HAYATI
Journal of Biosciences

Vol. 32 No. 6, November 2025 1551-1563
DOI:10.4308/hjb.32.6.1551-1563
ISSN: 1978-3019
EISSN: 2086-4094

Research Article

Check for updates

OPEN ACCESS

Assessing the Influence of Flowering Plants and Landscape Composition on Host-Parasitoid Food Webs

Mihwan Sataral[1], Akhmad Rizali[2], I Wayan Winasa[1], Hermanu Triwidodo[1,3], Damayanti Buchori[1,4*]

[1]*Department of Plant Protection, Faculty of Agriculture, IPB University, Bogor 16680, Indonesia*
[2]*Department of Plant Pests and Diseases, Faculty of Agriculture, University of Brawijaya, Jl. Veteran, Malang, East Java 65145, Indonesia*
[3]*Farmers and Fishermen Center (TNC) IPB University, Bogor 16680, Indonesia*
[4]*Center for Transdisciplinary and Sustainability Science (CTSS), IPB University, Bogor 16129, Indonesia*

ARTICLE INFO

Article history:
Received December 13, 2024
Received in revised form May 25, 2025
Accepted June 2, 2025
Available Online August 27, 2025

KEYWORDS:
habitat manipulation,
food-web metrics,
local scale,
landscape scale

ABSTRACT

The introduction of flowering plants into agricultural landscapes can significantly impact host-parasitoid food webs, although the extent of these effects varies depending on landscape characteristics. This study examined the effects of habitat manipulation by introducing flowering plants on the complexity of herbivore-parasitoid food webs in agricultural landscapes. Using Shannon diversity, links per species, linkage density, and vulnerability, we assessed the effects of flowers planted in maize fields. Herbivore collections were conducted at 2, 4, 6, 8, and 10 weeks after planting. Bipartite network analysis identified nine host morphospecies (Lepidoptera) in maize fields, revealing eight morphospecies in fields without flowering plants and six in fields with flowering plants. Eight major parasitoids were recorded, with *Paratetracnemoidea* sp.1 and *Telenomus remus* dominating fields without flowering plants, whereas *T. remus* was the most prevalent in fields with flowers. *Spodoptera frugiperda* emerged as the dominant host in both fields, whereas Lymantriidae sp.2 was present in low numbers in both field types. These results indicate that flowering plants enhance Shannon diversity and linkage density. However, the composition of the surrounding landscape can obscure these benefits, leading to simplified food web structures as the agricultural fields expand. Our findings underscore the significance of landscape context in shaping crop-herbivore-parasitoid interactions, offering valuable insights into sustainable agricultural management practices.

1. Introduction

Biodiversity and ecological functions within plant-insect communities are shaped by both local habitat conditions and broader landscape characteristics (Kruess 2003). Consequently, effective biodiversity conservation and biological control strategies must consider landscape effects at varying scales. Food webs illustrate the interactions between species across different trophic levels, and their structure significantly influences biodiversity and ecosystem function (Wang & Brose 2018). Furthermore, consumer-resource interactions are pivotal in driving population dynamics and community structures (Kawatsu *et al.* 2021). The conservation of natural enemies aims to enhance their effectiveness against plant pests by promoting the presence of nectar and pollen-rich plants in agroecosystems (Baggen *et al.* 1999). Variability in the trophic levels of natural enemies can influence the interactions between herbivores and

---

* Corresponding Author
E-mail Address: damayanti@apps.ipb.ac.id

their natural enemies, ultimately affecting tritrophic dynamics (Abdala-Roberts *et al*. 2019). Additionally, a diverse community of parasitoids may hinder biological control efforts (Yang *et al*. 2021) because hyperparasitoids can undermine the efficacy of primary parasitoids in these processes (Sullivan *et al*. 1999).

Investigating tritrophic interactions is crucial for understanding natural species dynamics and applying this knowledge to pest control strategies (Agrawal 2000). Herbivore-parasitoid interactions should be examined through a multitrophic and multispecies lens, as the strength and direction of effects across trophic levels can vary with spatial scale (Van De Koppel *et al*. 2005). Cuautle & Parra-Tabla (2014) found that parasitoids are generally less affected by spatial scales than herbivores, a phenomenon likely linked to the search behaviors of parasitoids at the patch level. In host-parasitoid interactions, species at the highest trophic levels are typically much smaller (Thies *et al*. 2005). Despite their size, these higher trophic level species may be more susceptible to extinction owing to habitat loss, fragmentation, and degradation resulting from agricultural intensification, as they face both direct effects on their populations and indirect effects on their hosts or prey (Cagnolo *et al*. 2009). A comprehensive understanding of agroecosystem responses and functioning, facilitated by a food web approach, could enhance the management of biological control in altered environments (Tylianakis *et al*. 2014).

