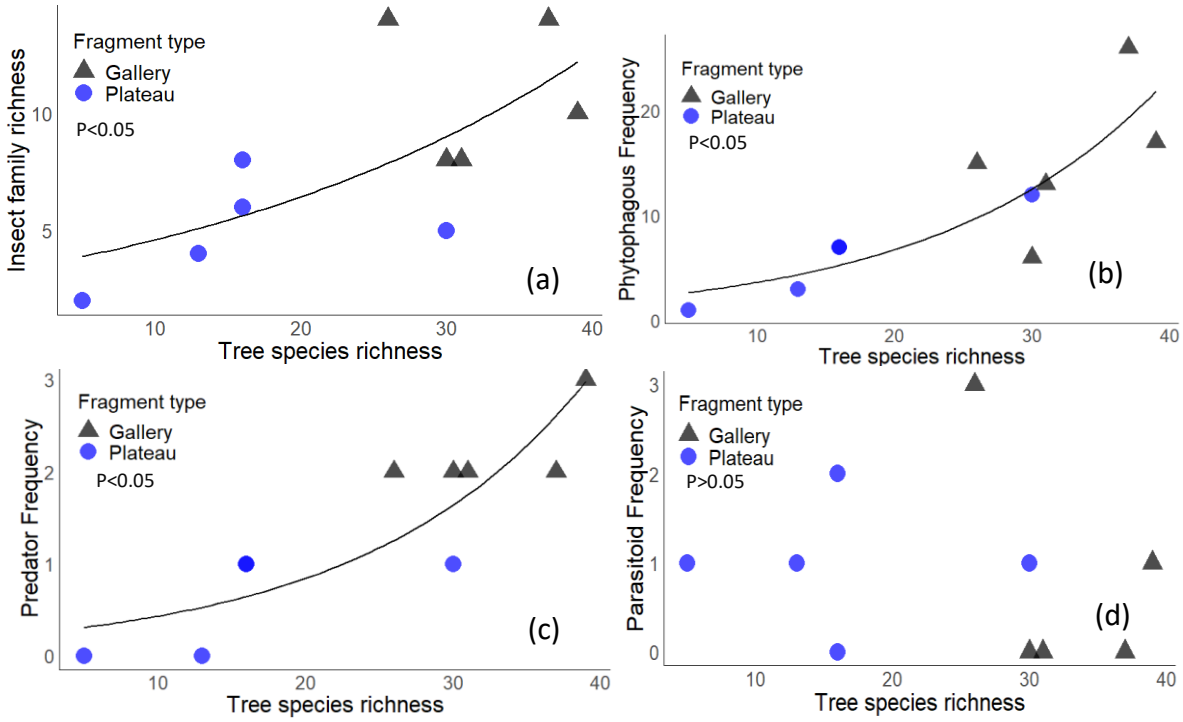

Figure 4. Relationship between tree species richness and insect family richness and frequency in 1000m2 forest fragment plots (2022). Insect family richness (a), phytophagous family frequency (b), predator family frequency (c) and parasitoid family frequency (d).

Relationships between family richness of insects in forest fragments and in sugarcane fields were significantly positive for total richness, phytophagous familiy and predator family richness indicating that insect diversity of sugarcane fields depends on adjacent forest fragments (Table 2; Figure 5). The relationship between family richness of parasitoids in forest fragments and sugarcane fields was also positive but only marginally significant (Table 2).

Table 2. Generalized linear mixed model (GLMM) testing the influence of insect family richness in forest fragments on the same variable in adjacent sugarcane fields. P-values in bold are significant at P<0.05, in italics at P<0.1.

	Estimate	Chi^2	P	Marginal R^2	Conditional R^2
All families	0.008±0.004	$\chi^2(1) = 4.907$	**0.027**	0.226	0.713
Phytophagous	0.059±0.028	$\chi^2(1) = 4.56$	**0.034**	0.349	0.349
Predators	0.075±0.036	$\chi^2(1) = 4.33$	**0.038**	0.296	0.296
Parasitoids	0.064±0.036	$\chi^2(1) = 3.22$	*0.073*	0.441	0.560

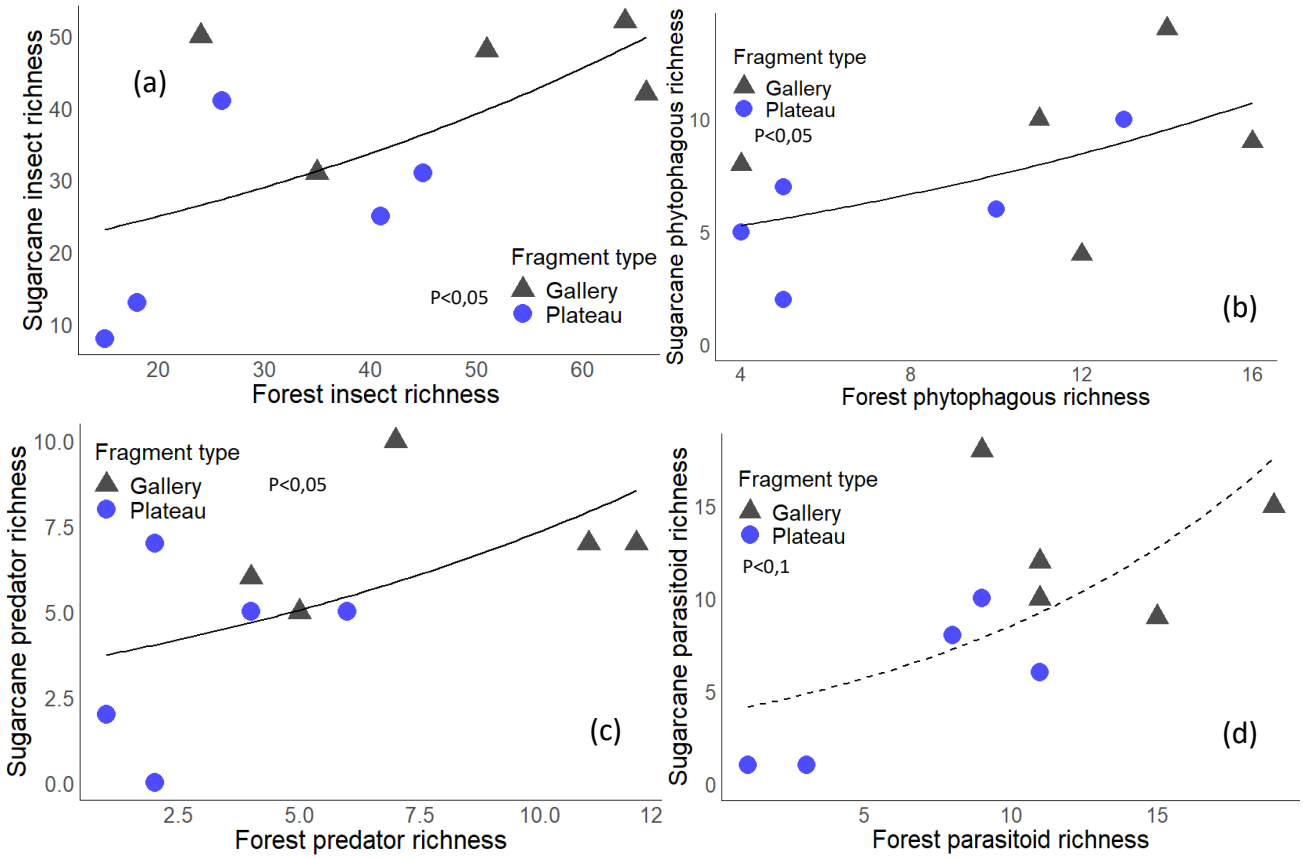

Figure 5. Influence of forest total insect family richness and functional group richness on the same parameters in sugarcane fields (2022). Total insects (a), phytophagous (b), predators (c) and parasitoids (d).

NMDS separated insect communities in sugarcane from those of forest fragments (Figure 6). Despite different trap types, there was, however, an overlap between both habitats. Habitat and forest fragment type explained 8,55% and 6.67% of the total variation, respectively. PERMANOVA still revealed a significant difference between sugarcane fields and forest fragments ($F = 1.6837$, $p = 0.011$).

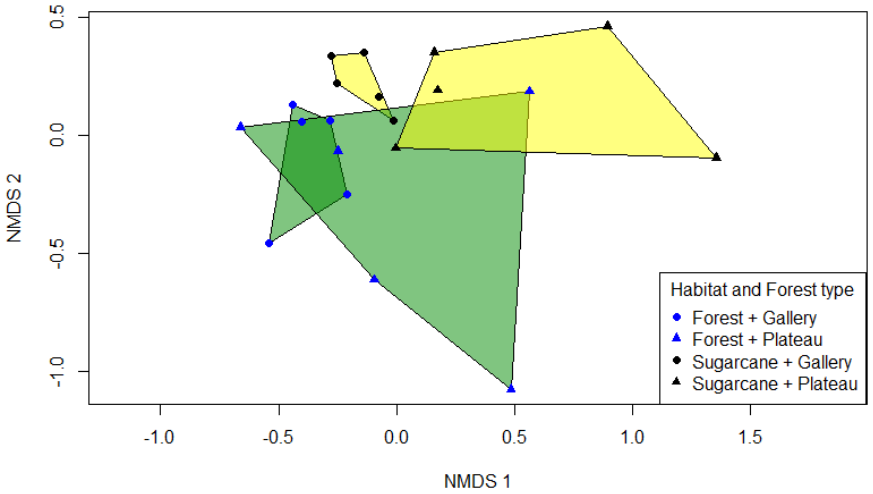

Figure 6. Non-metric Multidimensional Scaling (NMDS) of the insect family community in forest fragments and adjacent sugarcane fields. Yellow polygons: sugarcane, green polygons: forest fragments

4. Discussion

We found a positive influence of forest habitat quality (tree species richness and forest quality index) on arthropod richness and the frequency of functional groups involved in ecosystem services such as predators but also of phytophagous insects that may attack crop plants. While the preliminary data of 2020 showed significant relationships with habitat quality index only when spiders were included, the more detailed analyses of 2022 revealed significant relations for insect family richness and the frequency of several functional insect groups. We further demonstrated that the richness of insect families and functional groups in sugarcane fields were highly correlated to those of adjacent forest fragments suggesting a causal relationship and insect movements between the two habitats. However, although NMDS showed some overlap of insect family composition in forest fragments and sugarcane fields, the differences were still significant.

Previous studies have already identified a positive effect of tree species richness on arthropod diversity (Schuldt et al., 2019; Ampoorter, 2020), as well as a positive relationship between tree productivity and arthropod richness (Li et al., 2023). Such a positive influence of plant diversity on arthropod richness

across multiple trophic groups is known to improve ecosystem multifunctionality and to promote a wide range of ecosystem services (Soliveres et al., 2016). As diversity increases, the number of available niches increases and organisms are more likely to use resources in diverse, complementary, or mutually facilitative ways (Haan et al., 2021). Furthermore, biodiversity plays a crucial role in maintaining the stability of ecosystem processes by supporting different species that occupy similar functional niches but respond differently to environmental changes. The absence of a particular species may be compensated by the presence of another species with similar functional role (Elmqvist et al., 2003; Cadotte et al., 2011). Thus, our findings support the hypothesis that tree diversity and forest habitat quality are key drivers of arthropod diversity. In addition to the conservation of habitats, it is thus also important to preserve or restore habitat quality in order to support complex arthropod communities sustaining ecosystem services across landscapes.

The influence of tree species richness on phytophagous insects was expected as they directly depend on plants. Other studies found that habitats with greater tree diversity harbor more diverse and abundant herbivore communities (Leal et al., 2016; O'Brien et al., 2017). A higher number of plant species provides a greater variety of resources facilitating the coexistence of more herbivorous species (Lewinsohn and Roslin, 2008; Leal et al., 2016). However, increased plant diversity may also hamper insects to locate their host plants (Silva and Clarke, 2020). Hence, plant species richness may limit negative effects of herbivorous insects on individual plant species but other factors such as taxonomic distance of tree species and the proportion of non-host trees may be equally or more influential than species richness (Jactel et al., 2021; Gougherty and Davies, 2024). Although phytophagous insects are commonly perceived as pests in agriculture, they represent a vital trophic group in maintaining ecosystem services (Soliveres et al., 2016). A higher abundance of prey supports greater species richness and abundance of natural enemies (Fenoglio et al., 2012; Dominik et al., 2018). Additionally, most phytophagous insect species are not considered pest insects, since they do not attack crop plants. Therefore, the increase of phytophagous insects with increasing tree diversity cannot necessarily be considered as ecosystem disservice.

The effect of plant species on natural enemies is less evident than on phytophagous arthropods since they do not directly feed on plants (O'Brien et al., 2017). However, several important predator and parasitoid groups change nutrition from larval to adult stages. While larvae are carnivourous, adults feed on floral ressources such as pollen and nectar (Gardarin et al., 2018). Although food consumption is much higher during carnivorous larval stages, adult access to floral and extrafloral nectar can enhance longevity, fecundity and host searching activity (Gillespie et al., 2016; Benelli et al., 2017). This is particularly relevant in tropical forests, where many trees have extafloral nectaries that produce nectar to favour ants and parasitoids protecting plants from herbivory (Câmara et al., 2017; Miranda et al. 2022). Furthermore, several predator groups such as ladybirds use floral ressources and extrafloral as complementary food (Gardarin et al., 2018; Holm et al., 2021; Stowe et al., 2021). Finally, herbivores feeding on forest fragment vegetation represent alternative prey for predators including natural enemies feeding on pest insects (Gillespie et al., 2016; Stemmelen et al., 2022). Accordingly, our results showed an increase in predator richness in forest fragments of higher tree species richness. However, the frequency of parasitoid families was not significantly affected. Since many parasitoids are limited by their ability to access floral nectar, especially from deep flowers, they may rely on specific nectar sources not analyzed in our study, such as lianas or understory herbs (Garcia et al., 2014; Russell, 2015). Complete vegetation analysis is required to better understand relationships with insects at higher trophic levels (Garcia et al., 2014).

Although our study revealed relationships between tree species richness and the richness of certain insect functional groups, such as predators, we acknowledge that family richness alone may not fully reflect the functional contribution of these groups to ecosystem services. Therefore, it remains unclear whether the observed increase in predator richness translates into improved biological control (Chaplin-Kramer et al., 2011; Tscharntke et al., 2016). Furthermore, different predator families vary considerably in their hunting strategies, prey specificity, and efficiency, which limits the interpretation of potential impacts on pest suppression (Tylianakis and Romo, 2010). Our results suggest that species with potential for biological control are favored, but future

studies need to include more specific abundance measures to better assess the relationship between biodiversity and ecosystem service provision in agroecosystems.

The positive relationship between insect richness in forest fragments and sugarcane fields confirms that semi-natural habitats in agricultural landscapes favour species richness in crop fields and may thus promote the associated ecosystem services (Bartual et al., 2019; Medeiros et al., 2019). This positive effect can be explained by the movement of insects between habitats to search for resources, protection and a suitable microclimate (Sorribas et al., 2016; González et al., 2016). However, the comparison of community the comparison of community differences using PERMANOVA also showed that insect family composition is different between forests and agricultural habitats. These differences in community composition reflect habitat differences in terms of food resource availability, microclimate, and predator abundance limiting interaction between forests and agricultural habitats (Schneider et al., 2016; Alves et al., 2020). Although spillover likely results in taxa between habitats, habitat-specific conditions maintain distinct community assemblages. The placement of traps at different distances from the forest fragments or labelling of insects (Pollier et al., 2016) may help to better understand movements between forest fragments and sugarcane fields. Additionally, the use of different trap types in our study may have overestimated the differences between both habitats. Although yellow pan traps are not optimal for forest habitats, their use in both habitats may improve the comparison of insect communities and should be included in future studies.

Another limitation of our study is the use of larval feeding preference for functional group classification. This choice is justified by the amount of food consumption but may bias spillover dynamics, as adults are usually more mobile than larvae. In particular, holometabolous insects often change nutrition during their life cycle such as Lepidoptera, of which larvae are typically herbivorous while adults are pollinators (Wang et al., 2024). The separation of larvae and adults in different functional groups may help to overcome this limitation in future studies.

Our findings highlighted the critical role of natural habitats to preserve insect biodiversity and their associated ecosystem services within agricultural

landscapes. The diversity and quality of forest fragments had a significant influence on arthropod community composition. Beyond tree species richness, understory vegetation and climbers may also play an important role that need to be considered in future studies (Ampoorter, 2020; Staab and Schuldt, 2020). Our study does not only emphasize the necessity for policies and management strategies improving the conservation of semi-natural habitats, such as forest fragments in tropical agricultural landscapes but also shows the importance of examining the characteristics of these habitats more closely. Further studies are needed to fully understand the effects of tropical forest fragments on ecosystem service provision and to develop strategies for improving these services.

References

Ampoorter E et al. (2020) Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe. **Oikos** 129:133-146.

Asbjornsen H et al. (2014) Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. **Renewable Agriculture and Food Systems** 29:101-125.

Báldi A (2003) Using higher taxa as surrogates of species richness: a study based on 3700 Coleoptera, Diptera, and Acari species in Central-Hungarian reserves. **Basic and Applied Ecology** 4:589-593.

Bartual AM et al. (2019) The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. **Agriculture, Ecosystems & Environment** 279:43-52.

Benelli G et al. (2017) The impact of adult diet on parasitoid reproductive performance. **Journal of Pest Science** 90:807-823.

Blitzer EJ et al. (2012) Spillover of functionally important organisms between managed and natural habitats. **Agriculture, Ecosystems & Environment** 146:34-43.

Brockerhoff EG et al. (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. **Biodiversity and Conservation** 26:3005-3035.

Bartual AM et al. (2019) The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes. **Agriculture, Ecosystems & Environment** 279:43-52.

Benelli G et al. (2017) The impact of adult diet on parasitoid reproductive performance. **Journal of Pest Science** 90:807-823.

Blitzer EJ et al. (2012) Spillover of functionally important organisms between managed and natural habitats. **Agriculture, Ecosystems & Environment** 146:34-43.

Brockerhoff EG et al. (2017) Forest biodiversity, ecosystem functioning and the provision of ecosystem services. **Biodiversity and Conservation** 26:3005-3035.

Brown BV et al. (2009) **Manual of Central American Diptera**. Ottawa: NRC Research Press. 714 p., v. 1.

Brown BV et al. (2010) **Manual of Central American Diptera**. Ottawa: NRC Research Press. 728 p., v. 2.

Cadotte MW et al. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. **Journal of Applied Ecology** 48:1079-1087.

Câmara T et al. (2017) Habitat fragmentation, EFN-bearing trees and ant communities: Ecological cascades in Atlantic Forest of northeastern Brazil. **Austral Ecology** 42:31-39.

Castro TMMG, Moraes GJ (2010) Diversity of phytoseiid mites (Acari: Mesostigmata: Phytoseiidae) in the Atlantic Forest of São Paulo. **Systematics and Biodiversity** 8:301-307.

Chaplin-Kramer R et al. (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. **Ecology Letters** 14:922-932.

Correa CMA et al. (2024) How much biodiversity do we lose in planted forests? A case study with dung beetles in the Brazilian Amazon rainforest. **Biologia** 79:3549–3560.

Decocq G et al. (2016) Ecosystem services from small forest patches in agricultural landscapes. **Current Forestry Reports** 2:30–44.

Diniz S, Prado PI, Lewinsohn TM (2010) Species richness in natural and disturbed habitats: Asteraceae and flower-head insects (Tephritidae: Diptera). **Neotropical Entomology** 39:163–171.

Dominik C, Seppelt R, Horgan FG, Settele J, Václavík T (2018) Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. **Journal of Applied Ecology** 55:2461–2472.

Elmqvist T et al. (2003) Response diversity, ecosystem change, and resilience. **Frontiers in Ecology and the Environment** 1:488–494.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. **Annual Review of Ecology Evolution and Systematics** 34:487–515.

Felfili JM, Eisenlohr PV, de Melo MRF (2011) **Fitossociologia no Brasil**: métodos e estudos de casos. Viçosa: UFV. 558p.

Fenoglio MS, Srivastava D, Valladares G, Cagnolo L, Salvo A (2012) Forest fragmentation reduces parasitism via species loss at multiple trophic levels. **Ecology** 93:2407–2420.

Fernandez F, Sharkey MJ (2006) **Introducción a los Hymenoptera de la Región Neotropical**. Bogotá: Sociedad Colombiana de Entomología y Universidad Nacional de Colombia. 894p.

Gagic V, Paull C, Schellhorn NA (2018) Ecosystem service of biological pest control in Australia: the role of non-crop habitats within landscapes. **Austral Entomology** 57:194–206.

Garbach K, Milder JC, Montenegro M, Karp DS, DeClerck FAJ (2014) Biodiversity and ecosystem services in agroecosystems. **Encyclopedia of Agriculture and Food Systems** 2:21–40.

Garcia LC, Hobbs RJ, Maees dos SFA, Rodrigues RR (2014) Flower and fruit availability along a forest restoration gradient. **Biotropica** 46:114–123

Gardarin A, Plantegenest M, Bischoff A, Valantin-Morison M (2018) Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. **Journal of Pest Science** 91:943–955.

Gillespie MA, Gurr GM, Wratten SD (2016) Beyond nectar provision: the other resource requirements of parasitoid biological control agents. **Entomologia Experimentalis et Applicata** 159:207–221.

González E, Salvo A, Defagó MT, Valladares G (2016) A moveable feast: insects moving at the forest-crop interface are affected by crop phenology and the amount of forest in the landscape. **PLoS ONE** 11:e0158836.

Gougherty AV, Davies TJ (2024) Evolutionary history of host trees amplifies the dilution effect of biodiversity on forest pests. **PLoS Biology** 22:e3002473.

