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Programa de Pós-Graduação em Ecologia

Multi-scale biodiversity-ecosystem service relationship: The role of landscape, diversity and trophic networks on biological control by parasitoids

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Orientador: Prof. Dr. Pedro Henrique Brum Togni

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Brasília - DF, março de 2024.

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Relação biodiversidade-serviço ecossistêmico em múltiplas escalas: O papel das paisagens, da diversidade e das redes de interações locais no controle biológico por parasitoides

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GENERAL ABSTRACT

The threat suffered by the world's biodiversity has raised concern about the provision of ecosystem services essential for human life. Yet, biodiversity conservation does not guarantee ecosystem service provision, given species' interactions and variable responses to local and landscape factors. This work is divided into two chapters, both performed in 25 organic brassica crop fields from the Brazilian Federal District. In the first chapter, we evaluate how the landscape and local resources affect parasitoid diversity and aphid biological control. Locally, we compared parasitoid communities within the crops and on adjacent non-crop stripes and evaluated the effect of flower resource abundance on parasitoid diversity. At the landscape scale, we analyzed the effect of natural areas and their specific vegetational formations on parasitoid diversity and the scale of these effects. To close the first chapter, we evaluated the relationship between biodiversity and biological control. In the second chapter, we evaluate how non-crop plant stripes affect the network of interaction involving parasitoids and aphids in organic tropical brassica crops. First, we compared the topology of the interaction networks within the crops and on adjacent non-crop plants based on modularity and nestedness. Subsequently, we used the information from the networks to conduct simulate host-parasitoid population dynamics in scenarios of normal conditions, favoring an alternative native host, favoring an alternative pest, and favoring an alternative parasitoid. For that we used an adapted version of the generalized Lotka-Volterra model. In our first chapter, we showed that: non-crop plants sustain parasitoid richness, but their flower resource abundance disrupts it; landscape composition outweighs local resources in mediating parasitoid diversity; near-crop forests (0.42 km) aid parasitoid richness, while farther grasslands (1.75 km) aid abundance; savannas boost both forest benefits on parasitoid richness and grassland benefits on abundance; positive biodiversity-pest control relationships occur only in moderately rich fields. In our second chapter, we showed that: interactions in the lower trophic level tend to be more nested, while in the higher trophic level they are more modular; most significant differences in network metrics between crop fields and non-crop plant stripes occurred at the higher trophic level; differences in modularity between non-crop plants and brassica fields were significantly larger than expected at random, while differences in nestedness were significantly smaller than expected at random; the difference in nestedness between aphid-parasitoid networks sustained by different non-crop plants was significantly smaller than expected at random; alternative hosts and parasitoids can help control the populations of the main brassica pest *Brevicoryne brassicae*. Our findings show that natural vegetation formations with different tree densities have complementary effects in parasitoid diversity in tropical agroecosystems and represent a useful baseline for development of management and zoning plans. Furthermore, we show that parasitoid trophic interactions sustained by non-crop plants represent interesting targets for management plans since they can influence pest populations in these systems.

RESUMO GERAL

A ameaça sofrida pela biodiversidade mundial tem levantado preocupações sobre a provisão de serviços ecossistêmicos essenciais para a vida humana. No entanto, a conservação da biodiversidade não garante a provisão desses serviços, devidos as interações entre espécies e as respostas variáveis aos fatores locais e da paisagem. Este trabalho está dividido em dois capítulos, ambos realizados em 25 propriedades de cultivo orgânico de brássicas do Distrito Federal. No primeiro capítulo, avaliamos como a paisagem e os recursos locais afetam a diversidade de parasitoides e o controle biológico de pulgões. Localmente, comparamos as comunidades de parasitoides dentro das culturas e em faixas de plantas espontâneas adjacentes e avaliamos o efeito da abundância de recursos florais na diversidade de parasitoides. Na escala da paisagem, analisamos o efeito de áreas naturais e suas formações vegetais na diversidade de parasitoides e em qual escala ocorrem esses efeitos. Para encerrar o primeiro capítulo, avaliamos a relação entre biodiversidade e controle biológico. No segundo capítulo, avaliamos como faixas de plantas espontâneas afetam a rede de interação envolvendo parasitoides e pulgões. Primeiramente, comparamos a topologia das redes de interação dentro das culturas e em plantas não cultivadas adjacentes com base na modularidade e no aninhamento. Em seguida, usamos as informações das redes para simular a dinâmica populacional hospedeiro-parasitoide em cenários de condições normais, favorecendo um hospedeiro nativo alternativo, favorecendo uma praga alternativa e favorecendo um parasitoide alternativo. Para isso, utilizamos uma versão adaptada do modelo de Lotka-Volterra generalizado. Em nosso primeiro capítulo, mostramos que: as plantas não cultivadas sustentam a riqueza de parasitoides, mas a abundância de recursos florais é negativa; a composição da paisagem supera os recursos locais na mediação da diversidade de parasitoides; florestas próximas às culturas (0,42 km) auxiliam na riqueza de parasitoides, enquanto campos mais distantes (1,75 km) beneficiam a abundância; savanas impulsionam tanto os benefícios da floresta na riqueza de parasitoides quanto os benefícios da pastagem na abundância; as relações positivas entre biodiversidade e controle de pragas ocorrem apenas em campos moderadamente ricos. Em nosso segundo capítulo, mostramos que: as interações no nível trófico inferior tendem a ser mais aninhadas, enquanto no nível trófico superior são mais modulares; as diferenças mais significativas nas métricas de rede entre campos de cultivo e faixas de plantas não cultivadas ocorreram no nível trófico superior; as diferenças na modularidade entre plantas não cultivadas e campos de brássicas foram significativamente maiores do que o esperado ao acaso, enquanto as diferenças no aninhamento foram significativamente menores do que o esperado ao acaso; a diferença no aninhamento entre as redes de pulgões-parasitoides sustentadas por diferentes plantas espontâneas foi significativamente menor do que o esperado ao acaso; hospedeiros e parasitoides alternativos podem ajudar a controlar as populações da principal praga de brassicas *Brevicoryne brassicae*. Nossas descobertas mostram que formações de vegetação natural com diferentes densidades de árvores têm efeitos complementares na diversidade de parasitoides em agroecossistemas tropicais e representam uma linha de base útil para o desenvolvimento de planos de manejo e zoneamento. Além disso, mostramos que as interações tróficas de parasitoides sustentadas por plantas não cultivadas representam alvos interessantes para planos de manejo, pois podem influenciar as populações de pragas nesses sistemas.

KEYWORDS

Ecosystem services, Applied ecology, Agroecology, Cerrado

PALAVRAS-CHAVE

Serviços ecossistêmicos, Ecologia Aplicada, Agroecologia, Cerrado

GENERAL INTRODUCTION

The threat suffered by global Biodiversity generates concern about the maintenance of its ecosystem services (Cardinale et al., 2012). It is a fact that there is a relationship between biodiversity and ecosystem service provision (Tilman et al., 2001; Gamfeldt et al., 2013; Brockerhoff et al., 2017). However, a positive effect on service provision is not always achieved by increasing biodiversity (Straub et al., 2008; Letourneauet al., 2009; Macfadyen et al., 2011a; Forrester & Bauhus, 2016), and it is necessary to understand how species interact with each other. Biological control services, for example, can be negatively affected by increases in natural enemy diversity if the added species interact antagonistically, for example, through competition, intraguild predation, or hyperparasitism (Martin et al., 2013; Tougeron & Tena, 2019). Conversely, a positive effect of biodiversity on this service is expected when there is complementarity in resource utilization by the present natural enemies (Macfadyen et al., 2011a). In this context, the structure of these interaction networks is mediated by different landscape scales, which, influence from the regional pool of species to the need for them to compete for resources or the possibility of using them in a complementary way (Brose et al., 2004; Janssen et al., 2007; Cagnolo et al., 2009; Macfadyen et al., 2009; Tscharntke et al., 2012; Landis, 2017). In other words, different landscape scales can affect the provision of ecosystem services by mediating species diversity and their network of interactions.

Landscape structure, defined by the interaction between its composition and configuration can differentially influence the diversity of natural enemies in agroecosystems and their biological control service (Chaplin-Kramer et al., 2011; Woltz et al., 2012; Chaplin-Kramer et al., 2013; Rusch et al., 2016; Landis, 2017, Karp et al., 2018). Chaplin-Kramer et al (2011) suggest that natural enemies benefit from an increment in landscape complexity, with specialists being primarily influenced at smaller spatial scales, while generalists respond well to different scales. In a quantitative overview, Rusch and colleagues (2016) documented that biological control in areas with more complex landscapes almost doubled that found in areas with more homogeneous landscapes dominated by cropland. At the population level, higher proportions of natural habitats around a cultivated area can increase the density of aphid consumers, reducing its population growth and decreasing its density at harvest (Chaplin-Kramer, 2013). In addition to the proportion of natural areas, configuration metrics like edge density, and distance between cultivated and natural environments influence the spill-over of natural enemies into crop fields (Karp et al., 2018; Martin et al., 2019). At last, studies on the relationship between landscapes and biological control are lacking in the tropical region, which often show different responses compared to temperate regions (de Aquino et al., 2023; Novaes et al., 2024).

Thus, landscape composition and configuration, are key to understanding biological control provisioning, especially in the tropical region.

Apart from affecting the diversity of agroecosystems, the landscape can also mediate important features of its species interaction networks, such as interaction richness, modularity, and interaction nestedness (Post & Hairston, 2000; Tylianakis et al., 2007). In pollination networks, for example, interaction richness (the number of interactions in the network) decreases twice as fast as species richness with decreasing habitat area, but it also depends on the centrality of local species (Sabatino et al., 2010; Assunção et al., 2022). In networks of pest natural enemies, modularity (compartmentalization), had a positive relationship with the variety of habitats and their identities, suggesting that each module represents a set of interactions between species using the same habitats (Macfadyen et al., 2011b). Furthermore, modified and homogeneous habitats may decrease this measure as they are favorable for generalist species connecting the different modules (Tylianakis et al., 2007; Aizen et al., 2008). For interaction nesting, which reflects how much specialist interactions are a subset of more generalist ones, an increase is expected in homogeneous landscapes and with habitat suppression (Tylianakis et al., 2007; Gonzalez et al., 2011; Macfadyen et al., 2011b). Furthermore, habitat suppression can differentially affect different components and compartments of the network (Cagnolo et al., 2009), releasing species from top-down control and resulting in the loss of ecosystem services provided by higher trophic levels (Post & Hairston, 2000; Dobson, 2009).

Along with landscape structure, habitat management can also affect the diversity and network of natural enemies interactions (Landis et al. 2000; Macfadyen et al., 2009; Landis, 2017; Blassioli-Moraes et al., 2022). In this context, the Conservation Biological Control (CBC) strategies, which consists of favoring the action of natural enemies of agricultural pests through the conservation and management of resources and habitats in cultivated and adjacent areas, represents an alternative to increasing the availability of resources, shelter, prey, and alternative hosts of natural enemies (Shields et al., 2019; Venzon et al., 2021; Blassioli-Moraes et al., 2022). An economically viable CBC technique is spontaneous plant management (Venzon et al., 2019). Their use is a good alternative to increase the variety of habitats within cultivated areas, the permeability between cultivated and natural habitats, as well as floral, prey, and host resources allowing greater complementarity in resource use by natural enemies, resulting in an increase in biological control (Bianchi & Wäckers, 2008; Macfadyen et al., 2011b; Hatt et al., 2018; Martin et al., 2019). Moreover, the presence of non-crop plants has already been related to higher survival and attraction of native natural enemies over exotic representatives, preventing the destructuring of the interaction network by hyper generalist species (Aizen et al., 2008; Amaral et al., 2013). Given this, studying how spontaneous plants can contribute to the increase of natural enemies in CBC strategies, will contribute to the theoretical knowledge of the biodiversity-service relationship and to the reconciliation between biodiversity conservation and agricultural productivity.

Parasitoid wasps (Hymenoptera) comprise a large group of natural enemies of agricultural pests widely used in biological control strategies (Thies et al., 2003; Tylianakis et al., 2004; Plećaš et al., 2014; Gontijo et al., 2015; Eid et al., 2018; Kaser & Heimpel, 2018). These wasps are important in pest control because they oviposit on the hosts, which generally start to develop more slowly, consume less food, and upon hatching, the larvae feed on the host causing its death (Quicke, 2014). Although it is a much-studied group in relation to providing the ecosystem service of biological control, studies relating landscape characteristics to biological control efficiency shows contradictory results. While Thies and collaborators (2003) suggest that higher landscape complexity leads to increased parasitism and decreased herbivory in cultivation, other authors have shown that landscape complexity and farming systems did not affect parasitoid diversity and parasitoid-host interactions (Macfadyen et al., 2009; Hawro et al., 2017) or that both pest and parasitoid populations increase in response to landscape complexity (Plećaš et al., 2014). In this sense, it is necessary to study how parasitoids interact with factors at different spatial scales in order to support management strategies that effectively increase the biological control services of these natural enemies in the crops.

