



Universidade de Brasília
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Ecologia

**Conciliando agricultura e conservação: o papel da
paisagem natural e do sistema de produção para
o manejo ecológico da mosca-branca**

Danyelle Rocha Novaes

Orientador: Prof. Dr. Pedro Henrique Brum Togni

Brasília, DF

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Data da defesa: 20/08/2021

Banca examinadora

Prof. Dr. Pedro Henrique Brum Togni (Presidente/Orientador)
Departamento de Ecologia/UnB

Profa. Dra. Marina Regina Frizzas (Titular)
Departamento de Zoologia/UnB

Prof. Dr. Odair Aparecido Fernandes (Titular)
Departamento de Fitossanidade/UNESP

Prof. Dr. Ricardo Bomfim Machado (Suplente)
Departamento de Zoologia/UnB

Brasília, DF

Agosto de 2021

Dedico este trabalho à extraordinária e improvável sequência de eventos que culminou na magnífica, inconcebivelmente deslumbrante e vertiginosamente diversa vida no planeta Terra.

AGRADECIMENTOS

Agradeço à Universidade de Brasília por ter sido minha casa nos últimos anos, e que mesmo em tempos atribulados garantiu a possibilidade de desenvolvimento profissional e pessoal a mim e a muitos outros. Agradeço ao corpo docente do programa de pós-graduação em Ecologia pela dedicação e esmero para tornar e manter a excelência do curso. Ao CNPq pelo auxílio financeiro referente à minha bolsa, e também à FAPDF (Processo 00193-00000934/2019-11) e à FAPESP (Processo 2018/18274-3) pelo financiamento do projeto. O presente trabalho foi realizado com apoio financeiro da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001, através do Programa PROEX/CAPES.

Agradeço à professora Gabriela Bielefeld Nardoto, que disponibilizou espaço e materiais necessários para as atividades aqui executadas. Ao professor Ricardo Bomfim Machado pelas orientações importantíssimas. E ao colega Vinicius Tirelli Pompermaier pela ajuda e paciência.

Um agradecimento especial ao meu orientador, Pedro, que me recebeu de braços abertos no laboratório em uma situação pouco convencional, que acreditou em mim e estimulou o meu potencial desde o primeiro dia. Obrigada por ter garantido que eu me sentisse incluída e bem-vinda. Obrigada pelos conhecimentos compartilhados, pela paciência e pelo entusiasmo. E obrigada por ter sido um orientador amigo, e por ter permitido uma relação leve, transparente e horizontal. Você é um orientador admirável.

Agradeço ao querido Laboratório de Ecologia de Insetos, e a cada um de seus integrantes, sobretudo aos alunos de graduação, fundamentais para o bom andamento das atividades laboratoriais e na estação experimental. Agradeço especialmente à Camilla Alves e à Karen Mendes, pelo esforço na identificação dos inimigos naturais e nas atividades em campo. Também agradeço à equipe técnica, à equipe de limpeza, à equipe

de segurança, aos motoristas e demais trabalhadores do Departamento de Ecologia da UnB pelos serviços indispensáveis.

Agradeço aos agricultores Ivanildo, Osmany, Guilherme, Juã, Valdemar, Manoel, Zé, Gilliard, Eucácia, Daniel, Valter, Salvador, Francisco, Josimar, Paulo, César, Sebastião, Jair, Severino e Tânia, que gentilmente nos receberam em suas casas e permitiram a execução desse trabalho.

Agradeço às mulheres cientistas que vieram antes de mim, que arduamente pavimentaram o caminho. E também a todos aqueles que se dedicam à preservação do Cerrado e demais biomas.

Sou profundamente grata aos amigos que ganhei nessa jornada. Luan, Ana, Rafa e Amanda, obrigada por todas as trocas, pelo afeto, pela naturalidade dessa amizade que aliviou momentos difíceis e celebrou momentos felizes. Eu os amo e admiro, e quero tê-los sempre comigo, como amigos e colegas de profissão. Avante meus bacanas.

Muitíssimo obrigada à minha mãe Dona Glorinha e ao meu pai Seu Davilmar, que nunca pouparam esforços para estimular os meus estudos. Obrigada por todo o amor, por todo o apoio, por respeitarem o meu caminho e por celebrarem comigo todas as conquistas. Agradeço demais à minha irmã, Helzalyce, que é a minha maior parceira nessa vida, e que esteve sempre ao meu lado para me ajudar a superar todos os momentos de desânimo. Tamo junto sis, ano que vem é você.

Agradeço ao meu companheiro, Vasco, que é o meu maior fã e o maior entusiasta das minhas vitórias. Por todo carinho, afeto, compreensão e amor. Obrigada por navegar comigo. Te amo meu mel.

Por fim, agradeço à minha equipe espiritual que me guia e me auxilia a cada instante dessa experiência terrena que é amável e absurda. Saravá.

RESUMO

A intensificação da agricultura observada no último século resultou na ampla simplificação e fragmentação das paisagens agrícolas. Esse processo gera múltiplas escalas espaciais com as quais as espécies de insetos podem interagir. A resposta de insetos-praga e seus inimigos naturais a esse processo varia, uma vez que cada grupo funcional percebe e utiliza o habitat de forma distinta. O real efeito da fragmentação nas dinâmicas de infestação de insetos agrícolas ainda é motivo de debate na literatura, provavelmente devido à dificuldade de encontrar as escalas de resposta adequadas. O objetivo do presente estudo foi avaliar o efeito de fatores locais e da paisagem, em múltiplas escalas, nas dinâmicas de infestação e de dispersão do inseto praga *Bemisia tabaci*, a partir de interações bottom-up e top-down. Para isso, a abundância populacional de *B. tabaci* e a comunidade de seus inimigos naturais foram avaliadas em 20 propriedades rurais que cultivam tomate entre os anos de 2019 e 2021. Além disso, foi proposto um modelo de dispersão de longa distância para *B. tabaci* baseado na análise de fatores bióticos e abióticos relevantes para a movimentação da praga. Os resultados revelaram que *B. tabaci* responde a escalas maiores e é afetada principalmente pela paisagem. A composição da paisagem afetou *B. tabaci*, de forma que paisagens predominantemente agrícolas resultaram em maiores populações do inseto, sobretudo em cultivos convencionais. A configuração da paisagem também apresentou efeito significativo, revelando que a densidade de manchas nativas desfavorece as populações de *B. tabaci*, independentemente do sistema de manejo. Em contrapartida, inimigos naturais responderam principalmente a fatores locais, sendo beneficiados pelo sistema de manejo orgânico, sobretudo quanto à abundância e à diversidade das comunidades. Inimigos naturais foram também consistentemente beneficiados pela presença de vegetação nativa na paisagem, porém esse efeito foi mais evidente em escalas espaciais menores. O modelo de dispersão resultante prevê que o movimento de moscas-brancas entre propriedades no Distrito Federal aumenta à medida que a integridade da vegetação natural diminui. Nossas descobertas apontam que as características da paisagem podem mediar episódios de infestação pois afetam insetos-pragas e inimigos naturais de maneiras opostas. Demonstramos ainda que essas características interagem com fatores locais ao cultivo, o que evidencia a necessidade de estratégias de manejo em múltiplas escalas espaciais. Em conclusão, o trabalho aponta a importância da conservação de áreas naturais como estratégia de proteção de cultivos contra pragas. A vegetação nativa na paisagem é capaz de fortalecer pressões de controle bottom-up e top-down, mediando a dinâmica de infestação e arrefecendo episódios de dispersão em ampla escala.

Palavras-chave: agroecologia, Cerrado, serviços ecossistêmicos, multiescala, manejo ecológico de pragas, interações tritróficas, biodiversidade.

ABSTRACT

The intensification of agriculture observed in the last century has resulted in the vast simplification and fragmentation of agricultural landscapes. This process generates multiple spatial scales with which insect species can interact. The response of pest insects and associated natural enemies to this process varies, as each functional group perceives and uses the habitat differently. The real effect of fragmentation on infestation dynamics is still controversial, probably because studies might be missing the adequate scale of response. This study aimed to evaluate the effects of local and landscape factors, at multiple scales, on the infestation and dispersion dynamics of the pest insect *Bemisia tabaci*, based on bottom-up and top-down interactions. For this, we evaluated the abundance of *B. tabaci* populations and its natural enemies' community in 20 farms that cultivate tomatoes between the years 2019 and 2021. In addition, we proposed a long-distance dispersion model for *B. tabaci*, based on the analysis of biotic and abiotic factors that are relevant to this pest movement. The results revealed that *B. tabaci* responds to larger spatial scales and is mainly affected by the landscape. Landscape composition affected *B. tabaci*, and predominantly agricultural landscapes resulted in larger insect populations, especially in conventional farms. The landscape configuration also had a significant effect, revealing that the patch density of native patches disfavors pests populations, regardless of the management system. Conversely, natural enemies responded mainly to local factors and benefited from the organic management system, especially regarding the abundance and diversity of communities. Natural enemies also consistently benefited from native vegetation in the landscape, but this effect was more evident at smaller spatial scales. The resulting dispersion model predicts that the movement of whiteflies between farms in the Federal District increases as the integrity of natural vegetation decreases. Our findings demonstrate that landscape features can mediate infestation episodes, as they affect pest insects and natural enemies in opposite ways. We also shown that landscape characteristics interact with in-farm factors, which highlights the need for management strategies at multiple spatial scales. In conclusion, the study points out the importance of the conservation of natural areas as a strategy to protect crops against pests. The native vegetation in the landscape is able to strengthen bottom-up and top-down control pressures, mediating infestation dynamics and alleviating large-scale dispersal episodes.

Key words: agroecology, Cerrado, ecosystem services, multiscale, ecological pest management, tritrophic interactions, biodiversity.

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INTRODUCTION

Changes in land use driven by agricultural expansion and landscape fragmentation creates a mosaic of suitable and unsuitable habitats in multiple scales, affecting pests and beneficial insects in different ways (Turner, 2005; Fahrig et al., 2011; Tscharrntke et al., 2012; Turner & Gardner, 2015; Dainese et al., 2019). Agricultural landscapes exhibit abundant and concentrated food resources for pest insects (Root, 1973; Hambäck & Englund, 2005; Larsen & Noack, 2021), while reducing landscape functional, compositional and configurational heterogeneity for natural enemies (NE) (Landis et al., 2000; Thies et al., 2003; Bianchi et al., 2006; Concepcion et al., 2012). Such differences ultimately affect the provision of ecosystem services and disservices from one functional group or another in agricultural systems (Noriega et al., 2017; Ramos et al., 2020).

Attempts to deliver simple spatial models with accurate pest-control predictions enforced by natural habitats in the landscape have failed to find consistent patterns (Chaplin-Kramer et al., 2011; Karp et al., 2018). The direct effect on pests themselves is even harder to grasp and in some cases natural habitats were beneficial for pest populations (Tscharrntke et al., 2016). This lack of consistency across studies hinders accurate assessments on the role of conservation in agroecosystems and pest management. This may be due to the fact that functional groups interact and perceive habits differently and therefore might vary in the response to different spatial scales. Studies may be missing the adequate scale of response because they often focused on a single trophic level, either exclusively at an area-wide basis (Chaplin-Kramer et al., 2011; Karp et al., 2018), or at smaller local scales (Letourneau et al., 2011).