Gutierrez-Arellano C, Mulligan M (2018) A review of regulation ecosystem services and disservices from faunal populations and potential impacts of agriculturalisation on their provision globally. **Nature Conservation** 30:1–39.

Haan NL, Iuliano BG, Gratton C, Landis DA (2021) Designing agricultural landscapes for arthropod-based ecosystem services in North America. **Advances in Ecological Research** 64:191–250.

Haddad NM et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. **Science Advances** 1:e1500052.

Heisswolf A, Reichmann S, Poethke HJ, Schröder B, Obermaier E (2009) Habitat quality matters for the distribution of an endangered leaf beetle and its egg parasitoid in a fragmented landscape. **Journal of Insect Conservation** 13:165–175.

Hertzog LR et al. (2019) Forest fragmentation modulates effects of tree species richness and composition on ecosystem multifunctionality. **Ecology** 100:e02653.

Holm LL, He X, Sigsgaard L (2021) Flower diet enhances *Adalia bipunctata* larval development significantly when prey is limited. **Entomologia Experimentalis et Applicata** 169:750–757.

Jacobson AP, Riggio J, Tait AM, Baillie JEM (2019) Global areas of low human impact ('Low Impact Areas') and fragmentation of the natural world. **Scientific Reports** 9:14179.

Jactel H, Moreira X, Castagneyrol B (2021) Tree diversity and forest resistance to insect pests: patterns, mechanisms and prospects. **Annual Review of Entomology** 66:277–296.

Kaleka AS, Kaur N, Bali GK (2019) Larval development and molting. In: **Edible Insects**. London: IntechOpen. 98p.

Klein AM, Steffan-Dewenter I, Tscharntke T (2006) Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. **Journal of Animal Ecology** 75:315–323.

Leal LC, Andersen AN, Leal IR (2014) Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. **Oecologia** 174:173–181.

Leal CRO, Silva JO, Sousa-Souto L, Neves FS (2016) Vegetation structure determines insect herbivore diversity in seasonally dry tropical forests. **Journal of Insect Conservation** 20:979–988.

Lewinsohn TM, Roslin T (2008) Four ways towards tropical herbivore megadiversity. **Ecology Letters** 11:398–416.

Li Y et al. (2023) Multitrophic arthropod diversity mediates tree diversity effects on primary productivity. **Nature Ecology and Evolution** 7:832-840.

Losey JE, Vaughan M (2006) The economic value of ecological services provided by insects. **Bioscience** 56:311-323.

Mata RA, Tidon R (2013) The relative roles of habitat heterogeneity and disturbance in drosophilid assemblages (Diptera, Drosophilidae) in the Cerrado. **Insect Conservation and Diversity** 6:663-670.

Medeiros HR et al. (2019) Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes. **Biological Conservation** 238:108193.

Millennium Ecosystem Assessment MEA (2005) **Ecosystems and human well-being**. Washington DC: Island Press. 563 p.

Miranda VS, Rodrigues LG, Dutra SC, Alves-Araújo A (2022) Extrafloral nectaries of an Atlantic Forest conservation area in Southeastern Brazil. **Acta Botanica Brasilica** 36:e2021abb0187.

Mitchell MG, Bennett EM, Gonzalez A (2014) Forest fragments modulate the provision of multiple ecosystem services. **Journal of Applied Ecology** 51:909-918.

Newbold T et al. (2015) Global effects of land use on local terrestrial biodiversity. **Nature** 520:45-50.

O'Brien MJ et al. (2017) Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. **Ecology and Evolution** 7:8753-8760.

Parry HR et al. (2015) Plant composition modulates arthropod pest and predator abundance: evidence for culling exotics and planting natives. **Basic and Applied Ecology** 16:531-543.

Pollier A et al. (2016) Using the stable isotope marker 13C to study extrafloral nectar uptake by parasitoids under controlled conditions and in the field. **Entomologia Experimentalis et Applicata** 161:131-140.

Pywell RF et al. (2015) Wildlife-friendly farming increases crop yield: evidence for ecological intensification. **Proceedings of the Royal Society B Biological Sciences** 282:20151740.

Ramos DL et al. (2020) Ecosystem services provided by insects in Brazil: What do we really know? **Neotropical Entomology** 49:783-794.

Rand TA, Tylianakis JM, Tscharntke T (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. **Ecology Letters** 9:603-614.

R Core Team (2024) **R**: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Disponível em: https://www.R-project.org/. Acesso em: 11 ago. 2025.

Rezende CL et al. (2018) From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. **Perspectives in Ecology and Conservation** 16:208-214.

Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. **Biological Conservation** 142:1141-1153.

Rowe HI, Holland JD (2013) High plant richness in prairie reconstructions support diverse leafhopper communities. **Restoration Ecology** 21:174-180.

Russell M (2015) A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species. **Biological Control** 82:96-103.

Santos LA, Bischoff A, Fernandes OA (2018) The effect of forest fragments on abundance, diversity and species composition of predatory ants in sugarcane fields. **Basic and Applied Ecology** 33:58-65.

Schneider G, Krauss J, Boetzl FA, Fritze MA, Steffan-Dewenter I (2016) Spillover from adjacent crop and forest habitats shapes carabid beetle assemblages in fragmented semi-natural grasslands. **Oecologia** 182:1141-1150.

Schowalter TD, Noriega JA, Tscharntke T (2018) Insect effects on ecosystem services - Introduction. **Basic and Applied Ecology** 26:1-7.

Schuldt A et al. (2019) Multiple plant diversity components drive consumer communities across ecosystems. **Nature Communications** 10:1460.

Silva R, Clarke AR (2020) The “sequential cues hypothesis”: A conceptual model to explain host location and ranking by polyphagous herbivores. **Insect Science** 27:1136-1147.

Soliveres S et al. (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. **Nature** 536:456-459.

Sorribas J, González S, Domínguez-Gento A, Vercher R (2016) Abundance, movements and biodiversity of flying predatory insects in crop and non-crop agroecosystems. **Agronomy for Sustainable Development** 36:1-9.

Sousa EHS, Matos MCB, Almeida RS, Teodoro AV (2011) Forest fragments' contribution to the natural biological control of Spodoptera frugiperda Smith (Lepidoptera: Noctuidae) in Maize. **Brazilian Archives of Biology and Technology** 54:755-760.

Staab M, Schuldt A (2020) The influence of tree diversity on natural enemies—a review of the “enemies” hypothesis in forests. **Current Forestry Reports** 6:243-259.

Stemmelen A, Jactel H, Brockerhoff E, Castagneyrol B (2022) Meta-analysis of tree diversity effects on the abundance, diversity and activity of herbivores' enemies. **Basic and Applied Ecology** 58:130-138.

Stowe HE, Michaud JP, Kim TN (2021) Floral resources enhance fecundity, but not flight activity, in a specialized aphid predator, Hippodamia convergens (Coleoptera: Coccinellidae). **Frontiers in Ecology and Evolution** 9:748870.

Tscharntke T et al. (2016) When natural habitat fails to enhance biological pest control–Five hypotheses. **Biological Conservation** 204:449-458.

Tylianakis JM, Romo CM (2010) Natural enemy diversity and biological control: making sense of the context-dependency. **Basic and Applied Ecology** 11:657-668.

Wang X et al. (2024) Multiple interaction networks reveal that Lepidoptera larvae and adults prefer various host plants for diet and pollination. **Integrative Zoology** 19:763-776.

Wilson MC et al. (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. **Landscape Ecology** 31:219-227.

Winfree R, Aguilar R, Vázquez DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. **Ecology** 90:2068-2076.

Zhang K et al. (2016) Plant diversity accurately predicts insect diversity in two tropical landscapes. **Molecular Ecology** 25:4407-4419.

Supplementary Table 1: Frequency of plant species: number of occupied forest fragments (n=10)

Id	Family	Species	Frequency (no. of sites)
1	Anacardiaceae	*Astronium fraxinifolium* Schott	3
2	Anacardiaceae	*Astronium graveolens* Jacq.	9
3	Anacardiaceae	*Mangifera indica* L.	3
4	Anacardiaceae	*Myracrodruon urundeuva*	1
5	Anacardiaceae	*Schinus terebinthifolia* Raddi	1
6	Anacardiaceae	*Tapirira guianensis* Aubl.	3
7	Annonaceae	*Annona dolabripetala* Raddi.	1
8	Annonaceae	*Rollinia mucosa*	1
9	Annonaceae	*Xylopia aromatica* (Lam.) Mart.	1
10	Apocynaceae	*Aspidosperma cylindrocarpon* Mull.Arg.	1
11	Apocynaceae	*Aspidosperma* sp.	1
12	Apocynaceae	*Tabernaemontana catharinensis* A. DC.	4
13	Araliaceae	*Schefflera morototoni* (Aubl.) Maguire, Steyerm. and Frodin	1
14	Bignoniaceae	*Handroanthus impetiginosus* (Mart. Ex DC.) Mattos	1
15	Bignoniaceae	*Jacaranda micrantha* Cham.	3
16	Boraginaceae	*Cordia myxa* L.	5
17	Boraginaceae	*Cordia superba*	1
18	Calophyllaceae	*Calophyllum brasiliense* Cambess	2
19	Cannabaceae	*Celtis brasiliensis* (Gardner) Planch.	6
20	Cannabaceae	*Trema micrantha* (L.) Blume	5
21	Caryocaraceae	*Caryocar brasiliensis* Cambess.	2
22	Celastraceae	*Maytenus pittieriana* Steyerm.	1
23	Chrysobalanaceae	*Licania humilis* Cham. and Schtdl.	1
24	Clusiaceae	*Callophylum brasiliense*	1
25	Combretaceae	*Terminalia glabrescens* Mart.	1
26	Euphorbiaceae	*Alchornea sidifolia*	1
27	Euphorbiaceae	*Croton floribundus Spreng.*	9
28	Euphorbiaceae	*Maprunia guianensis* Aubl.	1
29	Fabaceae	*Acacia polyphylla* DC.	7
30	Fabaceae	*Albizia niopoides* (Spruce ex Benth.) Burkat	3
31	Fabaceae	*Anadenaterna pavonina* L.	1
32	Fabaceae	*Anadenaterna peregina* var. falcata (Benth.) Altschul	3
33	Fabaceae	*Bauhinia variegata L.*	3
34	Fabaceae	*Caesalpinia echinata* Lam.	3
35	Fabaceae	*Caesalpinia ferrea* C.Mart.	3
36	Fabaceae	*Copaifera langsdorffii* Desf.	1
37	Fabaceae	*Dimorphandra* sp.	1

38	Fabaceae	*Enterolobium contortisiliquum* (Vell.) Morong	3
39	Fabaceae	*Hymenaea courbaril* L.	6
40	Fabaceae	*Inga marginata* Willd.	4
41	Fabaceae	*Leucaena leucocephala* (Lam.) de Wit	2
42	Fabaceae	*Lonchocarpus cultratus* (Vell.) A.M.G. Azevedo and H.C.Lima	1
43	Fabaceae	*Machaerium aculeatum* Raddi	6
44	Fabaceae	*Machaerium acutifolium*	1
45	Fabaceae	*Machaerium brasiliense*	1
46	Fabaceae	*Machaerium stipitatim* Vogel	2
47	Fabaceae	*Ormosia arborea* (Vell.) Harms	4
48	Fabaceae	*Parapiptadenia rigida (Benth.)* Brenan	3
49	Fabaceae	*Piptadenia gonoacantha* (Mart.) J. F. Macbr	6
50	Fabaceae	*Platymenia reticulata*	1
51	Fabaceae	*Platypodium elegans Vogel*	6
52	Fabaceae	*Pterogyne nitens* Tul.	3
53	Fabaceae	*Schizolobium parahyba* (Vell.) S.F. Blake	2
54	Fabaceae	*Senegalia polyphylla* (DC.) Britton and Rose	1
55	Fabaceae	*Senna pendula*	1
56	Lamiaceae	*Aegiphila verticillata* Vell.	2
57	Lamiaceae	*Aegiphilla integrifolia*	1
58	Lamiaceae	*Callicarpa reevesii* Wall. Ex Walp	2
59	Lamiaceae	*Vitex megapotamica* (Spreng.) Moldenke	1
60	Lauraceae	*Endlicheria paniculata*	1
61	Lauraceae	*Nectandra megapotamica* (Spreng.) Mez	2
62	Lauraceae	*Ocotea corymbosa* (Meisn.) Mez	2
63	Lecythidaceae	*Cariniana estrellensis (Raddi) Kuntze*	4
64	Lecythidaceae	*Cariniana legalis*	1
65	Lythraceae	*Lafoensia pacari* A. St-Hill	2
66	Malvaceae	*Bombacopsis glabra* (Pasq.) A. Rob.o	1
67	Malvaceae	*Ceiba speciosa* (A.St.-Hil.) Ravenna	4
68	Malvaceae	*Heliocarpus popayanensis* Kunth	2
69	Malvaceae	*Luehea candicans* Mart.	3
70	Malvaceae	*Luehea paniculata*	1
71	Malvaceae	*Ochroma pyramidale* (Cav. ex Lam.) Urb.	1
72	Malvaceae	*Pachira aquatica* Aubl.	1
73	Malvaceae	*Pachira glabra* Pasq.	2
74	Meliaceae	*Cabralea canjerana* (Vell.)	1
75	Meliaceae	*Cedrela fissilis* Vell.	3
76	Meliaceae	*Guarea guidonia* (L.) Sleumer	4
77	Meliaceae	*Trichilia hirta*	1
78	Mimosoideae	*Piptocarpha sellowii*	1

79	Moraceae	*Castilla elastica Sessé*	1
80	Moraceae	*Ficus* sp.	1
81	Moraceae	*Morus alba*	1
82	Moraceae	*Morus nigra* L.	1
83	Muntingiaceae	*Muntingia calabura* L.	2
84	Myrtaceae	*Calyptranthes concinna* DC.	1
85	Myrtaceae	*Eugenia pitanga*	1
86	Myrtaceae	*Eugenia* sp.	3
87	Myrtaceae	*Myrcia fenzliana*	1
88	Myrtaceae	*Myrcia rostrata*	1
89	Myrtaceae	*Psidium guajava* L.	2
90	Myrtaceae	*Syzygium cumini (L.)* Skeels	3
91	Nyctaginaceae	*Pisonia ambigua*	1
92	Olacaceae	*Ximenia americana*	1
93	Phytolaccaceae	*Gallesia integrifolia* (Spreng.) Harms	3
94	Piperaceae	*Piper aduncun* L.	1
95	Piperaceae	*Piper arboreum* Aubl.	1
96	Polygonaceae	*Triplaris americana* L.	2
97	Polygonaceae	*Triplaris gardneriana*	1
98	Primulaceae	*Myrsine umbellata* Mart.	4
99	Rubiaceae	*Amaioua intermedia*	1
100	Rubiaceae	*Genipa americana* L.	1
101	Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl.	1
102	Rutaceae	*Metrodorea nigra*	1
103	Rutaceae	*Metrodoria nigra* A.St.-Hil.	1
104	Rutaceae	*Zanthoxylum* sp.	1
105	Salicaceae	*Casearia sylvestris* Sw.	3
106	Sapindaceae	*Alectryon tomentosum* Radlk.	1
107	Sapindaceae	*Cupania vernalis* Cambess	2
108	Sapindaceae	*Koelreuteria bipinata* Franch.	2
109	Sapindaceae	*Magonia glabrata* A.St.-Hil.	1
110	Sapindaceae	*Matayba elaeganoides*	1
111	Sapindaceae	*Urvillea laevis*	1
112	Ulmaceae	*Celtis iguanea*	3
113	Urticaceae	*Cecropia pachystachya* Trécul.	5
114	Urticaceae	*Urera baccifera* (L.) Gaudich. ex Wedd.	2
115	Vochysiaceae	*Vochysia tucanorum*	1

SupplementaryTable 2: Frequency of arthropod morphospecies sampled in 2020

Id	Order	Family	Arthropod Morphospecies	Frequency (no. of sites)
1	Aranea	Araneidae	Morphospecie 1	1
2	Aranea	Araneidae	Morphospecie2	1
3	Aranea	Araneidae	*Micrathena* 3	1
4	Aranea	Araneidae	Morphospecie 3	1
5	Aranea	Araneidae	Morphospecie 4	4
6	Aranea	Corinnidae	Morphospecie 1	7
7	Aranea	Corinnidae	Morphospecie 2	1
8	Aranea	Corinnidae	Morphospecie 3	2
9	Aranea	Gnaphosidae	Morphospecie 1	1
10	Aranea	Gnaphosidae	Morphospecie 2	1
11	Aranea	Lycosidae	Morphospecie 1	2
12	Aranea	Lycosidae	Morphospecie 2	1
13	Aranea	Oxyopidae	Morphospecie 1	1
14	Aranea	Salticidae	Morphospecie 1	1
15	Aranea	Salticidae	Morphospecie 2	1
16	Aranea	Salticidae	Morphospecie 3	1
17	Aranea	Salticidae	Morphospecie 4	1
18	Aranea	Salticidae	Morphospecie 5	1
19	Araneae	Salticidae	Morphospecie 6	1
20	Aranea	Salticidae	*Pachomius* sp.1	1
21	Aranea	Theridiidae	Morphospecie 1	1
22	Aranea	Theridiidae	Morphospecie 2	2
23	Aranea	Theridiidae	Morphospecie 3	2
24	Aranea	Thomisidae	Morphospecie 1	2
25	Aranea	Thomisidae	Morphospecie 2	1
26	Aranea	Thomisidae	Morphospecie 3	1
27	Aranea	Thomisidae	Morphospecie 4	1
28	Aranea	Thomisidae	Morphospecie 5	3
29	Aranea	Thomisidae	Morphospecie 6	3
30	Aranea	Unknown	Morphospecie 1	1
31	Aranea	Unknown	Morphospecie 2	1
32	Aranea	Unknown	Morphospecie 3	1
33	Aranea	Unknown	Morphospecie 4	2
34	Aranea	Unknown	Morphospecie 5	1
35	Aranea	Unknown	Morphospecie 6	1
36	Aranea	Unknown	Morphospecie 7	1
37	Aranea	Unknown	Morphospecie 8	1
38	Aranea	Unknown	Morphospecie 9	1
39	Aranea	Unknown	Morphospecie 10	1
40	Aranea	Unknown	Morphospecie 11	1
41	Aranea	Unknown	Morphospecie 12	1

42	Araneae	Unknown	Morphospecie 13	1
43	Aranea	Unknown	Morphospecie 17	2
44	Aranea	Unknown	Morphospecie 18	1
45	Aranea	Unknown	Morphospecie 19	1
46	Araneae	Unknown	Morphospecie 20	1
47	Aranea	Unknown	Morphospecie 21	1
48	Aranea	Unknown	Morphospecie 22	1
49	Coleoptera	Coccinellidae	Morphospecie 1	1
50	Coleoptera	Chrysomeloidae	*Charidotella* sp. 1	1
51	Coleoptera	Chrysomelidae	*Charidotella* sp. 2	1
52	Coleoptera	Chrysomelidae	Morphospecie 3	1
53	Coleoptera	Chrysomelidae	Morphospecie 4	1
54	Coleoptera	Chrysomelidae	Morphospecie 5	1
55	Coleoptera	Unknown	Morphospecie 1	1
56	Diptera	Muscidae	Morphospecie 1	1
57	Diptera	Tachinidae	Morphospecie 1	1
58	Hemiptera	Aphididae	Morphospecie 1	1
59	Hemiptera	Aphididae	Morphospecie 2	1
60	Hemiptera	Aphididae	Morphospecie 3	1
61	Hemiptera	Cicadellidae	Morphospecie 1	2
62	Hemiptera	Cicadellidae	Morphospecie 2	1
63	Hemiptera	Cicadellidae	Morphospecie 3	1
64	Hemiptera	Cicadellidae	Morphospecie 4	1
65	Hemiptera	Cicadellidae	Morphospecie 5	1
66	Hemiptera	Cicadellidae	Morphospecie 6	2
67	Hemiptera	Cicadellidae	Morphospecie 7	1
68	Hemiptera	Coccidae	*Ceroplastes cirripediformis*	4
69	Hemiptera	Coccidae	*Ceroplastes glometarus*	1
70	Hemiptera	Coccidae	*Ceroplastes rusci*	1
71	Hemiptera	Coccidae	*Ceroplastes* sp. 1	1
72	Hemiptera	Coccidae	Ceroplastes sp. 2	1
73	Hemiptera	Coccidae	Morphospecie 1	1
74	Hemiptera	Coccidae	Morphospecie 2	1
75	Hemiptera	Coccidae	Morphospecie 3	1
76	Hemiptera	Coccidae	Morphospecie 4	1
77	Hemiptera	Coccidae	Morphospecie 5	1
78	Hemiptera	Coccidae	Morphospecie 6	1
79	Hemiptera	Coccidae	Morphospecie 7	2
80	Hemiptera	Coccidae	*Parasaissetia nigra*	1
81	Coleoptera	Coccinellidae	Morphospecie 1	1
82	Hemiptera	Coreidae	Morphospecie 1	1
83	Hemiptera	Coreidae	*Leptoglossus zonatus*	1
84	Hemiptera	Diaspididae	Morphospecie1	1
85	Hemiptera	Diaspididae	Morphospecie 2	1
86	Hemiptera	Diaspididae	Morphospecie 3	2