Trophic interactions between herbivores and parasitoids are affected by the diversity of crops in the surrounding area, including the presence of flowering plants (Nitschke *et al*. 2017). Increasing crop heterogeneity effectively enhances and restores multitrophic biodiversity in agricultural landscapes (Sirami *et al*. 2019). Incorporating flowering plants that provide nutrients to their natural enemies can improve top-down control and support pest management (Balmer *et al*. 2013). A tritrophic study involving plants, sap-sucking Hemiptera, and ants demonstrated that higher local plant diversity stabilizes the mutualistic Hemiptera-ant network, while the antagonistic plant-Hemiptera network remains unaffected (Staab *et al*. 2015). These findings suggest that the bottom-up effects of plant diversity on trophic interactions may vary depending on the nature of the interaction, specifically whether it is mutualistic or antagonistic.

Understanding the effects of flowering plants on food webs is crucial for optimizing the use of floral resources in integrated pest management programs (Haro *et al*. 2018). Therefore, a deeper understanding of flowering plants is necessary to enhance habitat manipulation strategies for biological control and conservation (Begum *et al*. 2004). In addition, plant-herbivore-parasitoid interactions are influenced by landscape structure (Kruess 2003). Research by Syahidah *et al*. (2021) indicated that landscape composition, particularly the proportion of natural habitat and cropland, positively correlates with the structure of host-parasitoid food webs, notably in terms of connectance and compartment diversity. Conversely, Hawro *et al*. (2015) found no significant impact of landscape structure on the dynamics of the food web involving aphids and their parasitoids. Gagic *et al*. (2011) reported that increased landscape complexity led to simpler food webs between aphids and their parasitoids. While trophic interactions between herbivores and parasitoids have been extensively documented, the effects of flowering plants and landscape composition on the complexity of herbivore-parasitoid food webs remain underexplored. Food web complexity is a crucial factor that influences ecosystem function and stability (Tylianakis *et al*. 2007; Bukovinszky *et al*. 2008). Food web metrics serve as a means to characterize interactions among various trophic levels (Thompson *et al*. 2012). Understanding these metrics and their connections with local conservation practices at the landscape scale can enhance pest and natural enemy management strategies (Dong *et al*. 2019).

Maize is a crucial agricultural product in Indonesia, ranking second after rice as the most significant cereal crop (Erythrina *et al*. 2022). As the most extensively cultivated cereal, maize fosters intricate trophic interactions, highlighted by the swift adaptation of local parasitoids to invasive pests, such as Spodoptera frugiperda (Nurkomar *et al*. 2024). This invasive species has displaced native pests such as *Ostrinia furnacalis*, leading to yield losses of up to (Song *et al*. 2023) and disrupting the diversity of natural enemies in maize fields (Rizali *et al*. 2021). The tall structure of maize and the prevalence of monoculture landscapes make it an ideal setting for exploring floral resource provision and landscape habitat manipulation, which have been demonstrated to enhance parasitoid diversity and decrease dependence on chemical pesticides (Sarkar *et al*. 2018). Given its their expanding cultivation area and vulnerability to various pests, maize fields are vital habitat engineering models aimed at boosting natural enemies and herbivore-parasitoid food webs.

Previous studies have documented the connections between flowering plants and host-parasitoid food webs (Damien *et al*. 2017; Haro *et al*. 2018; Rizali *et al*. 2023), as well as the influence of landscape composition on these webs (Dong *et al*. 2019; Yang *et al*. 2021; Syahidah *et al*. 2021). However, the impact of flowering plants on herbivore-parasitoid food webs at the landscape scale remains unexplored. This study examined the effect of habitat manipulation through the planting of flowering plants at the landscape scale on the complexity of the herbivore-parasitoid food web, using metrics such as Shannon diversity, links per species, linkage density, and vulnerability. Specifically, this study aimed to determine whether the presence of flowering plants in maize fields and the surrounding landscape composition influence the structure of herbivore-parasitoid food webs. This study enhances our understanding of ecological interactions in agroecosystems and provides valuable insights into habitat manipulation strategies that promote biodiversity and improve pest control in agricultural landscapes.

2. Materials and Methods

2.1. Study Site and Pest Collection

This study was conducted in Bogor (Figure 1) from April to September 2022. It involved the examination of four maize fields with flowering plants (treatment) and four maize fields without flowering plants (control). The flowering plants were initially grown in polybags and then transplanted to the maize fields as they reached their flowering period. The selected species of flowering plants were *Cosmos* sp., *Turnera* sp., *Helianthus annuus*, *Vigna unguiculata*, *Arachis pintoi*, and *Antigonon leptopus*. These flowering plants were planted directly adjacent to the maize fields, approximately two weeks prior to maize planting, except for *V. unguiculata*, which was sown three weeks earlier. They were spaced 20 × 30 cm apart within three 5 × 5 m plots, with a 1 m gap between each plot. To maintain a continuous supply of flowers in the maize fields, new flowering plants were strategically planted alongside those nearing senescence. All flowering plants were supplied with organic fertilizer to optimize their growth.