These limitations extend to pest-insects dispersion models. Studies on habitat fragmentation are deeply rooted in island biogeography and metapopulation theories, and patches in a landscape were often considered isolated areas surrounded by an ecological

uniform and hostile matrix (McIntyre & Hobbs, 1999; Jules & Shahani, 2003; Rodewald, 2003; Manning et al., 2004; Murphy & Lovett-Doust, 2004; Kupfer et al., 2006). Although the importance of the matrix is now being recognized (Ricketts, 2001; Tworek, 2004; Bender & Fahrig, 2005; Fischer et al., 2005; Haynes et al., 2007; Prevedello & Vieira, 2010), models for pest dispersion frequently use stochastic particle simulations that focus mainly on abiotic characteristics and often fail to incorporate local factors (Conradt et al., 2003; Westbrook et al., 2011; Eagles et al., 2013; Wang et al., 2019; Koralewski et al., 2021).

Landscape factors will ultimately modulate the ability of a pest insect to move through habitats (Zaller et al., 2007; Benoît et al., 2012), whilst local factors, such as habitat quality and disturbance regimes, will determine the pest ability to establish populations (Concéption et al., 2012; Dassou & Tixier, 2016). Natural habitats in the landscape could function as bottle-necks for dispersing pest insect populations because they can physically impede movement and spillover (Schmidt & Tschardtke, 2005; Ricci et al., 2009); and impair the pests' ability to locate and colonize host plants (Root, 1973; Blackmer & Byrne, 1993; Mazzi & Dorn, 2012; Straub et al., 2014). Natural habitats can also exert a greater top-down control by favoring natural enemies at a landscape level (Chaplin-Kramer et al., 2013; Begg et al., 2017; Karp et al., 2018; Dainese et al., 2019). The presence of abundant and well connected natural patches in an agroecosystem tend to favor beta diversity and enhance the chances of spillover of natural enemies to the crops (Rand et al., 2006; Blitzer et al., 2012; Tschardtke et al., 2012). At the same time, suitable habitats such as crop patches provide favorable conditions that lead to pest population growth and subsequent harsher outbreaks (Ricci et al., 2009).

On an in-field scale, habitat diversity is known to alter habitat quality and the insect's ability to establish their populations (Bommarco & Banks, 2003; Plath et al., 2012; Concepción et al., 2012). For example, plant diversity promoted in organic farming will

positively affect natural enemy's abundance and diversity, especially for generalist species (Letourneau et al., 2011; Isbell et al., 2017). This will increase natural enemy activity and other related ecosystem services, consequently affecting pest insects at a local level (Tscharntke et al., 2012; Bommarco et al., 2013; Holland et al., 2016; Bartual et al., 2019). This is most likely due to the provision of supplementary and complementary food resources (e.g., prey, pollen, nectar) and favorable conditions for natural enemies (e.g., shelter, microclimatic conditions) (Landis et al., 2000; Bartual et al., 2019). Conversely, farming practices, such as harvest and use of synthetic broad-spectrum pesticides, can impair natural enemies' populations (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Veres et al., 2013; Togni et al., 2019)), while pest insects may be more resilient to such disturbances (Kruess & Tscharntke, 1994, 2000; Tscharntke & Brandl, 2004).

In this study we investigated the impacts of local and landscape factors on pest infestation, on associated natural enemies' community, and on pest dispersion dynamics. We used the worldwide pest species of whitefly *Bemisia tabaci* Gennadius (Aleyrodidae) Middle East- Asia Minor 1 (MEAM-1, former biotype B) as a model. *Bemisia tabaci* is a polyphagous insect, with a high efficiency in transmitting plant viruses to crops (Gilbertson et al., 2015). Whiteflies are highly mobile and can move approximately 2 km per day, depending on wind direction (Byrne, 1999; Isaacs et al., 1999; Riis & Nachman, 2006; Ludwig et al., 2019). Dispersing populations engage in long flights over the landscape, followed by periods of short movement between plants within the colonized crop (Byrne et al., 1996). Their movement across the landscape may be influenced by corridors where suitable habitats are available (Abdelkrim et al., 2017). After habitat colonization, individuals tend to be more responsive to local factors such as microclimatic conditions, spatial heterogeneity (Brewster et al., 1997), and semiochemical recognition (Togni et al., 2010). As whiteflies respond to local (Brewster et al., 1997; Togni et al., 2009, 2010, 2018) and

landscape factors (Abdelkrim et al., 2017; Ludwig et al., 2019), their spatial dynamics is expected to be influenced by different spatial scales simultaneously. They also have numerous well-known generalist natural enemies that are considered key-mortality factors of nymphs (Naranjo & Ellsworth, 2005; Karut & Naranjo, 2009), especially in organic crops (Togni et al., 2019).

Although crops represent the main source of resources for whiteflies, as polyphagous insects they should be able to explore many other habitats in the landscape. The presence of surrounding complex natural habitat types should impair population movement depending on its integrity and should influence local crops infestation. That is because landscape fragmentation facilitates the population movement among suitable patches (Mazzi & Dorn, 2012; Riotte-Lambert & Matthiopoulos, 2020) whilst reducing the available amount of suitable patches for natural enemies, consequently reducing top-down control (Thies et al., 2003; Fahrig et al., 2011; Tschardt et al., 2012).

To test these assumptions, we incorporated ecological infield data on pest and natural enemies and biotic and abiotic landscapes factors to create a dispersion model for the whitefly on a polygon of 5000 km². The question we addressed was how local and landscape factors determine infestation and dispersion dynamics of a flying pest insect, via both bottom-up and top-down forces. Specifically, we addressed the following questions: (i) do local factors such as management system (conventional and organic) interact with landscape factors to determine the abundance of whiteflies and associated natural enemies?; (ii) If so, how does the local management system interact with natural landscape composition and configuration in natural enemy conservation and pest incidence at different spatial scales?; (iii) Is there any relationship between pest incidence and natural enemies' conservation?; (iv) how natural enemies conservation, management system and landscape factors interact to affect whitefly dispersion among farms on an area-wide basis?

We hypothesize that: 1) local and landscape factors will interact to affect both whiteflies and associated natural enemies in opposite directions. Whiteflies will be negatively affected by the presence of natural vegetation in the landscapes while the abundance and diversity of natural enemies will be benefited; 2) whitefly abundance will be reduced in organic management systems, especially in predominantly natural landscapes, due to reinforced bottom-up and top-down constraints associated with habitat complexity; 3) greater patch density of natural habitats in the landscape will negatively impact pest populations because of further beneficial conditions for natural enemies and increased difficulties for pest colonization; 4) there will be a strong relationship between pest suppression and natural enemies' conservation, because of the enhanced service of top-down control provided by the latter; and 5) whitefly movement rates will be greater between simplified agricultural patches in the landscape, whilst the presence and integrity of natural vegetation might result in limitations for whitefly dispersion.

MATERIAL AND METHODS

- *Study area*

This study was conducted in 20 farms that crop tomatoes distributed in a 5,000 km² polygon in Brasilia, Federal District, Brazil (15°46'S; 47°44'W), from August 2019 to April 2021 (Fig. 1). We chose the tomato *Solanum lycopersicum* Lineu (Solanaceae) as a model crop because of its abundance, wide distribution and social relevance within the study area (IBGE, 2013). Tomato crops are also a high quality habitat for whiteflies and are particularly susceptible to yield loss due to whitefly transmitted viruses (Navas-Castillo et al., 2011; Quezado-Duval et al., 2014; Togni et al., 2019a). The minimum distance between the sampled farms was 8 km. All selected areas were located within small farms that employ mainly family labor. The average size of the sampled farms was 8 ± 4.9 ha and farms were located at different portions of the Brazilian Federal District, encompassing different landscape types.

The study area is located in the core of the Cerrado biome, the Brazilian tropical savanna that occupies approximately 204 million hectares of the Brazilian territory (Sano et al., 2010). The Cerrado is the most biodiverse savanna on the planet and is considered the last global agricultural frontier (Borlaug, 2002; Klink & Machado, 2005). It presents a wide range of phytophysionomies that ranges from grasslands, savanna-like vegetation, to tall riparian forests (Eiten, 1972; Ribeiro & Walter, 1998). The climate is type Aw according to the Köppen-Geiger classification, with dry winters and rainy summers (Cardoso et al., 2014). The average annual temperature ranges from 22°C to 27°C, and the average annual rainfall is around 1,500 mm (Klink & Machado, 2005). The Cerrado is a global biodiversity hotspot threatened mostly by large-scale agricultural expansion (Myers et al., 2000; Silva & Bates, 2002; Sano et al., 2019).

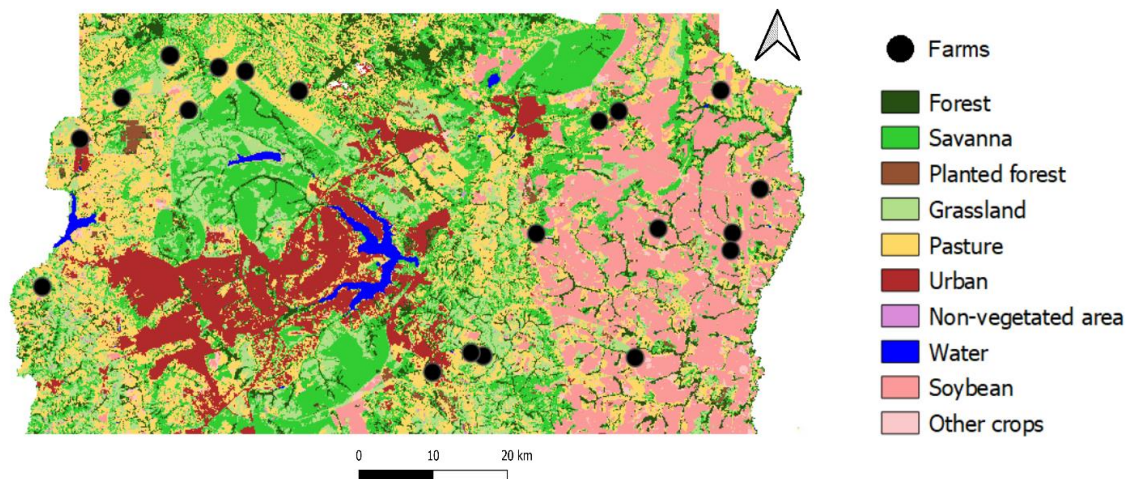


Fig. 1 Schematic representation of the landscape of the Brazilian Federal District around the capital city of Brasilia. The map illustrates the land coverage and usage and the spatial distribution of 20 tomato farms (black circles) distributed along the area. The landscape is characterized by different land-use classes. The land-use classes were defined based on a land-use map from the Brazilian Annual Mapping of Land Cover and Usage Project - MapBiomias.

- *Landscape and habitat management*

The landscape in the study area is highly fragmented and presents various types of agricultural patches that vary in size and configuration (Fig. 1). Large industrial farms occupy most of the area, but smaller farms that employ mostly familiar labor are greater in number (Codeplan, 2020). There is a predominance of soybean monoculture patches in the eastern portion of the region. The middle region is dominated by the urban infrastructure of the city of Brasilia, and includes the Paranoá lake, a large urban water body of approximately 38 km² (Codeplan, 2020). The northwestern region has a clear dominance of pasture patches, whilst the southwest presents relatively more preserved natural habitats (Codeplan, 2020). In general, natural vegetation is mainly present as branched and relatively narrow corridors that meander through the agricultural and urban patches (Codeplan, 2020). There are only three large and continuous natural patches within the landscape, which are all integral protected areas according to the IUCN classification: the Brasilia National Park in the northwestern region (42,300 ha); the Aguas Emendadas Ecological Station by the northeast

(9,100 ha); and the Environmental Protection Area Gama Cabeça de Veado in the furthest south (23,700 ha²) (Codeplan, 2020).