87	Hemiptera	Diaspididae	Morphospecie 4	1
88	Hemiptera	Diaspididae	Morphospecie 5	1
89	Hemiptera	Diaspididae	Morphospecie 6	1
90	Hemiptera	Diaspididae	Morphospecie 7	1
91	Hemiptera	Diaspididae	Morphospecie 8	1
92	Hemiptera	Diaspididae	Morphospecie 9	1
93	Hemiptera	Diaspididae	Morphospecie 10	2
94	Hemiptera	Fulgoridae	Morphospecie 1	1
95	Hemiptera	Largidae	Morphospecie 1	1
96	Hemiptera	Membracidae	Morphospecie 1	1
97	Hemiptera	Membracidae	Morphospecie 2	1
98	Hemiptera	Monophlebidae	Morphospecie 1	1
99	Hemiptera	Monophlebidae	Morphospecie 2	1
100	Hemiptera	Monophlebidae	Morphospecie 3	1
101	Hemiptera	Ortheziidae	Morphospecie 1	2
102	Hemiptera	Pentatomidae	Morphospecie 1	1
103	Hemiptera	Pseudococcidae	*Ferrisia* sp. 1	1
104	Hemiptera	Pseudococcidae	*Ferrisia* sp. 2	1
105	Hemipera	Pseudococcidae	*Ferrisia* sp. 3	1
106	Hemiptera	Pseudococcidae	Morphospecie 1	1
107	Hemiptera	Pseudococcidae	Morphospecie 2	1
108	Hemiptera	Pseudococcidae	Morphospecie 3	1
109	Hemiptera	Pseudococcidae	Morphospecie 4	4
110	Hemiptera	Pseudococcidae	Morphospecie 5	1
111	Hemiptera	Pseudococcidae	Morphospecie 6	1
112	Hemiptera	Pseudococcidae	Morphospecie 7	1
113	Hemiptera	Pseudoccocidae	Morphospecie 8	1
114	Hemipera	Pseudococcidae	Morphospecie 9	1
115	Hemipera	Pseudococcidae	Morphospecie 10	1
116	Hemipera	Pseudococcidae	Morphospecie 11	1
117	Hemiptera	Pseudococcidae	*Nipaecoccus* sp. 1	1
118	Hemiptera	Pseudococcidae	*Nipaecoccus* sp. 3	2
119	Hemiptera	Pseudococcidae	*Pseudococcus* sp. 1	2
120	Hemiptera	Pseudococcidae	*Pseudococcus* sp. 2	2
121	Hemiptera	Psyllidae	Morphospecie 1	1
122	Hemiptera	Reduviidae	Morphospecie 1	1
123	Hemiptera	Reduviidae	Morphospecie 2	3
124	Hemiptera	Reduviidae	Morphospecie 3	1
125	Hemiptera	Reduviidae	Morphospecie 4	1
126	Hemiptera	Reduviidae	Morphospecie 5	1
127	Hemiptera	Reduviidae	Morphospecie 6	1
128	Hemiptera	Reduviidae	Morphospecie 7	1
129	Hemiptera	Reduviidae	Morphospecie 8	1
130	Hemiptera	Tingidae	Morphospecie 1	1
131	Hemiptera	Tingidae	Morphospecie 2	2

132	Hemiptera	Tingidae	Morphospecie 3	1
133	Hemiptera	Tingidae	Morphospecie 4	1
134	Hemiptera	Tingidae	Morphospecie 5	2
135	Hemiptera	Unknown	Morphospecie 1	1
136	Hemiptera	Unknown	Morphospecie 1	1
137	Hymenoptera	Braconidae	Morphospecie 1	1
138	Hymenoptera	Ceraphronidae	Morphospecie 1	1
139	Hymenoptera	Formicidae	*Azteca* sp. 1	2
140	Hymenoptera	Formicidae	*Azteca* sp. 2	2
141	Hymenoptera	Formicidae	*Brachymyrmex* sp. 1	1
142	Hymenoptera	Formicidae	*Brachymyrmex* sp. 2	1
143	Hymenoptera	Formicidae	*Brachymyrmex* sp. 3	1
144	Hymenoptera	Formicidae	*Brachymyrmex* sp. 4	1
145	Hymenoptera	Formicidae	*Brachymyrmex* sp. 5	1
146	Hymenoptera	Formicidae	*Camponotus* sp. 1	1
147	Hymenoptera	Formicidae	*Camponotus* sp. 2	1
148	Hymenoptera	Formicidae	*Cephalotes* sp. 1	1
149	Hymenoptera	Formicidae	*Crematogaster* sp. 1	2
150	Hymenoptera	Formicidae	*Dorymyrmex brunneus*	1
151	Hymenoptera	Formicidae	*Ectatomma* sp. 1	1
152	Hymenoptera	Formicidae	*Monomorium* sp. 1	1
153	Hymenoptera	Formicidae	Morphospecie 1	1
154	Hymenoptera	Formicidae	Morphospecie 2	1
155	Hymenoptera	Formicidae	*Myrmelachista* sp. 1	1
156	Hymenoptera	Formicidae	*Myrmicinae* sp. 1	1
157	Hymenoptera	Formicidae	*Pheidole* sp. 1	1
158	Hymenoptera	Formicidae	*Pheidole* sp. 2	1
159	Hymenoptera	Formicidae	*Pheidole* sp. 3	4
160	Hymenoptera	Formicidae	*Pseudomyrmex* sp. 1	1
161	Hymenoptera	Formicidae	*Pseudomyrmex* sp. 2	2
162	Hymenoptera	Formicidae	*Pseudomyrmex* sp. 3	2
163	Hymenoptera	Formicidae	*Pseudomyrmex* sp. 4	1
164	Hymenoptera	Ichneumonidae	Morphospecie 1	5
165	Hymenoptera	Mutillidae	Morphospecie 1	1
166	Lepidoptera	Crambidae	Morphospecie. 1	1
167	Lepidoptera	Crambidae	Morphospecie 2	1
168	Lepidoptera	Crambidae	Morphospecie 3	1
169	Lepidoptera	Drepanidae	Morphospecie 1	1
170	Lepidoptera	Elachistidae	Morphospecie 1	1
171	Lepidoptera	Elachistidae	Morphospecie 2	1
172	Lepidoptera	Elastichidae	Morphospecie 3	1
173	Lepidoptera	Erebidae	Morphospecie 1	1
174	Lepidoptera	Geometridae	Morphospecie 1	1
175	Lepidoptera	Geometridae	Morphospecie 2	1
176	Lepidoptera	Geometridae	Morphospecie 3	1
177	Lepidoptera	Geometridae	Morphospecie 4	1

178	Lepidoptera	Geometridae	Morphospecie 5	1
179	Lepidoptera	Lycaenidae	Morphospecie 1	1
180	Lepidoptera	Noctuidae	Morphospecie 1	1
181	Lepidoptera	Noctuidae	Morphospecie 2	1
182	Lepidoptera	Nymphalidae	Morphospecie 1	1
183	Lepidoptera	Pyralidae	Morphospecie 1	1
184	Lepidoptera	Pyralidae	Morphospecie 2	1
185	Lepidoptera	Unknown	Morphospecie 1	2
186	Lepidoptera	Unknown	Morphospecie 3	1
187	Lepidoptera	Unknown	Morphospecie 4	1
188	Lepidoptera	Unknown	Morphospecie 5	1
189	Lepidoptera	Unknown	Morphospecie 6	1
190	Lepidoptera	Unknown	Morphospecie 7	1
191	Lepidoptera	Unknown	Morphospecie 8	1
192	Mesostigmata	Phytoseiidae	Morphospecie 1	1
193	Mesostigmata	Phytoseiidae	Morphospecie 2	1
194	Mesostigmata	Phytoseiidae	Morphospecie 3	1
195	Neuroptera	Chrysopidae	Morphospecie 1	1
196	Neuroptera	Chrysopidae	Morphospecie 2	1
197	Neuroptera	Chrysopidae	Morphospecie 3	1
198	Orthoptera	Unknown	Morphospecie 1	1
199	Pseudoscorpionida	Unknown	Morphospecie 1	1
200	Thysanoptera	Unknown	Morphospecie 1	1

Supplementary Table 3: Frequency of insect families sampled in 2022

Id	Order	Family	Functional group	Freaquency (no. of sites)
1	Coleoptera	Coccinellidae	Predator	1
2	Coleoptera	Nitidulidae	Omnivore	1
3	Coleoptera	Staphylinidae	Predator	1
4	Coleoptera	Unknown	Phytophagous	1
5	Diptera	Dolichopodidae	Predator	2
6	Diptera	Phoridae	Omnivore	1
7	Hemiptera	Aleyrodidae	Phytophageous	8
8	Hemiptera	Aphididae	Phytophageous	2
9	Hemiptera	Cicadellidae	Phytophageous	3
10	Hemiptera	Coccidae	Phytophageous	4
11	Hemiptera	Diaspididae	Phytophageous	5
12	Hemiptera	Membracidae	Phytophageous	1
13	Hemiptera	Miridae	Predator	1
14	Hemiptera	Pentatomidae	Phytophageous	1
15	Hemiptera	Psyllidae	Phytophageous	2
16	Hemiptera	Reduviidae	Predator	1
17	Hemiptera	Tingidae	Phytophageous	1
18	Hemiptera	Unknown	Phytophageous	9
19	Hymenoptera	Aphelinidae	Parasitoid	1
20	Hymenoptera	Braconidae	Parasitoid	1
21	Hymenoptera	Encyrtidae	Parasitoid	1
22	Hymenoptera	Eulophidae	Parasitoid	2
23	Hymenoptera	Figitidae	Parasitoid	1
24	Hymenoptera	Formicidae	Omnivore	5
25	Hymenoptera	Platygastridae	Parasitoid	2
26	Hymenoptera	Scelionidae	Parasitoid	1
27	Lepidoptera	Nymphalidae	Phytophageous	1
28	Lepidoptera	Unknown	Phytophageous	1
29	Neuroptera	Chrysopidae	Predator	7
30	Orthoptera	Gryllidae	Phytophageous	1
31	Phasmatodea	Unknown	Phytophageous	1
32	Psocoptera	Unknown	Omnivore	5
33	Thysanoptera	Unknown	Omnivore	3

Supplementary Table 4: Insect families sampled in traps of 2022.

Id	Order	Family	Functional group	Habitat presence
1	Hymenoptera	Bethylidae	Parasitoid	Both
2	Hymenoptera	Chrysididae	Parasitoid	Forest
3	Hymenoptera	Ichneumonidae	Parasitoid	Both
4	Hymenoptera	Pteromalidae	Parasitoid	Forest
5	Hymenoptera	Chalcididae	Parasitoid	Both
6	Hymenoptera	Diapriidae	Parasitoid	Both
7	Diptera	Tachinidae	Parasitoid	Both
8	Hymenoptera	Eulophidae	Parasitoid	Both
9	Hymenoptera	Eupelmidae	Parasitoid	Both
10	Hymenoptera	Perilampidae	Parasitoid	Sugarcane
11	Hymenoptera	Megaspilidae	Parasitoid	Forest
12	Hymenoptera	Tiphiidae	Parasitoid	Both
13	Hymenoptera	Figitidae	Parasitoid	Both
14	Hymenoptera	Braconidae	Parasitoid	Both
15	Hymenoptera	Mymaridae	Parasitoid	Both
16	Hymenoptera	Encyrtidae	Parasitoid	Both
17	Hymenoptera	Aphelinidae	Parasitoid	Both
18	Diptera	Pipunculidae	Parasitoid	Both
19	Hymenoptera	Ceraphronidae	Parasitoid	Both
20	Hymenoptera	Signiphoridae	Parasitoid	Sugarcane
21	Hymenoptera	Scelionidae	Parasitoid	Both
22	Hymenoptera	Trichogrammatidae	Parasitoid	Both
23	Hymenoptera	Platygastridae	Parasitoid	Both
24	Hymenoptera	Dryinidae	Parasitoid	Both
25	Hymenoptera	Proctotrupidae	Parasitoid	Forest
26	Diptera	Acroceridae	Parasitoid	Forest
27	Diptera	Empididae	Predator	Both
28	Neuroptera	Hemerobiidae	Predator	Forest

29	Diptera	Syrphidae	Predator	Both
30	Diptera	Bombyliidae	Predator	Sugarcane
31	Diptera	Asilidae	Predator	Sugarcane
32	Coleoptera	Coccinelidae	Predator	Both
33	Hemiptera	Reduviidae	Predator	Both
34	Diptera	Tabanidae	Predator	Both
35	Odonata	Calopterygidae	Predator	Forest
36	Hemiptera	Miridae	Predator	Both
37	Neuroptera	Chrysopidae	Predator	Both
38	Hymenoptera	Vespidae	Predator	Sugarcane
39	Hymenoptera	Sphecidae	Predator	Sugarcane
40	Hemiptera	Anthocoridae	Predator	Both
41	Diptera	Dolichopodidae	Predator	Both
42	Diptera	Therevidae	Predator	Both
43	Hymenoptera	Pompilidae	Predator	Both
44	Coleoptera	Staphylinidae	Predator	Both
45	Coleoptera	Melyidae	Predator	Both
46	Hymenoptera	Colletidae	Pollinator	Forest
47	Hymenoptera	Halictidae	Pollinator	Both
48	Hymenoptera	Andrenidae	Pollinator	Both
49	Hymenoptera	Apidae	Pollinator	Both
50	Coleoptera	Stratiomyidae	Decomposer	Both
51	Diptera	Sphaeroceridae	Decomposer	Both
52	Diptera	Sepcidae	Decomposer	Forest
53	Diptera	Ceratoponidae	Decomposer	Both
54	Diptera	Simullidae	Decomposer	Forest
55	Diptera	Scatopsidae	Decomposer	Forest
56	Diptera	Fannidae	Decomposer	Both
57	Diptera	Lauxanidae	Decomposer	Both
58	Diptera	Ulidiidae	Decomposer	Both
59	Diptera	Chironomidae	Decomposer	Both

60	Diptera	Milichiidae	Decomposer	Both
61	Hymenoptera	Formicidae	Detritivore (leafcutter)	Both
62	Coleoptera	Silvanidae	Detritivore	Sugarcane
63	Diptera	Keroplatidae	Detritivore	Both
64	Hymenoptera	Agaonidae	Herbivore	Both
65	Coleoptera	Bostrichidae	Herbivore	Forest
66	Hemiptera	Cicadellidae	Herbivore	Both
67	Coleoptera	Curculionidae	Herbivore	Forest
68	Hemiptera	Tingidae	Herbivore	Both
69	Hemiptera	Psyllidae	Herbivore	Both
70	Hemiptera	Aphididae	Herbivore	Both
71	Hemiptera	Aleyrodidae	Herbivore	Both
72	Hemiptera	Agromyzidae	Herbivore	Both
73	Hemiptera	Alydidae	Herbivore	Sugarcane
74	Orthoptera	Acrididae	Herbivore	Sugarcane
75	Lepidoptera	Noctuidae	Herbivore	Both
76	Hemiptera	Delphacidae	Herbivore	Both
77	Hemiptera	Flatidae	Herbivore	Forest
78	Hemiptera	Cercopidae	Herbivore	Sugarcane
79	Hemiptera	Rhopalidae	Herbivore	Forest
80	Coleoptera	Scolytidae	Herbivore	Forest
81	Orthoptera	Gryllidae	Herbivore	Forest
82	Hemiptera	Fulgoridae	Herbivore	Forest
83	Hemiptera	Ortheziidae	Herbivore	Forest
84	Hemiptera	Membracidae	Herbivore	Sugarcane
85	Coleoptera	Chrysomelidae	Herbivore	Both
86	Coleoptera	Curculionidae	Herbivore	Forest
87	Coleoptera	Platypodidae	Herbivore	Forest
88	Lepidoptera	Nymphalidae	Herbivore	Forest
89	Hemiptera	Lygaeidae	Herbivore	Both
90	Hemiptera	Coreidae	Herbivore	Forest

91	Coleoptera	Cerambycidae	Herbivore	Forest
92	Hemiptera	Derbidae	Herbivore	Both
93	Hemiptera	Cydnidae	Herbivore	Sugarcane
94	Orthoptera	Tettigonidae	Herbivore	Sugarcane
95	Lepidoptera	Hisperiidae	Herbivore	Sugarcane
96	Hemiptera	Rhyparochromidae	Herbivore	Both
97	Coleoptera	Mordellidae	Herbivore	Forest
98	Hymenoptera	Eurytomidae	Herbivore	Both
99	Coleoptera	Elateridae	Herbivore	Forest
100	Diptera	Clusiidae	Herbivore	Both
101	Coleoptera	Scarabaeidae	Herbivore	Sugarcane
102	Coleoptera	Tenebrionidae	Herbivore	Forest
103	Diptera	Ropalomeridae	Herbivore	Forest
104	Hymenoptera	Formicidae	Omnivore	Both
105	Diptera	Chloropidae	Omnivore	Both
106	Diptera	Muscidae	Omnivore	Both
107	Diptera	Sarcophagidae	Omnivore	Both
108	Diptera	Tipuliidae	Omnivore	Both
109	Diptera	Drosophilidae	Omnivore	Both
110	Diptera	Sciaridae	Omnivore	Both
111	Diptera	Calliphoridae	Omnivore	Forest
112	Diptera	Cecidomyiidae	Omnivore	Both
113	Diptera	Phoridae	Omnivore	Both
114	Diptera	Lonchaeidae	Omnivore	Both
115	Diptera	Micropezidae	Omnivore	Forest
116	Diptera	Pseudopomyzidae	Omnivore	Both
117	Diptera	Psychodidae	Omnivore	Both
118	Coleoptera	Nitidulidae	Omnivore	Both
119	Diptera	Ephydridae	Omnivore	Sugarcane
120	Psocoptera		Omnivore	Both
121	Diptera	Mycetophilidae	Omnivore	Both

Yellow pan trap in sugarcane fields (Jaboticabal, Brazil)

CHAPTER 3 – Functional Diversity and Seasonal Dynamics of Hymenoptera in Forest Fragments and Adjacent Sugarcane Fields

ABSTRACT - Hymenoptera provide essential ecosystem services such as parasitism, predation, and pollination, contributing to the regulation of pest populations and the maintenance of plant reproduction. However, these insects are sensitive to environmental disturbances, including habitat conversion and climate variability, that are common in agricultural landscapes. Understanding how Hymenoptera communities respond to temporal and spatial variation is key to promoting biodiversity and ecosystem functioning in managed systems. In this study, we investigated seasonal changes in Hymenoptera communities in forest fragments and adjacent sugarcane fields in southeastern Brazil. We tested four hypotheses: (1) the composition and abundance of Hymenoptera communities and functional groups vary between seasons; (2) forest fragments harbor higher richness and abundance than sugarcane fields; (3) forest fragments show greater temporal stability; and (4) Hymenoptera abundance in sugarcane fields is associated with that in nearby forest fragments, suggesting spillover. Sampling was conducted every three months, totaling four samples in one year. Yellow pan traps were placed in parallel in forest fragments and adjacent sugarcane fields for 48 hours. Hymenoptera were identified to family level and classified into functional groups (parasitoids, predators, and pollinators). Family composition varied significantly between seasons, but not between habitats. While total abundance did not differ across seasons or habitats, functional groups responded differently. Parasitoid, predator, and pollinator abundance changed between seasons. Predators and parasitoids showed a lower abundance in November while pollinator abundance increased. Habitat influenced parasitoid and pollinator abundance: parasitoid abundance was lower in sugarcane fields, whereas pollinators were more abundant. Richness and abundance were more stable in forest fragments, while sugarcane fields showed greater fluctuations, likely due to agricultural practices and microclimatic vaiation. No correlation was found between richness or abundance in forest fragments and adjacent fields. These findings demonstrate complementary habitat use by Hymenoptera and underscore the role of forest fragments as reservoirs of functional biodiversity. Conserving these fragments thus enhances ecosystem service provisioning, particularly during periods of environmental stress in crop fields.

Keywords: Agricultural landscape, Biodiversity conservation, Ecosystem services, Natural enemies, Seasonal variation

1. Introduction

The intensification of human land use, especially the expansion of agriculture, has led to the fragmentation and loss of natural and semi-natural habitats, compromising biodiversity and related ecosystem services (Haddad et al., 2015; Liu et al., 2018). This land-use change directly affects arthropod fauna, potentially reducing their abundance and functional diversity (Sánchez-Bayo and Wyckhuys, 2019; Uhler et al., 2021). However, remnants of native vegetation and non-crop areas can play an important role as refuges and reservoirs of biodiversity, contributing to the provision of ecosystem services (Decocq et al., 2016). To maintain insect diversity and the services they provide, it is necessary to implement measures that protect, restore, and improve habitats while mitigating the negative effects of land-use practices (Forister et al., 2019). A better understanding of interactions between insect communities of non-crop habitats and crop fields is required to evaluate ecosystem services.

Insects of the Hymenoptera provide important ecosystem services due to their wide functional diversity, including parasitism predation, and pollination (Noriega et al., 2018; Brock et al., 2021). However, several hymenopteran groups are vulnerable to environmental homogenization and structural simplification of vegetation (Escobero et al., 2025). Moreover, the abundance and richness of hymenopterans, especially parasitoids, are closely linked to overall arthropod diversity and may thus be indicators of biodiversity in agroecosystems (Anderson et al., 2011). The reinforcement of related ecosystem services provided by hymenopteran insect groups require strategies that enhance hymopteran populations in agricultural landscapes (Jankielsohn, 2018).

Non-crop habitats significantly contribute to biodiversity conservation and can benefit natural enemies of crop pests through spillover effects into cultivated areas (Dainese et al., 2017; Garratt et al., 2017). Heterogeneous environments with high structural and botanical complexity offer shelter, microhabitats, and food resources to a wide range of insect groups throughout the year (Dassou and Tixier, 2016; Gardarin et al., 2018). Among these resources, floral resources are particularly important for Hymenoptera, as most species depend on nectar and pollen during the adult stage. This is especially relevant for parasitoids, whose

larvae are carnivorous while adults require sugar-rich resources for energy, influencing their survival, dispersal, and reproductive success (Russell, 2015; Benelli et al., 2017). Although high plant diversity is generally associated with increased insect diversity and more stable ecosystem services (Jonsson et al., 2017; Eeraerts et al., 2020), resource quantity can also be critical. Even non-crop habitats with low plant diversity may support key hymenopteran groups if they provide abundant floral resources (González et al., 2022). However, it is also essential to consider community composition, not just diversity or abundance, as the ecological outcomes may vary depending on the specific plant and insect species involved, and the characteristics of each agroecosystem (Alhadidi et al., 2018; Crist et al., 2006; Deus et al., 2023).