The fields were separated by approximately 150 m to prevent any interactions between the treatments. Insect collection focused on the egg and larval stages, comparing plots with flowering plants (treatment) to those without (control). Three transects located 0, 10, and 20 m from the edge of the maize field (Figure 2) were used to collect pests at the egg, larval, and pupal stages. These collections were conducted 2, 4, 6, 8, and 10 weeks after planting. Pests in the egg, larval, and pupal stages were collected directly by hand from 100 maize plants at each distance along the transect lines. The collected pests were placed in labelled plastic containers, categorized by stage, and marked with the location, treatment, and collection times. Insects were

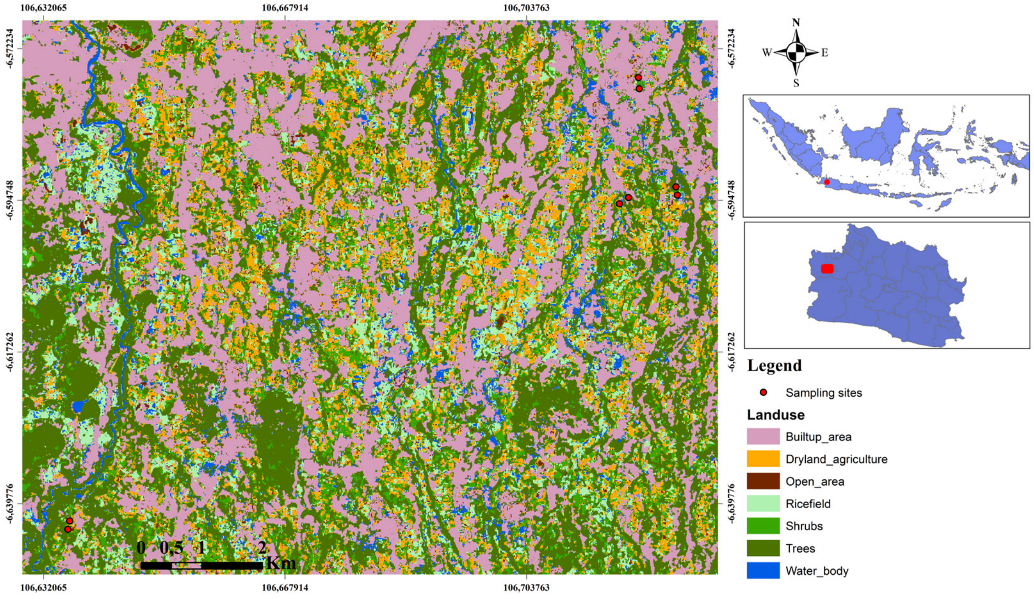


Figure 1. Map of research locations by land use type in Bogor, Indonesia

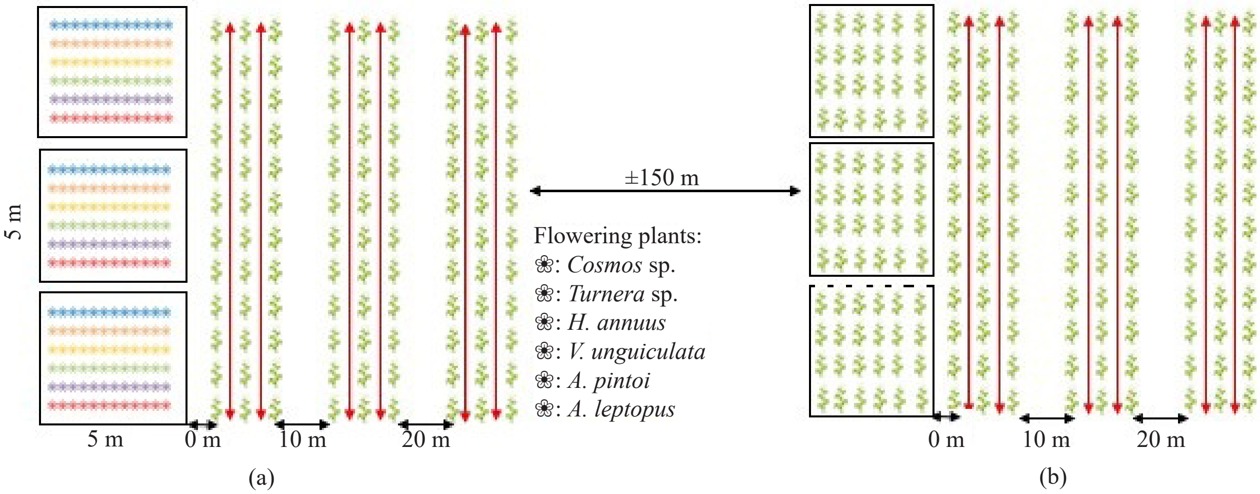


Figure 2. The experimental design in a maize field involved flowering plant enrichment (a) and without enrichment (b). Black arrows indicated the distance between the points of interest, while red arrows indicated the direction of the transect

identified at the Biological Control Laboratory of the Department of Plant Protection, Faculty of Agriculture, IPB University.