The most common crops in all farms besides tomato were brassicas, strawberry, cucumber and pumpkin. Nine farms were classified as organic, and 11 farms as conventional. The Brazilian legislation defines organic systems as all agricultural management systems that do not employ synthetic products and favor the use of biodiversity and ecosystem services on farm management, prioritizing socio economic benefits and environmental health (Brazil, 2003; Togni et al., 2019a). All organic farms must be certified and registered in the Brazilian Ministry of Agriculture and Livestock (Brazil, 2003). The sampled organic farms were certified for at least five years. The soil cover was predominantly made by spontaneous plants (i.e., weeds) in the organic farms, and by plastic mulching in the conventional farms. All farms presented sprinkler or micro sprinkler irrigation systems. Regarding fertilization strategies, the main product used in the organic crops was chicken manure, while conventional crops used a variety of chemical fertilizers and chicken manure. Pest control strategies varied greatly between organic and conventional farms. Organic farms used predominantly *Bt*-based products, Bordeaux mixture and released *Trichogramma pretiosum* Riley (Hymenoptera: Trichogrammatidae). Conventional farmers used different broad-spectrum chemical pesticides.

- *Insect sampling*

Yellow sticky traps (20 cm × 15 cm) were used to capture both whiteflies and associated arthropod natural enemies. We sampled each farm twice. The first sampling occurred within 40 days after tomato seedling transplanting to the field, during the vegetative tomato plant growth stage. In this first sampling we randomly placed five traps in the tomato plant canopy within the crop area 5 m apart from each other. The traps stayed in the field for five day and

were then removed and taken to the laboratory. The second sampling occurred within 70 days after tomato transplanting, during the initial flowering growth stage. We followed the same procedures from the first sampling for trap placement and removal. The growth stages for the two samplings were selected because they are particularly susceptible to whitefly infestation, and also to ensure we would capture both colonizing and established populations (Stansly & Naranjo, 2010; Oliveira et al., 2013). We also collected at least 10 adult whiteflies per farm with a manual aspirator to identify the cryptic species with random amplified polymorphic DNA (RAPD) markers (Barro & Driver, 1997). All sampled whiteflies were identified as *B. tabaci* MEAM-1 species.

In the laboratory we counted the number of whiteflies per trap and their natural enemies with a stereoscopic microscope. We were able to sample whitefly parasitoids in addition to predators using the same sampling procedure. All species were identified directly on the traps or were removed from them and sent to a taxonomist when needed. We restricted our identification to the *B. tabaci* natural enemy species described in Gerling et al., (2001); Oliveira et al., (2003), Arnó et al., (2010), Torres et al., (2014) and Togni et al. (2019b), focusing mostly on species occurring in the Neotropics.

- *Landscape characterization*

Geographic information (point data) was taken at the center of each sampled tomato area and imported to the QGIS software version 3.18.2 (QGIS Development Team, 2021). We then imported a land-use map of the Cerrado biome from the Brazilian Annual Land Use and Land Cover Mapping Project, Mapbiomas (collection 5.0; Souza et al., 2020). MapBiomas land-use maps use pixel-by-pixel classification of Landsat satellite images to classify land portions according to land usage and vegetation coverage during the period of study (Souza et al., 2020). The land-use map is a matricial map (raster format) and has a

resolution of 30 m (pixels represent areas of 30 m x 30 m) using only validated data. We used this map to analyze landscape structure by means of land-use composition and configuration (Martin et al., 2016).

In the QGIS we used the MMQGIS plugin (version 5.16) to create four circular buffers with 500, 1000, 1500, and 2000 m radius around each sampled farm. We used the Landscape Ecology Statistics (LecoS; Jung, 2019) module to calculate landscape structure in these four scales. We selected these radii because they correspond to half the maximum distance that whiteflies can disperse (from 2 – 8 km) (Riis and Nachman, 2006; Ludwig et al., 2019). To estimate landscape composition, LecoS calculated the land proportions of natural and agricultural habitats within each buffer. Land proportion is a simple, yet robust estimate of landscape composition (Walz, 2011) and it basically informs about the proportion of each land class relative to the entire map in each spatial scale. To estimate landscape configuration, we calculated the patch density of natural and agricultural habitats within each buffer. Patch density corresponds to the sum of patches from a class in the landscape, divided by the total landscape area. It is a fundamental aspect of landscape patterns and expresses the number of patches on a per unit area basis that facilitates comparisons among landscapes of varying size (Walz, 2011).

- *Statistical analyses*

We used a hierarchical cluster analysis to verify whether the abundance of whiteflies is clustered according to the management system and landscape type in each farm. We used the unweighted pair group method with an arithmetic mean (UPGMA) and the Euclidean distance based on the total abundance of whitefly populations per farm. A bootstrap of 100 randomizations was used to test the consistency of the nodes in the dendrogram (Quinn & Keough, 2002). Based on these results and on the landscape

composition, we tested how whitefly abundance was affected by the management system (organic and conventional) and by landscape type by fitting a Linear Mixed Effect model (LME) using the maximum likelihood method (Crawley, 2007). The log abundance of whitefly populations per farm was used as response variable and the management system and landscape type (agricultural or natural) as explanatory variables. The year and the month when sampling occurred were used as random factors. Only for this analysis we excluded the data of farms on urban landscapes. We assessed the significance of the variables included in the model using an F-test and the levels of the variables were compared by a model contrast analysis (Crawley, 2007). The goodness of fit of the model was tested by a model residual analysis. Using the same approach, we assessed how the management system, the percentage of natural vegetation (landscape composition) and the patch density of natural vegetation (landscape composition) affect the abundance of whiteflies per farm at different spatial scales. We used the log density of whiteflies per farm as response variables and the percentage or the patch density of natural total natural vegetation areas within the buffers of 500, 1000, 1500, and 2000 m as explanatory variables. We fitted separate models considering the explanatory variables and its interaction at each spatial scales, also using year and month as random factors (Crawley, 2007).

The same analyses performed for whitefly populations were made considering the abundance, species richness, and diversity of natural enemies as response variables. The diversity of natural enemies per farm was calculated using the Shannon-Wiener index (Shannon, 1948). We complemented the analyses on the role of landscape type to natural enemy diversity by calculating the Rényi diversity profiles of natural enemies in agricultural or natural landscapes, irrespective of the management system (Tóthmérész, 1995; Ricotta, 2003). This way we could explore the role of landscape type on natural enemy conservation in the landscape. To test if natural enemy abundance and species richness negatively

affected adult whitefly populations, we fitted a Generalized Linear Model (GLM), with a negative binomial error distribution (Crawley, 2007). We used the mean abundance of whiteflies per farm as response variable and the mean abundance of natural enemies per farm or the total number of natural enemy species per farm as explanatory variables. The significance of the model was assessed by a χ^2 test (Crawley, 2007). All analyses were performed in the software R (R Core Team, 2020).

- *Dispersion probability model*

The model represents an area of approximately 5,000 km² divided into cells measuring 0.03° latitude by 0.03° longitude (approximately 9 km²). The overall modeling approach comprised the overlay of three grid layers (Figs. 2 and 3). The first layer consisted in a raster map containing land usage and coverage data (see Landscape characterization), therefore encompassing biotic factors involved in whitefly dispersal, such as habitat availability, quality and distribution. The map was imported to QGIS and the land-use classes were reclassified. For that we used the *r.reclass* module from the Geographic Resources Analysis Support System (GRASS) Software, Version 7.8.5 (GRASS Development Team, 2020). The *r.reclass* tool creates an output map layer that is a reclassification, i.e. a substitution, of an input integer raster map layer (GRASS Development Team, 2020). The new values given to each land-use class (Table 1) were selected so as to represent the degree to which the land use impairs dispersal for the whitefly. The lowest value (1) was assigned to those land uses that represent highly suitable habitats. Based on previous analyzes of the whitefly ecology we determined that the most suitable habitat would be soybean crops due its prominence in the landscape, closely followed by other crops and pasture; less favorable habitats were assigned higher values (e.g., 5). In this category we included all types of natural habitats, and the highest values were assigned to taller and

more structurally complex vegetations (forest>savanna>grassland; Table 1); Highly unfavorable or inhospitable habitats were assigned much higher costs (e.g., 50). This category included patches of water, urban infrastructure and non-vegetated areas where whiteflies are not likely to find numerous hosts for landing or increase their population (Table 1).

Table 1. Values and respective justifications used for the reclassification of class values in the land-use map from Mapbiomas. The reclassification was intended to represent how different types of habitat impairs whitefly movement and therefore be used in the Least-Cost-Patch dispersion model.

Land-use class	Reclassified value	Justification	References
Forest	25	All natural habitats were designed intermediate to high values because our analyses revealed that they negatively affected whitefly populations. which is also confirmed by current literature. Furthermore. complex natural habitats can reduce dispersion rates of pests insects because they: represent higher energy and fitness costs; increase mortality risk; impair the pests' ability to locate host plants. We assumed that different phytophysognomies within the cerrado biome would differ in cost and permeability for the whitefly dispersion according to vegetation structure and complexity. The forests received the highest value among natural habitats because of their diversity. Dense and tall vegetation. The savanna received an intermediate value among natural habitats because of its shrubby and sparse vegetation. Grassland received the lowest value among natural habitats because of its short and relatively less complex and diverse vegetation.	Root, 1973; Sparks et al.. 1985; Bernays, 2001; Naranjo & Ellsworth, 2005; Schmidt & Tschamtkke. 2005; Fahrig, 2007; Ricci et al., 2009; Bonte et al., 2012; Cranmer et al., 2012; Mazzi & Dorn, 2012; Dingle, 2014; Aartsma et al., 2017; Cote et al., 2017; O'Rourke & Petersen, 2017
Savanna	20		
Grassland	15		
Pasture	5	Farm-related habitats receive lower cost values because they represent suitable and/or permeable habitats for whitefly dispersion. Pasture. although not itself suitable for the development of the whiteflies population. is a highly simplistic habitat and therefore must implicate low costs to flying insects dispersion. Crop habitats are undoubtedly the most favorable and attractive habits for the whitefly. since they account for their main source of food. Industrial soybean crops received a particularly low cost value because of its exceptional abundance and continuity across the study area. They are also simplistic and predictable environments. and therefore were represented as the most favorable habitats for the whitefly dispersion.	Root, 1973; Bernay,. 2001; Oliveira et al., 2001; Hambäck & Englund, 2005; Musa & Ren, 2005; Evans, 2007; Stansly & Naranjo. 2010; Mazzi & Dorn, 2012; Riotte-Lambert & Matthiopoulos, 2019; Larsen & Noack, 2020
Soybean	1		
Other crop	3		
Urban	45	Non-vegetated areas received the highest cost values because of their lack of favourable conditions to whitefly populations (i.e. food resources. oviposition sites and shelter) and because they lack visual and chemical cues that stimulate whitefly dispersion. Therefore such habitats should be considered as inhospitable to whiteflies (urban habitats received a slightly lower value because of the possible presence of ornamental plants and small vegetated areas like gardens and parks).	Willis & Byrne, 1999; Riis & Nachman, 2006; Stansly & Naranjo, 2010; Togni et al., 2018; Silva & Clarke 2019; da Silva Rodrigues et al., 2021
Non-vegetated	50		
Water	50		

The second layer was created in the software HYSPLIT 5.1.0 (Stein et al., 2015). For this layer we computed back-trajectories analysis to determine the origin of air masses and establish source-receptor relationships, simulating the dispersion of whiteflies as airborne particles, therefore encompassing the abiotic factor of the wind dynamics. The simulations started at the sampled points coordinates, 20 m above the ground level, at 12:00 UTC. We ran 20 independent simulations, one for each start point (sampled farm). The back-trajectories were computed for 1 July and 1 December. The periods were selected to exclude seasonal effects, since the average wind speed can undergo significant seasonal variations throughout the year (INMET, 2016). Both back-trajectories indicated remarkably similar air inflows from the northeastern regions of the study area. The third and final layer consisted in a topographic raster map from the Brazilian Agricultural Research Company (EMBRAPA; Miranda, 2021) that included terrain elevation and slope of the study area. This layer was used in order to represent the influence of the topography on whitefly dispersal as another abiotic landscape factor.