In addition to landscape structure, parasitoids also respond to resource availability at the local scale, making them useful models for the study and application of CBC (Hatt et al., 2018; Zhu et al., 2020). This influence occurs in two distinct ways: i) increasing these resources may allow for alternative hosts, i.e., new oviposition sites and food resources for the larvae (Holzschuh et al., 2010) and ii) increasing these resources may increase the abundance of floral resources, on which the adult parasitoids feed (Lavandero et al., 2005; Bianchi & Wäckers, 2008; Hatt et al., 2018; Zhu et al., 2020). Non-crop plant strips can promote an increase in host diversity and abundance and are important for maintaining, primarily, specialist parasitoids (Tscharntke, et al., 2005; Holzschuh et al., 2010). However, because adult parasitoids need resources to develop before ovipositing, their maintenance in cultivated habitats may be mediated primarily by floral resources at the expense of host abundance (Hatt et al., 2018). Strips with a high abundance of floral resources can increase the parasitism rate found in a crop by almost 100%, and this effect is affected by the distance from the resources (Lavandero et al., 2005), showing its importance in increasing habitat permeability to parasitoids. In addition, functional traits such as flower color and nectar availability are also important mediators of their attraction to parasitoids (Hatt et al., 2018). Therefore, it is necessary to understand how parasitoids interact with floral resources and alternative hosts in order to understand which features of these resources enhance their biological control service.

Given the above, it can be seen that the provision of biological control service by parasitoid wasps is affected by distinct features at different scales through changes in diversity and interactions between parasitoids and their main resources: hosts and floral resources (Tscharntke, et al., 2005; Macfadyen et al., 2009; Holzschuh et al., 2010; Hatt et al., 2018; Martin et al., 2019). At a regional scale, landscape composition is primarily responsible for mediating the pool of species able to colonize an area (Woltz et al., 2012; Chaplin-Kramer, 2013; Plećaš et al., 2014; Martin et al., 2019). While on a local scale, colonization will depend on the dispersal ability of parasitoids and how the landscape configuration mediates crop permeability by affecting the abundance and distribution of resources along its extent (Bianchi & Wäckers, 2008; Hatt et al., 2018; Martin et al., 2019). In this sense, spontaneous plants present an economically viable option to increase the abundance of floral resources and, consequently, the permeability of cultivated environments for parasitoid wasps (Venzon et al., 2019). Thus, these plants should affect the network of plant-host-parasitoid interactions, possibly increasing the biological control service depending on how this influence is expressed.

OBJECTIVES E HYPOTHESIS

The aim of this study is to answer how landscape and local resources mediate parasitoid diversity, their interactions with hosts, and biological control services in cultivated habitats. In order to answer this question, we will specifically investigate: i) How floral resources and host availability interact with the landscape in maintaining parasitoid diversity in cultivated habitats (first chapter); ii) How spontaneous plants affect the topology of crop-plant-host-parasitoid interaction networks (second chapter); iii) How the diversity and topology of interaction networks involving parasitoids influence the provision of biological control service in cultivated areas (both chapters).

As more natural landscapes provide a larger pool of species that could potentially colonize crop habitats, a greater abundance of local resources should attract more species by increasing habitat permeability, and concomitantly should allow subnetworks of interactions to take place across different habitat types. Therefore we expect that greater local resource availability and proportions of natural areas in the landscape will generate increases in parasitoid diversity and linkage richness as well as in the modularity of the network of aphid interactions and the complementarity of resource use among modules, culminating in more effective biological control. In this sense, our specific hypotheses are: i) Floral resource abundances and host densities have a positive relationship with parasitoid diversity, especially in landscapes dominated by natural areas; ii) In mostly natural landscapes, spontaneous plants will increase link richness, network modularity and decrease link nesting, increasing complementarity in resource use and presenting high link centrality by acting as connectors of different groups of interactions (modules). iii) More diverse communities of parasitoids will show higher parasitism rates and therefore intensity of biological control. Concomitantly, communities with more modular networks with less nesting between modules, by presenting greater complementarity, will increase the provision of this service.

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CHAPTER 1

Through the green mosaic: different tropical vegetation formations have complementary effects on parasitoid diversity and biological control in organic agroecosystems

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ABSTRACT

Land use change threaten global biodiversity, impacting ecosystem services, especially in diverse tropical regions. Yet, biodiversity conservation does not guarantee ecosystem service provision, given species' variable responses to local and landscape factors. Here we evaluate how the landscape and local resources affect parasitoid diversity and aphid biological control in a tropical organic crop. Locally, we compared parasitoid communities within the crops and on adjacent non-crop stripes and evaluated the effect of flower resource abundance on parasitoid diversity. At the landscape scale, we analyzed the effect of natural areas and their specific vegetational formations on parasitoid diversity and the scale of these effects. Finally, we evaluated the relationship between biodiversity and biological control. Non-crop plant stripes had higher parasitoid species richness and abundance than the crops, but similar species composition. Flower resource abundance in the non-crop stripes negatively affected parasitoid richness. Natural areas in the landscape benefited parasitoid richness at a close range (0.42 km) and reduced parasitoid abundance at a wider scale (1.75 km). Forests and savannas increased parasitoid richness and reduced abundance, while grasslands drive parasitoid abundance and disrupt species richness. Savannah areas, where trees and grasses coexist boosted the positive effects of forests on species richness and of grasslands on abundance. Parasitoid species richness benefited biological control exclusively in communities with intermediate number of parasitoid species. Our findings show that natural vegetation formations with different wood densities have complementary effects in parasitoid diversity in tropical agroecosystems and represent a useful baseline for development of management and zoning plans.

INTRODUCTION

The global threat to biodiversity due to land use change can directly affect the provision of ecosystem services (Cardinale et al., 2012; Oliver et al., 2015), especially in the tropics where most of the global biodiversity is concentrated (Willig et al., 2003; Jablonski et al., 2006; Ramos et al., 2020; Raven et al., 2020). However, biodiversity conservation does not guarantee the provision of ecosystem services because species may respond differently to local and landscape features (Straub et al., 2008; Letourneau et al., 2009; Forrester & Bauhus, 2016). In fact, the provision of biological control services by natural enemies has shown inconsistent responses to the presence of natural habitats in the landscape (Plećaš et al., 2014; Rusch et al., 2016; Karp et al., 2018). Differences in plant composition between these natural areas can be responsible for these responses, since natural enemies usually respond differently to environments with different wood densities (Fonseca et al., 2005; Togni et al., 2021). Still, habitat structure and local resources influence permeability by dictating attraction, colonization, and retention of natural enemy species (Landis, 2017; Togni et al., 2019b; Harterreiten-Souza et al., 2021). Thus, a multiscale approach is crucial for understanding how local and landscape features influence biological control services (Tscharntke et al., 2005, 2021).

Each habitat within a landscape provides distinct resources and conditions for natural enemies, which influence how species use and explore them (Fahrig et al., 2011). In this sense, the functional role of different habitats within the landscape is expected to affect the provision of biological control on crop habitats (Fahrig et al., 2011; Begg et al., 2017). Landscapes with higher functional heterogeneity that show different vegetational formations like forests, savannas, and grasslands, possibly have a more diverse pool of species able to colonize distinct habitat types due to a higher variety of resources, conditions, and pressures (Nyman, 2010). However, most of the knowledge on the relationship between landscape, biodiversity and ecosystem services are produced on temperate regions (Clarke et al., 2017). Tropical regions usually have higher landscape complexity and taxonomic diversity than temperate regions, which means that different patterns of complementarity and redundancy effects may arise (Cardoso et al., 2011; Monge-González et al., 2021). In this sense, it is essential to understand the importance of specific vegetational formations to the effect of natural area on tropical natural enemies and their services.

At the landscape scale, natural areas adjacent to crop fields can act as reservoirs of the pool of natural enemy species able to colonize the crops (Thies et al., 2003; Chaplin-Kramer et al., 2011, 2013; Rusch et al., 2016). However, the spillover from the natural areas to the crops depend on habitat permeability at the local scale and can be facilitated by reducing habitat disturbance (i.e., insecticide spraying) and increasing the provision of resources (alternative and supplementary) to natural enemies

(Amaral et al., 2013; Rezende et al., 2014; Snyder, 2019; Harterreiten-Souza et al., 2021; Blassioli-Moraes et al., 2022). Organic agriculture, for example, is known to benefit biodiversity by restricting the use of chemical pesticides and increasing plant diversity (Bengtsson et al., 2005; Garratt et al., 2011; Togni et al., 2019a; Venzon, 2021). Such benefits can be increased by maintaining non-crop plant stripes nearby the crops to increase the provision of supplementary plant-provided food (e.g., pollen and nectar) and alternative prey for natural enemies (Bianchi & Wäckers, 2008; Amaral et al., 2013; Hatt et al., 2018; Venzon et al., 2019). Combined, these two management strategies are expected to increase natural enemy diversity and biological control in agricultural systems and contribute to understand the relationship between biodiversity and ecosystem services on tropical areas (Macfadyen et al., 2009; Clarke et al., 2017).

Parasitoid wasps (Hymenoptera) are well-known natural enemies of agricultural pests (Thies et al., 2003; Plećaš et al., 2014; Gontijo et al., 2015). Some studies suggest higher landscape complexity boosts parasitism and diminishes herbivory (Thies et al., 2003), while others show no impact on parasitoid diversity or pest-parasitoid interactions (Macfadyen et al., 2009; Plećaš et al., 2014; Hawro et al., 2017). Parasitoids are constantly foraging for hosts and food (Tentelier et al., 2006), so their spillover from natural to agricultural areas should be mediated by their combination. In this sense, parasitoids respond well to the management of non-crop plants at a local scale, which provide alternative hosts and floral resources, on which the adult parasitoids feed (Lavandero et al., 2005; Bianchi & Wäckers, 2008; Hatt et al., 2018). Parasitoid diversity, which can benefit biological control and its stability, has been shown to respond positively to higher flower availability in non-crop habitats (Macfadyen et al 2011; González et al., 2022). Since agricultural fields usually have high host availability but little flower resource, non-crop plants may provide the necessary resources and conditions for an increased spillover.

We seek to understand how landscape features interact with local non-crop plant stripes to mediate parasitoid diversity and aphid biological control in tropical organic Brassicaceae crops. Specifically, we asked the following questions: i) How local non-crop plant floral resources interact with the landscape in mediating crop colonization by parasitoids. ii) How and in which scale natural areas in the landscape affect parasitoid diversity in organic crop fields? iii) How specific vegetational formations contribute to the effect of natural areas on parasitoids? iv) How the relationship between parasitoid diversity and their provision of biological control is affected by these multiscale factors? We predict that more natural landscapes will provide a larger pool of species, while a greater abundance of local resources provided by non-crop plant stripes will increase habitat permeability to these species. Therefore, we expect that local and landscape features benefiting parasitoid diversity will culminate in more effective biological control.

MATERIAL AND METHODS

Study area

This study was performed from August to October 2022 and 2023 in 25 organic farms cropping collards (*Brassica oleracea*, Brassicaceae) in the Brazilian Federal District (15°47’ S, 47°56′ W, 1000m above the sea level). The region is in the core of the Cerrado biome, the Brazilian tropical savanna, one of the 25 most important terrestrial biodiversity hotspots (Myers et al., 2000). The Cerrado is the second largest Brazilian biome (2 million km²) and 52,9% of its area is currently used for agricultural activities (Sano et al., 2019). The native vegetation of the biome is mostly within private properties and is formed by different plant physiognomies ranging from forest and savanna formations to grasslands (Ribeiro & Walter, 2008; De Marco et al., 2023), being potential reservoirs for beneficial insects like parasitoids.

The sampled farms were distributed within a land use gradient varying between areas dominated by large-scale monocultures to areas composed mostly by fragments of native vegetation. The farms belonged to small farmers (4 – 70 ha) and were certified as organic for at least 5 years (Brazil, 2003, 2007). Bt-based products (*Bacillus thurigiensis*), *Beauveria bassiana*, regular augmentative releases of *Trichogramma pretiosum* (Riley) (Hymenoptera: Trichogrammatidae) and different types of plant extracts were used for pest management according to Brazilian legislation (Togni et al., 2019c). Besides the input restrictions, the farmers usually use management practices to increase beneficial insect biodiversity in their fields, commonly maintaining strips of spontaneous non-crop vegetation nearby or among brassica crops (Assunção et al., 2022). The tropical savanna climate, with a dry winter and a hot and humid summer (da Silva et al., 2008; Alvares et al., 2013), forces farmers to grow collards during winter to avoid rainfall damage. Therefore, we conducted this study in the driest months of the dry season when aphids and parasitoids are abundant in organic brassica fields. The water supply for crops was provided by irrigation with sprinklers.

Landscape characterization

The characterization of the landscapes surrounding the fields was performed using satellite images from the land cover and use from the MapBiomas collections 7 and 8 (Souza Jr. et al., 2020). These collections use 30 m x 30 m pixels to differentiate more than 25 land cover types in the landscape. We reclassified the land cover types into eight groups based on the distinct functional responses of parasitoids to these land cover types (Fonseca et al., 2005) as follows: 1) Forests, 2) Savannas, 3) Natural Grasslands, 4) Pastures, 5) Urban areas, 6) Water bodies, 7) Soybean monocultures, 8) Other agricultural fields. The extent of the buffers used for landscape characterization was selected using the 'Scalescape' R package which avoids problems related with a priori extent and multiple-buffer methods for selecting the extent of the characterized landscape (Lowe et al., 2022).

Local resource sampling

In each farm, we measured the floral abundance in the non-crop stripes to estimate the abundance of floral resources available for parasitoids. To do this, we randomly selected ten points in the stripes of non-crop plants from 5 to 25 m distant from the crop. Each sampling point was at least 5 m apart from each other. In each sampling point, a 1 m² quadrat was stablished and photographed using a Canon EOS Rebel T6 digital camera. We positioned ourselves aside the quadrants avoiding shadowing the vegetation, positioned the camera at 1.5 m height at the center of the quadrant and took two photographs. The clearest image of each quadrant was divided using Inkscape software into units of 1 cm², each unit containing a flower receptacle was considered a floral unit as suggested by Carvalheiro et al. (2014), so that flowers of different sizes could have their resource abundances properly cataloged. Therefore, the abundance of flower resource was calculated as the average number of floral units per quadrat.