2.2. Host Rearing and Identification

Pests captured in the field were transferred to glass tubes for the egg stage, whereas larvae and pupae were placed in plastic cups for rearing. The reared larvae were provided with fresh corn as a daily food source. Daily observations were conducted to monitor the emergence of parasitoids from eggs, larvae, and pupae. The parasitoids were then preserved in 1.5 ml tubes containing 70% ethanol and labeled according to the pest labels from the field. The larvae and pupae were reared until they reached the adult stage. Unknown adult specimens were stored in a 30 ml plastic bottle of alcohol for identification purposes. The pests collected from the field and the parasitoids reared from the pests were counted. The identification process relied on morphological characteristics, referencing the books The Insects of Australia, Volume 1 and 2 (CSIRO 1990; CSIRO 1991), Hymenoptera of the world (Goulet *et al*. 1993), Nixon (1937), Nixon (1970), Nagaraja & Nagarkatti (1969), Gauld (1984), Van-Achterberg (1993), Zhang & Huang (2004), Ubaidillah (2003), Ubaidillah (2007), Buffington *et al*. (2020), and the official website, Identification Keys for Afrotropical Hymenoptera (http://www.waspweb.org/Keys/).

2.3. Landscape Composition Determination

Landscape composition was determined using Sentinel-2/S2 images processed using the Google Earth Engine (GEE) cloud computing platform. The image acquisition timeframe was adjusted to coincide with the sample collection period, from April 1, 2022, to September 30, 2022. The selected S2 image had a median digital number value and cloudiness level of <20% (Mahdianpari *et al*. 2020). The area of interest (AOI) was defined as a rectangular shape encompassing the Bogor Regency and its surrounding areas. The classification inputs consisted of the original band combinations of the multispectral bands, including B2, B3, B4, B5, B6, B7, B8, B8A, B11, and B12. The land-use classification encompassed seven categories: built-up areas, water bodies, trees, rice fields, dryland farming, shrubs, and open areas (Figure 3). The random forest algorithm was employed for land use classification (Gislason *et al*. 2006; Noi Phan *et al*. 2020) with a kappa coefficient value of >0.80 (Kumar *et al*. 2021). The image data were processed using ArcGIS 10.8 software to assess the landscape conditions within a 500 m radius of the observation land (Bonato *et al*. 2023). The landscape parameters considered were the class area (CA), number of patches (NumP) of farmland (encompassing rice fields and dryland farming), and semi-natural habitats (comprising shrubs and trees).

2.4. Data Analysis

Trophic relationships between hosts and parasitoids were established based on direct observations of pests in maize crops and the emergence of parasitoids from reared insect pests. Trophic interactions were analyzed and visualized using the 'bipartite' package (Dormann *et al*. 2022). The food web indices utilized included Shannon diversity, which measures the number of host and parasitoid species in each compartment (Murakami