Several studies have shown that forest habitats adjacent to croplands enhance the diversity, abundance, and activity of hymenopteran species in agricultural landscapes (Klein et al., 2006; Banks et al., 2013). However, the strength of this relationship may be influenced by habitat quality such as plant community composition, the composition of insect functional groups, and seasonality (Proesmans et al., 2019; Coutinho et al., 2020). Despite advances in the understanding of functional biodiversity in agricultural landscapes, there are still important gaps regarding how different functional groups of Hymenoptera respond simultaneously to seasonality and plant species composition, especially in tropical monocultures such as sugarcane.

In this study, we investigated how flying Hymenoptera communities change across seasons and habitats (forest fragments and sugarcane fields). We further analysed whether hymenoptera communities in sugarcane fields are influenced by those of adjacent forest fragments to obtain information on refuge function. Specifically, we aimed to (1) assess the effects of seasonality and habitat type on Hymenoptera community composition; (2) examine the effect of these factors on total hymenoptera abundance, family richness, and functional group abundance across; and (3) analyse correlations between insect abundance in sugarcane fields and adjacent forest fragments. We hypothesize that:

1. the composition and abundance of Hymenoptera communities and functional groups change between seasons;

2. forest fragments support greater insect richness and abundance than sugarcane fields;

3. forest fragments present greater temporal stability in insect communities; and

4. the abundance of Hymenoptera in sugarcane fields is associated with that in nearby forest fragments, indicating movement between habitats.

2. Material and methods

2.1. Study sites and design

The study was carried out between 2023 and 2024 in Atlantic Forest (Mata Atlântica) fragments and adjacent sugarcane fields located in the municipality of Jaboticabal, São Paulo state, Brazil (21°15′19″ S, 48°19′21″ W). The landscape in this region is dominated by sugarcane fields, with a low proportion of remaining gallery and plateau forest fragments. The climate is tropical, with relatively dry winters and a rainy summer. Average annual rainfall is approximately 1300 mm and temperature of 22 °C. The western and more continental section of the Atlantic Forest is classified as semi-deciduous and forms a transitional zone towards the drier savanna (Cerrado). Prior to European colonization in the early XVI century, the Atlantic Forest was the predominant vegetation type in the region.

We selected ten forest fragments adjacent to sugarcane fields based on the following criteria: absence of commercial tree plantations within the fragments, and a minimum distance of 1 km between fragments. Five of the selected fragments were located on shallow slopes and classified as plateau forests, while the remaining five were gallery forest remnants situated near rivers

or streams. Plateau fragments generally exhibited greater cover of shrubs and lianas, whereas gallery fragments were characterized by proximity to water bodies and are legally protected as Permanent Preservation Areas (PPAs), primarily to safeguard water quality in public supply catchment zones (Santos et al., 2018). Within each forest fragment, data were collected in a randomly selected 50m × 20m plot, located 5 meters from the fragment edge.

Sugarcane cultivation in the region follows a rotational harvesting system, with different areas harvested at different times of the year. In our study, all sugarcane fields adjacent to forest fragments were harvested by early July, and sampling was conducted afterward, during the regrowth phase. Although all areas had been harvested by this time, the interval since harvest varied across sites, leading to differences in sugarcane regrowth stages during sampling. This temporal pattern reflects typical management regimes in commercial sugarcane landscapes of southeastern Brazil, where most harvests occur during the dry season, particularly between May and October.

2.2. Insect sampling

We conducted insect sampling using yellow pan traps (42 × 28 × 8cm) placed both in forest fragments and in adjacent sugarcane fields in 2023 and 2024 (Table 1). In each habitat, two traps were installed 15 meters apart and 5 meters from the field edge, with those in the forest fragment positioned parallel to the adjacent crop. For the statistical analyses, we summed the counts from both traps to obtain a cumulative value of insect abundance and family richness per habitat. Each trap was filled with 2L of water and 10 drops of detergent, and remained exposed for 48 hours. Sampling was conducted every three months over a one-year period, totaling four sampling events (August 2023, November 2023, February 2024 and May 2024).

Collected insects were preserved in 70% diluted ethanol. Hymenoptera specimens were later sorted and identified to family level (excluding ants). Based on predominant life-history traits described for each family, hymenopterans were

classified into the following functional groups: parasitoids, predators, and pollinators (Fernandez and Sharkey, 2006). Families that could not be clearly assigned to a single functional group were categorized as omnivorous and subsequently excluded from functional group analyses. For taxa that change feeding between larval and adult stages, we used larval feeding habits, as larvae generally have higher resource demands and represent the main consumers in the life cycle (Kaleka et al., 2019).

Table 1. Monthly precipitation (mm), temperature and relative humidity (%) in the evaluation periods of the 2023/2024 growing season in Jaboticabal, SP, data from the agroclimatological station of Unesp-Jaboticabal.

Month/year	Precipitation (mm)	Average temperature (°C)	Relative humidity (%)
August/2023	15.2	22.5	59.4
September/2023	29.5	26.2	55.1
October/2023	141.3	26.1	69.9
November/2023	100.5	26.7	60.8
December/2023	127.4	27.0	65.3
January/2024	118.5	25.5	73.8
February/2024	88.7	25.3	75.5
March/2024	128.2	25.7	75.9
April/2024	8.1	25.4	68.2
May/2024	3.7	23.3	62.1
June/2024	0.0	22.2	54.1
July/2024	2.0	21.5	54.8

2.3. Data analysis

We compared Hymenoptera family composition across different seasons and habitats (forest fragments and sugarcane fields) using non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity of presence–absence data. The NMDS was run using the metaMDS function of the vegan package with a maximum of 100 random starts (trymax = 100) to avoid local

minima. To test for differences in community composition, we used permutational multivariate analysis of variance (PERMANOVA) implemented with the adonis2 function in vegan, using 999 permutations and stratifying by plot to account for repeated measures across time. Additionally, we applied an analysis of similarities (ANOSIM) to further evaluate seasonal differences in community composition. ANOSIM was performed using Jaccard dissimilarity with 999 permutations and grouping samples by sampling month. This analysis was used to identify which sampling periods differed most in community composition, complementing the PERMANOVA results.

To assess the effects of season and habitat (forest fragment vs. sugarcane) on Hymenoptera abundance and on each functional group (parasitoids, predators, and pollinators), we fitted generalized linear mixed models (GLMMs) with a negative binomial distribution (family = nbinom2) using the glmmTMB package, as overdispersion was detected. In all models, site and fragment type were included as random effects to account for the nested structure of the data and for repeated sampling in the same locations. Because both habitats were sampled within each plot across seasons, this structure allowed us to test for habitat and seasonal effects while controlling for spatial dependency and avoiding pseudoreplication. The same modeling approach was used to analyze family richness (the number of Hymenoptera families), with the model structure: glmmTMB(Family ~ Season * Habitat + (1|Site) + (1|Fragment), family = nbinom2).

Additionally, we tested whether insect abundance or family richness in the forest fragment influenced the corresponding metric in the adjacent sugarcane field. To avoid temporal pseudoreplication, we calculated the mean abundance and richness for each plot across all sampling dates. We then used linear models (LMs) to assess the relationship between forest fragment and sugarcane field values. Model assumptions (normality and homoscedasticity of residuals) were checked by Shapiro–Wilk and Breusch–Pagan tests. When assumptions were not met, we fitted generalized linear models (GLMs) with a negative binomial distribution. Separate models were fitted for each functional group (e.g.,

parasitoids, predators, pollinators, and phytophagous). All analyses were performed using R 3.6.2 software (R Core Team, 2024).

3. Results

A total of 1440 specimens were collected and belonged to 36 families. Of this total number, 965 of the specimens were classified as parasitoids (67.01%), 322 as predators (22.36%), 112 as pollinators (7.78%), and the remaining individuals (2.85%) could not be associated to functional groups and were thus omitted from analysis (Supplementary Table 1).

3.1. Hymenoptera community

We found a significant difference between seasons in hymenopteran family composition ($F = 2.293$, $p = 0.001$; Figure 1). However, no significant differences were detected between habitats (forest fragment and sugarcane; $F = 1.457$, $p = 0.105$), and for the season × habitat interaction ($F = 0.950$, $p = 0.537$). Pairwise ANOSIM tests showed that the Hymenoptera community composition in August differed significantly from November ($R = 0.14$, $p = 0.003$), February ($R = 0.16$, $p = 0.002$), and May ($R = 0.07$, $p = 0.045$). November also differed significantly from February ($R = 0.11$, $p = 0.010$) and May ($R = 0.09$, $p = 0.023$), while no significant difference was detected between February and May ($R = 0.04$, $p = 0.128$).

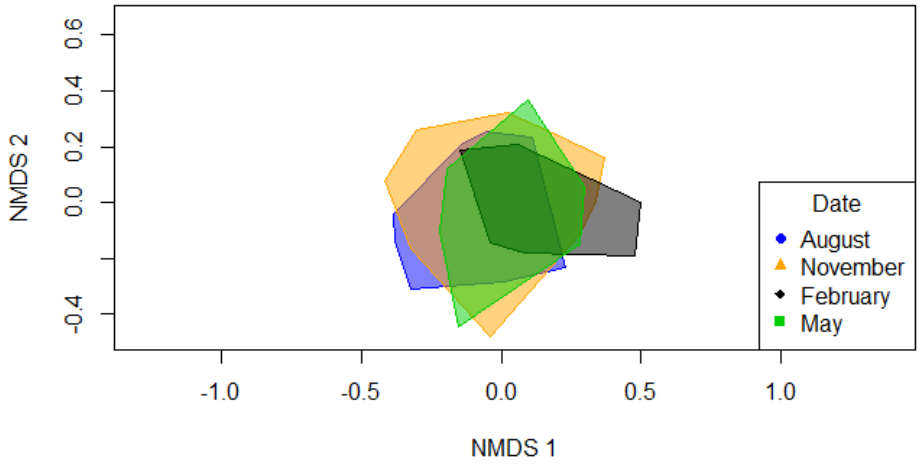

Figure 1. Non-Metric Multidimensional Scaling (NMDS) ordination of Hymenoptera family composition based on Jaccard dissimilarity in forest fragments and adjacent sugarcane fields sampled across four seasons.

3.2. Functional group abundance and richness

There was no significant effect of season or habitat on total Hymenoptera abundance, and the season x habitat interaction was also non-significant. In contrast, parasitoid abundance was significantly affected by both factor and their interaction. For most of the year, parasitoid abundance was lower in the sugarcane fields compared to the forest fragments, but this pattern is reversed in May. The abundance of predators was affected by the season, being greater in sugarcane fields in August, but not in the following months. The abundance of pollinators was significantly influenced by both season and habitat. Being pollinators greater in the sugarcane field most of the year, but contrary to the other groups the largest number was observed in November (Table 2; Figure 2).

Table 2. Generalized linear mixed models (GLMM) testing the effects of season and habitat on Hymenoptera abundance. p-values in bold are significant ($p<0.05$).

	Season		Habitat		Season*Habitat	
	χ^2	p	χ^2	P	χ^2	p
Total	3.601	0.307	0.004	0.951	3.286	0.350
Parasitoids	27.724	**<0.001**	5.728	**0.017**	12.605	**0.006**
Predators	35.460	**<0.001**	1.184	0.277	4.999	0.172
Pollinators	19.313	**<0.001**	7.620	**<0.001**	4.077	0.253

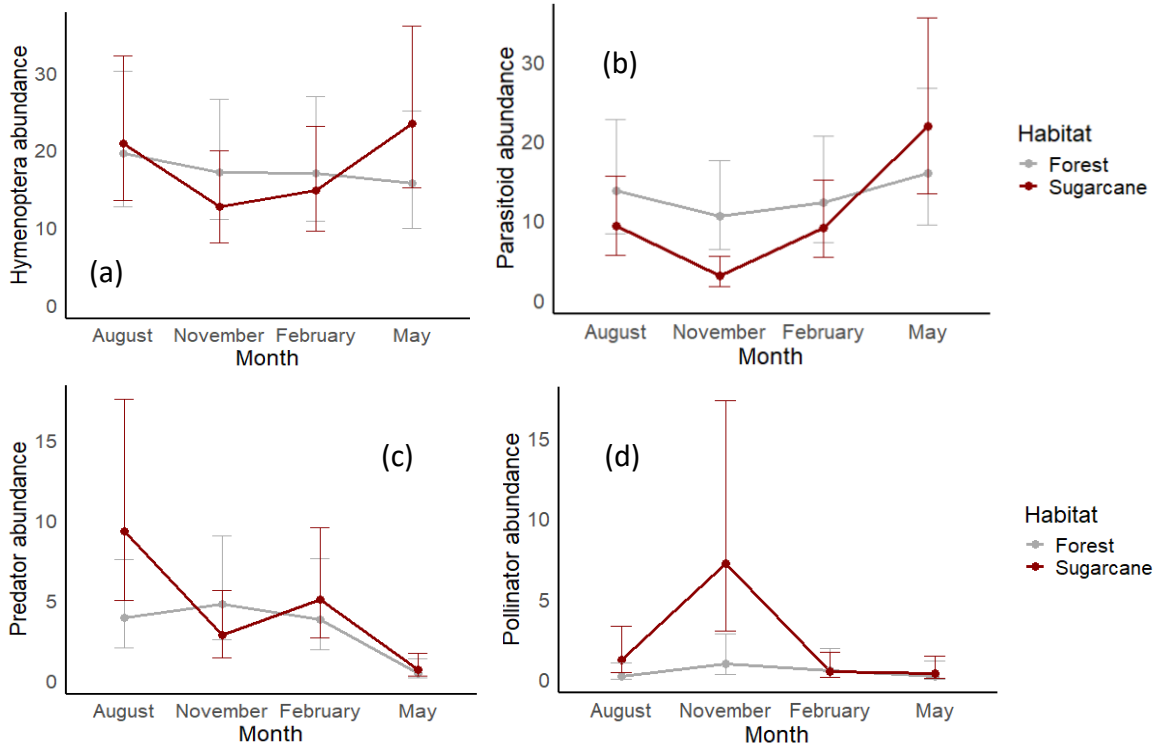

Figure 2. Predicted mean (± 95% confidence interval) total abundance of Hymenoptera and functional groups across seasons and habitats (individuals per site). Lines represent predictions from generalized linear mixed models with a negative binomial distribution. Total Hymenoptera (a), parasitoids (b), predators (c) and pollinators (d).

We also analyzed family richness in both seasons and habitats. There was no effect of season (χ^2= 4.860, p= 0.183) or habitat (χ^2=2.772, p= 0.096), but the

effect of season × habitat interaction was significant (χ^2= 11.503, p= 0.009) (Figure 3).

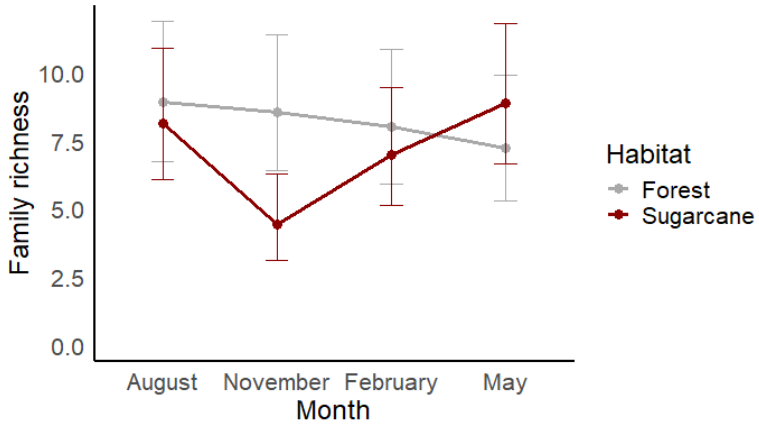

Figure 3. Predicted mean (± 95% confidence interval) Hymenoptera family richness in different seasons habitats.

We did not find an effect of family richness in the forest fragment on family richness in adjacent sugarcane field (χ^2 = 0.313, p = 0.576). Similarly, there were no significant correlations between the abundances of hymenopteran functional groups (predators, parasitoids, pollinators) in forest fragments and sugarcane fields (Table 2; Figure 4).

Table 3. Linear models (LMs) testing whether the Hymenoptera abundance in sugarcane fields increases with increasing abundance in adjacent forest fragments.

Total		Parasitoids		Predators		Pollinators	
χ^2	p	χ^2	p	χ^2	p	χ^2	p
2.105	0.147	2.976	0.085	1.005	0.316	<0.001	0.995

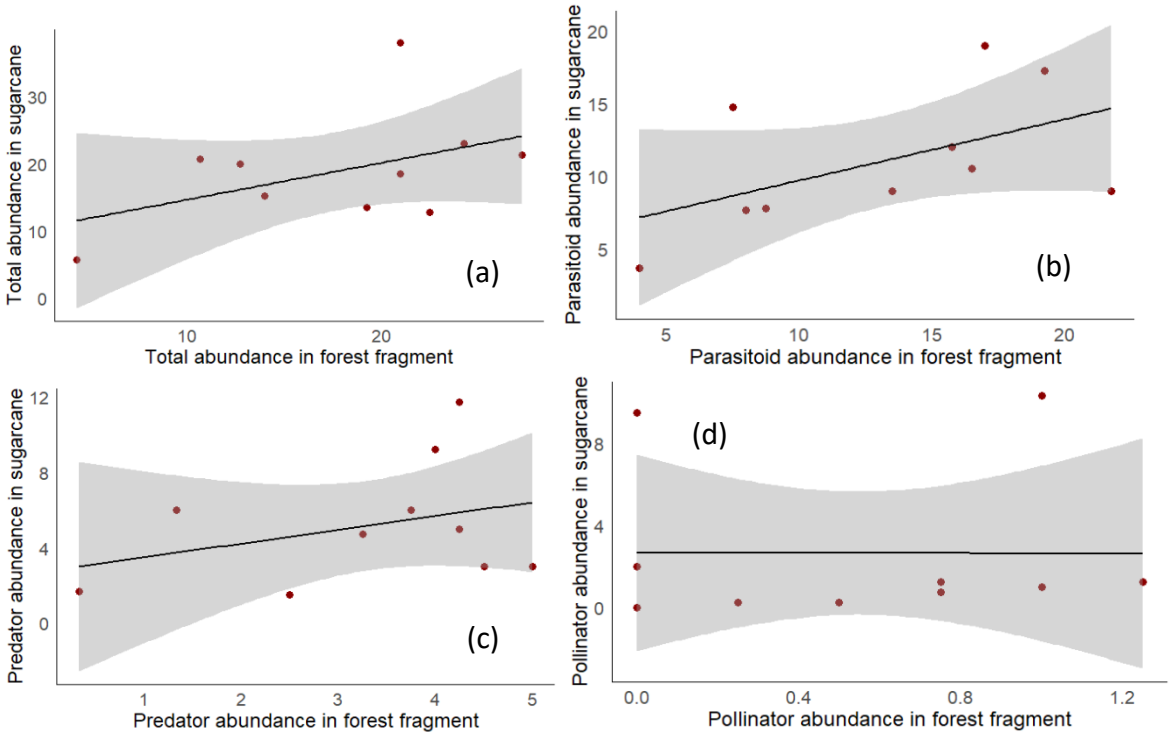

Figure 4. Relationship between the mean abundance of Hymenoptera and functional groups in forest fragments and adjacent sugarcane fields. Total Hymenoptera (a), parasitoids (b), predators (c) and pollinators (d).

4. Discussion

The analysis of Hymenoptera community composition revealed a significant effect of seasonality, indicating that the structure of this community varies throughout the year. The community in August differed significantly from that of November, February, and May. This was mainly explained by a decrease in parasitoid and predator populations in sugarcane fields from August to November but also by an increase of pollinator abundance. The family richness also decreased from August to November with a subsequent increase in February and May, which was already observed for parasitoids. Surprisingly, the Hymenoptera abundance was not lower in sugarcane fields than in adjacent forest fragments. Parasitoid abundance was siginficantly lower in sugarcane fields, but pollinator abundance was higher. In contrast to our hypothesis, we did

not find significant relationships between abundances of different functional groups in sugarcane fields and forest fragments.

The seasonal shifts in family composition may be associated with changes in resource availability, such as nectar and prey, biotic factors that directly influence insect development and activity, and in particular with disturbance related to agricultural practices in sugarcane fields (Aranda and Graciolli, 2015; Kishinevsky et al., 2017; Osorio-Canadas et al., 2018). The absence of a habitat effect on community composition suggests that, despite structural differences between forest fragments and sugarcane fields, most families may be broadly distributed or use both environments at different times during the annual cycle. Moreover, many hymenopteran species are quite mobile, and the relatively small distance between forest and sugarcane plots may have limited the differentiation of communities. Finally, the taxonomic resolution (family level) may have been insufficient to detect fine-scale differences in Hymenoptera communities.

While season and habitat did not affect total Hymenoptera abundance, they did influence functional groups. This result shows that general patterns may mask specific trends within functional groups because the decrease of a group may be compensated by the increase of another. The finding highlights the importance of analyzing groups separately to gain more accurate ecological insights (Coutinho et al., 2020).