Both second and third layers were imported to QGIS and reclassified following the same methods used for the first layer in order to represent how landscape would impair whitefly dispersion. The second layer was used to reveal the main direction of the wind currents in the city area. Furthermore, cells within the calculated trajectories were assigned with higher values than the ones outside the trajectories; in the third layer we attributed higher values to higher altitudes and more abrupt slopes. Finally, we summed the three raster layers using the raster calculator function in QGIS. The result map was then converted to an ASCII grid in order to be used as input for the software Circuitscape 4.0.5 (Anantharaman et al., 2019). In Circuitscape we performed a pairwise least-cost-path model. This model simulates the dispersal of a

species between designated source and destination points on a surface, or map grid, known as a cost-raster. The cost-values given to each cell in the grid represent the degree to which each cell impairs dispersal for the target species (Anantharaman et al., 2019).

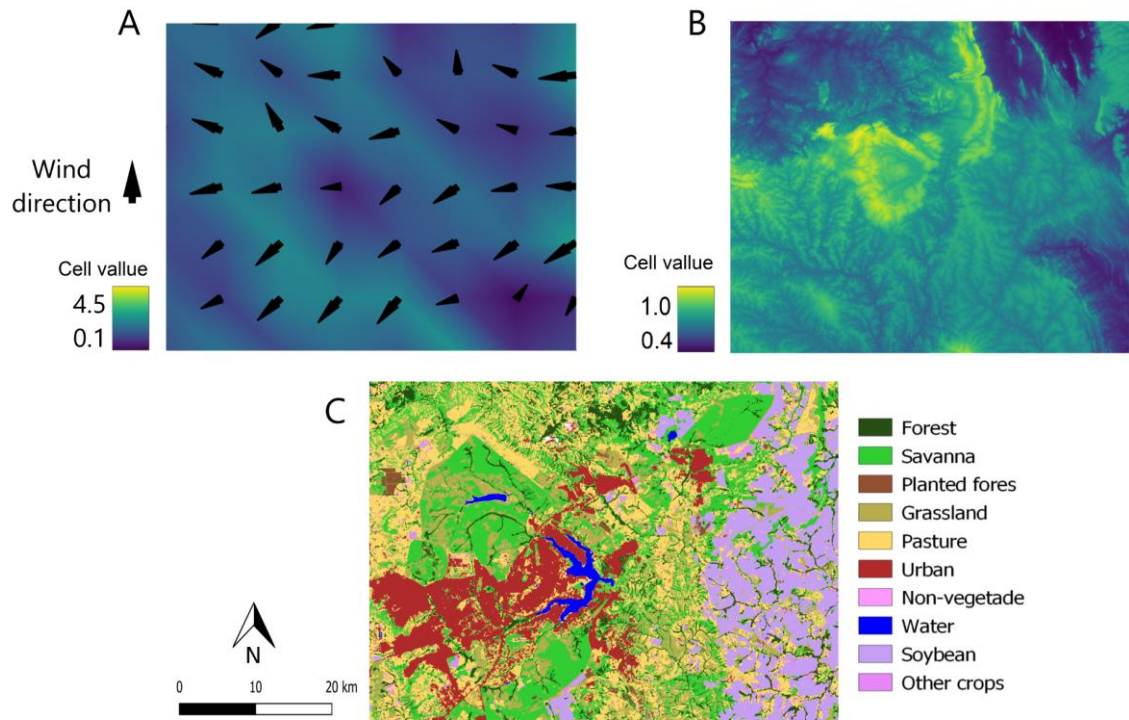


Fig 2. Representation of the three raster layers used for the composition of the whitefly dispersion model. The layers encompassed wind dynamics (A); landscape topography (B); and land coverage and usage (C). The layers were reclassified in order to represent the degree of impediment to whitefly movement across the landscape. Higher cell values indicate downwind areas (A) and higher terrain elevations (B).

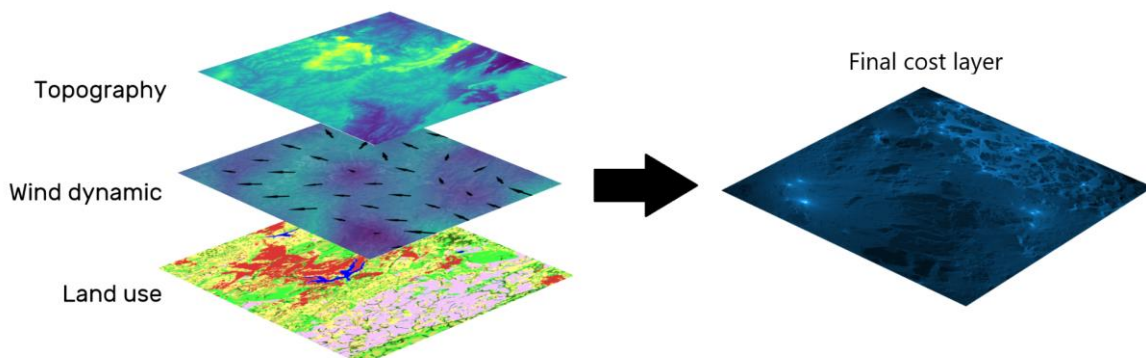


Fig 3. Composition of the final layer used as cost surface for the dispersion model for whiteflies in the Brazilian Federal District. The final layer was based on the overlap of three raster layers

(wind dynamics, land coverage and usage; and terrain topography) and the abundance data of whiteflies in conventional and organic farms cropping tomato plants.

RESULTS

- *Landscapes characteristics*

The conventional and organic farms we sampled were embedded on three broad landscape types. Ten farms were embedded in natural landscapes, eight farms in agricultural landscapes, and two farms in urban landscapes (Fig. 4). In natural landscapes, patches of Savanna represented an average of 21.35% ± 10.51% of the landscape, while Grassland and Forest represented averages of 18.97% ± 11.01% and 5.15% ± 2.10%, respectively. In agricultural landscapes, soybean crops were abundant and represented an average percentage of 49.97% ± 16.14%, while the sum of all other crops totaled an average of only 6.85% ± 4.84%. In the urban landscapes, the urban class represented an average of 28.8% ± 11.57% of the total area.

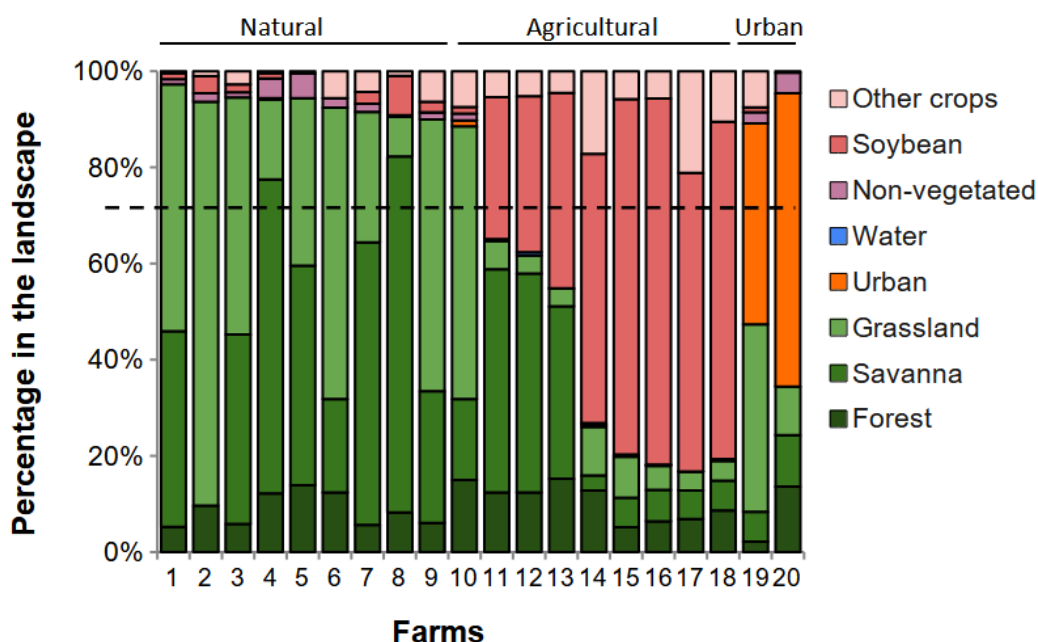


Fig. 4 Composition of the landscape around 20 tomato farms in the Federal District, Brazil. The landscapes were characterized based on the percentage of different land-use classes present in a map of land usage and coverage from the year 2019 provided by the Project MapBiomass. Landscapes with >70% of natural vegetation were classified as natural

landscapes; landscapes with <70% of natural vegetation and <40% of urban infrastructure were classified as agricultural landscapes; and landscapes with >40% of urban infrastructure were classified as urban landscapes.

- *Whitefly infestation*

The cluster analysis based on whitefly abundance revealed three distinct groups of farms that clustered according to landscape type and management system (Fig. 5). The first group contained conventional and organic farms in agricultural landscapes with high densities of whiteflies. The second group included conventional and organic farms in natural landscapes and the third group comprised conventional farms in agricultural landscapes. The latter group was closer to natural landscapes because whitefly densities were lower in these farms and consequently closer to farms in natural landscapes. This suggests that whitefly abundance can be influenced by both landscapes and local factors (Fig. 5).