Parasitoid sampling

To sample parasitoid diversity, 18 200 ml pan traps were distributed in each farm, within the crop and the non-crop plant stripes. The sampling points were distributed along the crop and stripes at least 25 m from each other, and 5 m apart from the edges of the crop fields and non-crop plant stripes. In each point (replicates), the three traps (pseudo replicates) were placed 5 m apart, forming a triangle around the sampling point. This design was selected to reduce the chance of sample loss and to increase attractiveness of the sampling points. The pan traps were filled with 200 ml of a solution with 50%

water, 30% etilenoglicol and 20% alcohol. The traps were colored with UV reflecting yellow spray acrylic paint to increase parasitoid attraction (Hatt et al., 2018). The traps were installed 1.20 m above ground crops to increase the chances of collecting foraging parasitoids above the non-crop and crop plants (Chan-Canché et al., 2020). The traps were supported by perforated steel bands tied to plastic stakes. They were kept in the field for five days, after which the material was taken to the laboratory for sorting and identification. The sampled parasitoids were identified to the family level using Goulet & Huber (1993) and separated into morphospecies. Samples of each point were poll together to avoid pseudo replications.

Biological control experiment

To estimate biological control services in each farm, an exclusion experiment was conducted based on Gardiner at al. (2009). In each farm, 30 brassica plants were randomly selected and subjected to the following treatments: 1) exclusion bags (natural enemies had no access); 2) open leaf marked with a colored ribbon (allowing natural enemy access). Therefore, each treatment was composed of a plant with a bagged leaf paired with an open leaf. Using this procedure, we avoided differences between the treatments that could be attributed to factors such as plant physiology. The exclusion bags (30 x 20 cm) were made of voil fabric, allowing only light and air to pass through. When setting up the experiment, all organisms other than aphids were removed from the leaves. The number of apterous, winged, and parasitized aphids was counted on each treatment. When necessary, the aphids were removed so that the number was similar in both leaves. The leaves used for this experiment had, between 10 and 100 aphids, depending on the aphid infestation in each farm. After five days, the number of apterous, winged, and parasitized aphids on these leaves were counted again. We then calculated the biological control service index (BSI) proposed by Gardiner et al. (2009), which is an estimate of average biological control per farm.

$$\mathrm{BSI} = \frac{\sum_{p=1}^{4} \frac{(A_{c,p} - A_{o,p})}{A_{c,p}}}{n}$$

(1)

where, $A_{c,p}$ is the number of aphids found in the closed leaf at the end of the experiment, $A_{o,p}$ is the number of aphids found on the open leaf and n is the number of plants used in the experiment.

Data analysis

To analyze the differences between the communities of parasitoids inside the crop fields and in the non-crop plant stripes, we began with an individual based rarefaction analysis using the ‘iNext’ R package (Hsieh et al., 2016). To further understand how the abundances were distributed, we fitted species abundance distribution (SAD) models to each habitat using the ‘sads’ R package (Prado et al., 2024). We fitted four SAD models: i) Power law, ii) Poisson log-normal, iii) Log series, and iv) Broken stick, which were than compared through likelihood and Akaike information criterion (AIC) values. Berger-Parker dominance index (D) and Pielou equitability index (J) were calculated to support SAD predictions.

The dissimilarity in the species composition between habitats was initially analyzed with a Permutational Analysis of Variance (PERMANOVA) and a Similarity Percentage Analysis (SIMPER), to identify which taxa are primarily responsible for the difference between habitat types. The Non-Metric Multidimensional Scaling (nMDS) followed by permutational fit of richness and abundance vectors to analyze the contribution of these variables to the dissimilarity within and between farms. The SIMPER and nMDS analysis were based on Bray-Curtis distance matrices. These procedures were conducted using the ‘vegan’ R package (Oksanen et al., 2007).

To analyze the effect of multiscale factors on parasitoid species richness and abundance, we used the ‘Scalescape’ R package, which estimates distance-weighted landscape effects on a response variable based on a previous local model (Lowe et al., 2022). The local models consisted of generalized linear mixed models (GLMMs), on the effect of floral resource abundance on parasitoid species richness and abundance, with the sampling year as random variable. Models with different error distributions were tested and compared based on AIC values. For the landscape model, ‘Scalescape’ identifies: i) the buffer range that improves model fit, ii) the weight loss of landscape predictors as the distance increases and, iii) the direction and magnitude of the landscape effect. Two landscape GLMMs were built for each response variable starting from the local models and differing on the included landscape predictors. In the first, the landscape predictor was total natural area, while in the second we decomposed natural area into specific vegetational formations (forests, savannas, grasslands). In all the landscape models, agricultural area was included as a covariate. The models with the specific vegetational formations as predictors was submitted to a hierarchical partitioning analysis to estimate their relative importance to parasitoid species richness and abundance. This procedure was conducted using the ‘glmm.hp’ R package (Lai et al., 2022).

Finally, to estimate the biodiversity-ecosystem service relationship (BES), we used segmented regressions, with parasitoid species richness and abundance as predictors and biological control service index (BSI) as response. The segmented regression allowed us to identify different BES for communities within a gradient from low to high parasitoid richness and abundance. This procedure enables us to understand the responses to increasing parasitoid diversity in farms with different parasitoid species richness and abundance. The correlation between parasitoid species richness and abundance was tested to help interpret BES results.

RESULTS

Parasitoid communities in the crop and non-crop habitats

We sampled 1950 hymenopteran parasitoids classified into 314 (morpho) species within 32 families (Tab. 1). Crops presented 717 individuals from 173 species and the non-crop plant stripes 1233 individuals of 239 species. The mean abundance was 78.0 ± 15.1 individuals/farm (± SE) and the mean species richness was 26.2 ± 4.6 species/farm. The five most abundant families represent 78.7% of the total abundance, which were Pteromalidae (811 individuals), Figitidae (258), Encyrtidae (224), Diapriidae (157), and Braconidae (86). The families with higher species richness were Diapriidae (40 species), Braconidae (38), Encyrtidae (31), Mymaridae (28), and Pteromalidae (23).

Table 1 – Hymenopteran parasitoid families, their richness and abundance in the different habitats sampled in Brassica organic fields.

Family	Richness	Abundance		
		Crop fields	Non-crop stripes	Total
Diapriidae	40	68	89	157
Braconidae	38	33	53	86
Encyrtidae	31	45	179	224
Mymaridae	28	20	41	61
Pteromalidae	23	278	533	811
Scelionidae	21	13	46	59
Figitidae	21	146	114	260

Eulophidae	16	12	15	27
Ichneumonidae	11	4	17	21
Tetracampidae	11	5	13	18
Torymidae	11	31	8	39
Platygastridae	10	5	15	20
Bethylidae	9	11	15	26
Ceraphronidae	8	13	22	35
Aphelinidae	7	11	14	25
Signiphoridae	6	4	3	7
Eupelmidae	5	2	14	16
Dryinidae	4	1	4	5
Trichogrammatidae	4	3	4	7
Chrisydidae	3	2	1	3
Elasmidae	3	4	4	8
Megaspilidae	3	2	11	13
Tanaostigmatidae	3	1	2	3
Chalcididae	2	0	4	4
Evaniidae	2	0	8	8
Proctotrupidae	2	1	3	4
Agaonidae	1	1	1	2
Perilampidae	1	1	0	1

Although the estimated number of species in the crop fields was lower (Chao 1 = 366 species), than in the non-crop plant stripes (Chao 1 = 518 species), the individual-based rarefaction curves did not show any difference in species richness in both habitats (crop fields S = 173; non-crop plant stripes S = 239). The parasitoid communities were formed by many rare and a few abundant species. The species abundance distribution in both habitats fitted to a Power Law model (Tab. 2). The lower α values found in the crop fields indicates a steeper decline in abundance with increasing abundance rank, although dominance (Crop D = 0.38 ± 0.04; Non-crop D = 0.32 ± 0.03) and equitability (Crop J = 0.83 ± 0.04; Non-crop J= 0.84 ± 0.03 [± SE]) were similar in both habitats (Fig. 1).

Table 2 - Log-likelihood and Akaike Information Index (AIC) comparison between species abundance distribution models for crop fields and non-crop stripes.

		Log-likelihood	AIC	dLog-likelihood	dAIC	Weight
Crop Fields						
	Power law	-274.83	551.65	150	0	0.75
	Poisson lognormal	-274.92	553.85	149.9	2.19	0.25
	Log series	-314.03	630.06	110.8	78.41	$< 10^{-15}$
	Broken stick	-424.83	849.65	0	298	$< 10^{-65}$
Non-crop stripes						
	Power law	-414.58	831.16	205.27	0	0.7
	Poisson lognormal	-414.41	832.83	205.44	1.67	0.3
	Log series	-464.55	931.1	155.3	99.94	$< 10^{-20}$
	Broken stick	-619.85	1239.7	0	408.54	$< 10^{-80}$

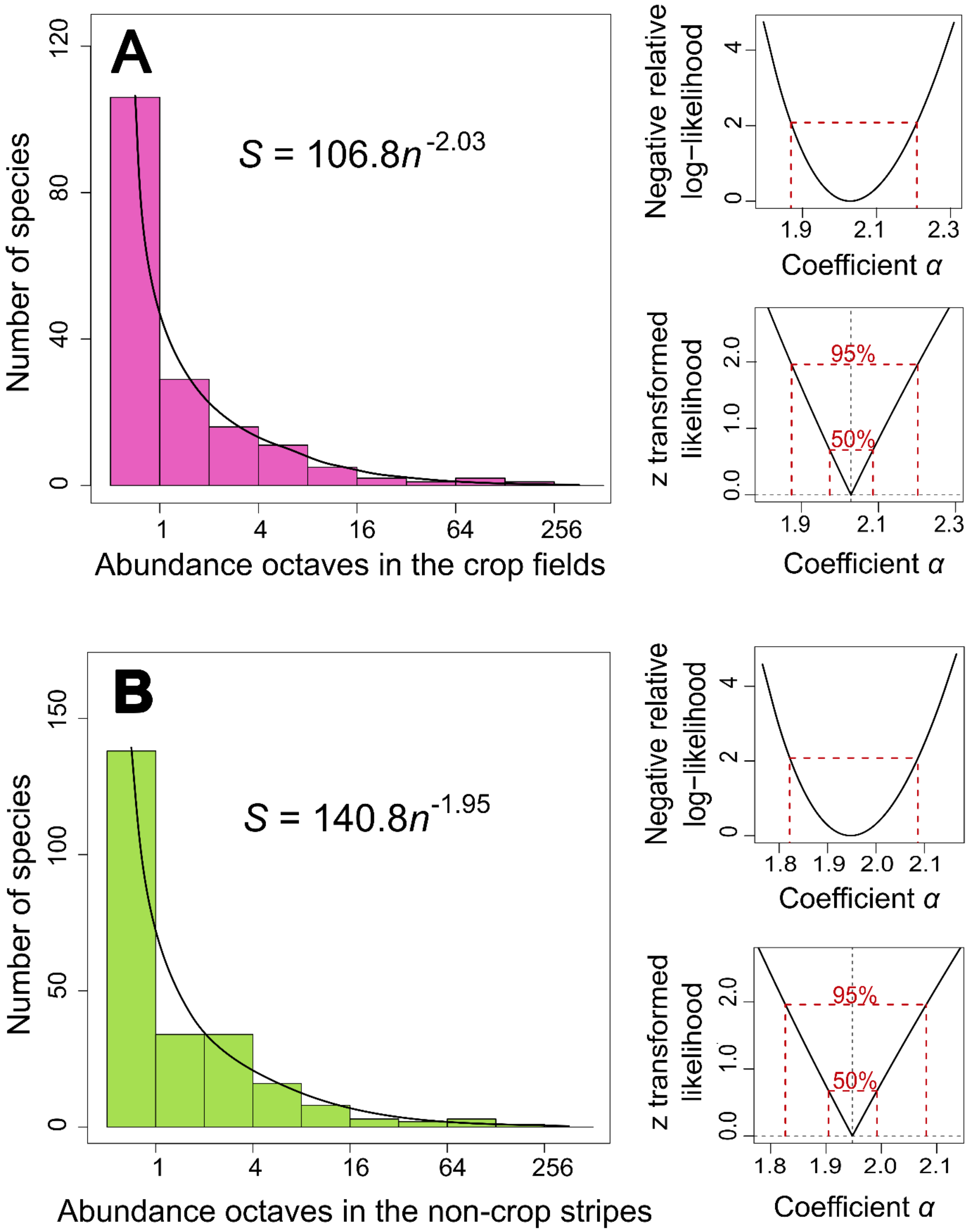

Figure 1 – Hymenopteran parasitoids species abundance distribution models (SADs) for crop fields (A) and non-crop plant stripes (B) in organic farms in the Brazilian Federal District. For each habitat, are shown the power law model fitted to Preston abundance octaves (left plot) the log-likelihood profiles for relative (top right) and z transformed (bottom right) likelihood of the α coefficient. *S*

represents the number of species and *n* the number of individuals. The likelihood profiles are shown to provide background for the comparison of the α coefficients between habitats. In them the red lines represent likelihood thresholds (the -2 loglikelihood threshold in top plot and the probability of the coefficient lying with these thresholds based on standard deviation in the bottom plot).

The PERMANOVA showed that crop fields have similar species composition to the non-crop plant stripes ($R^2 = 0.009$; d.f. = 1, 138; $F = 1.307$; $p = 0.0970$) with an overall average similarity of 91.91%, according to the SIMPER analysis using the Bray-Curtis index (Tab. 3). Species richness was responsible for 64% of the explained differences in species composition ($R^2 = 0.34$; $p = 0.0010$) between farms while abundance accounted for 36% of such differences ($R^2 = 0.19$; $p = 0.0130$) (Fig. 2).