Parasitoid abundance was significantly influenced by season, habitat, and their interaction. This significant interaction reflects the complex and specific ecological needs of hymenopteran insects, including suitable hosts and microhabitats (Vogel et al., 2021; Scherr et al., 2023). Their foraging behavior may shift seasonally in response to changes in resource distribution (Eoche-Bosy et al., 2016). Although higher humidity and temperature in November would typically favor insect activity, the drastic drop in parasitoid abundance between August and November suggests a delay in recolonisation, or dispersal limitations related to their small body size (Silva et al., 2011; Yan et al., 2024). Actually, the dry season lasts until October and sugarcane plants show poor regrowth after harvest in summer resulting in a decline of resources for potential host or prey species. Common sugarcane herbivores such as the sugarcane borer, *Diatraea*

saccharalis (Lepidoptera: Crambidae), and the sugarcane mealybug, *Saccharicoccus sacchari* (Hemiptera: Pseudococcidae), tend to be more abundant at the end of the rainy season or at the beginning of the dry season in subtropical regions of Brazil (Borges Filho et al., 2019). Parasitoid phenology may be synchronized with host availability, ensuring that offspring emerge when resources are more abundant (Aranda and Graciolli, 2015). Finally, the lower abundance of parasitoids in sugarcane fields may be related to the reduced structural complexity and lower host diversity typically found in managed agricultural habitats (Letourneau et al., 2015).

Predator abundance was also significantly different between seasons. Similar to parasitoids, abundances strongly decreased in sugarcane fields between August and November. Additionally, predator abundance also decreased in May across both habitats. Similarly to host availability for parasitoids, this pattern may reflect responses to abiotic conditions, such as the end of the rainy season, but also to fluctuations in prey availability (Nadeau and Stamp, 2003; Canevazzi et al., 2011). Water availability is a key driver of survival of predator affectling directly insect physiology, and affects at the same time food resources such as nectar and nectar-feeding prey (Elpino-Campos et al., 2007). The drop in abundance in May may also be explained by sugarcane harvest, starting at the beginning of the dry season and representing a strong disturbance for all insect groups. The absence of a significant habitat effect on predators may reflect the generalist habit of these predatory insects, indicating that both habitats provide adequate or complementary food sources and nesting sites (Coutinho et al., 2020; Ferreira et al., 2020). The absence of a significant habitat effect on predator abundance may reflect their generalist habits and high mobility, which allow them to exploit resources in both habitats (Coutinho et al., 2020; Ferreira et al., 2020). Moreover, even within the same taxonomic group, predators may differ in their degree of specialization, using similar or distinct resources depending on local conditions (Moura et al., 2019; Deus et al., 2023).

Pollinator abundance was significantly affected by both season and habitat, with higher values recorded in sugarcane fields compared to forest fragments. Abundance was particularly high in November, but this seasonal

increase occurred only in sugarcane fields, whereas fluctuations in forest fragments were small. The higher abundance in sugarcane fields was unexpected, considering that sugarcane is usually harvested before flowering and even flowers only produce pollen and lack nectar, reducing their attractiveness to pollinators (Dinesh Babu et al., 2022). Nevertheless, bee activity in sugarcane fields has been previously documented and may be explained by increasing cover of weeds that provide floral resources, attracting pollinators (Pinheiro and Schlindwein, 2005; Bretagnolle and Gaba, 2015). Sugarcane harvest in the dry season may favor the emergence of such plants due to reduced light competition, resulting in temporary increase in flower density. Due to poor sugarcane regrowth until the beginning of the rainy season the crop is not very competitive allowing the development of weeds. Escobedo-Kenefic et al. (2020) suggest that bees concentrate in such floral patches during short windows of high resource availability. To confirm this explanation, vegetation analyses should not be limited to forest fragments but need to include the spontaneous flora of sugarcane fields in future studies.

Although total Hymenoptera abundance was not significantly affected by season and habitat, family richness showed a significant interaction between season and habitat. Similarly to predator and parasitoid abundance, richness remained relatively stable in forest fragments across all sampling periods, but decreased strongly in sugarcane fields in November. Again, sugarcane harvest, that occurred during the dry season, combined with the beginning of rainfall in November, may have contributed to this decline by altering habitat structure and increasing insect mortality (Barbosa et al., 2019; Oliveira et al., 2025). In contrast, the more complex vegetation structure in forest fragments may buffer such effects, reducing direct contact between raindrops and insects (Ruiz-Guerra et al., 2013). These findings demonstrate the role of forest fragments as seasonal refuges for Hymenoptera, particularly during stressful periods, while also suggesting that sugarcane fields may provide complementary resources during other times of the year (Banks et al., 2013; Santos et al., 2009).

Contrary to our expectations, none of the functional groups showed a significant abundance correlation between forest fragments and adjacent

sugarcane fields. This may indicate that, even if the overall composition of the community is similar, the movement dynamics and habitat use of individual taxa vary between groups or seasons. Nevertheless, our previous results indicate that forest fragments may represent a source of colonization of agricultural lands (Schüepp et al., 2012; Santos et al. 2018). Such spillover from semi-natural habitats to adjacent crops is documented in several studies (Tscharntke et al., 2005; Medeiros et al., 2012). However, the movement dynamics is complex, varying according to the temporal availability of resources, specific characteristics of each habitat, insect mobility and abiotic factors (Cole et al., 2017).

Our results emphasize the importance of maintaining forest fragments within agricultural landscapes. These natural habitats do not only contribute to biodiversity conservation but also support the seasonal availability of beneficial insects, that may provide ecosystem services such as biological control and pollination. However, as our study was conducted at family level, it is likely that many of the collected individuals do not have a direct influence on agricultural systems. Therefore, more specific studies are needed to identify the beneficial species that provide ecosystem service and may affect crop productivity.

References

Alhadidi SN, Griffin JN, Fowler MS (2018) Natural enemy composition rather than richness determines pest suppression. **BioControl** 63:575–584.

Anderson A et al. (2011) The potential of parasitoid Hymenoptera as bioindicators of arthropod diversity in agricultural grasslands. **Journal of Applied Ecology** 48:382–390.

Aranda R, Graciolli G (2015) Spatial–temporal distribution of the Hymenoptera in the Brazilian Savanna and the effects of habitat heterogeneity on these patterns. **Journal of Insect Conservation** 19:1173–1187.

Ávalos-Hernández O, Trujano-Ortega M, García-Vázquez UO, Yánez-Ordóñez O (2019) Diversity and resource use patterns of bees and flies that visit flowers in the Cuatro Ciénegas Basin. **Animal Diversity and Biogeography of the Cuatro Ciénegas Basin** 105–116.

Banks JE et al. (2013) Effects of proximity to forest habitat on hymenoptera diversity in a Costa Rican coffee agroecosystem. **The Pan-Pacific Entomologist** 89:60–68.

Barbosa BG et al. (2019) Factors affecting thrips (Thysanoptera: Thripidae) population densities in watermelon crops. **The Florida Entomologist** 102:10–15.

Benelli G et al. (2017) The impact of adult diet on parasitoid reproductive performance. **Journal of Pest Science** 90:807–823.

Borges Filho RC et al. (2019) Population dynamics of pests and natural enemies on sugar cane grown in a subtropical region of Brazil. **Florida Entomologist** 102:526–530.

Bretagnolle V, Gaba S (2015) Weeds for bees? A review. **Agronomy for Sustainable Development** 35:891–909.

Brock RE, Cini A, Sumner S (2021) Ecosystem services provided by aculeate wasps. **Biological Reviews** 96:1645–1675.

Canevazzi NCDS, Noll FB (2011) Environmental factors influencing foraging activity in the social wasp Polybia paulista (Hymenoptera: Vespidae: Epiponini). **Psyche: A Journal of Entomology** 2011:542487.

Crist TO, Pradhan-Devare SV, Summerville KS (2006) Spatial variation in insect community and species responses to habitat loss and plant community composition. **Oecologia** 147:510–521.

Cole LJ, Brocklehurst S, Robertson D, Harrison W, McCracken DI (2017) Exploring the interactions between resource availability and the utilisation of semi-natural habitats by insect pollinators in an intensive agricultural landscape. **Agriculture, Ecosystems & Environment** 246:157–167.

Coutinho JG, Angel-Coca C, Boscolo D, Viana BF (2020) Heterogeneous agroecosystems support high diversity and abundance of trap-nesting bees and wasps among tropical crops. **Biotropica** 52:991–1004.

Dainese M, Montecchiari S, Sitzia T, Sigura M, Marini L (2017) High cover of hedgerows in the landscape supports multiple ecosystem services in Mediterranean cereal fields. **Journal of Applied Ecology** 54:380–388.

Dassou AG, Tixier P (2016) Response of pest control by generalist predators to local-scale plant diversity: a meta-analysis. **Ecology and Evolution** 6:1143–1153.

Decocq G et al. (2016) Ecosystem services from small forest patches in agricultural landscapes. **Current Forestry Reports** 2:30–44.

Deus JPAD, Araujo G, Buschini MLT, Moura RR (2023) Habitat types in the Atlantic Forest differently influence community structure and species interaction of cavity-nesting Hymenoptera and their natural enemies. **Journal of Insect Conservation** 27:129–140.

Dinesh Babu KS et al. (2022) A short review on sugarcane: its domestication, molecular manipulations and future perspectives. **Genetic Resources and Crop Evolution** 69:2623–2643.

Eeraerts M, Smagghe G, Meeus I (2020) Bumble bee abundance and richness improves honey bee pollination behaviour in sweet cherry. **Basic and Applied Ecology** 43:27–33.

Eoche-Bosy D, Outreman Y, Oliveira Andrade T, Krespi L, Van Baaren J (2016) Seasonal variations of host resources influence foraging strategy in parasitoids. **Entomologia Experimentalis et Applicata** 161:11–19.

Elpino-Campos Á, Del-Claro K, Prezoto F (2007) Diversity of social wasps (Hymenoptera: Vespidae) in Cerrado fragments of Uberlândia, Minas Gerais State, Brazil. **Neotropical Entomology** 36:685–692.

Escobedo-Kenefic N et al. (2020) Disentangling the effects of local resources, landscape heterogeneity and climatic seasonality on bee diversity and plant-pollinator networks in tropical highlands. **Oecologia** 194:333–344.

Escobero C, Gómez-Martínez C, Cursach J, González-Estévez MA, Lázaro A (2025) Traits of hymenopterans, dipterans and plants that indicate vulnerability to landscape homogenization. **Basic and Applied Ecology** (no prelo).

Ferreira JVA et al. (2020) Effect of habitat amount and complexity on social wasps (Vespidae: Polistinae): implications for biological control. **Journal of Insect Conservation** 24:613–624.

Forister ML, Pelton EM, Black SH (2019) Declines in insect abundance and diversity: we know enough to act now. **Conservation Science and Practice** 1:e80.

Gardarin A, Plantegenest M, Bischoff A, Valantin-Morison M (2018) Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. **Journal of Pest Science** 91:943–955.

Garratt MP, Senapathi D, Coston DJ, Mortimer SR, Potts SG (2017) The benefits of hedgerows for pollinators and natural enemies depends on hedge quality and landscape context. **Agriculture, Ecosystems & Environment** 247:363–370.

Gontijo LM (2019) Engineering natural enemy shelters to enhance conservation biological control in field crops. **Biological Control** 130:155–163.

González E et al. (2022) Artificial temporary non-crop habitats support parasitoids on arable land. **Biological Conservation** 265:109409.

Haddad NM et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. **Science Advances** 1:e1500052.

Harrison T, Gibbs J, Winfree R (2018) Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. **Global Change Biology** 24:287–296.

Jankielsohn A (2018) The importance of insects in agricultural ecosystems. **Advances in Entomology** 6:62–73.

Jonsson M, Kaartinen R, Straub CS (2017) Relationships between natural enemy diversity and biological control. **Current Opinion in Insect Science** 20:1–6.

Kishinevsky M, Keasar T, Bar-Massada A (2017) Parasitoid abundance on plants: effects of host abundance, plant species, and plant flowering state. **Arthropod-Plant Interactions** 11:155–161.

Klein AM, Steffan-Dewenter I, Tscharntke T (2006) Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. **Journal of Animal Ecology** 75:315–323.

Letourneau DK, Bothwell Allen SG, Kula RR, Sharkey MJ, Stireman JO III (2015) Habitat eradication and cropland intensification may reduce parasitoid diversity and natural pest control services in annual crop fields. **Elementa** 3:000069.

Liu J et al. (2018) How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? **Landscape Ecology** 33:341–352.

Matos MCB, Silva SS, Teodoro AV (2016) Seasonal population abundance of the assembly of solitary wasps and bees (Hymenoptera) according to land-use in Maranhão state, Brazil. **Revista Brasileira de Entomologia** 60:171–176.

Medeiros HR et al. (2022) Landscape composition regulates the spillover of beneficial insects between forest remnants and adjacent coffee plantations. **Perspectives in Ecology and Conservation** 20:111–116.

Milet-Pinheiro P, Schlindwein C (2005) Do euglossine males (Apidae, Euglossini) leave tropical rainforest to collect fragrances in sugarcane monocultures? **Revista Brasileira de Zoologia** 22:853–858.

Moura RR, Pitilin RB, Buschini MLT (2019) Specialisation in prey capture drives coexistence among sympatric spider-hunting wasps. **Ecological Entomology** 44:639–647.

Nadeau H, Stamp N (2003) Effect of prey quantity and temperature on nest demography of social wasps. **Ecological Entomology** 28:328–339.

Noriega JA et al. (2018) Research trends in ecosystem services provided by insects. **Basic and Applied Ecology** 26:8–23.

Oliveira SJ, Cesarin V, Fernandes OA (2025) Dynamics of natural mortality factors of immature *Diatraea saccharalis* (Fabricius) (Lepidoptera: Crambidae) in sugarcane adjacent to forest fragments. **Journal of Applied Entomology** 149:278–291.

Osorio-Canadas S, Arnan X, Bassols E, Vicens N, Bosch J (2018) Seasonal dynamics in a cavity-nesting bee-wasp community: shifts in composition, functional diversity and host-parasitoid network structure. **PLoS One** 13:e0205854.

Proesmans W, Bonte D, Smagghe G, Meeus I, Verheyen K (2019) Importance of forest fragments as pollinator habitat varies with season and guild. **Basic and Applied Ecology** 34:95–107.

Ruiz-Guerra B, Hanson P, Guevara R, Dirzo R (2013) Richness and abundance of Ichneumonidae in a fragmented tropical rain forest. **Neotropical Entomology** 42:458–465.

Russell M (2015) A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species. **Biological Control** 82:96–103.

Sánchez-Bayo F, Wyckhuys KA (2019) Worldwide decline of the entomofauna: a review of its drivers. **Biological Conservation** 232:8–27.

Santos GDM, Bispo PC, Aguiar CML (2009) Fluctuations in richness and abundance of social wasps during the dry and wet seasons in three phyto-physiognomies at the tropical dry forest of Brazil. **Environmental Entomology** 38:1613–1617.

Santos LA, Bischoff A, Fernandes OA (2018) The effect of forest fragments on abundance, diversity and species composition of predatory ants in sugarcane fields. **Basic and Applied Ecology** 33:58–65.

Scherr A, Quinn NF, Tallamy D, Duan JJ (2023) Effect of forest microhabitat and larval stage on overwintering survival, development, and phenology of *Spathius galinae* (Hymenoptera: Braconidae), biological control agent of emerald ash borer, *Agrilus planipennis* (Coleoptera: Buprestidae). **Florida Entomologist** 106:104–109.

Schüepp C, Rittiner S, Entling MH (2012) High bee and wasp diversity in a heterogeneous tropical farming system compared to protected forest. **PLoS One** 7:e52109.

Silva NAPD, Frizzas MR, Oliveira CM (2011) Seasonality in insect abundance in the "Cerrado" of Goiás State, Brazil. **Revista Brasileira de Entomologia** 55:79–87.

Tscharntke T, Rand TA, Bianchi FJ (2005) The landscape context of trophic interactions: insect spillover across the crop—noncrop interface. **Annales Zoologici Fennici** 42:421–432.

Uhler J, Redlich S, Zhang J, Hothorn T, Tobisch C, Ewald J, et al. (2021) Relationship of insect biomass and richness with land use along a climate gradient. **Nature Communications** 12:5946.

Vogel S et al. (2021) Abundance, not diversity, of host beetle communities determines abundance and diversity of parasitoids in deadwood. **Ecology and Evolution** 11:6881–6888.

Yan S et al. (2024) Effects of rainfall on parasitism and survival of *Telenomus remus*, an egg parasitoid of fall armyworm. **CABI Agriculture and Bioscience** 5:1–11.

SupplementaryTable 1: Hymenoptera families sampled with functional classification and abundance.

Id	Family	Classification	Abundance
1	Encyrtidae	Parasitoid	84
2	Ichneumonidae	Parasitoid	37
3	Braconidae	Parasitoid	53
4	Diapriidae	Parasitoid	69
5	Mymaridae	Parasitoid	74
6	Aphelinidae	Parasitoid	16
7	Bethylidae	Parasitoid	19
8	Figitidae	Parasitoid	35
9	Ceraphronidae	Parasitoid	125
10	Dryinidae	Parasitoid	8
11	Chrysididae	Parasitoid	1
12	Platygastridae	Parasitoid	31
13	Scelionidae	Parasitoid	156
14	Trichogramatidae	Parasitoid	4
15	Eupelmidae	Parasitoid	4
16	Eulophidae	Parasitoid	13
17	Mutilidae	Parasitoid	6
18	Signiphoridae	Parasitoid	5
19	Azotidae	Parasitoid	6
20	Chalcididae	Parasitoid	18
21	Tiphiidae	Parasitoid	9
22	Megaspilidae	Parasitoid	5
23	Perilampidae	Parasitoid	1
24	Agaonidae	Phytophagous	2
25	Tanaostigmatidae	Phytophagous	4
26	Sphecidae	Predator	2
27	Eucharitidae	Predator	1
28	Crabronidae	Predator	134
29	Pompilidae	Predator	208
30	Vespidae	Predator	95
31	Andrenidae	Pollinator	4
32	Apidae	Pollinator	21
33	Halictidae	Pollinator	94
34	Colletidae	Pollinator	3
35	Pteromalidae	Not classified	21
36	Eurytomidae	Not classified	11

Sticky traps in vineyard (Luberon, France)

CHAPTER 4 – Effect of forest fragment vegetation on arthropod abundance, composition and predation in adjacent vineyards

ABSTRACT - Natural habitats in agricultural landscapes increase heterogeneity and supports diverse arthropod communities with multiple ecosystem functions. However, it remains unclear which vegetation characteristics most influence insect richness, community composition, and the provision of ecosystem services in agroecosystems. This study analysis how forest vegetation affects the abundance and composition of arthropods of different functional groups in both forest fragments and adjacent vineyards, as well as predation rates across habitats. It was set up in 13 vineyards bordering forest fragments in the Luberon Mountains, southeastern France. Plant species were identified, and the cover of flowers, trees, shrubs and herbaceous vegetation were estimated. Insects were sampled using sticky traps placed in the forest, at the vineyard border, and in centre of vineyards. After five days, captured arthropods were identified and assigned to functional groups: parasitoids, predators, phytophagous insects, omnivores, and pollinators (bees). Additionally, predation rates were measured using sentinel cards with *Lucilia* sp. larvae. Insect community composition differed among forest fragments, vineyard borders, and vineyard interiors, although total abundance did not. At the vineyard border, insect composition and abundance differed between the trap sides facing the forest and those facing the vineyard, but this pattern was not observed within the vineyard indicating insect movements from the forest into the vineyards. Insect abundance in forest fragments influenced abundance at vineyard borders, but not inside vineyards. Vegetation effects were strongest at the vineyard border, particularly floral cover, which positively influenced nearly all arthropod groups except pollinators. Herbaceous and tree cover were also relevant, indicating that different vegetation components support distinct ecological functions. Predation rates were highest in forest fragments and vineyard predation was positively related to predation in adjacent forests confirming a potential resource function of forests. While plant parameters did not affect predation in forest fragments, total vegetation and shrub cover affected predation in vineyards. Although many effects were concentrated at the vineyard border, our findings highlight the key role of forest fragments in maintaining arthropods diversity and promoting ecosystem services in agricultural landscapes, particularly through floral resources. These fragments may serve as functional refuges for beneficial insects and enhance recolonization of vineyards, in particular, after disturbance. Conservation and management strategies that preserve or restore forest vegetation may thus strengthen ecological interactions and support sustainable agriculture.

Keywords: Conservation biological control, Ecosystem services, Flower resources, Habitat spillover, Landscape complexity, Natural enemies

1. Introduction

Agricultural intensification has caused a series of negative effects on biodiversity, including landscape simplification and the fragmentation of natural habitats (Haddad et al., 2015; Zabel et al., 2019). These changes affect both population and ecosystem levels, ultimately influencing the capacity of these systems to provide essential ecosystem services (González et al., 2015; Liu et al., 2018). However, fragments of natural and semi-natural habitats still contribute to biodiversity and the provision of ecosystem services in agricultural landscapes (Inclan et al., 2015; Holland et al., 2016). While crop fields provide food resources, non-crop habitats are less disturbed areas that are important for the survival and recolonization of organisms (Tscharntke et al., 2005; Medeiros et al., 2022). Thus, landscape fragmentation can either facilitate or hinder the movement of organisms between habitats, affecting ecosystem services (Mitchell et al., 2015; Novaes et al., 2024). The effect of fragmentation on service provision depends on the involved species, the ecosystem functions considered, and local characteristics (Mitchell et al., 2015).

Insect movement between habitats is often associated with spillover effects between crop and non crop areas (Tscharntke et al., 2012; González et al., 2016) that may occur from semi-natural habitats to crop field, but also in the opposite direction (Blitzer et al., 2012; Frost et al., 2015). The spillover from semi-natural habitats to crop fields can benefit crops by increasing the abundance of biological control agents or pollinators (Aviron et al., 2016; Segre et al., 2020). However, the magnitude and direction of these movements depend on many factors, including the vegetation structure of fragments and the distance to the habitat edge (Ferrante et al., 2017; Proesmans et al., 2019).