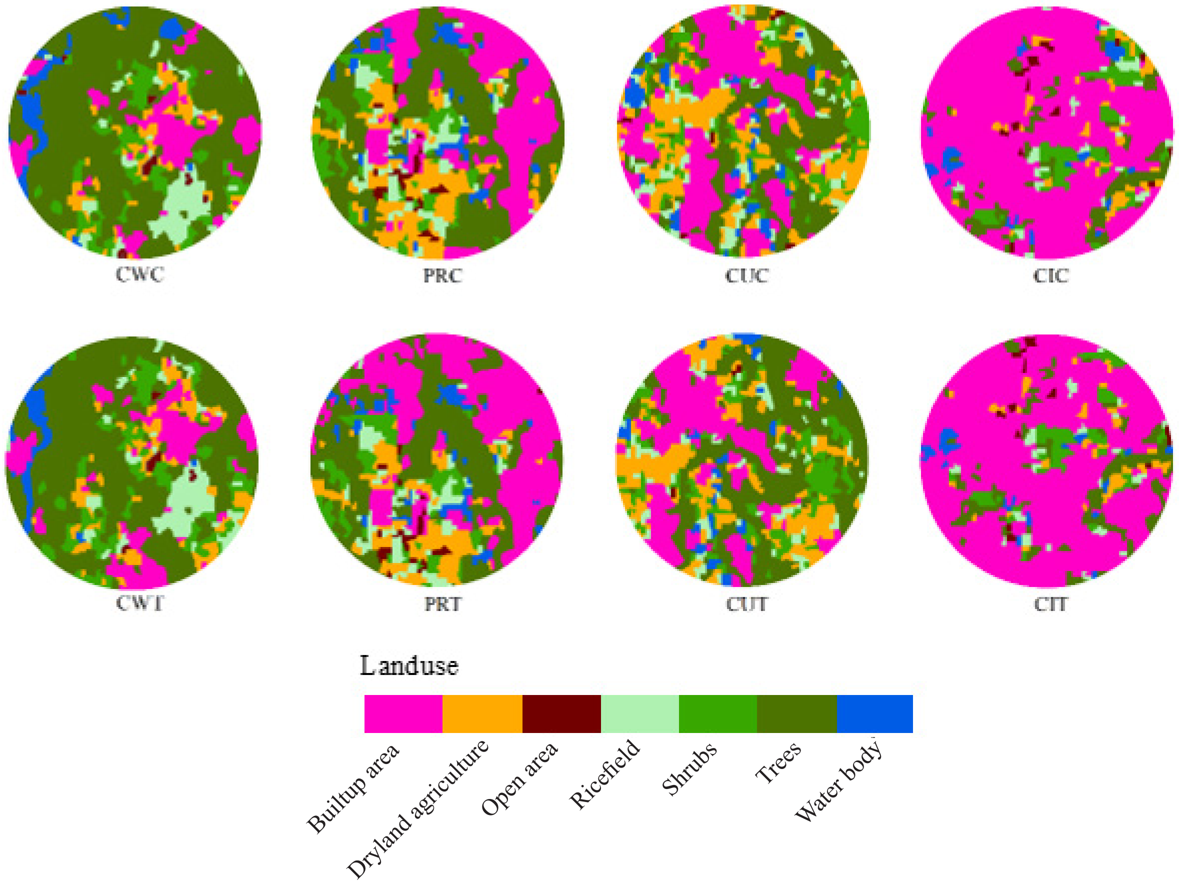


Figure 3. Landscape composition at the study site within a 500-meter radius. CWC, PRC, CUC, and CIC are fields without flowering plant enrichment, and CWT, PRT, CUT, and CIT are fields with flowering plant enrichment

et al. 2008); linkage density, which quantifies the number of links or relationships between species in the network (Bersier *et al*. 2002); links per species, which is the average number of links per species (Montoya *et al*. 2006); and vulnerability, which represents the weighted average number of parasitoids per host species (Maunsell *et al*. 2015). These indices were calculated using the 'network level' function (Dormann *et al*. 2008). To assess the influence of treatments and landscape structure on food webs, a generalized linear model (GLM) with a quasi-Poisson distribution was employed to address data overdispersion (Demétrio *et al*. 2014). The predictor variables included treatment (with or without flowering plants), maize age, number of patches (NumP), and class areaareas (CA) of semi-natural habitats and farmlands. We also examined the interactions between the treatments and the class areas of farmland and semi-natural areas to assess the effectiveness of flowering plants at the landscape scale. All data were analyzed using R statistical software version 4.4.0 for Windows (R Core Team 2024).

3. Results

The landscape composition within a 500-meter radius of the maize fields revealed that the number of farmland patches varied from 76 to 192, whereas semi-natural patches ranged from 69 to 134. The area of farmland was between 5.50 and 22.83 ha, whereas the semi-natural area spanned from 12.74 to 53.30 ha. Overall, the landscape conditions at the study site exhibited a proportion of semi-natural habitats exceeding 20%, indicating a highly complex landscape.

3.1. Host and Parasitoid Composition in Maize Fields With and Without Flowering Plants

The bipartite network visualization revealed the presence of nine host morphospecies of Lepidoptera in maize fields, specifically *Aloa lactinea*, *Helicoverpa armigera*, Lepidoptera sp., Lymantriidae sp.1., Lymantriidae sp.2., *Ostrinia furnacalis*, *Plusia* sp., *Spodoptera frugiperda* and *Spodoptera litura*. Additionally, there were ten parasitoid morphospecies, including