Table 3 – Species contribution to dissimilarity calculated with SIMPER analysis (until 60% cumulative dissimilarity).

Species	Average dissimilarity	Contribution (%)	Cumulative (%)	Mean Crop	Mean Non-crop
Pteromalidae2	14.83	16.13	16.13	1.94	3.09
Pteromalidae1	7.752	8.434	24.56	0.971	1.6
Pteromalidae3	6.18	6.724	31.29	0.486	1.47
Figitidae2	5.973	6.499	37.79	1.47	0.971
Encyrtidae4	2.442	2.656	40.44	0.243	1.06
Pteromalidae6	2.204	2.398	42.84	0.143	0.414
Diapriidae1	1.348	1.467	44.31	0.0571	0.243
Scelionidae2	1.162	1.264	45.57	0.0286	0.186
Figitidae1	0.9889	1.076	46.65	0.143	0.186

Pteromalidae19	0.9225	1.004	47.65	0.0143	0.186
Ceraphronidae2	0.9048	0.9844	48.64	0.0714	0.0714
Diapriidae6	0.8933	0.9719	49.61	0.271	0.0714
Mymaridae1	0.8886	0.9668	50.57	0.0143	0.143
Bethylidae2	0.8781	0.9554	51.53	0.0857	0.0857
Encyrtidae18	0.8184	0.8904	52.42	0	0.643
Ceraphronidae1	0.7873	0.8566	53.28	0.0429	0.143
Pteromalidae14	0.7839	0.8529	54.13	0.0286	0.157
Diapriidae18	0.7659	0.8332	54.96	0.0571	0.257
Torymidae6	0.723	0.7866	55.75	0.2	0.0143
Pteromalidae10	0.7085	0.7709	56.52	0.1	0.114
Diapriidae8	0.7063	0.7684	57.29	0.1	0.0857
Megaspilidae3	0.6956	0.7568	58.05	0.0286	0.1
Aphelinidae3	0.6719	0.731	58.78	0.0714	0.1
Figitidae3	0.6095	0.6631	59.44	0.129	0.0429
Encyrtidae3	0.5865	0.6381	60.08	0	0.143
Encyrtidae10	0.5814	0.6325	60.71	0.1	0.129

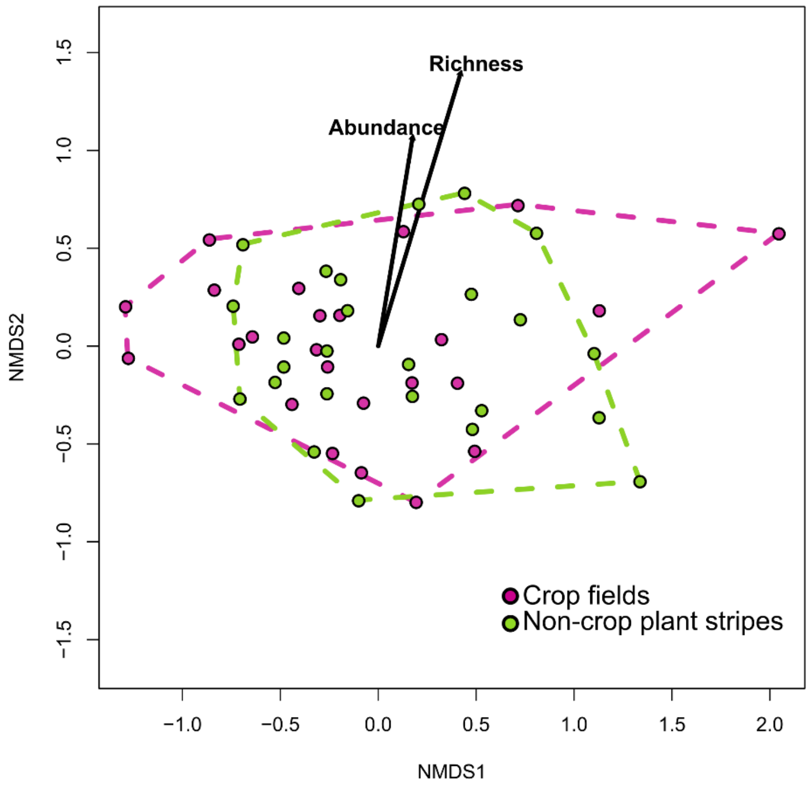

Figure 2 – Non-metric multidimensional scaling (nMDS) of the parasitoid community composition in brassica crops (crop fields) and in the non-crop plant stripes in organic farms in the Brazilian Federal District (stress = 0.18). Arrows represent abundance and richness fitted vectors, which explained 52% of the variation in the species composition between habitats.

Multiscale factors affecting parasitoid communities

Local floral resource abundance (floral units) showed a significant slightly negative effect on parasitoid species richness (β = -0.0015; F = 9.201; d.f. = 1, 22; p = 0.0026) in the farms (Fig. 3), but no effects on parasitoid abundance (β = 0.0003; F = 1.306; d.f. = 1, 22; p = 0.2734). At the landscape scale, the effects of natural areas diverged between species richness and abundance (Fig. 4). The multiscale model explained 50% of the variation in parasitoid species richness, with a positive effect of natural areas in parasitoid richness (β = -6.010; F = 21.690; d.f. = 1, 16; p < 0.0001) (Fig. 4A). Natural areas positively affected parasitoid richness until a 1 km radius from the crop area, but the strongest effect was observed at a 0.42 km radius. In terms of parasitoid abundance, the multiscale model explained 47% of the deviation. Natural areas in the landscape negatively affected parasitoid abundance (β = -7.970; F = 265. 300; d.f. = 1, 16; p < 0.001) (Fig. 4B). The effect on abundance happened until 5 km from the crop area but the strongest effect was observed at a 1.75 km radius buffer (Fig. 4B).

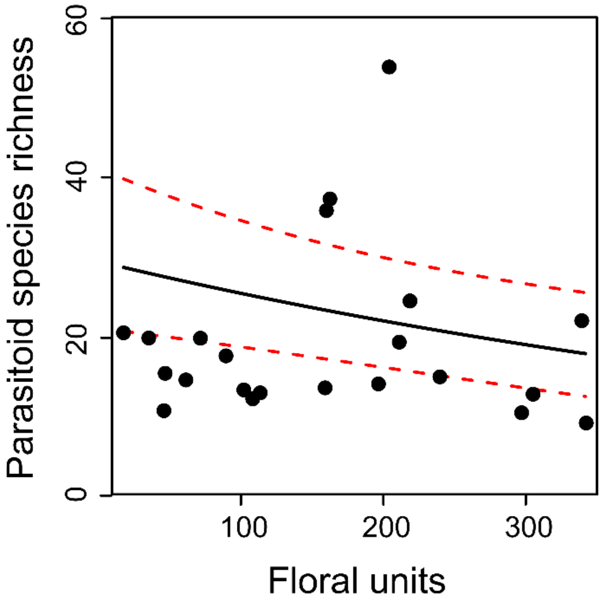

Figure 3 – Poisson generalized linear mixed-effects model on the relationship between floral resource abundance (floral units) on the non-crop plant stripes and parasitoid species richness in Brassica organic crops in the Brazilian Federal District.

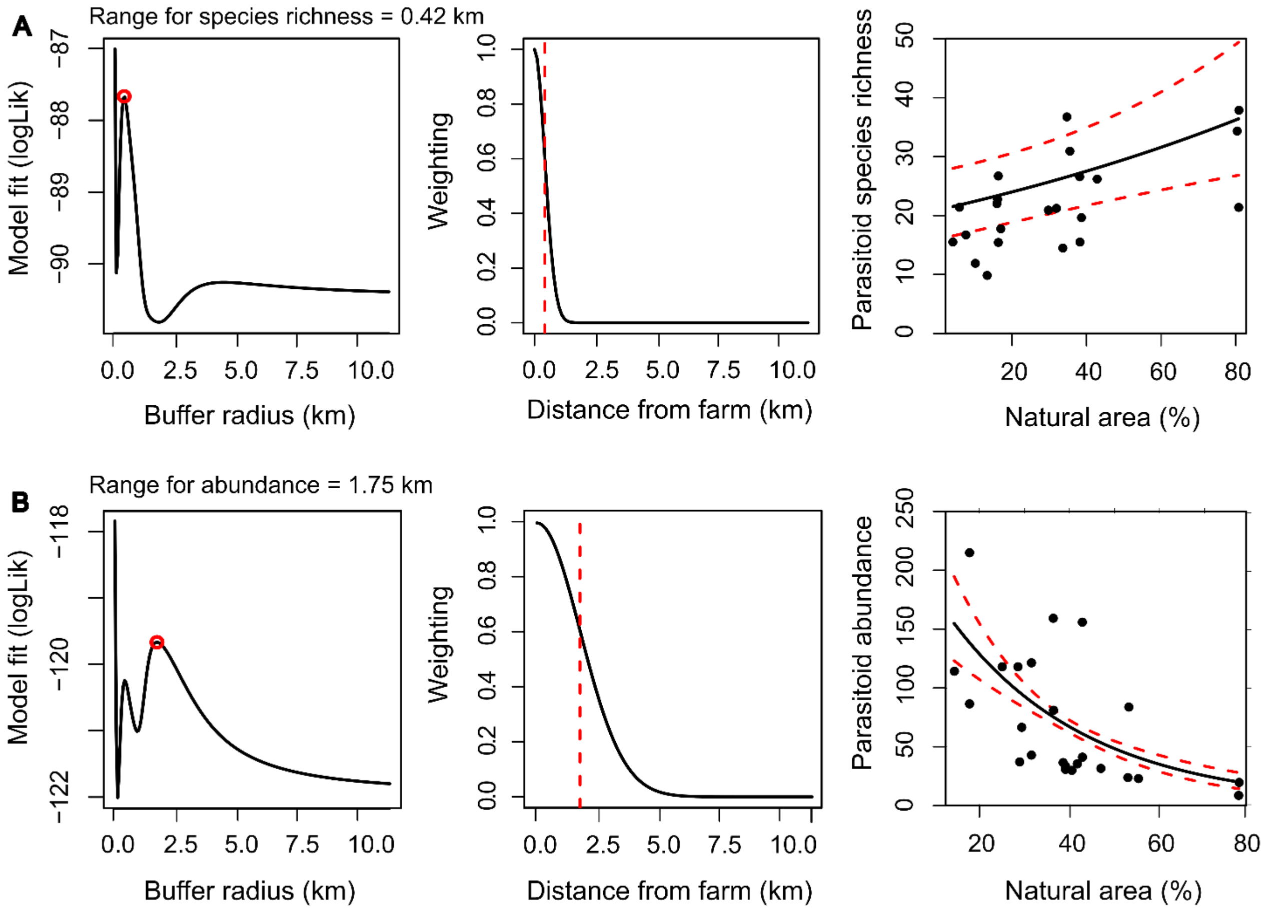

Figure 4 – Relationships between the percentage of natural areas in the landscape (landscape composition) and parasitoid species richness (A) and abundance (B). For each response variable were calculated: the ideal buffer radius to improve model fit (left plot), the natural area weight loss with distance from farm (center plot) and the effect of natural areas on the response variable within the buffer that improves model fit (right plot) according to a generalized mixed-effects model. In the center plots, the red dashed lines represent the range parameter value. While in the right plot the red dashed lines represent the 95% confidence intervals.

When assessing the role of each natural vegetation formation in the landscape, the interaction between forests and savannas positively affected species richness (β = 129.612; F = 6.130; d.f. = 1, 16; p = 0.0066), where the higher percentages of savanna formations in the landscape boost the positive effects of forests (Fig. 5A). Nevertheless, the independent effects of forests and savannas on parasitoid species richness were not significant (forest: β = - 31.532; F = 0.456; d.f. = 1, 16; p = 0.4562; savanna: β = -9.446; F = 0.120; d.f. = 1, 16; p = 0.4615). Grasslands had a negative effect on species richness

(β = -7.573; F = 3.964; d.f. = 1, 16; p = 0.0403) and its interaction with savannas was not statistically significant although savanna environments can reverse the negative effects of grassland on parasitoid species richness (β = 13.5678; F = 2.79; d.f. = 1, 16; p = 0.0840) (Fig. 5A). Grasslands were the most important component for species richness (27.67%), but the grouping of forests, savannas and their interaction summed more that 50% of the relative importance to species richness (Fig. 6A).