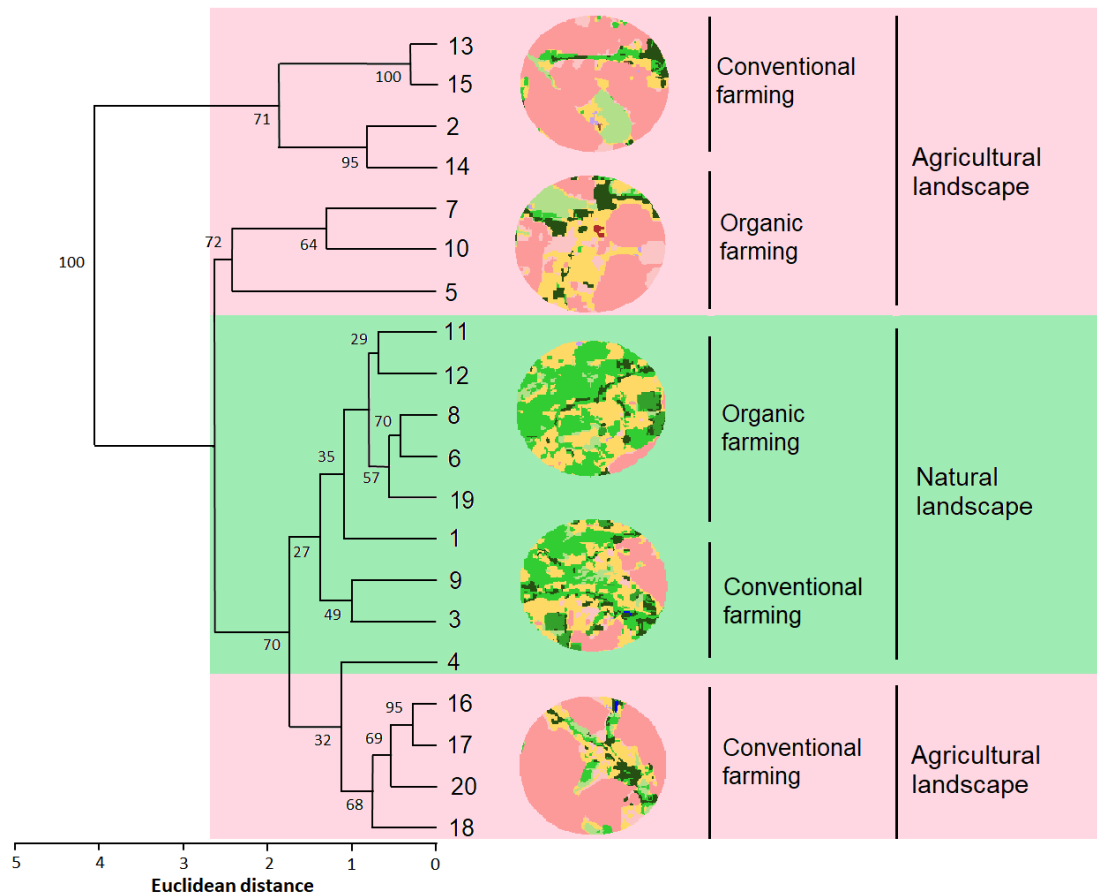


Fig. 5 Hierarchical clustering dendrogram based on the Euclidean distance of whitefly abundance on 20 organic and conventional farms cropping tomatoes at different landscape types in the Brazilian Federal District (Cophenetic correlation = 0.7668). The height of the nodes represents the distance between groups. The number in each node represents the consistency of the nodes based on a bootstrap procedure with 100 randomizations. The numbers in the end tips of the cluster represent the sampled farm identities. The circles in the image are schematic representations of examples of the landscape types at the spatial scale of 2000 m.

This assumption was confirmed by the LME analyses which revealed that whitefly abundance was not affected by the management system ($F = 7.67$, $d.f. = 1$, $P = 0.0062$). However, whitefly abundance was affected by landscape type ($F = 41.63$, $d.f. = 1$, $P < 0.0001$) and by the interaction of the management system and landscape type ($F = 31.49$, $d.f. = 1$, $P < 0.0001$). Whitefly populations presented higher densities in conventional farms in agricultural landscapes (Fig. 6). The mean (\pm SE) whitefly abundance in conventional farms in agricultural landscapes (391.8 ± 135.8 individuals per farm) was ten times higher than in organic farms in agricultural landscapes (38.1

± 4.1 individuals per farm). Conversely, in natural landscapes whitefly abundance was three times higher in organic farms (50.1 ± 27.8 individuals per farm) than in conventional farms (15.3 ± 4.5 individuals per farm).

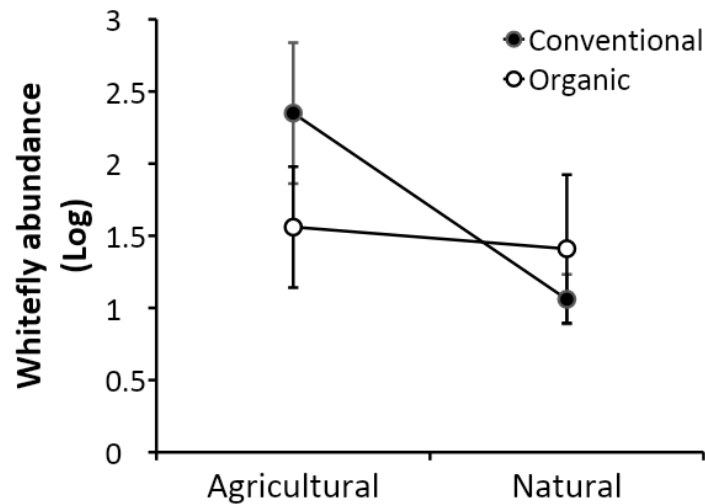


Fig. 6 Mean log abundance (\pm SD) of whiteflies per farm based on landscape type (agricultural and natural) and management system (conventional and organic) in farm cropping tomatoes in the Brazilian Federal District, based on a Linear Mixed Effect Model analysis.

We proceed to verify how the percentage of natural vegetation in the landscapes (composition) of all farms in different landscape types affected the abundance of whiteflies at different spatial scales. Whitefly abundance was affected by the interaction between the percentage of natural vegetation and management systems at the scales of 500, 1000 and 1500 m (Table 2; Figs. 7A, B, C), but not at the scale of 2000 m (Table 2; Fig. 7D). There was also no significant effect on whitefly abundance from the amount of natural vegetation alone, nor from the management system alone (Table 2). The amount of natural vegetation negatively impacted whitefly densities in conventional farms but did not affect the abundance of whiteflies in organic systems (Table 2; Figs. 7A, B, C). To verify if the landscape effect on whitefly abundances was also due to landscape configuration, we fitted other LME models based on the patch density of natural fragments within the landscapes at all spatial

scales. Differently from the landscape compositional analyses, natural patch density affected whitefly populations at larger spatial scales of 1000, 1500 and 2000 m, but not in the smaller scale of 500 m (Table 2). The effect of natural patch density was negative in all significant cases, regardless of the management system (Figs. 7F, G, H). There was no significant effect of the interaction between natural patch density and management at any scale, and also no significant effect was found from the management system alone (Table 2).

Table 2. Effects of local and landscape factors in the abundance of whiteflies. The values refer to insects sampled in 20 tomato conventional and organic farms located around the city of Brasilia. Federal district. Brasil. during the years of 2019-2021. The results were calculated by linear mixed-effect models (LMEs). Values in bold indicate significant effect at $P < 0.05$.

Response variables	Explanatory variables	F	d.f.	P
Whitefly abundance (Buffer 500 m)	% of natural vegetation	0.19	1	0.6675
	Management system	0.49	1	0.4975
	% of natural vegetation: management system	9.94	1	0.0182
Whitefly abundance (Buffer 1000 m)	% of natural vegetation	0.65	1	0.4395
	Management system	0.51	1	0.4901
	% of natural vegetation: management system	5.87	1	0.0359
Whitefly abundance (Buffer 1500 m)	% of natural vegetation	2.40	1	0.1526
	Management system	1.22	1	0.2953
	% of natural vegetation: management system	5.34	1	0.0434
Whitefly abundance (Buffer 2000 m)	% of natural vegetation	2.31	1	0.1599
	Management system	1.02	1	0.3353
	% of natural vegetation: management system	1.82	1	0.2068
Whitefly abundance (Buffer 500 m)	Natural vegetation patch density	0.38	1	0.5525
	Management system	0.02	1	0.8851
	Natural vegetation patch density : management system	0.20	1	0.6614
Whitefly abundance (Buffer 1000 m)	Natural vegetation patch density	6.10	1	0.0331
	Management system	0.01	1	0.9139
	Natural vegetation patch density : management system	2.43	1	0.1498
Whitefly abundance (Buffer 1500 m)	Natural vegetation patch density	34.9	1	0.0001
	Management system	0.04	1	0.8545
	Natural vegetation patch density : management system	3.23	1	0.1024
Whitefly abundance (Buffer 2000 m)	Natural vegetation patch density	25.4	1	0.0050
	Management system	0.48	1	0.5049
	Natural vegetation patch density : management system	0.75	1	0.4066

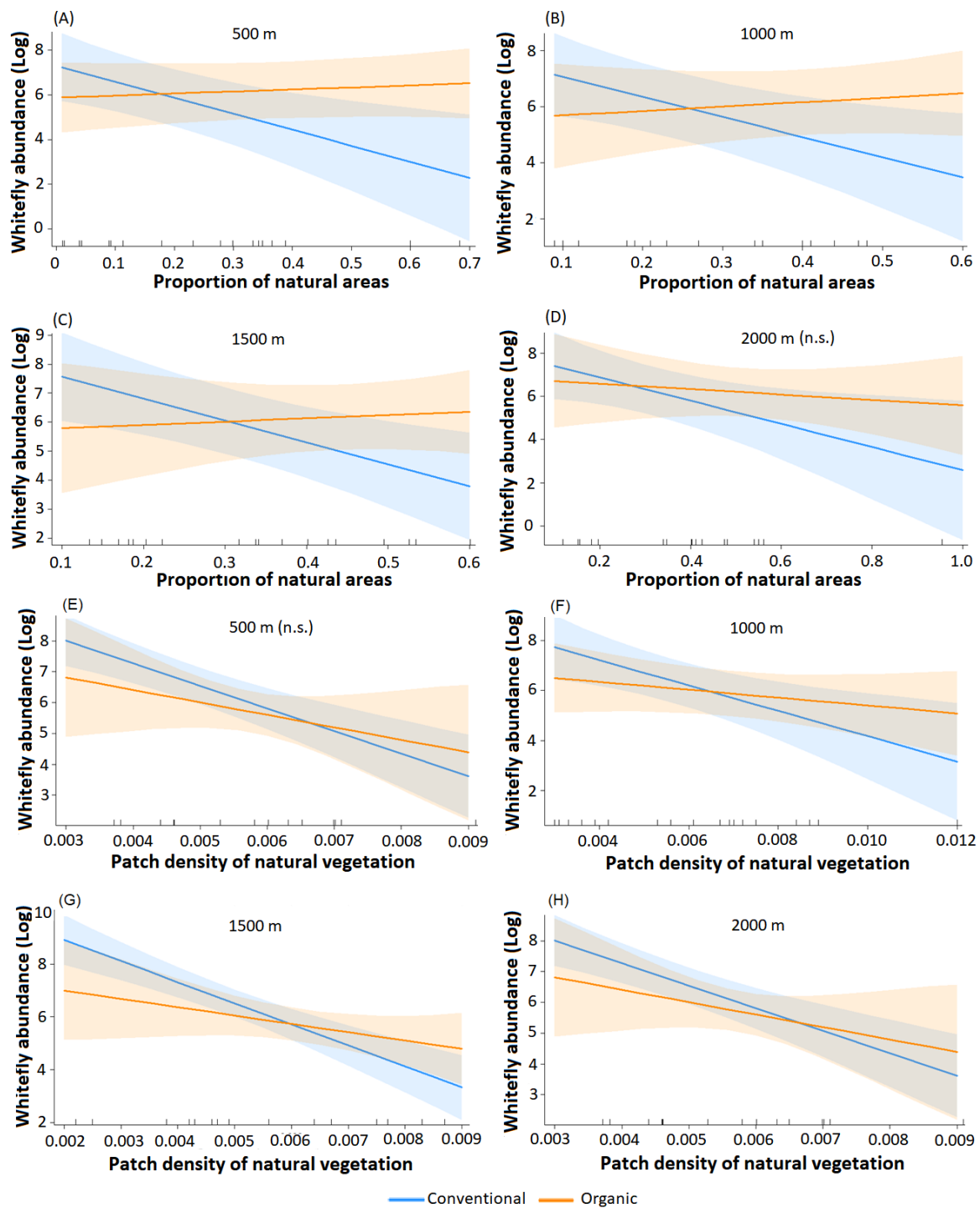


Fig. 7 Effects on the log abundance of whitefly populations of the percentage of natural vegetations (landscapes composition) in the spatial scales of 500 m (A), 1000 m (B), 1500 m (C) and 2000 m (D); and from the density of natural patches (landscape configuration) in the spatial scale of 500 m (E), 1000 m (F), 1500 m (G) and 2000 m (H), in farms cropping tomatoes in conventional and organic management systems, in the Brazilian Federal District. n.s = not significant according to the Linear Mixed Effect Models fitted for each explanatory variable at different spatial scales.