Forest fragments in agricultural landscapes represent such natural or semi-natural habitat types that may preserve insect populations and thus contribute to ecosystem services (Decocq et al., 2016; Milligan et al., 2016; Medeiros et al., 2022). Several studies demonstrated this role of forest fragments but focused on habitat quantity and configuration, whereas the habitat quality has rarely been tested (Martin et al., 2016; Schuldt et al., 2018; Haan et al., 2020). Vegetation and habitat stratification are important habitat quality parameters

since they have a strong influence on resource provision and thus on insect movement (Randlkofer et al., 2010), directly affecting the occurrence and activity of different functional groups (Ober and Hayes, 2008; Obermaier et al., 2008).

Greater plant species richness and structural heterogeneity can enhance the availability of key resources, including shelter, food sources such as pollen, nectar, honeydew, and extrafloral nectar, as well as alternative prey (Landis et al., 2000; Gurr et al., 2017). Vegetation also helps create favorable microclimatic conditions that support insect development and activity, while offering protection against abiotic stressors and pesticide applications. In addition, more heterogeneous vegetation structure may reduce antagonistic interactions, such as intraguild predation, by increasing spatial separation and niche availability (Landis et al., 2000; Gontijo et al., 2019). Floral resources are particularly important for natural enemies, which often depend on them during part or all of their life cycles, either obligatorily or as a supplemental food source (Gardarin et al., 2018). Beyond direct nutritional benefits, floral resources can enhance other aspects, such as those related to longevity and reproduction (He et al., 2021). Specific vegetation characteristics, such as species composition, flower abundance, canopy cover, and shrub density, have been associated with variation in the composition of insect communities in forests (Hanula et al., 2015; Perone et al., 2018; Knuff et al., 2020). However, studies that comprehensively assess how these vegetation features influence the functional structure of insect communities and, consequently, the provision of ecosystem services in agroecosystems are still rare.

Biological control is an important ecosystem service that is related to semi-natural habitat quality and may contribute to the reduction of chemical pest control (Holland et al., 2017; Noriega et al., 2018). Predation of sentinel prey has been widely used as a proxy to evaluate this service, as it reflects the abundance and activity of natural enemies in agroecosystems (Lövei and Ferrante, 2017; Puliga et al., 204). Studies in southern France vineyard landscapes have shown that predation pressure is favoured by species-rich inter-row vegetation (Blaise et al., 2021; Rocher et al., 2024). These findings highlight the potential of preserving

semi-natural vegetation to enhance natural pest control in vineyards through habitat provision for beneficial arthropods.

The present study aims at evaluating the role of forest vegetation in shaping arthropods communities and mediating ecosystem service provision in adjacent vineyards. Specifically, we analysed how woodland vegetation affects insect abundance and community composition in both woodlands and adjacent vineyards, and whether forest fragments act as sources and refuges for insects moving into vineyards. Additionally, we investigated whether woodland vegetation affects insect predation rates, using sentinel prey as an indicator of biological control service. We hypothesize that: (1) the plant community composition of forest fragments affects the abundance, composition of arthropods communities and predation function in both woodlands and adjacent vineyard habitats, (2) arthropods move from woodlands to adjacent vineyards, (3) beneficial arthropods abundance and predation are mainly influenced by floral resources in forest fragments and, (4) predation rates in woodlands positively influence predation rates in vineyards, suggesting a spillover of ecosystem services.

2. Material and methods

2.1. Study sites and design

The study was conducted between May and June 2024 in 13 vineyards and adjacent woodlands located in the Luberon mountains, Southeastern France (Figure 1). This region has a Mediterranean climate, characterized by hot, dry summers, mild winters, and peak rainfall in spring and autumn, with an annual average of 700 mm (1991–2020 data from the Pertuis meteorological station). We selected vineyards with spontaneous inter-row vegetation and adjacent woodlands. Usually, one out of two inter-rows were tilled whereas the other half was covered with vegetation that was mown once to twice in May and June. No

insecticide treatments were applied during the sampling period, but winegrowers used fungicides and in some cases herbicides during the study season. The surrounding landscape was predominantly covered with vineyards, interspersed with few other crops such as cherry, apple, and olive orchards, fields of durum wheat and lavender, and semi-natural habitats including woodlands.

Figure 1: Geographical position of analysed vineyards in Luberon, France.

2.2. Vegetation analysis

To plant species composition of forest fragments, all plant species in an area of 10 x 20 m around the sticky traps were identified. The percentage cover of each plant was estimated as the vertical projection of aboveground plant organs. Additionally, the cover of flowers, trees, shrubs and herbaceous vegetation as well as total vegetation cover were estimated.

2.3. Arthropod sampling

Sticky traps were placed mid-May in the forest fragment (5m from the border), in the first vineyard row (vineyard border), and at a distance of 10m from the first vineyard row (inner part of the vineyard). At each of these three distances, three yellow sticky traps (20 x 25cm) spaced by 10m were placed resulting in nine

traps per site and 117 traps in total (Figure 2). The traps were removed after five days of exposure. For vineyard traps, insects were analysed separately at both sides of the traps. We assumed that insects with a higher abundance on the forest than on the vineyard side had moved from the forets into the vineyards. The sampled arthropods (insects, spiders and harvestman) were identified to order and family level. Additionally, arthropods were classified into functional groups using knowledge on life-history feeding features of the majority of species in each order or family: parasitoids, predators, phytophagous, omnivores and pollinators (bees). For insects that change feeding between larval and adult stages, we used the larval feeding behaviour, as larvae generally have higher resource demands and are the primary consumers in the life cycle.

Figure 2: Sampling design. Sticky traps were fixed in three lines, in the forest fragment in the first vineyard row, and inside the vineyard. Moreover, *Lucilia* sp. larvae predation cards were fixed in the forest fragment and inside vineyards.

2.4. Predation rate

In order to evaluate the influence of forest fragments on insect predation, sentinel cards (2 × 2cm) were placed in the forest fragment and vineyard transects at a distance of 10 m from the field border (Figure 3). In each habitat, twenty white cards were placed 5m apart containing one living larva of *Lucilia* sp.

(Diptera: Calliphoridae) resulting in 40 cards per vineyard and 520 cards in total. *Lucilia* larvae have a similar size and shape as caterpillars attacking grapevine and were purchased from a fishing store. The cards were pinned to the trunks and branches of grapevine plants at a height of 1m. The larvae were exposed for a period of 24 hours, and damage to the larvae or absence were considered predation events.

2.5. Statistical analysis

To compare community composition across the three habitats (woodland, vineyard border, and vineyard center) and betwee trap sides of vineyard traps (facing the forest fragment vs. facing the vineyard), we used non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity. Differences among habitats were tested using permutational multivariate analysis of variance (PERMANOVA). Statistical tests were performed using the adonis2 function of the vegan package in R with 999 permutations.

We ran generalized linear models (GLMs) to analyze the influence of insect abundance in forest fragments on insect abundance at the vineyard border and within the vineyard. We further included trap side (facing the forest fragment vs. facing the vineyard) as a factor in the model to analyse the direction of movements. A Poisson distribution was used when data were not overdispersed, while a negative binomial error distribution was applied in cases of overdispersion. A similar model was run to test the relationships between *Lucilia* larvae predation in forest fragments and vineyards using the proportion of predated larvae in the vineyard as a function of the proportion of predated larvae in the forest fragment. Since no overdispersion was detected, we fitted a GLM with a binomial error distribution and logit link function.

Prior to fitting the models with vegetation characteristics, we tested for multicollinearity using the variance inflation factor (VIF) of the car package. This analysis was performed separately for each habitat type (woodland, vineyard border, and vineyard center). Variables with VIF values above 2 were excluded

to avoid collinearity. In all cases, plant species richness showed high collinearity (VIF > 2) and was therefore excluded. We analyzed the effects of forest plant parameters (total, flower, tree, shrub, and herbaceous cover) on the abundance of insects using generalized linear mixed models (GLMM) in the glmmTMB package with a negative binomial distribution to account for overdispersion. "Site" was included as a random effect to control for potential spatial variation among sampling locations. Larval predation was analysed in the same way using binomial error distribution and logit link function. All analyses were run using R version 3.6.2 (R Core Team, 2025).

3. Results

We found 187 plant species in the woodlands of our study. *Quercus pubescens* (Fagaceae), *Hedera helix* (Araliaceae) and *Cornus sanguinea* (Cornaceae) were the most frequent species (Supplementary Table 1). We collected 24,629 arthropods, including 2665 parasitoids, 1632 predators, 9038 phytophagous, 20 pollinators and 11274 omnivorous (Supplementary Table 2).

3.1. Arthropod community composition in vineyards and adjacent woodlands

The arthropod community composition was significantly different between woodland, vineyard border and vineyard center ($F = 9.440$, $p = 0.001$) (Figure 4a). At the border of vineyards, the community composition also differed between the trap side facing forest and vineyards ($F = 3.448$, $p = 0.007$) (Figure 4b). However, comparing the two sides of the traps in the vineyard center there is no difference in arthropod community composition ($F = 1.159$, $p = 0.292$).

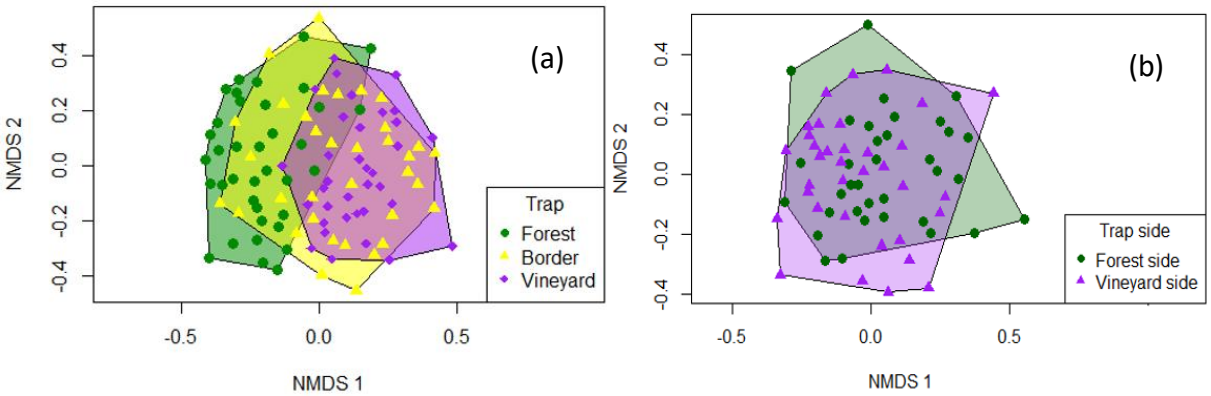

Figure 4. Non-Metric Multidimensional Scaling (NMDS) of arthropod family communities (a) in forest fragments and adjacent vineyards (border, central rows), (b) in border trap sides (facing forest vs facing vineyard).

3.2. Relationships between arthropod abundance in woodlands and adjacent vineyards

We did not find differences in the total abundance of arthropods between the three habitat types ($\chi^2 = 0.829$, $p = 0.363$) but the abundance of arthropods in vineyard borders was significantly related to the abundance in forest fragments ($\chi^2 = 4.335$, $p = 0.037$). However, there was no effect of arthropod abundance in the forest fragments on arthropods abundance inside vineyards ($\chi^2 = 1.698$, $p = 0.193$).

In the border of the vineyards, trap side had a significant effect on insect abundance ($\chi^2 = 7.359$, $p = 0.007$) being higher at side facing the forest fragment (Figure 5a). In the center of the vineyards, the trap side effect on insect abundance disappeared ($\chi^2 = 0.829$, $p = 0.363$) (Figure 5b).

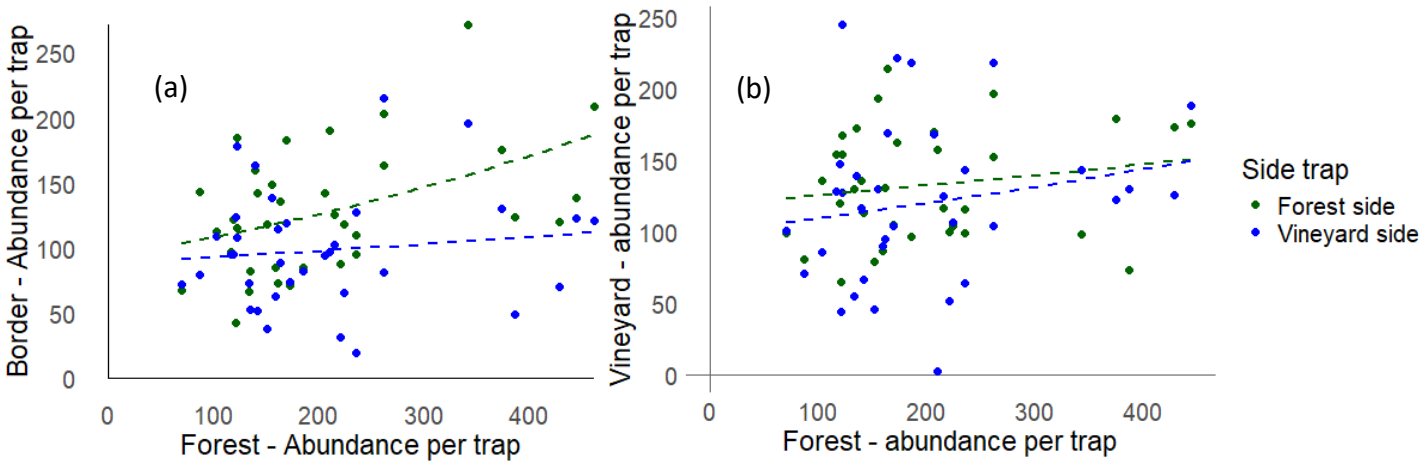

Figure 5. Relationship between arthropod abundance in forest fragments and vineyards and effect of trap side (facing forest vs facing vineyard) (a) in the vineyard border (b) in the vineyard center.

3.3. Relationships between woodland plant community composition and arthropod groups

Within woodlands, vegetation characteristics were weakly correlated with the abundance of benefial and phytophagous insects. The only significant relationship was detected between shrub cover and parasitoid abundance being positive (Supplementary Table 3). The relationships between woodland vegetation characteristics and arthropod groups were stronger in vineyard borders. Flower cover had the strongest effect, being significantly positive for almost all analysed insect groups, except for pollinators. Furthermore, tree cover showed significant relationships with total arthropod and omnivore abundance. Herbaceous cover significantly influenced abundance of predators, phytophagous and total arthropod abundance (Table 1, Fig. 6). At a distance of 10 m in the vineyard center, most significant relationships between woodland vegetation characteristics and abundance of beneficial and phytophagous groups disappeared. Significant relationships were still detected between total plant cover and parasitoid abundance, between flower cover and predator abundance and between herbaceous cover and pollinator abundance (Table 2, Fig. 6).

Table 1. Results of Generalized Linear Mixed Models analysing relationships between woodland vegetation characteristics and the abundance of arthropod groups in **adjacent vineyard borders**. P-values in bold are significant at P<0.05.

Cover (%)	Total arthropod abundance		Parasitoid abundance		Predator abundance		Phytophagous abundance		Omnivorous abundance		Pollinator abundance	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Total	0.0056	0.4216	0.0286	**0.0101**	0.0080	0.4862	0.0115	0.3312	-0.0044	0.6486	-0.0869	0.1010
Flower	0.1076	**0.0010**	0.1351	**0.0062**	0.1045	**0.0468**	0.1420	**0.0104**	0.1223	**0.0070**	-12.900	0.9998
Tree	-0.0079	**0.0001**	0.0031	0.2775	-0.0011	0.7613	-0.0056	0.1065	-0.0136	**<0.001**	0.0155	0.3871
Shrub	-0.0013	0.6250	0.0039	0.3181	-0.0049	0.3043	0.0029	0.5220	-0.0040	0.2882	0.0050	0.8514
Herbaceous	0.006	**0.0299**	0.0038	0.3420	0.017743	**0.0002**	0.0128	**0.0084**	-0.0009	0.8128	0.0097	0.7323

Table 2. Results of Generalized Linear Mixed Models (glmmTMB) analysing the relationships between woodland vegetation characteristics and the abundance of arthropod groups in **central rows of adjacent vineyards**. P-values in bold are significant at P<0.05.

Cover (%)	Total arthropod abundance		Parasitoid abundance		Predator abundance		Phytophagous abundance		Omnivorous abundance		Pollinator abundance	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Total	0.0001	0.9895	0.0355	**0.0144**	-0.0040	0.7798	0.0032	0.7873	-0.0106	0.4790	0.0032	0.7873
Flower	0.0282	0.5801	0.0656	0.3272	0.1817	**0.0034**	0.0347	0.5329	0.0236	0.7341	0.0347	0.5329
Tree	-0.0031	0.3428	0.0068	*0.0914*	-0.0023	0.5929	0.0009	0.8022	-0.0076	*0.0827*	0.0009	0.8022
Shrub	0.0019	0.6577	0.0052	0.3205	-0.0072	0.1853	0.0040	0.3874	0.0011	0.8438	0.0040	0.3874
Herbaceous	0.0058	0.1894	0.0063	0.2596	-0.0057	0.3323	0.0123	0.0116	0.0021	0.7315	0.0123	**0.0116**

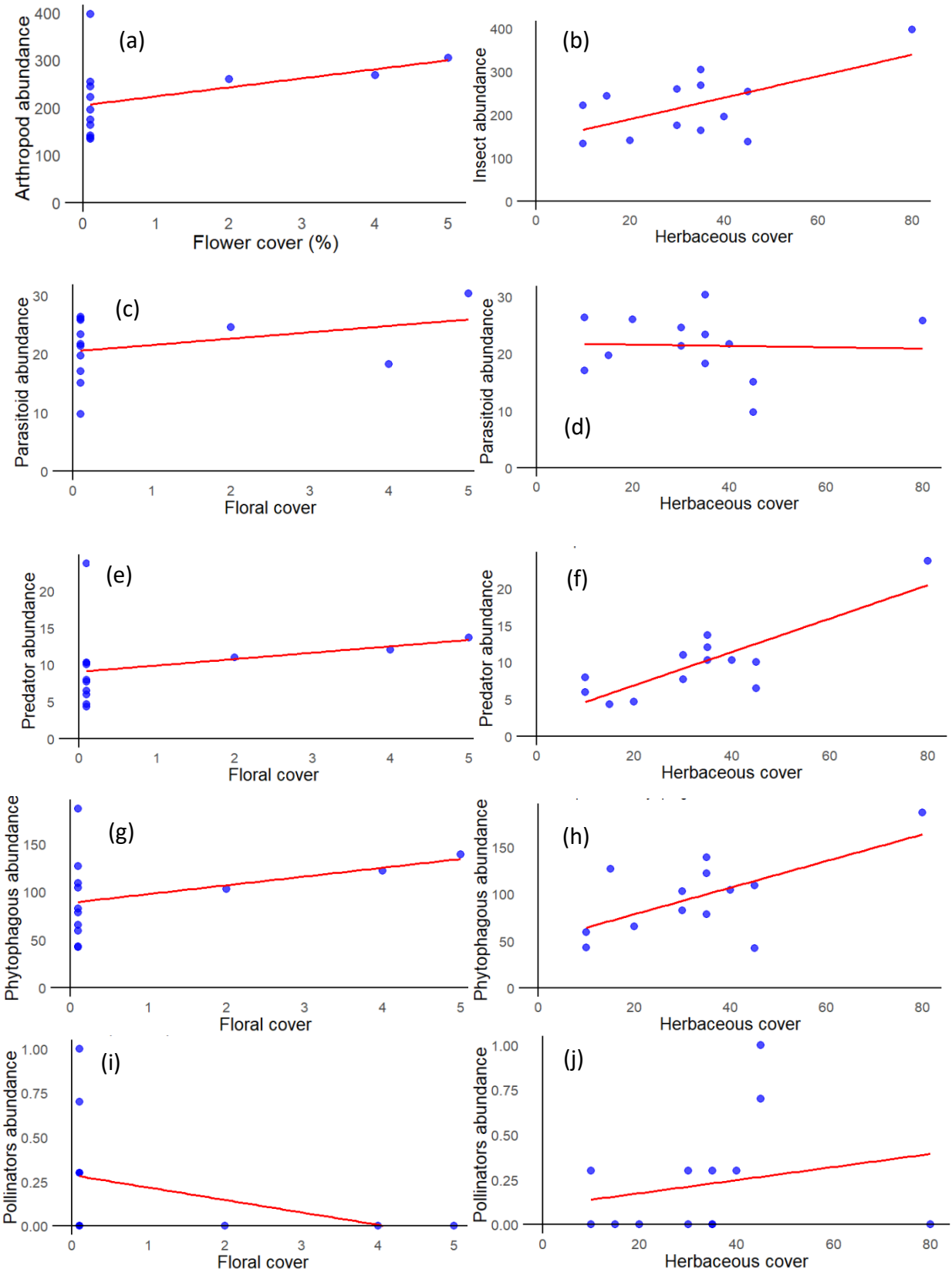

Figure 6. Influence of flower cover (a, c, e, g, i) and herbaceous cover (b, d, f, h, j) on the abundance of different arthropod groups in adjacent vineyard borders.

3.4. Relationships between predation in woodlands and vineyards

Habitat (forest fragment or vineyard) had a significant effect on the predation rate of *Lucilia* larvae (χ^2= 33.212, $p < 0.001$) being higher in forest fragments (Figure 7). The influence of the forest predation rate on the predation rate in the vineyard center was significantly positive (χ^2= 3.8742, $p = 0.049$).