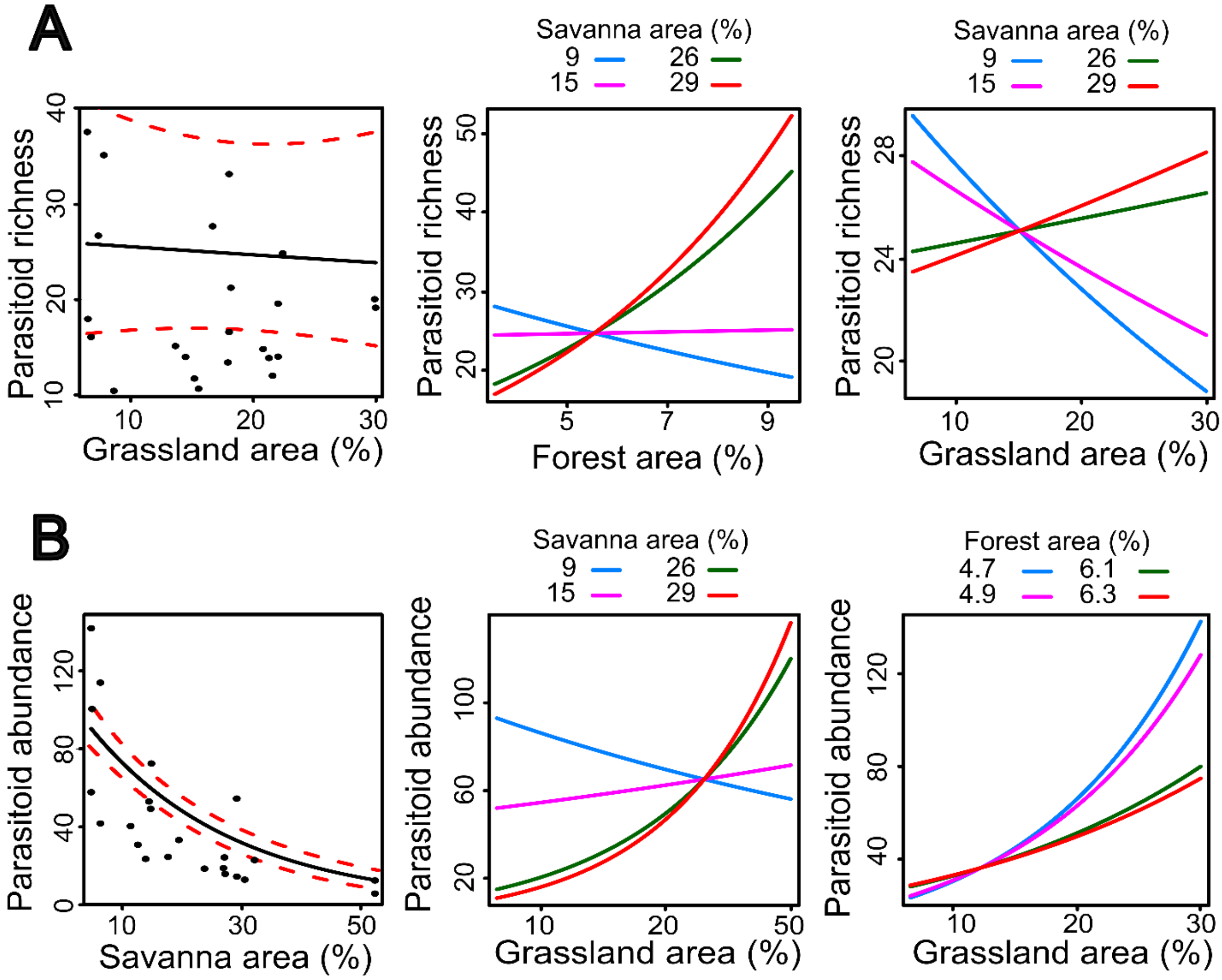

Figure 5 – Effects of the significant components of the specific vegetational formation GLMM on parasitoid species richness (A) and abundance (B) in organic crop farms from the Brazilian savanna. The effect of the interaction between grasslands and savannas on parasitoid richness was not statistically significant, but probably biologically important (p = 0.0840).

Parasitoid abundance was negatively affected by savannas (β = -15.157; F = 143.800; d.f. = 1, 16; p < 0.0001) (Fig. 5B). The interaction between grassland and forests (β = -217.909; F = 40.446;

d.f. = 1, 16; p < 0.0001) and grasslands and savannas (β = 64.756; F = 182.451; d.f. = 1, 16; p < 0.0001) also had a significant effect in abundance. Grasslands tend to have a positive effect on parasitoid abundance, but this effect is highly dependent on savanna environments, while forests can lower the magnitude of these effects (Fig. 5B). Forests and grasslands did not independently affect parasitoid abundance (Forests: β = 25.892; F = 0.854; d.f. = 1, 16; p = 0.2984. Grasslands: β = 4.211; F = 54.503; d.f. = 1, 16; p = 0.4531). The relative importance analysis show that savannas and their interaction with the other two formations comprise over 65% of the relative importance to parasitoid abundance (Fig. 6B).

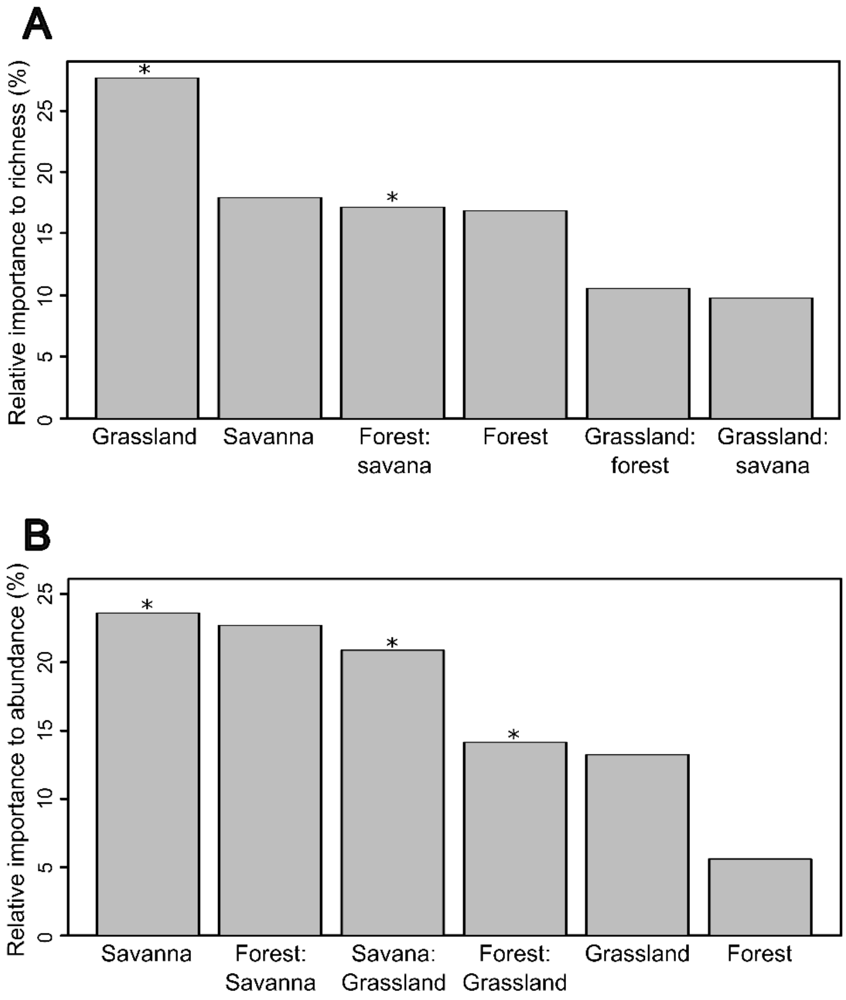

Figure 6 – Relative importance of natural vegetation formations and their interactions to parasitoid species richness (A) and abundance (B) GLMMs. Terms containing ":" indicate interactions between the landscape components. The * above the bars indicate the significant predictors from the GLMMs.

Biological control response to parasitoid species richness showed divergent results between communities with low, intermediate, and high species richness (Fig. 7). The segmented regression explained 37% of the variation in biological control. The first breaking point was fixed at 31.00, while the second breaking point was estimated to be 58.74 ± 11.86 (± SE). For communities with less parasitoid species, increasing diversity showed a detrimental effect ($\beta = -0.025$; $F = 6.657$; d.f. = 1, 19; $p = 0.0183$). When the community reaches 31 species, increasing parasitoid species richness generates a steep increase in biological control, until around 58 species ($\beta = 0.038$; $F = 7.703$; d.f. = 1, 19; $p = 0.0120$), when redundancy is reached and biological control stabilizes ($\beta = -0.010$; $F = 5.674$; d.f. = 1, 19; $p = 0.0278$). We did not find any significative effect of parasitoid abundance on aphid biological control (Tab. 4), although parasitoid richness and abundance were highly correlated ($r = 0.711$; d.f. = 22; $p < 0.0001$).

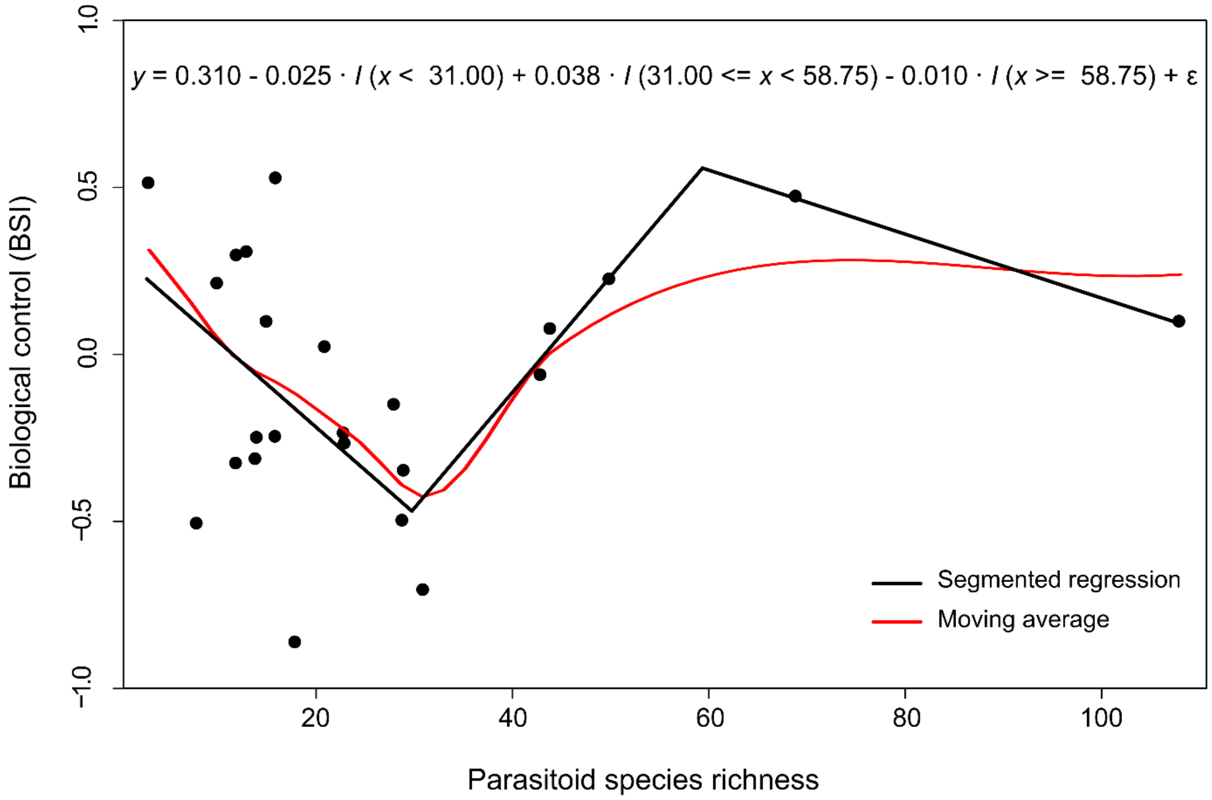

Figure 7 – Segmented regression on the relationship between Parasitoid species richness and biological control in organic farms cropping brassicas in the Brazilian Federal District. The black lines represent the segmented regression model and the red line represent the moving average, which is presented to avoid misinterpretation of segments with fewer points.

Table 4 - Segmented regression results for the realtioship between parasitoid abundance and biological control.

Segment	Estimate	Sum Sq	F value	Df	P
Before 1st breaking point	-0.0125	0.125173	0.899112	1, 18	0.355578
Between 1st and 2nd breaking points	0.01671	0.217753	1.564109	1, 18	0.227078
After 2nd breaking point	-0.01942	0.090569	0.650554	1, 18	0.430443

DISCUSSION

We showed that landscape context may be more important than local non-crop plant resources in benefitting parasitoids and related biological control services in tropical organic farms. Higher abundances of local floral resources may be detrimental for parasitoid richness most likely increasing negative interactions with hyperparasitoids, but these habitats were naturally diverse, and their functional redundancy may sustain service provision (Oliver et al., 2015). Parasitoid abundance and species richness are affected by distinct natural vegetation formations and by different spatial scales because natural components of landscapes are functionally complementary (Biggs et al., 2020). Forest and savanna areas adjacent to the crop fields (0.42 km) increased parasitoid richness, while grasslands at broader spatial scales (≥ 1.75 km) drive parasitoid abundance. Such complex and interdependent interactions of landscape composition on parasitoid communities influenced biological control services. Biological control was positively affected by parasitoid richness only in communities with intermediate number of parasitoid species.

Tropical organic collard crops using non-crop plant stripes can sustain a high diversity of parasitoid species within the farm, but communities are dominated by families that include hyperparasitoids of aphidophagous parasitoids (Pteromalidae, Figitidae and Encyrtidae). Such diverse communities can sustain parasitoids of different pests because species with different functional traits may coexist locally (Roxburgh et al., 2004). However, our results indicate that antagonistic interactions between parasitoids and hyperparasitoids may arise frequently, which can disrupt complex trophic networks by excluding important biological control agents (Duffy et al., 2007; Ji & Wang, 2022). In this context, it is essential to comprehend the interactions between parasitoids and their hosts in order to develop appropriate plans to manage them.

The similarities in species composition and richness between crop and non-crop areas indicates that the parasitoids are constantly foraging between and within both habitats. The non-crop plant stripes may retain parasitoid species when harvest occurs and promote a rapid colonization when a new crop cycle starts (Obanyi et al., 2024). However, the abundance of floral resource on the non-crop plant stripes had a negative effect on parasitoid richness. This highlights the importance of managing the functional diversity of the non-crop plants to parasitoids, since their resources must be appropriate to the natural enemies' requirements (Blassioli-Moraes et al., 2022). Nectar suitability and accessibility, for example, plays an important role in parasitoid maintenance and may diverge between plant species (Wäckers, 2004; Calderón-Arroyo et al., 2023). Moreover, parasitoids depend on hosts for oviposition, resource that is usually more abundant in the crop fields. In this sense, analyzing the tri-trophic networks, in which the plants that sustain host-parasitoid interactions are identified, can indicate the beneficial plants that should be prioritized in management plans (Venzon et al., 2019).