- *Natural enemy conservation and top-down effects*

We collected a total of 2,927 individuals from 35 species and 10 families (Table 3). All species are known to be natural enemies of whiteflies. Most species collected were predators, with most species belonging to the Coccinellidae family. We also found the parasitoids *Encarsia* spp. and *Eretmocerus* spp. (Hymenoptera: Aphelinidae) (Table 3). The three most abundant species were *Diomus* sp. 1 (Coleoptera: Coccinellidae; 12.9%), *Orius* sp. (Hemiptera: Anthocoridae; 6.9%) and *Diomus* sp. 3 (Coleoptera: Coccinellidae; 6.4%).

Table 3. Mean number (\pm SE) per farm and percentage of the total *Bemisia tabaci* natural enemy species occurring on 20 tomato farms in conventional and organic systems, as well as in natural and agricultural landscapes, in the Brazilian Federal District during the periods between August 2019 and April 2021.

Taxon	Management system		Landscape type		% of total
	Conventional	Organic	Agricultural	Natural	
Coleoptera					
Coccinellidae					
<i>Hyperaspis festiva</i>	2.7 \pm 1.17	6.5 \pm 1.27	5.1 \pm 2.06	7.2 \pm 1.73	2.89%
<i>Hyperaspis</i> sp.	0.2 \pm 0.13	6.2 \pm 152	0.1 \pm 0.13	3.8 \pm 1.00	0.15%
<i>Diomus</i> sp. 1	11.6 \pm 0.13	0.2 \pm 0.25	20.5 \pm 7.70	0.2 \pm 0.22	12.88%
<i>Diomus</i> sp. 2	3.1 \pm 1.68	27.4 \pm 7.40	2.9 \pm 1.25	18.7 \pm 4.72	4.15%
<i>Diomus</i> sp. 3	3.4 \pm 1.24	8.6 \pm 1.71	8.0 \pm 4.10	7.9 \pm 2.32	6.37%
<i>Scymnus</i> sp.	6.3 \pm 2.55	15.9 \pm 7.26	5.6 \pm 1.60	9.7 \pm 6.29	5.55%
<i>Cycloneda sanguinea</i>	1.5 \pm 0.45	10.5 \pm 2.32	4.1 \pm 1.71	10.9 \pm 3.23	2.30%
<i>Harmonia axyridis</i>	1.7 \pm 0.47	5.9 \pm 1.51	3.1 \pm 0.74	2.9 \pm 0.93	1.74%
<i>Hippodamia convergens</i>	0.5 \pm 0.25	3.5 \pm 1.13	1.6 \pm 1.35	1.8 \pm 0.97	1.41%
<i>Eriopis connexa</i>	1.7 \pm 0.95	4.1 \pm 1.37	2.7 \pm 1.68	2.6 \pm 0.94	3.55%
<i>Psyllobora</i> sp.	1.6 \pm 0.86	9.6 \pm 4.11	1.1 \pm 0.55	7.9 \pm 3.78	2.07%
<i>Azya bioculata</i>	0.7 \pm 0.34	4.6 \pm 1.66	0.5 \pm 0.33	3.9 \pm 1.59	0.26%
<i>Azya scutata</i>	0.6 \pm 0.38	0.0 \pm 0.00	0.5 \pm 0.38	0.0 \pm 0.00	0.44%
<i>Brachiacantha</i> sp. 1	2.4 \pm 1.51	0.5 \pm 0.27	5.4 \pm 3.28	0.3 \pm 0.24	2.33%
<i>Brachiacantha</i> sp. 2	0.0 \pm 0.00	4.6 \pm 2.88	0.0 \pm 0.00	1.4 \pm 0.77	0.04%
<i>Chronodes brasiliensis</i>	0.0 \pm 0.00	0.1 \pm 0.13	0.0 \pm 0.00	0.1 \pm 0.11	0.01%
<i>Coleomegilla maculata</i>	0.4 \pm 0.21	0.0 \pm 0.00	0.5 \pm 0.27	0.0 \pm 0.00	0.15%
<i>Serangium</i> sp.	0.2 \pm 0.19	0.0 \pm 0.00	0.5 \pm 0.33	0.0 \pm 0.00	0.52%
<i>Nephaspis</i> sp. 1	0.1 \pm 0.09	1.5 \pm 0.57	0.1 \pm 0.13	1.1 \pm 0.54	0.22%
<i>Nephaspis</i> sp. 2	2.8 \pm 0.87	5.1 \pm 2.62	9.1 \pm 6.74	5.0 \pm 2.35	3.33%
<i>Coccidophilus</i> sp.	0.3 \pm 0.20	0.6 \pm 0.32	0.4 \pm 0.26	0.4 \pm 0.29	0.52%

<i>Delphastus</i> sp.	0.2 ± 0.12	1.2 ± 0.31	0.2 ± 0.16	0.9 ± 0.31	0.15%
<i>Olla v-nigrum</i>	0.0 ± 0.00	0.2 ± 0.16	0.0 ± 0.00	0.2 ± 0.15	0.07%
<i>Tenuisvalvae notata</i>	1.8 ± 0.39	1.1 ± 0.66	2.0 ± 1.01	1.3 ± 0.48	0.07%
<i>Tenuisvalvae</i> sp.	0.9 ± 0.55	10.4 ± 5.11	0.4 ± 0.18	7.0 ± 4.41	8.63%
Cybocephalidae					
<i>Cybocephalus</i> sp.	4.8 ± 1.85	0.1 ± 0.13	5.1 ± 2.41	0.1 ± 0.11	0.07%
Hemiptera					
Anthocoridae					
<i>Orius insidiosus</i>	6.2 ± 2.80	0.5 ± 0.19	8.8 ± 4.77	0.2 ± 0.15	3.41%
Geocoridae					
<i>Geocoris</i> sp.	0.0 ± 0.00	13.5 ± 5.01	0.1 ± 0.13	8.7 ± 3.69	0.93%
Neuroptera					
Hemerobiidae					
	5.4 ± 1.79	1.2 ± 1.11	5.1 ± 1.65	1.2 ± 0.98	6.89%
Chrysopidae					
	1.8 ± 0.77	52.6 ± 18.31	2.0 ± 1.65	38.0 ± 16.6	0.19%
Hymenoptera					
Aphelinidae					
<i>Encarsia formosa</i>	0.2 ± 0.13	5.7 ± 1.42	0.1 ± 0.13	4.4 ± 1.11	0.04%
<i>Eretmocerus</i> sp.	1.4 ± 0.31	0.0 ± 0.00	3.4 ± 2.68	0.1 ± 0.11	1.07%
Dermaptera					
Forficulidae					
<i>Doru luteipes</i>	0.1 ± 0.04	18.5 ± 12.4	0.1 ± 0.12	16.7 ± 9.44	3.92%
Aranae					
	1.8 ± 0.39	1.1 ± 0.66	2.0 ± 1.01	1.3 ± 0.48	0.07%

Natural enemies abundance was significantly affected by the management system alone ($F = 67.78$, $d.f. = 1$, $P < 0.0001$), and by the interaction between landscape type and management system ($F = 4.99$, $d.f. = 1$, $P = 0.0267$), but not by landscape type alone ($F = 0.02$, $d.f. = 1$, $P = 0.8961$). Contrary to what was observed for whiteflies, natural enemies were more abundant in organic farms within agricultural landscapes (Fig. 8A). However, in conventional management systems, natural landscapes slightly favored NE abundance (Fig. 8A). Nevertheless, species richness was not significantly affected by management system ($F = 4.04$, $d.f. = 1$, $P = 0.0722$), or landscape type ($F = 0.05$, $d.f. = 1$, $P = 8282$), nor the interaction between these two factors ($F = 0.26$, $d.f. = 1$, $P = 0.6220$) (Fig. 8B). Nevertheless, when we considered the effect of landscape type on NE diversity regardless of the management system,

we found that they were more diverse in natural than in agricultural landscapes (Fig. 9).

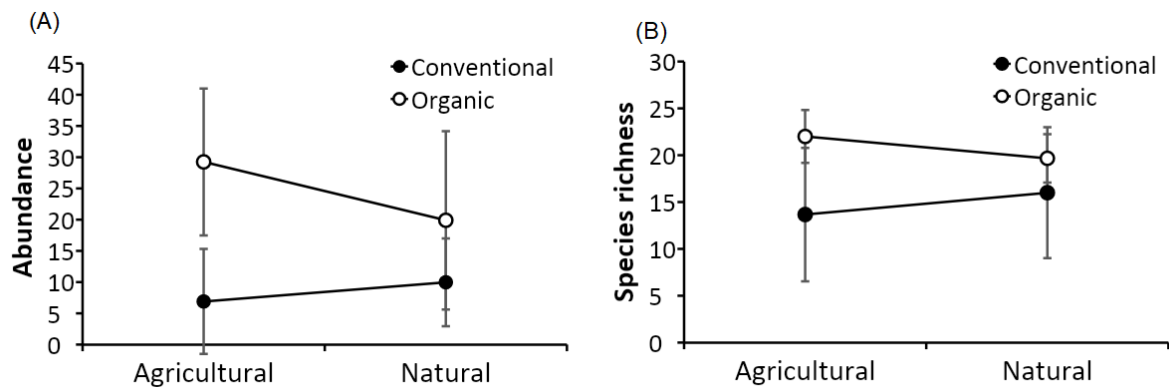


Fig. 8 Mean abundance (\pm SD) (A) and species richness (B) of whiteflies' natural enemies sampled in 20 tomato farms cropping tomatoes in conventional and organic management systems and located on different landscape types (agricultural and natural) in the Brazilian Federal District. Both results are based on Linear Mixed Effect Models fitted to different response variables (abundance and species richness) separately.

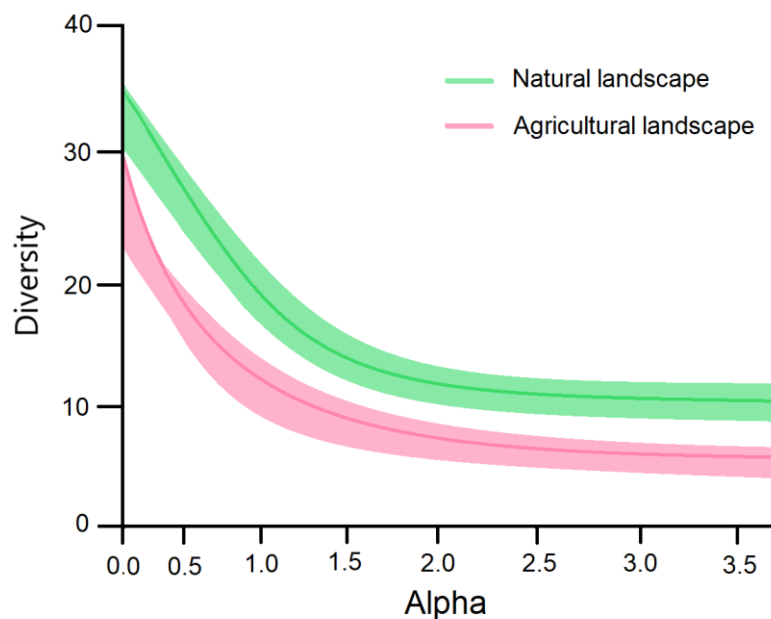


Fig. 9 Rényi diversity profiles (95% confidence intervals) of whitefly natural enemies sampled in 20 farms cropping tomatoes and located in natural and agricultural landscapes in the Brazilian Federal District.