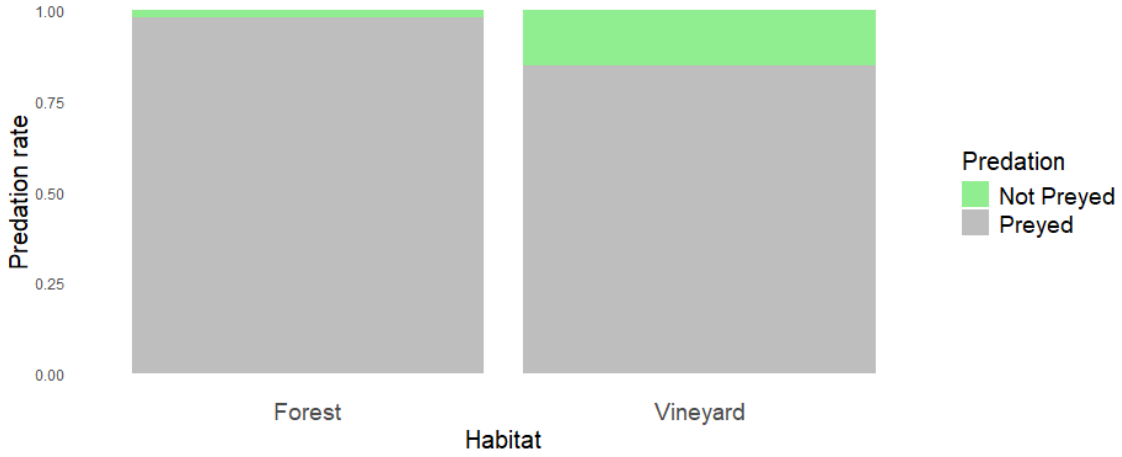

Figure 7. Predation rate of *Lucilia* larvae in woodlands and the center of adjacent vineyards.

Woodland plant community characteristics were not related to predation in forest fragments. In the vineyard center, total cover had a negative effect and shrub cover had a marginally significant positive effect on predation rate (Table 4).

Table 4. Results of generalized linear mixed models analysing the relationships between woodland vegetation characteristics and the predation rate of *Lucilia* larvae within woodlands and in the center of adjacent vineyards.

Cover (%)	Forest predation rate		Vineyard predation rate	
	Estimate	P	Estimate	P
Total	0.0590	0.4932	-0.1268	**0.0441**
Flower	-0.0939	0.7790	-0.4234	0.1166
Tree	0.0396	0.2785	0.0092	0.5305
Shrub	0.0176	0.5699	0.0321	*0.0883*
Herbaceous	0.0543	0.2197	0.0038	0.8324

4. Discussion

Arthropod communities differed in composition between vineyard center, border and adjacent forest although total insect abundance was similar. However, communities of these three habitats shared many taxa, suggesting inter-habitat insect movements. Such movements were further supported by positive relationships between insect abundance in forests and vineyard border. Additionally, relationships were stronger on the vineyard trap side facing the forest indicating directional movements from forests into vineyards. However, these relationships did not extend into the vineyard center suggesting that the exchange between forests and vineyards is limited to the vineyard borders. Our analysis of vegetatation characteristics in adjacent forest demonstrated particularly positive effects of flowering nectariferous plants and plant species richness on beneficial arthropod abundance in vineyard borders. Some of these effects were also visible in central parts of vineyard but most positive relationships vanished.

Previous studies have documented arthropods movements both from natural habitats to agricultural crops and vice versa, depending on local conditions (Frost et al., 2015; Zumoffen et al., 2018). In agricultural landscapes, such flows are highly dynamic. Under stable environmental conditions, insects may move into crops, whereas after disturbance, the movement may reverse

(Schellhorn et al., 2014; Segoli et al., 2020). Insect-specific traits, such as their degree of generalism and sex, also influence their ability to move between habitats (Schellhorn et al., 2008; Frost et al., 2015; Rösch et al., 2015). In this way, forest fragments may function as refuges, enabling insects to recolonize nearby crops after disturbances such as harvesting or pesticide application, thereby reinforcing their role in maintaining biodiversity and ecosystem services over time (Santos et al., 2018). Vineyards are regularly disturbed by cultural practices such as mowing, tillage of non-vegetated inter-rows, grapevine pruning, herbicide and fungicide treatments (Rocher et al. 2024). Thus, refuges outside vineyards are crucial for recolonisation. Habitat quality such as plant species composition providing resources and shelter may largely influence this refuge function (Bischoff et al. 2016; Pollier et al. 2018).

Despite similar total arthropods abundance between habitats and positive relationships between beneficial insect abundance in forest and vineyards, compositional differences still reflect the strong differences in abiotic conditions related to crop management and vegetation structure (Schaffers et al., 2008; Sinclair et al., 2024). This underscores the importance of community composition analyses, rather than relying solely on richness or abundance metrics when assessing ecological impacts of environmental change. The dilution of positive relationships between insect abundances in crop fields and neighbouring semi-natural habitats towards central parts of crop fields is well documented and explains the weaker correlations between forest fragments and the vineyard center compared to the vineyard border (Tylianakis et al., 2004; Pollier et al. 2019. The limited mobility may be the result of lower resource availability in vineyards and the energetic costs of movements (Heimpel & Jervis 2005; Wanner et al. 2006). This explanation is supported by the absence of differences in insect community composition between the two sides of the traps in the vineyard center.

The influence of vegetation characteristics in forest fragments on arthropod communities varied among functional groups, possibly due to differences in resource use and ecological roles, as reported in earlier studies (Šálek et al., 2015; Knuff et al., 2020). Moreover, the effect of vegetation also differed among habitats, being more evident at the vineyard border. In the forest

fragments and vineyard interiors, vegetation parameters had a limited influence on insect abundance. This suggests that the influence of forest fragments is stronger in adjacent areas and progressively weakens toward the interior of the crop field. Vegetation structure had no effect on predation rates within forest fragments, which may indicate that other factors are more decisive in structuring insect communities in these environments. Alternatively, the combination of different vegetation strata may create sufficient heterogeneity to support high functional diversity and maintain ecosystem services such as predation (Leidinger et al., 2021; Bastida et al., 2024). In forest fragments, only shrub and herbaceous cover influenced parasitoid abundance. Previous studies have reported positive effects of herbaceous and shrubby vegetation on parasitoids, likely due to increased habitat complexity and additional resources that enhance parasitoid persistence and reproductive success (Arnan et al., 2011; Burks and Philpott, 2017).

At the vineyard border, floral cover was the key driver of the abundance all benificial arthropods groups except pollinators. This highlights the role of flowers as resources for a variety of insect groups, including predators and parasitoids (Carrié et al., 2012; Lu et al., 2014). Floral resources are particularly important for insects such as hoverflies, lacewings, and parasitoids, that change nutrition between life cycle stages. Often larvae are carnivorous, but adults require nectar and pollen (Russell, 2015; Leman et al., 2023; González et al., 2024). Although predatory throughout their life cycle, other natural enemies, such as ladybirds, may additionally benefit from floral resources, because they increase adult longevity and fecundity by complementing their carnivorous diet (Pollier et al., 2018; Hameed et al., 2024). The lack of a response among pollinators may be linked to floral preference specificity or the low attractiveness of available floral species (Alignier et al., 2023), or the low number of specimens collected. Furthermore, pollinators are more mobile than most other insect groups considered in this study. Local vegetation characteristics may thus be less important if more distant floral resources are available (Rocher et al. 2024). The effect of floral resources for predators was also apparent in central parts of vineyards, suggesting effective spillover. This finding highlights the importance of flowering, nectar-producing plants in field margins as a sustainable management

strategy potentially increasing the abundance of natural enemies in crops (Saunders et al., 2018; Gontijo, 2019).

Tree cover was negatively associated with omnivore and total arthropod abundance. Additionally, total vegetation cover had a negative effect on predation rates. These effects may be related to the structure of adjacent forest fragments, where taller vegetation may act as physical barriers to arthropod movement (La Cava et al., 2024), or reduce light availability and temperature (Perone et al., 2018). However, the negative effect of tree cover may also be indirect since a dense tree canopy hampers the development of herbaceous understory vegetation. Herbaceous cover positively influenced total arthropod abundance, particularly predators and herbivores. In Europe, nectar production is largely limited to herbaceous vegetation whereas trees are usually wind-pollinated and do not provide nectar as the most important floral resource. However, the simultaneous significance of flower cover and herbaceous plant species suggests that herbacous vegetation also provides other habitat functions such as shelter, palatable vegetative biomass (herbivores) alternative prey (predators) and structural heterogeneity (Wenninger and Inouye, 2008; Scherber et al., 2014; Shapira et al., 2018). Herbaceous cover in forest fragments also affected pollinator abundance but only in central parts of the vineyard but not in the border. The higher mobility of pollinators may explain this effect at a higher distance from the forest edge. However, it is still a bit surprising that herbaceous but not flower cover positively influenced pollinator abundance in vineyards. Similarly to predators, the effect may be related to other habitat functions such as shelter (Quinlan et al., 2022).

Although predation rates on *Lucilia* larvae reached high values in both environments, they were significantly higher in forest fragments than in central parts of vineyards. This highlights the importance of such natural or semi-natural habitats in maintaining ecological interactions such as predation (Rusch et al., 2016). Furthermore, predation rates in the vineyard increased in response to predation observed in adjacent forest fragments, confirming a potential spillover of natural enemies into vineyards. However, we did not find a positive effect of flower cover on predation in vineyards whereas the relationship was positive for

predator abundance. The effect size of forest flower cover on predators may have been too small to obtain a significant effect on predation. Furthermore, predators captured by sticky traps may not be the same attacking *Lucilia* larvae. Previous studies showed that ant were major predators of *Lucilia* larvae in vineyards (Blaise et al., 2022; Rocher et al., 2022) and sticky traps are not the best method to obtain information on ant abundance. We still found an influence of forest vegetation characteristics (shrub, total vegetation cover) on predation in central vineyard row confirming that the conservation of forests or forest fragments may be an effecient strategy for promoting functional biodiversity and associated ecosystem services in vineyards.

Our results demonstrated that forest fragments contribute significantly to arthropod diversity in vineyards promoting essential ecological interactions such as predation or pollination. Although effects are partially limited to the vineyard border, management and conservation strategies should involve these natural or semi-natural habitats. Agri-environment schemes including adaptive forest management (préservation of herbaceous understory vegetation) and restoration (planting native tree and shrub species) may help to maintain or enhance diversity and ecosystem services.

References

Alignier A et al. (2023) Floral resource maps: a tool to explain flower-visiting insect abundance at multiple spatial scales. **Landscape Ecology** 38:1511–1525.

Arnan X, Bosch J, Comas L, Gracia M, Retana J (2011) Habitat determinants of abundance, structure and composition of flying Hymenoptera communities in mountain old-growth forests. **Insect Conservation and Diversity** 4:200–211.

Aviron S, Poggi S, Varennes YD, Lefèvre A (2016) Local landscape heterogeneity affects crop colonization by natural enemies of pests in protected horticultural cropping systems. **Agriculture, Ecosystems & Environment** 227:1–10.

Bastida JM et al. (2024) Effects of plant leaf traits, abundance and phylogeny on differentiation of herbivorous insect assemblages in Mediterranean mixed forest. **European Journal of Forest Research** 143:1149–1164.

Bischoff A et al. (2016) Effects of spontaneous field margin vegetation and surrounding landscape on *Brassica oleracea* crop herbivory. **Agriculture, Ecosystems & Environment** 223:135–143.

Blaise C et al. (2021) The key role of inter-row vegetation and ants on predation in Mediterranean organic vineyards. **Agriculture, Ecosystems & Environment** 311:107327.

Blaise C et al. (2022). Vegetation increases abundances of ground and canopy arthropods in Mediterranean vineyards. **Scientific Reports** 12: 3680.

Blitzer EJ et al. (2012) Spillover of functionally important organisms between managed and natural habitats. **Agriculture, Ecosystems & Environment** 146:34–43.

Burks JM, Philpott SM (2017) Local and landscape drivers of parasitoid abundance, richness, and composition in urban gardens. **Environmental Entomology** 46:201–209.

Carrié RJ, George DR, Wäckers FL (2012) Selection of floral resources to optimise conservation of agriculturally-functional insect groups. **Journal of Insect Conservation** 16:635–640.

Decocq G et al. (2016) Ecosystem services from small forest patches in agricultural landscapes. **Current Forestry Reports** 2:30–44.

Ferrante M, González E, Lövei GL (2017) Predators do not spill over from forest fragments to maize fields in a landscape mosaic in central Argentina. **Ecology and Evolution** 7:7699–7707.

Frost CM, Didham RK, Rand TA, Peralta G, Tylianakis JM (2015) Community-level net spillover of natural enemies from managed to natural forest. **Ecology** 96:193–202.

Gardarin A, Plantegenest M, Bischoff A, Valantin-Morison M (2018) Understanding plant–arthropod interactions in multitrophic communities to improve conservation biological control: useful traits and metrics. **Journal of Pest Science** 91:943–955.

González E, Salvo A, Valladares G (2015) Arthropods on plants in a fragmented Neotropical dry forest: a functional analysis of area loss and edge effects. **Insect Science** 22:129–138.

González E, Salvo A, Defagó MT, Valladares G (2016) A moveable feast: insects moving at the forest-crop interface are affected by crop phenology and the amount of forest in the landscape. **PLoS One** 11:e0158836.

Gontijo LM (2019) Engineering natural enemy shelters to enhance conservation biological control in field crops. **Biological Control** 130:155–163.

González E, Bianchi FJJA, Eckerter PW, Entling MH (2024) Linking landscape structure, floral resource distribution, pollen use and movement distances of a generalist predator. **Journal of Applied Ecology** 61:2798–2808.

Gurr GM, Wratten SD, Landis DA, You M (2017) Habitat management to suppress pest populations: progress and prospects. **Annual Review of Entomology** 62:91–109.

Haan NL, Zhang Y, Landis DA (2020) Predicting landscape configuration effects on agricultural pest suppression. **Trends in Ecology and Evolution** 35:175–186.

Haddad NM et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. **Science Advances** 1:e1500052.

Hameed O, Ugine T, Westbrook A, Losey J (2024) Consumption of nectar-like sugar solutions promotes longevity and fecundity in the ladybird beetles *Harmonia axyridis* and *Hippodamia convergens*. **Arthropod-Plant Interactions** 18(4):763–770.

Hanula JL, Horn S, O'Brien JJ (2015) Have changing forests conditions contributed to pollinator decline in the southeastern United States? **Forest Ecology and Management** 348:142–152.

He X, Kiær LP, Jensen PM, Sigsgaard L (2021) The effect of floral resources on predator longevity and fecundity: A systematic review and meta-analysis. **Biological Control** 153:104476.

Holland JM et al. (2016) Structure, function and management of semi-natural habitats for conservation biological control: a review of European studies. **Pest Management Science** 72(9):1638–1651.

Holland JM et al. (2017) Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. **Agronomy for Sustainable Development** 37:1–23.

Inclan DJ, Cerretti P, Marini L (2015) Landscape composition affects parasitoid spillover. **Agriculture, Ecosystems & Environment** 208:48–54.

Knuff AK et al. (2020) Insect abundance in managed forests benefits from multi-layered vegetation. **Basic and Applied Ecology** 48:124–135.

La Cava S et al. (2024) Moths in space: The below-canopy structure of forest drives abundance and mobility-related traits of moth communities. **Science of The Total Environment** 921:171056.

Landis DA, Wratten SD, Gurr GM (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. **Annual Review of Entomology** 45(1):175–201.

Leidinger J et al. (2021) Shifting tree species composition affects biodiversity of multiple taxa in Central European forests. **Forest Ecology and Management** 498:119552.

Leman A et al. (2023) Sugar and pollen supply enhances aphid control by hoverflies in strawberry. **Biological Control** 186:105347.

Liu J et al. (2018) How does habitat fragmentation affect the biodiversity and ecosystem functioning relationship? **Landscape Ecology** 33:341–352.

Lövei GL, Ferrante M (2017) A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. **Insect Science** 24:528–542.

Lu ZX et al. (2014) Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: prospects for enhanced use in agriculture. **Insect Science** 21:1–12.

Martin EA, Seo B, Park CR, Reineking B, Steffan-Dewenter I (2016) Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. **Ecological Applications** 26:448–462.

Mazzi D, Dorn S (2012) Movement of insect pests in agricultural landscapes. **Annals of Applied Biology** 160:97–113.

Medeiros HR et al. (2022) Landscape composition regulates the spillover of beneficial insects between forest remnants and adjacent coffee plantations. **Perspectives in Ecology and Conservation** 20:111–116.

Milligan MC, Johnson MD, Garfinkel M, Smith CJ, Njoroge P (2016) Quantifying pest control services by birds and ants in Kenyan coffee farms. **Biological Conservation** 194:58–65.

Mitchell MG et al. (2015) Reframing landscape fragmentation's effects on ecosystem services. **Trends in Ecology and Evolution** 30(4):190–198.

Noriega JA et al. (2018) Research trends in ecosystem services provided by insects. **Basic and Applied Ecology** 26:8–23.

Novaes DR et al. (2024) Natural habitat connectivity and organic management modulate pest dispersal, gene flow, and natural enemy communities. **Ecological Applications**, 34(2): e2938.

Ober HK, Hayes JP (2008) Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. **Forest Ecology and Management** 256:1124–1132.

Obermaier E, Heisswolf A, Poethke HJ, Randlkofer B, Meiners T (2008) Plant architecture and vegetation structure: two ways for insect herbivores to escape parasitism. **European Journal of Entomology** 105:233.

Pollier A, Guillomo L, Tricault Y, Plantegenest M, Bischoff A (2018) Effects of spontaneous field margin vegetation on the regulation of herbivores in two winter crops. **Basic and Applied Ecology** 27: 71-82.

Pollier A, Tricault Y, Plantegenest M, Bischoff A (2019) Sowing of margin strips rich in floral resources improves herbivore control in adjacent crop fields. **Agricultural and Forest Entomology** 21:119–129.

Proesmans W, Bonte D, Smagghe G, Meeus I, Verheyen K (2019) Importance of forest fragments as pollinator habitat varies with season and guild. **Basic and Applied Ecology** 34:95–107.

Puliga GA, Sprangers T, Huiting H, Dauber J (2024) Management practices influence biocontrol potential of generalist predators in maize cropping systems. **Entomologia Experimentalis et Applicata** 172:132–144.

Quinlan GM et al. (2022) Grassy–herbaceous land moderates regional climate effects on honey bee colonies in the Northcentral US. **Environmental Research Letters** 17:064036.

Randlkofer B, Obermaier E, Hilker M, Meiners T (2010) Vegetation complexity—the influence of plant species diversity and plant structures on plant chemical complexity and arthropods. **Basic and Applied Ecology** 11:383–395.

R Core Team (2025) **R**: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rocher L, Melloul E, Blight O, Bischoff A (2024) Effect of spontaneous vegetation on beneficial arthropods in Mediterranean vineyards. **Agriculture, Ecosystems & Environment** 359:108740.

Rösch V, Tscharntke T, Scherber C, Batáry P (2015) Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. **Oecologia** 179: 209-222.

Rusch A et al. (2016) Agricultural landscape simplification reduces natural pest control: A quantitative synthesis. **Agriculture, Ecosystems & Environment** 221:198–204.

Russell M (2015) A meta-analysis of physiological and behavioral responses of parasitoid wasps to flowers of individual plant species. **Biological Control** 82:96–103.

Šálek M et al. (2015) Edges within farmland: Management implications of taxon specific species richness correlates. **Basic and Applied Ecology** 16:714–725.

Santos LA, Bischoff A, Fernandes OA (2018) The effect of forest fragments on abundance, diversity and species composition of predatory ants in sugarcane fields. **Basic and Applied Ecology** 33:58–65.

Saunders ME, Luck GW (2018) Interaction effects between local flower richness and distance to natural woodland on pest and beneficial insects in apple orchards. **Agricultural and Forest Entomology** 20:279–287.

Schaffers AP, Raemakers IP, Sýkora KV, Ter Braak CJ (2008) Arthropod assemblages are best predicted by plant species composition. **Ecology** 89:782–794.

Schellhorn NA, Bellati J, Paull CA, Maratos L (2008) Parasitoid and moth movement from refuge to crop. **Basic and Applied Ecology** 9:691–700.

Schellhorn NA, Bianchi FJJA, Hsu CL (2014) Movement of entomophagous arthropods in agricultural landscapes: links to pest suppression. **Annual Review of Entomology** 59:559–581.

Scherber C, Vockenhuber EA, Stark A, Meyer H, Tscharntke T (2014) Effects of tree and herb biodiversity on Diptera, a hyperdiverse insect order. **Oecologia** 174:1387–1400.

Schuldt A et a.l (2018). Biodiversity across trophic levels drives multifunctionality in highly diverse forests. **Nature communications** 9: 2989.

Segoli M, Kishinevsky M, Rozenberg T, Hoffmann I (2020) Parasitoid abundance and community composition in desert vineyards and their adjacent natural habitats. **Insects** 11:580.

Segre H, Segoli M, Carmel Y, Shwartz A (2020) Experimental evidence of multiple ecosystem services and disservices provided by ecological intensification in Mediterranean agro-ecosystems. **Journal of Applied Ecology** 57:2041–2053.

Shapira I et al. (2018) Habitat use by crop pests and natural enemies in a Mediterranean vineyard agroecosystem. **Agriculture, Ecosystems & Environment** 267:109–118.

Sinclair JS et al. (2024) Effects of land cover and protected areas on flying insect diversity. **Conservation Biology** e14425.

Tscharntke T, Rand TA, Bianchi FJ (2005) The landscape context of trophic interactions: insect spillover across the crop—noncrop interface. **Annales Zoologici Fennici**:421–432.

Tscharntke T et al. (2012) Moderação da paisagem em padrões e processos de biodiversidade – oito hipóteses. **Biological Reviews** 87:661–685.

Tylianakis JM, Didham RK, Wratten SD (2004) Improved fitness of aphid parasitoids receiving resource subsidies. **Ecology** 85:658–666.

Wenninger EJ, Inouye RS (2008) Insect community response to plant diversity and productivity in a sagebrush–steppe ecosystem. **Journal of Arid Environments** 72:24–33.

Zabel F et al. (2019) Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. **Nature Communications** 10:2844.