At the landscape scale natural areas can be sources of parasitoid species for organic crops. The most prominent effect of natural areas in species richness in the crops occur at more restricted spatial scales (0.42 km) because parasitoid foraging behavior is more conditioned to the availability of hosts for their progeny, favoring spillover effects from natural vegetation to the crops (Tscharntke et al., 2005; Rand et al., 2006; Evans, 2018). Therefore, habitat interfaces can favor natural enemy activity with natural habitats sustaining natural enemy populations readily available for crop colonization (Togni et al., 2019a; Harterreiten-Souza et al., 2021). Adjacent natural areas can act as sources of parasitoid species able to colonize agricultural fields, but their abundances depend highly on the abundance of hosts (May et al., 1981; Thies et al., 2005; Macfadyen et al., 2011). Since natural areas can act as barriers for pests, which can disperse for longer distances and in higher abundances than natural enemies (Corbett & Rosenheim, 1996; Castro et al., 2023; Novaes et al., 2023), the effects on parasitoid abundances should operate at wider scales (1.75 km) than on species richness. Such effects show that in order to increase beneficial insects, maintaining natural vegetation inside private lands should be economically and politically encouraged (Belcher et al., 2003; Metzger et al., 2019; Novaes et al., 2023).

However, not all natural vegetation formations at the landscape scale have the same effects on parasitoid communities. Beneficial effects rely mostly on the structural complexity and diversity of vegetation formations which in turn affect their functional roles for parasitoids (Fahrig et. al, 2011; Concepcion et al., 2012; Begg et al., 2017). Parasitoid species richness has been positively correlated with wood density, while abundance showed a negative relationship with it (Fonseca et al., 2005). Forests usually have higher insect species richness, probably favoring the coexistence of multiple parasitoid species, while grasslands provide more plant-provided food for adult individuals (Crist & Peters, 2014; Baude et al., 2016). In savanna environments, the coexistence of trees and grasses boost the positive effects of forests and grasslands on parasitoid species richness and abundance, respectively. Our results show that part of the inconsistencies in natural enemies' response to landscape context (Karp et al., 2018) may be related to the different roles that each natural vegetation formation within the landscape may have in natural enemy richness and abundance in tropical agroecosystems. This can be especially important for non-forested tropical biomes, which have high compositional and configurational diversity.

The biodiversity-ecosystem service relationships were also influenced by these multiscale features, revealing distinct patterns on parasitoid communities with low, intermediate, and high species richness of parasitoid species. Communities with fewer species tend to have its services concentrated on a few keystone species (Longland & Ostoja, 2013). This makes them more susceptible to disruption by increasing complexity and antagonistic interactions (Aizen et al., 2008; Martin et al., 2013; Qian & Akçay, 2020). At an intermediate species richness level, a positive biodiversity-ecosystem service relationship is observed indicating the arising of complementarity patterns (Snyder, 2019). Since species that come from adjacent natural areas have alternative resources beyond the ones shared by the species present only in the crop fields, niche overlap is reduced increasing coexistence and complementarity in resource use (Pastore et al., 2021). Additionally, farm management also has influence on these complementarity patterns and their effects on the ecosystem services (Togni et al., 2019a). At last, redundancy patterns arise for communities with high species richness, what plays an important role on biological control stability (Macfadyen et al., 2011). In this sense, biodiversity-ecosystem service relationships are unlikely to be linear in tropical regions, as the number of species varies greatly between sites and specific local management and landscape contexts need to be considered.

CONCLUSIONS

In summary, we show that non-crop plant stripes can shelter a high diversity of parasitoids for organic tropical crops, increasing the permeability of the crop fields and possibly sustaining their populations when the main crop is absent. However, these plant stripes need to be managed according to the suitability and availability of their floral resources to the target biological control agent. In addition, we show that natural areas within 420 m are the sources of these parasitoid species, although its different vegetation formations play different and complementary functional roles for biodiversity and related ecosystem services. These results can subsidize the management of tropical landscapes based on the functional role of its habitats for agro-ecosystems services. Our study also contributes to the knowledge on the relationship between biodiversity and biological control in tropical agro-ecosystems, which are more diverse than in temperate regions, raising the complexity of interference, complementarity, and redundancy patterns. In this sense, we show that this relationship is not always linear and can depend directly on interactions with the landscape. Therefore, the management of tropical natural areas combined with more biodiversity-friendly farming practices, can help to reconcile sustainable agricultural production with the conservation of remnants of native vegetation in priority environments (e.g. hotspots).

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CHAPTER 2

From field to theory: using trophic networks and mathematical modelling to understand biological control by parasitoids in space and time

ABSTRACT

The threat suffered by the world's biodiversity has raised concern about the provision of ecosystem services essential for human life. However, an increase in biodiversity does not always result in greater provision, due to differences in how species interact with each other and their habitats. Here we evaluate how non-crop plant stripes affect the network of interaction involving parasitoids and aphids in organic tropical brassica crops. First, we compared the topology of the interaction networks within the crops and on adjacent non-crop plants based on modularity and nestedness. Subsequently, we used the information from the networks to conduct data driven simulations of host-parasitoid population dynamics using an adapted version of the generalized Lotka-Volterra model. We simulated scenarios of normal conditions, favoring an alternative native host, favoring an alternative pest, and favoring an alternative parasitoid. The most important pest in organic brassica fields was *Brevicoryne brassicae*, which presented a specialized interaction with the parasitoid *Diaretiella rapae*, responsible for ~90% of its parasitism. *Myzus persicae* was the most abundant alternative pest while *Uroleucon* species were the most common native host. *Praon volucre* was the most abundant alternative parasitoid. In general, we show that interactions in the lower trophic level tend to be more nested, while in the higher trophic level they are more modular. We show that most significant differences in network metrics between crop field and non-crop plant stripes were observed at the higher trophic level of parasitoid-hyperparasitoid interactions. Differences in modularity between non-crop plants and brassica fields were significantly larger than expected at random, while differences in nestedness were significantly smaller than expected at random. Additionally, we showed that the difference in nestedness between aphid-parasitoid networks sustained by different non-crop plants was significantly smaller than expected at random, suggesting that factors beyond plant identity define this metric in the non-crop plant stripes. Through the population dynamics simulations, we show that alternative hosts and parasitoids can help control the populations of the main brassica pest *B. brassicae*, but it is necessary to further understand these interactions to avoid chaotic dynamics.

INTRODUCTION

Global Biodiversity loss generates concern about the maintenance of future ecosystem services (Cardinale et al., 2012). It is a fact that there is a relationship between biodiversity and ecosystem service provision (Tilman et al., 2001; Gamfeldt et al., 2013; Brockerhoff et al., 2017). However, a positive effect on service provision is not always achieved by increasing biodiversity (Straub et al., 2008; Letourneauet al., 2009; Macfadyen et al., 2011a; Forrester & Bauhus, 2016), and it is necessary to understand how species interact with each other. Biological control, for example, can be negatively affected by increases in natural enemy diversity if the added species interact antagonistically, for example, through competition, intraguild predation, or hyperparasitism (Martin et al., 2013; Tougeron & Tena, 2019). Conversely, a positive effect of biodiversity on this service is expected when there is complementarity in resource utilization by the present natural enemies (Macfadyen et al., 2011a). In this context, the structure of these interaction networks is mediated by habitat features, which influences the need for species to compete for resources or the possibility of using them in a complementary way (Brose et al., 2004; Janssen et al., 2007; Cagnolo et al., 2009; Macfadyen et al., 2009; Tscharntke et al., 2012; Landis, 2017). Ultimately, habitat features and the structure of interaction networks will determine how the provision of ecosystem services is maintained in space and time.

Spatial relatioshnships mediate important features of its species interaction networks, such as interaction richness, modularity, and interaction nestedness (Post & Hairston, 2000; Tylianakis et al., 2007). In pest-natural enemy networks, modularity may be benefited by habitat diversification and species identity, suggesting that each habitat comprises a specific set of interactions, with specialists being primarily influenced at smaller spatial scales, while generalists respond well to different scales (Chaplin-Kramer et al., 2011; Macfadyen et al., 2011b). Furthermore, modified and homogeneous habitats may decrease modularity as they are favorable for generalist species connecting the different modules (Tylianakis et al., 2007; Aizen et al., 2008). Conversely, interaction nestedness, is benefited by habitat suppression (Tylianakis et al., 2007; Gonzalez et al., 2011; Macfadyen et al., 2011b), releasing species from top-down control and resulting in the loss of ecosystem services provided by higher trophic levels (Post & Hairston, 2000; Dobson, 2009). At the population level, higher proportions of natural habitats around the cultivated area can increase the density of pest consumers, reducing its population growth and decreasing its density at harvest (Chaplin-Kramer et al., 2013). Habitat management can also affect the network of natural enemy interactions through alternative prey and resources (Landis et al. 2000; Macfadyen et al., 2009; Landis, 2017; Blassioli-Moraes et al., 2022). In this context, managing non-crop plants can increase alternative prey and host resources allowing greater complementarity in resource use by natural enemies (Venzon et al., 2019; Bianchi & Wäckers, 2008; Macfadyen et al., 2011b; Hatt et al., 2018).

The interactions that natural enemies sustain with their preys, hosts and environments constrain their population dynamics over time (Yoo & O'Neil, 2009; Welch & Harwood, 2014; Rosero et al., 2024). With a theoretical model, Rosero et al. (2024) showed that the same set of species interactions can result in different dynamics depending on habitat heterogeneity. Plant resources can benefit natural enemies in heterogenous habitats, but they benefit pest populations in homogeneous habitats due to the liberation of top-down regulation (Rosero et al., 2024). The success of biological control services depend widely on these cyclical dynamics. If natural enemy populations are established before the population peak of the pest, biological control may succeed, while if this happens after a pest populational boom, the crops may be already damaged by pests (Yoo & O'Neil, 2009). Crop environments are cyclical by nature, from crop-management cycles to phenological cycles of the managed plants. In this sense, understanding the temporal dynamics of pest-natural enemy interactions is essential to conduct overlapping management cycles that benefit natural enemies and biological control (Welch & Harwood, 2014).

Parasitoid wasps (Hymenoptera) comprise a large group of natural enemies of agricultural pests widely used in biological control strategies (Thies et al., 2003; Tylianakis et al., 2004; Plećaš et al., 2014; Gontijo et al., 2015; Eid et al., 2018; Kaser & Heimpel, 2018). Parasitoids respond well to habitat structure, making them useful models for the study of spatially explicit interaction networks (Hatt et al., 2018; Zhu et al., 2020). This response occurs in part due to the increase in alternative hosts, i.e., new oviposition sites and food resources for the larvae (Holzschuh et al., 2010). Non-crop plant strips can promote an increase in host diversity and abundance and are important for maintaining, primarily, specialist parasitoids through the diversification of habitats and resources (Tscharntke, et al., 2005; Holzschuh et al., 2010). Additionally, parasitoids show characteristic cyclical dynamics with their hosts, which can be influenced by habitat features (Welch & Harwood, 2014; Rosero et al., 2024). Therefore, understanding how parasitoid interactions with their primary and alternative hosts influence their population dynamics over time is essential to develop management plans appropriate for each farm contexts and cycles.

We seek to understand how non-crop plant stripes mediate interactions sustained by aphid parasitoids and how these interactions influence parasitoid population dynamic over time in tropical organic Brassicaceae crops. Specifically, we asked the following questions: i) How local non-crop plants influence network structure in aphid-parasitoid interaction networks. ii) How host-parasitoid interactions sustained by non-crop plant stripes modulate population dynamics in normal conditions and when we artificially favor alternative hosts and alternative parasitoids. We predict that parasitoid interaction networks will show higher nestedness inside the crop filed, due to the higher frequency of generalists and a higher modularity in the non-crop plant stripes, where resource diversity can allow parasitoid to use their preferred resources creating different modules. Therefore, we expect that an increase in the population of alternative hosts and parasitoids benefited by the non-crop plant stripes will result in a decay off pest populations over time.

MATERIAL AND METHODS

Study area

This study was performed from August to October 2022 and 2023 in 25 organic farms cropping collards (*Brassica oleracea*, Brassicaceae) in the Brazilian Federal District (15°47’ S, 47°56′ W, 1000m above the sea level). The region is in the core of the Cerrado biome, the Brazilian tropical savanna, one of the 25 most important terrestrial biodiversity hotspots (Myers et al., 2000). The Cerrado is the second largest Brazilian biome (2 million km²) and 52,9% of its area is currently used for agricultural activities (Sano et al., 2019). The native vegetation of the biome is mostly within private properties and is formed by different plant physiognomies ranging from forest and savanna formations to grasslands (Ribeiro & Walter, 2008; De Marco et al., 2023), being potential reservoirs for beneficial insects like parasitoids.

The sampled farms were distributed within a land use gradient varying between areas dominated by large-scale monocultures to areas composed mostly by fragments of native vegetation. The farms belonged to small farmers (4 – 70 ha) and were certified as organic for at least 5 years (Brazil, 2003, 2007). Bt-based products (*Bacillus thurigiensis*), *Beauveria bassiana*, regular augmentative releases of *Trichogramma pretiosum* (Riley) (Hymenoptera: Trichogrammatidae) and different types of plant extracts were used for pest management according to Brazilian legislation (Togni et al., 2019c). Besides the input restrictions, the farmers usually use management practices to increase beneficial insect biodiversity in their fields, commonly maintaining strips of spontaneous non-crop vegetation nearby or among brassica crops (Assunção et al., 2022). The tropical savanna climate, with a dry winter and a hot and humid summer (da Silva et al., 2008; Alvares et al., 2013), forces farmers to grow collards during winter to avoid rainfall damage. Therefore, we conducted this study in the driest months of the dry season when aphids and parasitoids are abundant in organic brassica fields. The water supply for crops was provided by irrigation with sprinklers.