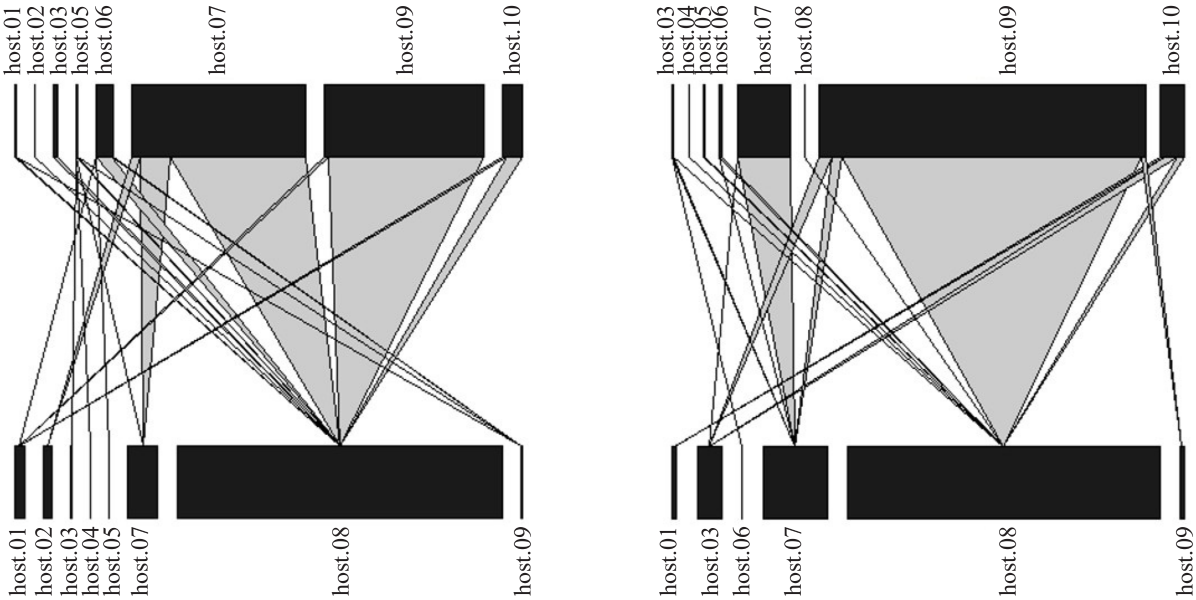
Charops sp., *Euplectrus* sp., Figitidae sp., *Megaselia* sp., *Microplitis* sp.1., *Microplitis* sp.2., *Paratetracnemoidea* sp.1., *Paratetracnemoidea* sp.2., *Telenomus remus*, and *Trichogramma chilotraea* (Table 1). Differences in food web structures were observed between fields with and without flowers (Figure 4). Specifically, the field without flowers exhibited eight host morphospecies, whereas the field with flowers had six host morphospecies. Eight primary parasitoids were identified in maize fields without flowering plant enrichment, with *Paratetracnemoidea* sp.1 and *T. remus* being the dominant species. Conversely, *T. remus* emerged as the dominant species in maize fields enriched with flowering plants. In both treatments, *S. frugiperda* was the prevailing host, representing a new invasive pest in Indonesia. Notably, all ten parasitoid morphospecies were observed to parasitize *S. frugiperda*. This finding suggests that, despite its invasive nature, local parasitoids have adapted to the presence of this new species. *Paratetracnemoidea* sp.1 and *T. remus* are potential parasitoids for controlling *S. frugiperda*.

3.2 Effect of Flowering Plants and Landscape Composition on Host-Parasitoid Food Webs Complexity

This analysis revealed that flowering plants at the edges of maize fields contribute to the formation of a complex host-parasitoid food web structure. The study found significant effects of flowering plants on various metrics of host-parasitoid food webs, including links per species (P= 0.039), linkage density (P= 0.067), Shannon

Table 1. List of parasitoid species and their hosts recorded from maize fields in Bogor

Parasitoid	Code	Parasitoid function	Host	Code
Braconidae				
Microplitis sp.1	par.05	larval parasitoid	Lepidoptera sp.	host.03
			Lymantriidae sp.1	host.04
			Plusia sp.	host.07
			S. frugiperda	host.08
			S. litura	host.09
Microplitis sp.2	par.06	larval parasitoid	*A. lactinea*	host.01
			Lymantriidae sp.2	host.05
			Plusia sp.	host.07
			S. frugiperda	host.08
			S. litura	host.09
Encyrtidae				
Paratetracnemoidea sp.1	par.07	egg and larval parasitoid	*H. armigera*	host.02
			Lepidoptera sp.	host.03
			Plusia sp.	host.07
			S. frugiperda	host.08
Paratetracnemoidea sp.2	par.08	egg parasitoid	*S. frugiperda*	host.08
Eulophidae				
Euplectrus sp.	par.02	larval parasitoid	*S. frugiperda*	host.08
Figitidae				
Figitidae sp.	par.03	larval parasitoid	*O. furnacalis*	host.06
			Plusia sp.	host.07
			S. frugiperda	host.08
Ichenemonidae				
Charops sp.	par.01	larval parasitoid	*S. frugiperda*	host.08
			S. litura	host.09
Phoridae				
Megaselia sp.	par.04	larval parasitoid	*S. frugiperda*	host.08
Scelionidae				
T. remus	par.09	egg parasitoid	*A. lactinea*	host.01
			Lepidoptera sp.	host.03
			Plusia sp.	host.07
			S. frugiperda	host.08
			S. litura	host.09
Trichogrammatidae				
T. chilotraeae	par.10	egg parasitoid	*A. lactinea*	host.01
			Lepidoptera sp.	host.03
			S. frugiperda	host.08