Zumoffen L, Signorini M, Salvo A (2018) Bidirectional movement of aphid parasitoids (Braconidae: Aphidiinae) between crops and non-crop plants in agroecosystems of central Argentina. **Applied Entomology and Zoology** 53:1–9.

Supplementary Table 1: Frequency of plant species: number of occupied forest fragments (n=10)

Family	Species	Frequency (no. of sites)
Fagaceae	*Quercus pubescens*	13
Rubiaceae	*Rubia peregrina*	11
Araliaceae	*Hedera helix*	13
Geraniacea	*Geranium robertianum*	4
Orchidadeae	*Orchis purpurea*	3
Crassulaceae	*Umbilicus rupestris*	1
Cornaceae	*Cornus sanguinea*	12
Fagaceae	*Quercus ilex*	9
Orobanchaceae	*Orobanche hederae*	1
Rubiaceae	*Galium aparine*	4
Rosaceae	*Rubus ulmifolius*	5
Orchidadeae	*Cephalanthera damasonium*	6
Rosaceae	*Prunus spinosa*	6
Caprifoliaceae	*Lonicera xylosteum*	3
Crassulaceae	*Sedum album*	1
Poaceae	*Trisetum flavescens*	1
Aspleniaceae	*Asplenium trichomanes*	1
Aspleniaceae	*Asplenium ceterach*	1
Poaceae	*Melica ciliata*	1
Boraginaceae	*Myosotis ramosissima*	1
Geraniacea	*Geranium rotundifolium*	1
Saxifracea	*Saxifraga tridactylites*	1
Plantaginaceae	*Veronica arvensis*	2
Rosaceae	*Crataegus monogyna*	8
Adoxaceae	*Viburnum tinus*	2
Campanulaceae	*Campanula sp*	2
Lamiaceae	*Aeollanthus*	1
Fabaceae	*Medicago minima*	3
Caryophyllaceae	*Stellaria media*	2
Orobanchaceae	*Odontites luteus*	3
Asteraceae	*Senecio vulgaris*	1
Brassicaceae	*Cardamine hirsuta*	1
Poaceae	*Bromus sterilis*	1
Santalaceae	*Osyris alba*	4
Ranunculaceae	*Clematis flammula*	8
Orchidadeae	*Epipactis sp*	5
Pinaceae	*Pinus nigra*	2
Pinaceae	*Pinus halepensis*	1
Fabaceae	*Genista cinerea*	5
Cupressaceae	*Juniperus communis*	6
Rosaceae	*Amelanchier ovalis*	1
Buxaceae	*Buxus sempervirens*	1
Asparagaceae	*Ruscus aculeatus*	2

Euphorbiaceae	*Euphorbia characias*	1
Rosaceae	*Rosa agrestis*	3
Rhamnaceae	*Rhamnus alaternus*	1
Fabaceae	*Genista hispanica*	2
Oleaceae	*Phillyrea latifolia*	2
Asteraceae	*Hieracium murorum*	8
Adoxaceae	*Viburnum lantana*	2
Lamiaceae	*Teucrium chamaedrys*	2
Rosaceae	*Sorbus aria*	1
Thymelaeaceae	*Daphne laureola*	1
Cyperaceae	*Carex halleriana*	1
Rosaceae	*Rosa canina*	5
Oleaceae	*Jasminum fruticans*	1
Fabaceae	*Hippocrepis emerus*	1
Orchidadeae	*Himantoglossum robertianum*	2
Fabaceae	*Coronilla minima*	1
Cupressaceae	*Juniperus oxycedrus*	3
Asparagaceae	*Asparagus acutifolius*	2
Rubiaceae	*Galium obliquum*	1
Caryophyllaceae	*Silene italica*	8
Poaceae	*Festuca rubra*	7
Fabaceae	*Trifolium angustifolium*	1
Fabaceae	*Vicia hybrida*	5
Asparagaceae	*Muscari neglectum*	1
Fabaceae	*Lathyrus cicera*	3
Asteraceae	*Picris hieracioides*	5
Apiaceae	*Daucus carota*	4
Fabaceae	*Trifolium campestre*	2
Asteraceae	*Crepis vesicaria*	1
Caprifoliaceae	*Scabiosa maritima*	3
Fabaceae	*Medicago rigidula*	1
Ranunculaceae	*Clematis vitalba*	3
Lamiaceae	*Calamintha nepeta*	1
Rosaceae	*Sanguisorba minor*	4
Campanulaceae	*Campanula rapunculus*	3
Caryophyllaceae	*Arenaria serpyllifolia*	1
Caryophyllaceae	*Minuartia hybrida*	1
Poaceae	*Helictochloa bromoides*	1
Fabaceae	*Vicia sativa*	3
Poaceae	*Lolium rigidum*	1
Fabaceae	*Trigonella esculenta*	2
Fabaceae	*Trifolium stellatum*	1
Fabaceae	*Trifolium campestre*	1
Rubiaceae	*Galium mollugo*	2
Fabaceae	*Lathyrus aphaca*	1
Fabaceae	*Lathyrus sphaericus*	1
Fabaceae	*Vicia peregrina*	1
Fabaceae	*Vicia pannonica*	2

Lamiaceae	*Clinopodium vulgare*	1
Elaeagnaaceae	*Eleagnus sp*	1
Fabaceae	*Medicago marina*	1
Orchidadeae	*Ophrys scolopax*	1
Poaceae	*Festuca arundinacea*	2
Equisetaceae	*Equisetum ramosissimum*	1
Orchidadeae	*Anacamptis pyramidalis*	1
Poaceae	*Poa pratensis*	3
Asteraceae	*Taraxacum sp*	1
Plantaginaceae	*Plantago lanceolata*	2
Taxaceae	*Taxus sp*	1
Fabaceae	*Bituminaria bituminosa*	2
Rubiaceae	*Galium obliquum*	1
Rosaceae	*Agrimonia eupatoria*	2
Scrophulariaceae	*Verbascum sp*	2
Vitaceae	*Vitis vinifera*	1
Malvaceae	*Tilia sp*	1
Betulaceae	*Corylus sp*	1
Ulmaceae	*Ulmus minor*	3
Caprifoliaceae	*Lonicera estrusca*	6
Pinaceae	*Pinus pinaster*	1
Poaceae	*Elytrigia repens*	3
Cyperaceae	*Carex flacca*	5
Poaceae	*Brachypodium phoenicoides*	3
Oleaceae	*Phillyrea angustifolia*	0
Salicaceae	*Populus alba*	2
Rosaceae	*Prunus sp.*	5
Salicaceae	*Salix alba*	1
Adoxaceae	*Sambucus ebulus*	1
Poaceae	*Arrhenaterum elatius*	1
Poaceae	*Dactylis glomerata*	1
Rosaceae	*Potentilla recta*	1
Violaceae	*Viola* (cf odonata)	1
Fabaceae	*Medicago arabica*	1
Aristolochiaceae	*Aristolochia rotunda*	1
Fabaceae	*Trifolium pratense*	2
Asteraceae	*Cirsium vulgare*	1
Caryophyllaceae	*Silene latifolia alba*	2
Fabaceae	*Lathyrus annuus*	1
Rosaceae	*Rubus caesius*	3
Fabaceae	*Melilotus sp.*	1
Cyperaceae	*Scirpoides holoschoenus*	1
Poaceae	*Poa trivialis*	1
Cyperaceae	*Carex sp.*	1
Poaceae	*Cynodon dactylon*	1
Celastraceae	*Euonimus sp.*	1
Asteraceae	*Artemisia vulgaris*	1
Fagaceae	*Quercus robur*	1

Convolvulaceae	*Convolvulus arvensis*	1
Adoxaceae	*Viburnum rugosum*	2
Anacardiaceae	*Rhus coriaria*	0
Juglandaceae	*Juglans regia*	0
Euphorbiaceae	*Euphorbia cyparissias*	1
Lauraceae	*Laurus nobilis*	0
Sapindaceae	*Acer campestre*	0
Fabaceae	*Coronilla varia*	1
Lamiaceae	*Clinopodium nepeta*	3
Cannabaceae	*Celtis australis*	1
Orchidadeae	*Cephalanthera purpurea*	1
Pinaceae	*Pinus silvestris*	1
Violaceae	*Viola* (cf hirta)	1
Rosaceae	*Prunus*	1
Brassicaceae	*Arabis hirsuta*	1
Asparagaceae	*Aphyllanthes monspeliensis*	1
Hypericaceae	*Hypericum perforatum*	2
Poaceae	*Catapodium rigidum*	2
Fabaceae	*Spartium junceum*	1
Poaceae	*Bromus diandrus*	1
Gentianaceae	*Blackstonia perfoliata*	1
Brassicaceae	*Capsella bursa-pastoris*	2
Euphorbiaceae	*Euphorbia helioscopia*	1
Fabaceae	*Vicia sp.*	1
Geraniacea	*Geranium molle*	1
Poaceae	*Poa angustifolia*	1
Apiaceae	*Eryngium campestre*	1
Fabaceae	*Lotus corniculatus*	1
Caryophyllaceae	*Silene vulgaris*	1
Fabaceae	*Trifolium repens*	1
Caryophyllaceae	*Cerastium glomeratum*	1
Asteraceae	*Pentanema squarrosum cf*	1
Poaceae	*Hordeum murinum*	1
Poaceae	*Bromus madritensis*	1
Ranunculaceae	*Helleborus foetidus*	1
Papaveraceae	*Fumaria officinalis*	1
Oleaceae	*Fraxinus angustifolia*	1
Fabaceae	*Melilotus officinalis cf* (Trigonella)	1
Apiaceae	*Tordylium maximum*	1
Poaceae	*Bromus erecta*	1
Poaceae	*Phleum pratense*	1
Fabaceae	*Anthylis vulneraria*	1
Oleaceae	*Ligustrum vulgare*	1
Asteraceae	*Lactuca seriola*	1
Asteraceae	*erigeron sumatrensis*	1
Poaceae	*Aegilops ovata*	1
Poaceae	*Bromus hordeaceus*	1
Papaveraceae	*Papaver rhoeas*	1

Supplementary table 2. Arthropods sampled with functional classification and abundance.

Id	Order	Family	Functional group	Abundance
1	Hymenoptera	Unidentified	Parasitoid	2652
2	Hymenoptera	Chrysididae	Parasitoid	13
3	Hymenoptera	Formicidae	Predator	204
4	Araneae	Unidentified	Predator	216
5	Neuroptera	Hemerobiidae	Predator	2
6	Neuroptera	Chrysopidae	Predator	25
7	Odonata	Unidentified	Predator	1
8	Diptera	Empididae	Predator	149
9	Coleoptera	Coccinelidae	Predator	17
10	Hemiptera	Reduviidae	Predator	1
11	Coleoptera	Staphylinidae	Predator	54
12	Hemiptera	Anthocoridae	Predator	2
13	Hymenoptera	*Vespoidea*	Predator	65
14	Diptera	Syrphidae	Predator	33
15	Coleoptera	Carabidae	Predator	2
16	Coleoptera	Meloidae	Predator	1
17	Hymenoptera	Pompilidae	Predator	8
18	Raphidioptera	Unidentified	Predator	75
19	Hemiptera	Miridae	Predator	63
20	Dermaptera	Unidentified	Predator	3
21	Coleoptera	Cantharidae	Predator	709
22	*Dromopoda*	Unidentified	Predator	1
23	Coleoptera	Drilidae	Predator	1
24	Hemiptera	Aphididae	Phytophagous	3097
25	Auchenorrhyncha	Unidentified	Phytophagous	3900
26	Hemiptera	Psyllidae	Phytophagous	1207
27	Coleoptera	Buprestidae	Phytophagous	152
28	Hemiptera	Membracidae	Phytophagous	1

29	Hemiptera	Tingidae	Phytophagous	1
30	Coleoptera	Cerambycidae	Phytophagous	31
31	Coleoptera	Anobiidae	Phytophagous	1
32	Lepidoptera	Unidentified	Phytophagous	79
33	Hemiptera	Pentatomidae	Phytophagous	3
34	Coleoptera	Brentidae	Phytophagous	29
35	Hymenoptera	*Symphyta*	Phytophagous	13
36	Coleoptera	Chrysomelidae	Phytophagous	19
37	Hemiptera	Aleyrodidae	Phytophagous	156
38	Coleoptera	Elateridae	Phytophagous	132
39	Hemiptera	*Heteroptera*	Phytophagous	28
40	Coleoptera	Bostrichidae	Phytophagous	3
41	Coleoptera	Tenebrionidae	Phytophagous	1
42	Coleoptera	Oedemeridae	Phytophagous	97
43	Coleoptera	Curculionidae	Phytophagous	88
44	Hymenoptera	Halictidae	Pollinator	13
45	Hymenoptera	Apidae	Pollinator	7
46	Thysanoptera	Unidentified	Omnivorous	4466
47	Diptera	Unidentified	Omnivorous	6490
48	Coleoptera	Dermestidae	Omnivorous	28
49	Coleoptera	Mordellidae	Omnivorous	68
50	Plecoptera	Unidentified	Omnivorous	5
51	Coleoptera	Melyridae	Omnivorous	24
52	Coleoptera	Scraptiidae	Omnivorous	141
53	Coleoptera	Corylophidae	Omnivorous	14
54	Mecoptera	Unidentified	Omnivorous	28
55	Coleoptera	Scarabaeidae	Omnivorous	2
56	Blattodea	Unidentified	Omnivorous	3
57	Coleoptera	Ptinidae	Omnivorous	4
58	Coleoptera	Lycidae	Omnivorous	1

Table 3. Results of Generalized Linear Mixed Models analysing relationships between woodland vegetation characteristics and the abundance of arthropod groups **within forest fragments**. P-values in bold are significant at P<0.05, P-values in italics at P<0.1.

Cover (%)	Total arthropod abundance		Parasitoid abundance		Predator abundance		Phytophagous abundance		Omnivorous abundance		Pollinator abundance	
	Estimate	P	Estimate	P	Estimate	P	Estimate	P	Estimate	P	Estimate	P
Total	0.0034	0.8638	0.0020	0.8369	0.0195	0.5203	-0.0073	0.54290	0.0300	0.8625	-0.0869	0.1010
Flower	0.0126	0.8901	-0.0474	0.2989	0.0783	0.5792	-0.0367	0.5180	0.2211	0.6382	-12.1859	0.9998
Tree	-0.0025	0.6619	0.0008	0.7736	0.0083	0.3425	-0.0026	0.4571	2.1790	0.1399	0.0155	0.3871
Shrub	0.0071	0.3233	0.0078	**0.0301**	0.0104	0.3478	0.0033	0.4659	0.6266	0.4286	0.0050	0.8514
Herbaceous	0.0088	0.2521	0.0072	*0.0609*	0.0197	*0.0957*	0.0067	0.1757	0.3070	0.5796	0.0097	0.7323

Sentinel card in woodlands (Luberon, France)

CHAPTER 5 – Conclusions and perspectives

In my thesis, I aimed to understand how vegetation and landscape structure of natural or semi-natural habitats influence flying insect communities and their potential role in the provision of ecosystem services in tropical and Mediterranean agroecosystems. The research was conducted in two contrasting regions: sugarcane fields adjacent to Atlantic Forest fragments in Brazil and vineyards in southeastern France. This comparative approach allowed us to evaluate whether ecological patterns observed in tropical landscapes are repeated or modified in Mediterranean agroecosystems. The three parts of the thesis were designed to be complementary, with each chapter addressing specific knowledge gaps and building upon the previous one. I started with the effects of tree diversity on insect communities in forest fragments, which was followed by seasonal dynamics and habitat associations of Hymenoptera in tropical landscapes, and ended with the analysis of vegetation structure and predation rates in temperate vineyard systems.

In the first part (second chapter), we used tree species richness as a parameter of forest habitat quality and found a positive influence on the richness and frequency of functional insect groups. We also identified a strong correlation between insect richness in the fragments and in adjacent sugarcane fields, suggesting insect movement between habitats and a potential role of the fragments as sources of biodiversity for cultivated areas. However, there were some limitations due to the different trap types used in each habitat (yellow pan traps in sugarcane and Malaise traps in forest fragments). Furthermore, although data were collected in two different years, sampling was conducted only once per year, which limits temporal inferences.

In the second part (third chapter), we were able to use the same trap type (yellow pan traps) in both habitats and analyzed community variation throughout the year. We focused on Hymenoptera, a group of great ecological importance, that revealed high seasonal variations in family composition and abundance, with distinct effects across habitats and functional groups. Parasitoids, for example, were more abundant in forest fragments, while pollinators increased in sugarcane

fields in certain seasons. These results highlight the role of forest fragments as seasonal refuges, especially during periods of disturbance or resource scarcity in the crops.

Interestingly, unlike the patterns found in Chapter 2, we did not observe significant correlations in the richness or abundance of Hymenoptera families between habitats. However, even in Chapter 2 there was only a marginally significant relationship for the richness of parasitoids (group with a large number of Hymenoptera) between the two habitats. This may indicate that the interactions of this group between the habitats differ from other insect groups. In addition, there was no difference in family composition between the forest fragments and sugarcane fields, in contrast to the results reported earlier. Nevertheless, questions remained about specific vegetation characteristics that drive insect community composition and the variation of insect at different distances from the forest fragment. Moreover, ecosystem service evaluation would need a more direct measure of services provided by insect groups showing a spillover from forest fragments.

In the third part (fourth Chapter), we expanded the analysis to a Mediterranean agroecosystems, evaluating insect communities in French vineyards. We confirmed that adjacent forest fragments positively influence the abundance of beneficial insects at vineyard borders, even under contrasting climatic and management conditions, a pattern consistent with Chapter 2. Additionally, we found that flower cover and plant species richness positively affect different insect functional groups. However, these effects tend to weaken towards central parts of the vineyards, indicating limitations in the spillover of individuals. We also observed significant differences in insect community composition between habitats (forest fragments, vineyard borders and centers), as in Chapter 2, but in contrast to Chapter 3. This discrepancy may be the result of differences in the taxonomic scope (Hymenoptera only in Chapter 3 vs. all flying insects in Chapter 2 and 4), as well as temporal resolution, Chapter 3 included seasonal sampling, that revealed high temporal variability, and consequently potentially mask spatial correlations. We also used sentinel cards as models to assess predation rates, inferring the provision of ecosystem

services. This confirmed that forest fragments contribute to higher predation rates in vineyards, suggesting their influence on biological pest control.

This thesis, therefore, contributes to scientific knowledge in:

1. **Demonstrating that the quality of semi-natural habitats, rather than just its presence, is crucial for maintaining insect biodiversity in agricultural landscapes**.

Although this was not the main focus of the study, differences between gallery and plateau fragments were evident. Gallery forests are protected by law and are subject to ecological restoration. Although exotic species are often planted, higher plant richness supports insect communities. Plateau fragments, on the other hand, remain vulnerable to human impact and are rarely restored. In many cases, they resemble abandoned areas with few tree species, mostly covered by shrubs and lianas. The contribution to biodiversity depends on the situation of fragments in river valley and plateaus. It is crucial to consider the preservation of both habitat types in order to maintain biodiversity in sugarcane dominated agricultural landscapes.

2. **Integrating functional approaches (trophic groups, ecosystem services) in insect diversity analyses, allowing more applied interpretations for agricultural sustainability**.

In this study, we did not only focus on richness or abundance but also on functional groups in order to relate their contribution to ecosystem services, such as biological control and pollination. Due to differences in habits between groups, many results only became apparent when analyzed separately. This finding relates scientific results closer to agricultural practice because it clarifies how landscape and vegetation features influence different groups and their role in agroecosystem functioning.

3. **Showing that the positive effects of vegetation on insects are spatially limited, being more apparent in crop edges.**

Although we evaluated the influence of forest fragments in crop fields, sampling was conducted close to the crop edge. When analysing vineyard insect abundance and composition at greater distances from the forest (Chapter 4), significant relationships disappeared. Thus, it is possible to infer limitations in insect movement between habitats, possibly due to structural barriers, species-specific habits, or resource limitation. Despite these limitations, there is a significantly positive effect of these natural or semi-natural habitats on crop fields. Moreover, such limitations vary according to local conditions and the choice of insect traits.

4. **The need to characterize vegetation in ecological studies, moving beyond the simple analysis of plant cover in order to understand how different components (flowers, herbaceous plants, shrubs, trees) influence insect communities**.

In this study, we aimed to draw conclusions on specific vegetation characteristics of semi-natural habitats. Rather than considering only the presence of vegetation, we evaluated species richness, plant functional groups and/or plant community composition. The contrasting effects on insect communities depending on each vegetation parameter expand our understanding of the importance of vegetation conservation in agricultural landscapes and indicate that these relationships may be even more complex.

Despite considerable success, this thesis also highlights limitations and gaps that should be addressed in future research. Taxonomic identification at order and family level, while adequate for broad analyses, limits inferences about specific ecological interactions. Functional classification based only on the larval stage may not accurately reflect the ecological role of adult insects, especially in holometabolous groups with distinct life-stage habits. Classification as parasitoid or predator also does not mean that these individuals act in the biological control of pests, because many of them feed on spiders and other natural enemies. Although plant species were identified, we did not assess whether one or few species play a key role in supporting specific insect groups.

Future studies may overcome these limitations by:

- Including species-level insect identification or focusing on groups with well-defined ecosystem service contribution;
- Distinguishing functional groups for larval and adult stages;
- Directly quantifying ecosystem services such as parasitism rates, predation on specific pests, and pollination;
- Using marking or tracking methods to assess real insect movements between habitats;
- Analysing vegetation more in detail, particularly the abundance of flowering species that may provide critical resources for beneficial insects.

By integrating results obtained in distinct environments with different land-use pressure, this thesis provided a baseline for the development of more sustainable, ecologically informed agricultural practices capable of reconciling food production with biodiversity conservation. The findings underscore the need for public policies that promote the conservation of natural or semi-natural habitats and the restoration of native vegetation as fundamental strategies to ensure the resilience and functioning of agroecosystems under increasing environmental pressures.