Sampling plants, aphids and parasitoids

To assemble the networks of interactions between plant, host, and parasitoids, we sampled the insects inside the crops and on non-crop plant flower stripes nearby the crops. We performed direct collections of 20 plants, 10 brassica plants and 10 non-crop plants collected on the adjacent stripes. The non crop stripes were at most 25m apart from the crop fields and the plants were collected at least 5m apart from the stripe edges. Due to the aggregate distribution of the aphids, our sample was directed to plants infested with aphids, this was especially important in the non-crop stripes where a higher plant diversity was available. In each habitat, the search had a 20 minutes limit, so it ended either when the 10 plants were found or when the time was over. During the collections, the species of plants where the aphids were found were identified using a weed identification manual (Moreira & Bragança, 2011). Afterward, the infested plants were taken to the laboratory where the parasitized aphids were placed in glass tubes, in which adult parasitoids emerged and were then bathed in alcohol. Since some aphids could have been recently parasitized, thus not appearing so, each plant with the rest of the colonies was placed in 20 x 30 cm (diameter x height) cylindrical cage closed with a fine mesh net. The base of the plants was placed inside 10 x 10 cm cups filled with water and the cages were maintained at 25°C with a 12h photoperiod. Every three days the cages were monitored to spot the presence of apparent parasitized aphids, which were carefully removed from the plants using brushes and placed in glass tubes where we proceeded like the ones spotted on the field. The aphids and parasitoids were identified to the level of species and the hyper parasitoids to the level of family and morphospecies.

Building the network of plant-pest-parasitoid interactions

To understand how the plant-pest-parasitoid interactions were structured and how the habitat type influence these interactions, we modeled the network of interactions among parasitoids, aphids, brassicas and non-crop plants. The current study system enables that the interaction network is assembled based on confirmed consumption interactions. Our network was conceptually a multilayer network comprised of an array of interaction matrices. Each interaction matrix was composed of weighted pairwise interactions with the resources at the rows and the consumer at the columns (plants x aphids, aphids x parasitoids, parasitoids x hyperparasitoids). We then calculated modularity and link nestedness for aphid-parasitoid and parasitoid-hyperparasitoids interaction in each observed plant. Modularity measures whether the network is organized into groups of interactions (modules), while nestedness measures the extent to which specialist species interactions are a subset of generalist species interactions. Afterwards we used a randomization process to compare these metrics between networks. The networks were constructed and their metrics calculated using ‘bipartite’ package for R software

(Dormann et al., 2008). With this, it was possible to investigate how non-crop plants mediate aphid-parasitoid and parasitoid-hyperparasitoid interactions in organic tropical fields.

Simulating the effects of network structure on the population dynamics of pests and parasitoids

To simulate how the structure of the interaction network affect the population dynamics of the host-parasitoid system we used the generalized Lotka-Volterra (gLV) model. To properly conduct the gLV two main datasets are needed: 1) A community matrix with the intensity of each interaction's influence on each species; 2) A matrix of intrinsic growth values for each species. The matrix of intrinsic growth values was built from reference values obtained in literature. To design the community matrix, we need to know which interactions are occurring (the zeros and ones of the community matrix), the interaction types (the sign-pattern of the community matrix) and the per capita interaction strength (the short-term effect of one individual on an individual of another species). The first two, we got directly from our ecological network and the third we estimated using field observations of interaction rates as follows (Rott & Godfray, 2000; Jordan et al., 2003; Wootton & Emmerson, 2005):

i) Direct interactions: the strength of a single direct interaction was calculated as the ratio of parasitism frequency.

$$a_{i,j} = \frac{\alpha_{i,j}}{\sum\limits_{j} \alpha_{i,j}}, \tag{1}$$

where $a_{i,j}$ is the interaction matrix, i is our host, j is the parasitoid and $\alpha_{x,y}$ is the number of parasitoid link shared by host species (hereon frequency matrix).

ii) Indirect interactions between hosts: the strength of indirect interactions between host species was quantified based on frequency of links shared by these species with parasitoids. Calculated as:

$$a_{i,j} = \sum_{k=1}^{n} \frac{\alpha_{k,j}}{\sum\limits_{l=1}^{m} \alpha_{k,l}} \cdot \frac{\alpha_{i,k}}{\sum\limits_{k=1}^{n} \alpha_{i,k}}, \tag{2}$$

where $a_{i,j}$ is the strength of the indirect effect of species *j* on species *i*, *n* and *m* are the number of parasitoid and host species, respectively. $\alpha_{x,y}$ is our frequency matrix. While *k* and *l* are parasitoids and hosts, respectively. In this expression, the strength of the indirect interactions is given by the product of the strength of two direct interactions.

With these data we were able to conduct data driven simulations of the effect of network structure on population dynamics of pest and parasitoids through the following gLV model

$$\begin{cases} \dfrac{dX_i}{dt} = r_i X_i - r_i \dfrac{X_i}{K_i} \displaystyle\sum_{j=0}^{R} \omega_{ij} X_j - X_i \sum_{j=0}^{P} a_{ji} \dfrac{Y_j}{1 + h a_{ji} X_i} \\ \dfrac{dY_i}{dt} = Y_i \displaystyle\sum_{j=0}^{R} a_{ij} k_j \dfrac{X_j}{1 + h a_{ij} X_j} - Y_i m_i \end{cases} \tag{3}$$

where X_i represents the population level of aphid *i* and *Yi* the population of parasitoid *i* on time *t*, *r* represents the intrinsic growth rate, *Ki* is the carrying capacity of aphid *i*, *ωij* represents the indirect interaction between aphids *i* and *j*, a_{ij} represents the interaction between parasitoid *i* and aphid *j*, (parasitism probability), *h* is the time parasitoids need to handle the hosts, *k* is the conversion rate of resource into offspring, R and P represent the number of aphids and parasitoid, respectively. All procedures related with the gLV were conducted on Python programming language

RESULTS

Network characterization

In terms of host-parasitoid interactions, the most frequent was the parasitism of the aphid *Brevicoryne brassicae* (L.) by the parasitoid *Diaretiella rapae* (McIntosh). *Brevicoryne brassicae* was the most important brassica pest and *D. rapae* was responsible for ~ 90% of its control (Tab. 1). Within the brassica fields, a Figitidae hyperparasitoid dominates at the fourth trophic level, followed by a Pteromalidae species (Tab. 2). In the non-crop plant stripes, aphids were found in *Sonchus oleraceus* (L.) and *Bidens pilosa* (L.) (Fig. 1). The network sustained by *S. oleraceus* were dominated by a native aphid *Uroleucon sonchi* (L.), which were responsible for maintaing the populations of the alternative parasitoids, *Praon volucre* and *Aphidius* sp. *Diaretiella rapae* was able to parasitize *U. sonchi*, but their populations still account on the individuals of the pest aphids that were occasionaly found on the non-crop plant stripes (Fig. 1). Nevertheless, the combination of *S. oleraceus* and *U. sonchi*, can maintain parasitoid populations between harvests. The same hyper-parasitoid species found on the brassica field were sampled in *S. oleraceus*, but with more equitative numbers and different host preferences. In them, the figitidae hyper-parasitoid prefered *D. rapae* and *P. volucre*, while the Pteromalidae prefered *Aphidius sp*. The Encyrtidae hyperparasitoid, which was nearly absent from the crop fields, had a steep increase in number in *S. oleraceus*, and was the one to show the more generalistic habits. The other non-crop plant in which aphids were found was *B. pilosa*, which showed the most simple network, with only two species of aphids, two primary parasitoids, and no hyperparasitoids. The main aphid found in *B. pilosa* was *Uroleucon ambrosiae*, a different species from the same native genus from the ones found in *S. oleraceus*. However *U. ambrosiae* were more suitable for *D. rapae* than *U. sonchi*, which was dominated by *P. volucre* and *Aphidius sp*. (Fig. 1).

Table 1 – Number of aphid-parasitoid interactions from organic brassica crops from the Federal District and their non-crop plant stripes.

Plant	Aphid	Parasitoid		
		Diaretiella rapae	*Praon volucre*	*Aphidius sp.*
Brassica oleracea				
	Brevicoryne brassicae	*1018*	*16*	*1*
	Myzus persicae	85	20	0
	Lipaphis pseudobrassicae	11	1	0
	Uroleucon sonchi	1	1	1
Sonchus oleraceus				
	Brevicoryne brassicae	2	1	0
	Myzus persicae	5	12	0
	Uroleucon sonchi	9	38	25
Bidens pilosa				
	Myzus persicae	1	1	0
	Uroleucon ambrosiae	4	3	0

Table 2 – Number of parasitoid-hyperparasitoid interactions from organic brassica crops from the Federal District and their non-crop plant stripes.

Plant	Parasitoid	Hyperparasitoid		
Brassica oleracea		Figitidae spp.	Pteromalidae spp.	Encyrtidae spp.
	Diaretiella rapae	410	123	2
	Praon volucre	16	3	1
	Aphidius sp.	1	1	0
Sonchus oleraceus				
	Diaretiella rapae	3	1	1
	Praon volucre	3	2	2
	Aphidius sp.	1	4	1

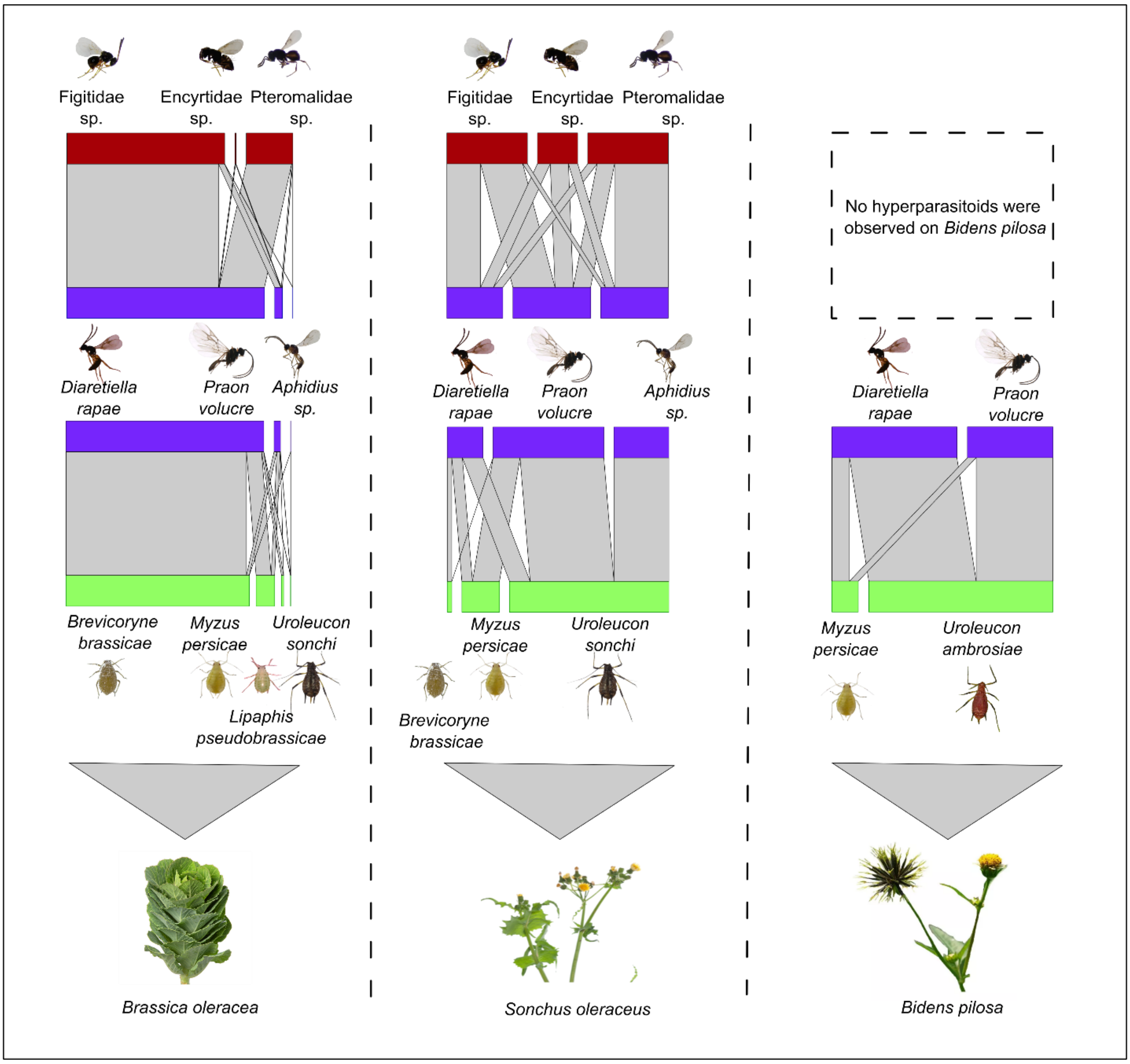

Figure 1 – Aphid parasitoid and parasitoid-hyper interactions in brassica fields and non-crop plants stripes for organic farms in the Brazilian Federal District. The interactions were identified by isolating a mummy, identifying its species and waiting for the parasitoid to emerge. In case of hyperparasitoid emergence, the primary parasitoid were identified through the mummy when possible, and when unidentifiable, proportional values from the identifiable cases were used.