Using the same approach we used for whitefly regarding landscape composition and configuration at different spatial scales, we fitted a LME model for NE abundance and species richness. The interaction between the percentage of natural

habitat and management systems had a significant and positive effect on the abundance of natural enemies at the scales of 1000 m and 1500 m (Table 4). At the larger scale of 2000 m the abundance of natural enemies was positively affected by the percentage of natural habitat alone (Table 4). In terms of landscape configuration, abundance of natural enemies was not affected by natural patch density at any scale. Conversely, species richness and diversity of natural enemies were not affected by percentage of natural vegetation at any scale but were both affected by natural vegetation patch density in the smaller scale of 500 m (Table 4). The mean abundance of whiteflies was not affected by natural enemies' abundance ($\chi^2 = 1.24$, *d.f.* = 19, *P* = 0.2653) nor by natural enemies' species richness ($\chi^2 = 0.25$, *d.f.* = 19, *P* = 0.6176) (Table 4).

Table 4. Effects of local and landscape factors in the abundance of whiteflies, and in the abundance, richness and diversity of whitfly's natural enemies. The values refer to insects sampled in 20 tomato conventional and organic farms located around the city of Brasilia, Federal District. Brasil, during the years of 2019-2021. The results were calculated by linear mixed-effect models(LMEs). Values in bold indicate significant effect at $P < 0.05$.

Response variables	Explanatory variables	F	d.f.	P
Natural enemies abundance (Buffer 500 m)	% of natural vegetation	1.33	1	0.2764
	Management system	16.57	1	0.0022
	% of natural vegetation: management system	2.16	1	0.1728
Natural enemies abundance (Buffer 1000 m)	% of natural vegetation	2.18	1	0.1709
	Management system	19.36	1	0.0013
	% of natural vegetation: management system	5.33	1	0.0436
Natural enemies abundance (Buffer 1500 m)	% of natural vegetation	2.09	1	0.1785
	Management system	22.56	1	0.0008
	% of natural vegetation: management system	7.02	1	0.0244
Natural enemies abundance (Buffer 2000 m)	% of natural vegetation	14.18	1	0.0037
	Management system	8.90	1	0.0137
	% of natural vegetation: management system	0.28	1	0.6063
Natural enemies richness (Buffer 500 m)	% of natural vegetation	3.74	1	0.0820
	Management system	2.74	1	0.1289
	% of natural vegetation: management system	4.26	1	0.0659
Natural enemies richness (Buffer 1000 m)	% of natural vegetation	4.85	1	0.0522
	Management system	1.87	1	0.2010
	% of natural vegetation: management system	2.39	1	0.1527
Natural enemies richness (Buffer 1500 m)	% of natural vegetation	1.65	1	0.2276
	Management system	2.40	1	0.1524

Natural enemies richness (Buffer 2000 m)	% of natural vegetation: management system	0.17	1	0.6884
	% of natural vegetation	2.03	1	0.1846
	Management system	1.95	1	0.1925
	% of natural vegetation: management system	0.07	1	0.7922
Natural enemies diversity (Buffer 500 m)	% of natural vegetation	4.23	1	0.0668
	Management system	0.19	1	0.6730
	% of natural vegetation: management system	2.97	1	0.1156
Natural enemies diversity (Buffer 1000 m)	% of natural vegetation	4.84	1	0.0524
	Management system	0.03	1	0.8690
	% of natural vegetation: management system	0.47	1	0.5075
Natural enemies diversity (Buffer 1500 m)	% of natural vegetation	1.78	1	0.2126
	Management system	0.13	1	0.7255
	% of natural vegetation: management system	0.09	1	0.7671
Natural enemies diversity (Buffer 2000 m)	% of natural vegetation	0.09	1	0.7664
	Management system	1.31	1	0.2794
	% of natural vegetation: management system	0.55	1	0.4759
Natural enemies abundance (Buffer 500 m)	Natural vegetation patch density	4.51	1	0.0597
	Management system	17.97	1	0.0017
	Natural vegetation patch density:management system	1.16	1	0.3074
Natural enemies abundance (Buffer 1000 m)	Natural vegetation patch density	0.24	1	0.6321
	Management system	18.55	1	0.0015
	Natural vegetation patch density : management system	0.27	1	0.6156
Natural enemies abundance (Buffer 1500 m)	Natural vegetation patch density	0.19	1	0.6695
	Management system	15.79	1	0.0026
	Natural vegetation patch density : management system	0.72	1	0.4157

Natural enemies abundance (Buffer 2000 m)	Natural vegetation patch density	0.18	1	0.6752
	Management system	14.35	1	0.0036
	Natural vegetation patch density : management system	0.04	1	0.8504
Natural enemies richness (Buffer 500 m)	Natural vegetation patch density	13.49	1	0.0043
	Management system	6.10	1	0.0331
	Natural vegetation patch density : management system	0.39	1	0.5482
Natural enemies richness (Buffer 1000 m)	Natural vegetation patch density	0.01	1	0.9282
	Management system	4.04	1	0.0723
	Natural vegetation patch density : management system	0.04	1	0.8480
Natural enemies richness (Buffer 1500 m)	Natural vegetation patch density	0.20	1	0.6650
	Management system	3.83	1	0.0787
	Natural vegetation patch density : management system	0.40	1	0.5404
Natural enemies richness (Buffer 2000 m)	Natural vegetation patch density	0.13	1	0.7271
	Management system	3.83	1	0.0789
	Natural vegetation patch density : management system	0.17	1	0.6899
Natural enemies diversity (Buffer 500 m)	Natural vegetation patch density	33.30	1	0.002
	Management system	1.43	1	0.2592
	Natural vegetation patch density : management system	4.89	1	0.0514
Natural enemies diversity (Buffer 1000 m)	Natural vegetation patch density	0.15	1	0.7056
	Management system	1.02	1	0.3353
	Natural vegetation patch density : management system	1.02	1	0.3353
Natural enemies diversity (Buffer 1500 m)	Natural vegetation patch density	1.45	1	0.2549
	Management system	0.58	1	0.4643
	Natural vegetation patch density : management system	1.19	1	0.2996

Natural enemies diversity (Buffer 2000 m)	Natural vegetation patch density	0.96	1	0.3500
	Management system	0.84	1	0.3796
	Natural vegetation patch density : management system	0.80	1	0.3925

- *Dispersion probability model*

The final dispersion model identified at least three clusters of highly vulnerable areas, or infestation “hotspots” (Fig. 10). The geographical distribution of whitefly dispersion probabilities approximately mirrored the proportion of agricultural land cover. The eastern portion of the study appears as highly permeable to whitefly dispersion due to abundant and well connected large scale soybean crops (Fig. 10). The wind's general direction (from east to west) indicates that the most critical dispersion episodes must occur from the eastern infestation cluster to both southern and western clusters. In terms of whitefly dispersion probability, the farms in the furthest west appear as almost isolated from the other sampled farms (Fig. 10). The presence of roads and other interruptions in the natural patches increased permeability and decreased natural habitat capacity to function as a barrier. The large natural vegetation patches in the conservation units were able to considerably reduce the connectivity between east and west infestation clusters (Fig. 10).

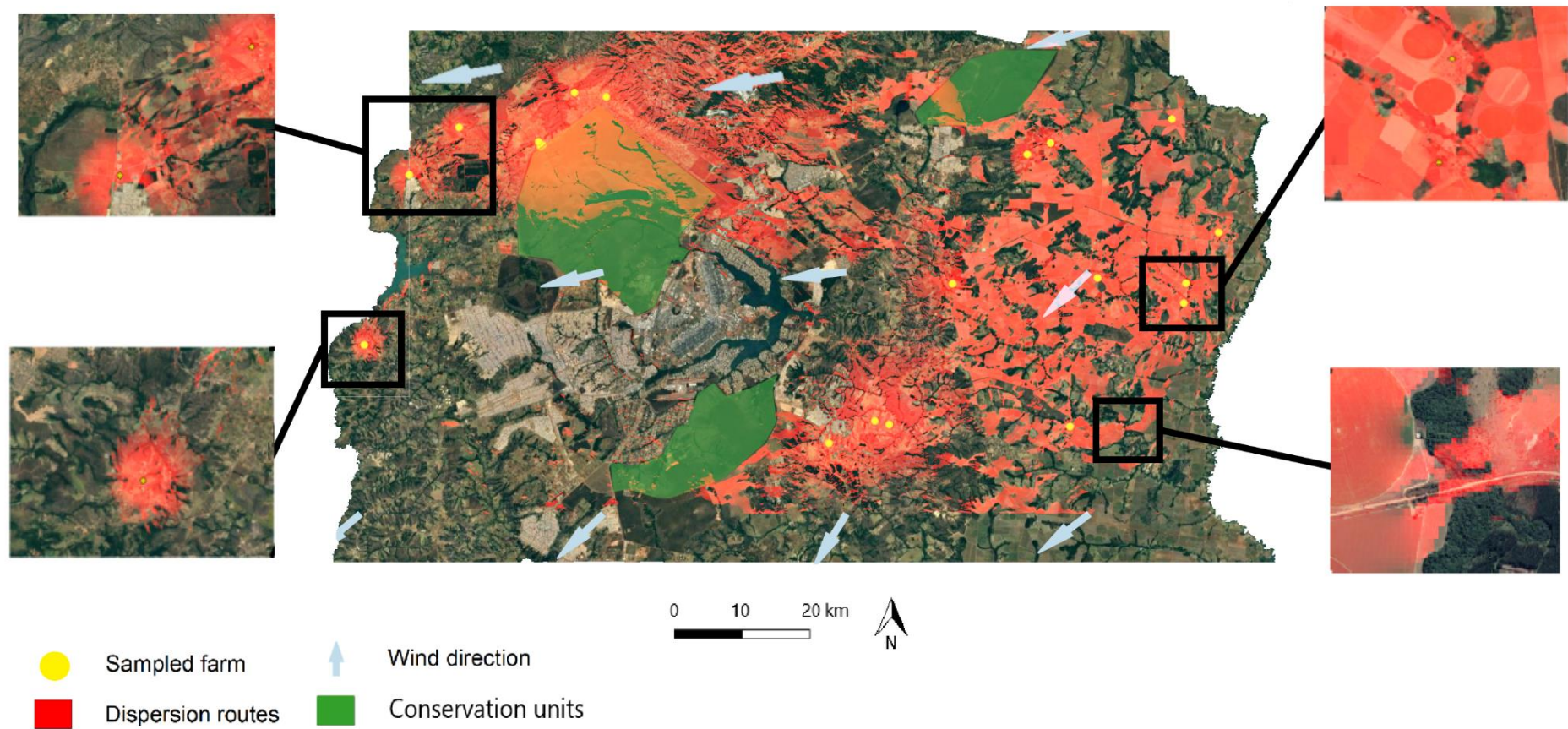


Fig. 10 Dispersion model for whiteflies (*Bemisia tabaci*) at an 5000 km² polygon considering 20 farms cropping tomatoes in the Brazilian Federal District. The dispersion model was based on data related to the land coverage and usage, wind dynamics, and terrain topography and in a surface for whitefly dispersion in each layer. The figure highlights four areas that illustrate how natural vegetation can impair whitefly movement in the landscape.