(a)

(b)

Figure 4. The food web illustration portrays the host-parasitoid trophic system in maize fields under two scenarios: (a) fields without flowering plant enrichment and (b) fields with flowering plant enrichment. The horizontal bars indicate the abundance of each parasitized host species (bottom bar) and its primary parasitoid (top bar). Codes on the bars, see Table 1

diversity (P= 0.095), and vulnerability (P= 0.056) (Table 2). The interaction between flowering plant treatment and farmland class area had a negative effect on Shannon diversity (P = 0.042). Additionally, a positive correlation was observed between farmland class area and linkage density (P= 0.087), as well as between vulnerability and the number of semi-natural patches (P= 0.033), semi-natural class area (P= 0.089), and farmland class area (P= 0.013). Conversely, the number of farmland patches was negatively correlated with vulnerability (P= 0.038).

4. Discussion

This research suggests that introducing flowering plants at the edges of maize fields can create complex host-parasitoid food webs. This observation aligns with findings by O'Gorman & Emmerson (2009) and Haro *et al*. (2018), who indicated that flowering plants in agroecosystems influence food web connectivity. Additionally, Tylianakis *et al*. (2007) highlighted the significant impact of habitat modification on food web interactions. Our results further suggest that landscape composition is a crucial factor in shaping the structure of host-parasitoid food webs.

Our findings revealed significant disparities in the composition of hosts and parasitoids between fields with and without flowering plants. Specifically, host abundance was more significant in non-flowering fields, with *S. frugiperda* emerging as the predominant host under both scenarios. Notably, *S. frugiperda*, an invasive pest identified in Indonesia in 2019 (Sartiami *et al*. 2020). It exhibits remarkable adaptability to its new environment, posing a substantial threat to maize yield (Hutasoit *et al*. 2020). In flower-planted fields, *T. remus* emerged as the predominant parasitoid. Conversely, *Paratetracnemoidea* sp.1 and *T. remus* were the primary species in the non-flowering fields. *T. remus* has been documented as an egg parasitoid of various lepidopteran species (Kenis *et al*. 2019) and has been found to dominate in parasitizing the eggs of *S. frugiperda* in the field (Sisay *et al*. 2019). This indicates its effectiveness as a natural enemy of this pest (Sari *et al*. 2020). Its dominance suggests a robust capacity for the survival and colonization of *S. frugiperda* (Wengrat *et al*. 2021). Remarkably, *T. remus* can parasitize entire egg masses, including those shielded by scales (Laminou *et al*. 2020), which is a trait uncommon among other egg parasitoids (Laminou *et al*. 2023). Additionally, this parasitoid effectively locates hosts through volatile compounds emitted by maize plants during pest attacks (Peñaflor *et al*. 2011; Michereff *et al*. 2019). The landscape conditions surrounding the maize field may have favored this parasitoid, as described by Pascual *et al*. (2022), facilitating its abundance in both flowering and non-flowering fields.

Table 2. Relationships between flowering plants, maize age, and landscape composition, including the number of farmland patches (NumP.Agri), number of semi-natural patches (NumP.SemNat), farmland class area (CA.Agri), and semi-natural class area (CA.SemNat) with Shannon diversity, links per species, linkage density, and vulnerability. Significance level: *$P < 0.1$; **$P < 0.05$.

Response variables	Predictor variables	Estimate	SE	*P*	R^2
Shannon diversity	(Intercept)	-4.475	6.501	0.501	0.501
	Flowering plants	3.035	1.717	0.095*	
	Maize age	0.061	0.078	0.442	
	NumP.Agri	-0.009	0.082	0.912	
	NumP.SemNat	0.012	0.110	0.914	
	CA.Agri	0.163	0.261	0.540	
	CA.SemNat	0.017	0.070	0.810	
	Flowering plants x CA.Agri	-0.227	0.103	0.042**	
	Flowering plants x CA.SemNat	0.005	0.059	0.930	
Links per species	(Intercept)	-1.672	1.685	0.335	0.339
	Flowering plants	0.741	0.331	0.039**	
	Maize age	-0.021	0.021	0.334	
	NumP.Agri	-0.011	0.020	0.597	
	NumP.SemNat	0.017	0.028	0.564	
	CA.Agri	0.052	0.064	0.429	
	CA.SemNat	0.010	0.017	0.563	
	Flowering plants x CA.Agri	-0.010	0.025	0.689	
	Flowering plants x CA.SemNat	-0.016	0.015	0.284	
Linkage density	(Intercept)	-2.192	1.369	0.128	0.519
	Flowering plants	0.527	0.269	0.067*	
	Maize age	0.012	0.017	0.496	
	NumP.Agri	-0.023	0.017	0.185	
	NumP.SemNat	0.033	0.023	0.161	
	CA.Agri	0.096	0.053	0.087*	
	CA.SemNat	0.015	0.014	0.299	
	Flowering plants x CA.Agri	-0.022	0.020	0.295	
	Flowering plants x CA.SemNat	-0.008	0.012	0.490	
Vulnerability	(Intercept)	-4.985	1.985	0.022	0.623
	Flowering plants	0.840	0.410	0.056*	
	Maize age	0.021	0.025	0.407	
	NumP.Agri	-0.055	0.024	0.038**	
	NumP.SemNat	0.077	0.033	0.033**	
	CA.Agri	0.213	0.076	0.013**	
	CA.SemNat	0.036	0.020	0.089*	
	Flowering plants x CA.Agri	-0.026	0.030	0.383	
	Flowering plants x CA.SemNat	-0.017	0.018	0.348	