Network metrics

In terms of Nestedness of the aphid-parasitoid interctions, the one sustained by *B. oleracea* had the smallest value of nestedness (-0.034), followed by the ones on *B. pilosa* (0.470) and *S. oleraceus* (0.513). When considering the parasitoid-hyper interactions, the ones sustained by *B. oleracea* (0.101) are more nested than the ones sustained by *S. oleraceus* (0.094). Through a randomization process, we saw that for the aphid-parasitoid interactions, the only pair that showed significant differences from the randomized and observed nestedness was the *S. oleraceus* – *B. pilosa* pair (Fig. 2A). It shows that the observed differences (OD) in nestedness between these two non-crop plants were smaller than expected at random (RD) (OD = 0.018; RD = 0.446 ± 0.008; p = 0.0241[± SE]), what suggests that factors beyond plant identity are modulating interaction nestedness in non-crop plant stripes, but differences between theses stripes and crop fields are maintained as expected (p = 0.3430). Opposingly, the parasitoid-hyper interactions of the crop fields and the non-crop stripes showed differences significantly smaller than expected at random (OD = 0.029; RD = 0.334 ± 0.005; p = 0.0477) (Fig. 2B), what suggests that the non-crop plants modulate interaction nestedness of the crop fields at this trophic level.

In terms of modularity, the most modular networks were the ones sustained by *S. oleraceus*, in which parasitoid-hyper interactions were more modular (0.265), followed by the aphid parasitoid interactions (0.114). The aphid-parasitoid interactions in the brassica fields followed with a modularity of 0.030, but the parasitoid-hyper interactions in these fields had the lowest value of modularity (0.006). At last, the aphid-parasitoid interaction sustained by *B. pilosa* showed the smallest modularity of this trophic level (0.018). The only pairwise difference in modularity that was significantly different from the expected at random was the difference between the parasitoid-hyper interactions sustained by *S. oleraceus* and *B. oleracea* (OD = 0.259; RD = 0.106 ± 0.001; p < 0.0001) (Fig. 2C). It shows that the difference in modularity between the main non-crop plant and brassica plants doubled what was expected at random for these interactions, suggesting that in the non-crop plants the hyperparasitoids can select their preferred resource, while in the brassica fields they show generalistic behavior.

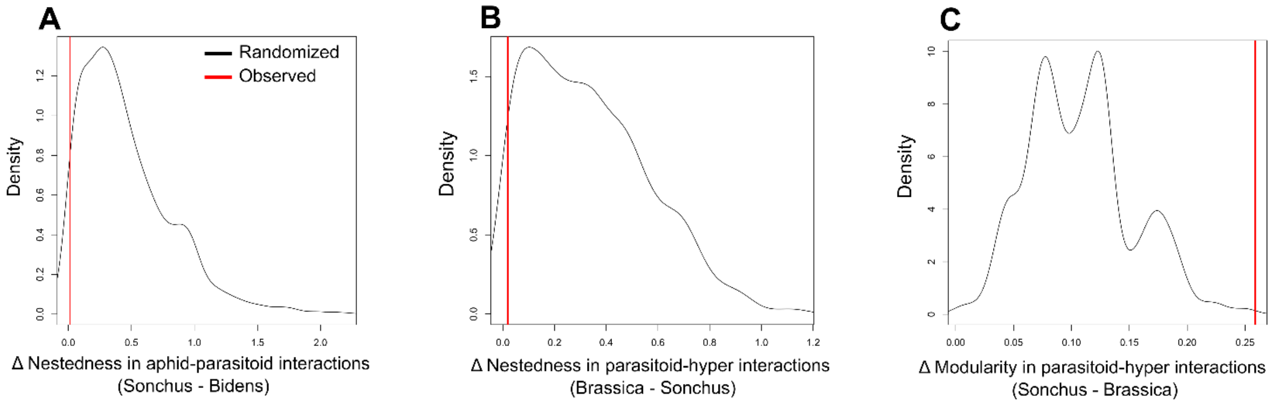

Figure 2 – Comparison between observed pair wised differences in network metrics and the expected at random with 2000 permutations. A) pair wised differences in nestedness between aphid parasitoid interactions sustained by *S. oleraceus* and *B. Pilosa*. B) Pair wised differences in nestedness between

parasitoid-hyper interactions sustained by *B. oleracea* and *S. oleraceus*. C) pair wised differences in modularity between parasitoid-hyper interactions sustained by *B. oleracea* and *S. oleraceus*.

Population dynamics simulation

In a first simulation with normal conditions found in the literature we were able to see a community dominated by *B. brassicae* with *D. rapae* being the only parasitoid that can reach a stable cycle (Fig. 3A). In a second simulation, the main alternative host, *U. sonchi*, was favored by a 10% increase in fecundity (represented by the produced offspring by resource used [k]). In this scenario the apparent competition caused a drastic decrease in the population of the pest *B. brassicae*, which stabilized at low levels, but parasitoid population accompanied this decrease (Fig. 3B). In the third simulation, which favored the secondary pest *M. persicae* with a 15 % increase in fecundity, the populations of *B. brassicae* were also controlled and the *M. persicae* populations peaks were half the size of *B. brassicae* in the first simulations. Additionally, *D. rapae* was also able to stablish stable cycles in this third scenario (Fig. 3C). In the fourth simulation, in which the alternative parasitoid *P. volucre* was favored with a 20% decrease in mortality, *B. brassicae* populations were controlled, but *M. persicae* followed chaotic dynamics with occasional peaks almost twice as high as *B. brassicae* population peaks in normal conditions. Additionally, increasing the populations of the alternative parasitoid *P. volucre*, caused the extinction of the native aphid *U. sonchi*, which may be linked to the populational increase in *M. persicae* (Fig 3D).

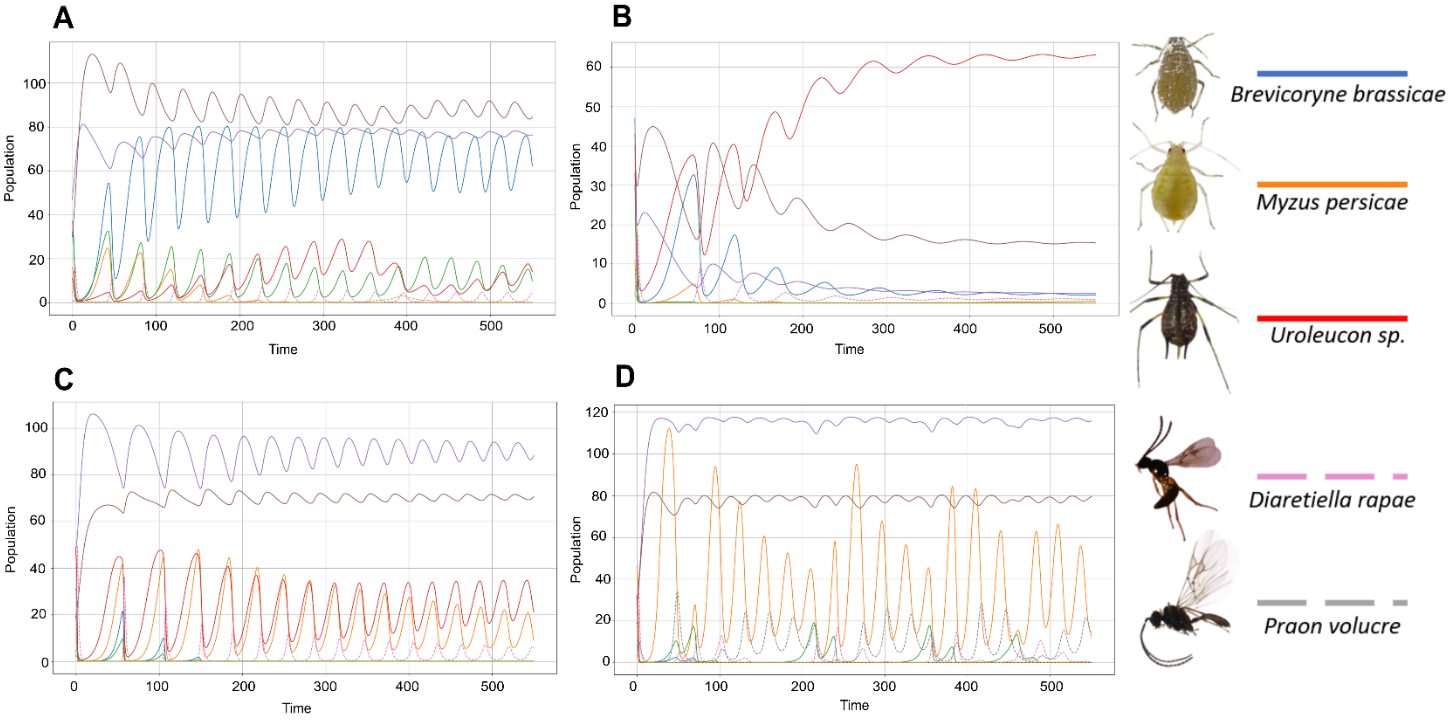

Figure 3 – Host-parasitoid population dynamics through generalized Lotka-Volterra equations. A) Normal condition simulation. B) Favoring the alternative native host *Uroleucon spp.* C) Favoring the alternative pest *M. persicae*. D) Favoring the alternative parasitoid *P. volucre*. The green line represents L. pseudobrassicae, but its parameters were not manipulated. The brown and purple lines represent two unidentified aphids from which no parasitoid emerged, generating independent dynamics and were removed from network analysis.

DISCUSSION

Our results show that the interactions undergone by parasitoids in organic tropical agroecosystems tend to be more modular in the non-crop plant stripes than in the crop fields but interaction nestedness was more similar between these habitats than it would be expected at random. Additionally, the non-crop plants favored the alternative hosts and parasitoids, and the main biological control agent was relatively more frequent than pests in these environments. We also show that the inclusion of alternative hosts and parasitoid in these agroecosystems can result in a decay of pest populations, but is important to understand stability in these scenarios, because some generate chaotic dynamics that can result in occasional pest populational peaks, which can lead to yield and economic losses for the farmers.

The differences in modularity observed between the trophic interactions networks that involve parasitoids from non-crop plant stripes and crop fields suggest the alternative resources found in these stripes allow parasitoid to select their preferred resources, using them complementarily in different modules. In fact, modularity tends to be benefited by habitat diversification and identity, suggesting that each habitat comprises a specific set of complementary interactions (Chaplin-Kramer et al., 2011; Macfadyen et al., 2011b). Despite this trend, differences in interaction nesting between non-crop plant stripes and crop fields were smaller than expected at random what may reflect the high specialization found in parasitoids or the high habitat heterogeneity of tropical organic agroecosystems, since the contrary is usually expected (Tylianakis et al., 2007; Gonzalez et al., 2011; Macfadyen et al., 2011b; Togni et al., 2019). At last, most of the significant differences observed in the network metrics were observed at the last trophic level of the hyperparasitoids, which represent a threat to the disruption of biological control and shows that local non-crop plant management can modulate these interactions.

Favoring alternative hosts and parasitoids in organic tropical agroecosystems can result in a decay of pest populations. This explains part of the effects of habitat heterogeneity on the population dynamics of natural enemies, since habitat heterogeneity is directly related to alternative resources (Rosero et al., 2024). This lack of alternative resources can also explain theoretical predictions that show that resource abundance benefit pests in homogenous crop habitats and natural enemies in heterogenous habitats (Rosero et al., 2024). It is also important to mention that the stability of these dynamics must be taken in consideration since some scenarios reflected on chaotic dynamics and this is essential to conceal the management cycles of the crop fields with the pest-parasitoids cycles and ensure proper biological control (Yoo & O'Neil, 2009; Welch & Harwood, 2014).

Based on the above we show the importance of non-crop plants on modulating modularity and nestedness in organic tropical agroecosystems, as well as providing alternative hosts and parasitoids that can reduce pest populations over time. The results from this chapter help us understand the ones presented on the first chapter. Flower resource abundance alone was not beneficial for parasitoids because plant diversity and identity must influence this pattern. Meaning that specialized interactions need to be maintained so that modularity and complementarity patterns maintain host-parasitoid cycles in the log term. In this sense, we suggest that future studies go deeper in the methodological novelty suggested in this work, developing methodologies that unite field sampling, experimental ecology and mathematical biology to predict and manage the future of biological control in agroecosystems.

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GENERAL CONCLUSION

Our study helps to answer how landscape and local resources mediate parasitoid diversity, their interactions with hosts, and biological control services in cultivated habitats. We showed that non-crop plants can sustain parasitoid richness even if their flower resource abundance is detrimental. Landscape composition was more important than local resources in mediating parasitoid diversity and specific vegetation formations had complementary effects on parasitoid diversity. Near-crop forests (0.42 km) benefited parasitoid species richness, while farther grasslands (1.75 km) benefited abundance. Furthermore, savannas, where trees and grasses coexist, boost both forest benefits on parasitoid richness and grassland benefits on abundance. Additionally, we showed that biodiversity-pest control relationships can show divergent responses in communities with different number of species. The interactions in the lower trophic level tend to be more nested, while in the higher trophic level they are more modular and most significant differences in network metrics between crop fields and non-crop plant stripes occurred at the higher trophic level. The mathematical modelling tool was useful to show that alternative hosts and parasitoids can help control the populations of the main brassica pest *B. brassicae*. Our result show that natural areas do act as a pool of parasitoid species for organic tropical ecosystems, but knowing specific vegetation formation identity is important when developing management plans for these areas. Additionally, non-crop plant can act as banks of these insect inside farms and the interactions sustained by these plants may be of high importance for biological control services in tropical organic crop fields.