DISCUSSION

We demonstrated that local and landscape factors interact to affect whitefly populations and associated natural enemies in opposite directions. Different from general current patterns (Chaplin-Kramer., 2011), natural landscape complexity was more detrimental for whitefly populations than local factors, especially in conventional farms. Conversely, natural enemies were mainly affected by on-farm characteristics, and were benefited by organic management, particularly in agricultural landscapes. These multiple interacting factors resulted in a probabilistic dispersal model on an area-wide basis predicting that whiteflies movement will be facilitated by natural vegetation suppression and fragmentation. Therefore, habitat permeability for natural enemies is determined by local factors, while landscape complexity conserves natural enemies and impairs pest dispersion and establishment, producing negative bottom-up and top-down effects on pest insects (Tscharncke et al., 2012; Karp et al., 2018). Our results indicate that the conservation of natural habitats in the landscape can enhance pest control in industrial conventional farms. At the same time, we have shown that vegetation diversity inside farms can buffer the negative effects of highly simplified and homogeneous landscapes on pest infestations. However, these local and landscape beneficial effects are context dependent and not necessarily additive, which emphasizes the need for targeted management plans and case-by-case assessments.

Management system itself did not affect whitefly populations. This was partially expected because adult whiteflies are highly polyphagous and mobile insects (Stansly & Naranjo, 2010), therefore they can explore a variety of host plants and are less affected by crop diversity and management strategies (Bernays, 1999; Togni et al.,

2009; Togni et al., 2018). Previous studies have shown a similar trend for aphids (Rusch et al., 2013), and even for less polyphagous but highly mobile pest insects, such as the codling moth (*Cydia pomonella* Lineu, Lepidoptera: Tortricidae; Ricci et al., 2009). Moreover, the high genotypic plasticity of whiteflies makes their populations highly resistant to most pesticides available (Basit, 2019; Horowitz, et al., 2020; Mota-Sanchez & Wise, 2021). As a consequence, recent evidence has shown that pesticide application has failed in controlling whitefly infestations, especially in agricultural landscapes (Dângelo et al., 2018). Thus, landscape rather than local factors may dictate population dynamics for highly mobile phytophagous insects such as whiteflies.

Such prediction is reinforced by the fact that whitefly populations in conventional farms decreased with the percentage of natural vegetation at broader spatial scales. Phytophagous insects occurring in intensively managed landscapes should be able to move between suitable habitats in a continuous source and sink spatial dynamic (Wissinger, 1997; Bianchi et al., 2006). Mobile organisms will adjust foraging decisions to habitat features such as distribution and quality (Dwyer & Morris, 2006; Mazzi & Dorn, 2012) that will modulate their patch/host selection (Silva & Clarke, 2019). As whiteflies recognize specific wavelengths to find suitable habitats in the landscape (Isaacs et al., 1999; Riis & Nachman, 2006), and use plant volatiles for host targeting (Visser, 1988; Bruce et al., 2005), natural areas may be confounding factors for migrant individuals. Due to the neuronal limitations of polyphagous insects, their patch choice will rely in more homogenous visual and chemical cues as those present in agricultural landscapes (Bernays, 2001; Vallat & Dorn, 2005; Togni et al., 2010; Togni et al., 2018; Silva & Clarke, 2019). However, our results show that such effects may manifest at larger spatial scales than previously thought.

Our results for landscape configuration also indicate that whiteflies respond to habitat fragmentation at wider spatial scales. Nevertheless, whiteflies were less abundant whenever the patch density of natural habitats was higher. Increases in configurational heterogeneity of natural patches may increase landscape complementation regarding bottom-up effects (Brotons et al., 2004; Fahrig et al., 2011) and difficult population spillover across habitat interfaces (Haan et al., 2020), reducing pest population inside crops. Landscape configuration will therefore interact with landscape composition so that the former will produce mostly bottom-up effects and the latter will impair the population movement (Dominik et al., 2018; Redhead et al., 2020).

However, the positive effects of natural habitats on pest control also depend on in-field features to some degree (Concepción et al., 2008). Some plants can allow pest populations to go from adjacent vegetation to crops (Pickett et al., 2004, Macfadyen et al., 2015, Klick et al., 2016), and natural habitats can increase whitefly population in crops due to spillover effect in some cases (Togni et al., 2021). This is because the importance of natural patches for natural enemies' movement and pest-control activity diminishes when habitat-matrix differences are smaller (Forman, 1995; Hudgens & Haddad, 2003; Concepción et al., 2012) This can possibly explain why in this study natural vegetation favored whitefly's population inside organic farms, and why natural habitats sometimes are beneficial for pest insects (Tscharntke et al., 2016).

Contrary to what was observed for whiteflies, natural enemies were mainly affected by local factors such as the organic management system. Crop and non-crop diversity promoted in organic farming is known to benefit both parasitoides (Derocles et al., 2014) and generalist predators (Letourneau et al., 2011; Harterreiten-Souza et al., 2014; Isbell et al., 2017). The lack of effect on natural enemies' richness was

probably a result from our targeted sampling that focused on a restricted group of species known as whitefly's natural enemies. Diversity, on the other hand, was increased by natural vegetation regardless of the management strategy, which indicates a buffering effect of landscape type on the management system. In fact, previous studies have shown that the landscape context can buffer the negative effects of management on natural enemies' communities even when the pesticide pressure is high (Lee et al., 2001; Geiger et al., 2010).

Adjacent natural habitat further benefits natural enemies because they offer alternative and supplementary food resources (Landis et al., 2000; Quispe-Tarqui, 2015; Quispe et al., 2017), and refuges and shelters when no prey is available (Lee et al., 2001). For instance, it has been found that fecundity and body size of predator beetles are positively correlated with landscape complexity, which suggests poorer food availability in simplified landscapes (Bommarco, 1998; Östman et al., 2001). Similarly, parasitoid fecundity and longevity have been found to be enhanced when supplied with more abundant and diverse floral resources in complex landscapes (Olson & Wäckers, 2007). Heterogeneous natural patches in the landscape close to the cropped area will then sustain natural enemies' populations and ensure crop recolonization when a new crop cycle starts (Tscharrntke et al., 2007; Macfadyen et al., 2015). Therefore, agroforestry systems (Harterreiten-Souza et al., 2014) and forest fragments (Togni et al., 2019a) can act as shelter for natural enemies throughout seasonal variations. In our study this effect was enhanced in smaller scales, probably because natural enemies will prefer habitats closest to the food sources inside the crops and will be more abundant and active near habitat interfaces (Nicholls et al., 2001; Harterreiten-Souza et al., 2021). This could be especially relevant for vegetable

crops that have a short cycle and demand a rapid colonization of natural enemies coming from adjacent areas (Togni et al., 2019b).

Conversely, natural enemies' richness and diversity were both affected by landscape configuration, as predicted by theory and recent empirical studies (Chaplin-Kramer et al., 2011; Duarte et al., 2018; Haan et al., 2020). Fine-grained landscapes present smaller and more complex patches that will increase the length of border among habitats, increasing habitat complementation and resource accessibility (Fahrig et al., 2011). This will influence natural enemies' richness (Concepción et al., 2012; Dominik et al., 2018), diversity (Hendrickx et al., 2007; Holzschuh et al., 2010; Fahrig et al., 2011; Tscharrntke et al., 2012), and abundance (Martin et al., 2016). Furthermore, natural enemies in our study also responded to configuration at smaller spatial scales, which can be due to the fact that the presence of natural enemies is conditioned to the amount of close and accessible prey (Nicholls et al., 2001; Harterreiten-Souza et al., 2021).

The fact that natural enemies did not affect the abundance of adult whiteflies in this study was partially expected. Most of whitefly's natural enemies are nymph predators and only a few species are known to prey on adults (Gerling et al., 2001; Oliveira et al., 2003; Arnó et al., 2010; Torres et al., 2014; Togni et al., 2019a). However, predation has been shown to be the key mortality factor of whitefly nymphs in Brazilian organic tomato farms (Togni et al., 2019b) and in other crops around the world (Naranjo & Ellsworth 2005; Asimwe et al., 2007; Karut & Naranjo, 2009). Increasing the abundance and richness of natural enemies had led to higher rates of *B. tabaci* nymph predation and parasitism (Togni et al., 2019a) and of other pest species (Snyder et al., 2006; Macfadyen et al., 2011). This suggests that biodiversity can promote ecosystem services of biological control and compensate for the use of

chemical pesticides. Therefore, although pest populations may be the same in conventional and organic systems, the mechanisms underlying whitefly adult recruitment are different in each management system.

All the above-mentioned effects of local and landscape factors interacted to produce our dispersal model of whitefly populations on an area-wide basis. Clearly, the presence of large and well connected agricultural habitats facilitated pest movement among farms, and natural areas' integrity and amount produced the opposite effect. Habitat boundaries, especially structurally complex ones such as forest edges in protected areas, may disrupt visual and olfactory cues for pest insects (Cranmer et al., 2012; Aartsma et al., 2017) and increase foraging time and predation risk (Fahrig, 2007; Cote et al., 2017).

In fact, dispersal is a particularly vulnerable stage in insect life cycles (Ronce, 2007) with mortality rates during this period ranging from 63% (Nealis & Regniere, 2009) to 99.99% (Johnson, 1969). These rates may be influenced by how long insects travel and are exposed to natural enemies (O'Rourke & Petersen, 2017), the energetic costs they experience (Rankin & Burchsted, 1992; Zera & Denno, 1997; Dingle, 2014), and the fitness costs associated to their movement (Zera et al., 1999; Lazzaro & Little, 2009; O'Rourke et al., 2010; Guerra, 2011). Additionally, dispersing species, especially small and relatively weak flyers such as whiteflies, count on the probability of randomly landing at a suitable habitat, and have no energetic reserves to survive for long periods in unsuitable temporary patches (Hambäch & Englund, 2005; O'Rourke & Jones, 2011; Martinson & Fagan, 2014).

Therefore, complex landscapes may increase mortality factors for dispersing pest insects, when compared to simpler and homogeneous landscapes that are easier to cross and navigate (Charrier et al., 1997; Ries & Debinski, 2001; Kallioniemi et al.,

2014). Combined with the intrinsic barrier-like effect promoted by tall and complex vegetation (O'Rourke & Petersen, 2017), these factors explain why whiteflies are less abundant in the more natural portion of the Brazilian Federal District. This demonstrates that abiotic conditions, such as wind and topography, interact with biotic factors to determine pest insects dispersion, but the biotic factors are more likely to modulates colonization rates and directions.

CONCLUSION

This study has demonstrated that different insect functional groups respond to landscape features at different spatial scales. While pest insects responded more strongly to the conservation of natural habitats on a wider basis, natural enemies were mainly affected by in-farm characteristics, or by surrounding areas that are closer to the target crop. These results highlight the importance of simultaneously considering multiple spatial scales for different trophic levels in agricultural ecosystems, as well as the role of natural enemies on the broad response of phytophagous insects to multiscale interacting factors.

We also demonstrated that natural vegetation has a potentially crucial role in alleviating pest harshness in farms, regardless of the management system or landscape type. The conservation of natural vegetation affected not only local and regional trophic interactions, but also long-range pest dispersal patterns at much larger spatial scales. These findings can signal to farmers and decision-makers that sustainable area-wide management strategies may be more efficient than in-field management for pest control and suppression.

Such results open up the possibility of creating protected natural areas in strategic points of the landscape as an integrated and coordinated effort to manage

pests across regions. This approach would add yield value to protected areas, in addition to their role in the urgent need for conservation, and could represent an exciting and important step towards the goal of conciliating nature conservation and farming productivity.

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