This study confirms the positive impact of flowering plants on Shannon diversity within food webs, as Landis *et al*. (2000) noted. However, the interaction between flowering plants and farmland size had a detrimental effect on this diversity. In landscapes characterized by intensive farming, the advantages of planting flowers may be diminished, leading to a less pronounced increase in biodiversity (Nilsson *et al*. 2021). These findings indicate that broader landscape factors often mask the influence of flowering plants. Consequently, more than flowering plants alone may be needed to adequately support diverse parasitoid species in regions dominated by extensive agricultural land. Thus, a comprehensive understanding of host-parasitoid food webs, including Shannon diversity, must account for local conditions, surrounding habitat, and geographical context (Rizali *et al*. 2024).

Analyzing links per species can illuminate patterns of interaction and specialization among species. This metric represents the average number of interactions that each species engages in within the food web (Montoya *et al*. 2006). A higher average indicates a more interconnected network, whereas a lower average suggests that species are more isolated with fewer interactions (Dormann *et al*. 2009). The positive correlation between flowering plants and links per species is closely tied to its relationship with Shannon diversity, which facilitates increased interactions among host-parasitoid species. This study demonstrates that local conservation practices significantly enhance the complexity of herbivore-parasitoid food webs in agricultural land (Lohaus *et al*. 2013). This study found no significant impact of landscape composition on the number of links per species within host-parasitoid food webs. In tropical agricultural settings, landscape composition may not substantially influence host-parasitoid interactions, suggesting that other factors could be more critical in shaping these dynamics (Ulina *et al*. 2019). As Rizali & Buchori (2024) noted, identifying key factors that affect host-parasitoid interactions in tropical agricultural landscapes may enhance our understanding of the complexities within these food webs.

The positive correlation between flowering plants and linkage density suggests that flowers enhance resource availability for parasitoid survival. A high linkage density indicates greater interactions among species within a network (Bersier *et al*. 2002). Wang *et al*. (2024) also reported a positive association between linkage density and plant richness. Generally, parasitoid richness significantly influences linkage density (Gagic *et al*. 2011; Rizali *et al*. 2023). However, some studies have indicated that habitat modification practices do not significantly affect linkage density in host-parasitoid food webs (Tylianakis *et al*. 2007). Interestingly, this study found a positive relationship between farmland area class and linkage density.

An increase in agricultural land cover typically correlates with decreased parasitoid richness owing to resource limitations (Jonsson *et al*. 2012; Letourneau *et al*. 2015). This reduction negatively impacts food web complexity, including the density of linkages. However, Gagic *et al*. (2011) found that food webs can exhibit greater complexity, characterized by higher linkage density, in more straightforward landscapes with a high proportion of agricultural land. Larger crop areas generally support greater densities of host species (Root 1973) and tend to harbor more parasitoids than non-crop areas (Dong *et al*. 2019). This increased host availability can elevate parasitoid populations and parasitism rates (Cuny *et al*. 2019), leading to more host-parasitoid interactions within the food web. Consequently, extensive crop areas can significantly drive host-parasitoid interactions (Jonsson *et al*. 2012), as evidenced by the lack of a significant effect of patch number and class area of semi-natural habitat on linkage density.

Beyond flower planting, increasing the number of semi-natural patches and the extent of semi-natural and agricultural class areas can increase vulnerability. Greater vulnerability suggests that a higher number of parasitoids are capable of attacking their hosts (Dong *et al*. 2019). This may be because parasitoids thrive on the enhanced availability of host resources in extensively cropped areas or those surrounded by semi-natural patches (Tscharntke *et al*. 2016; Laterza *et al*. 2023). Syahidah *et al*. (2021) also found that a higher proportion of agricultural land has a positive influence on host-parasitoid connectivity. Conversely, Dong *et al*. (2019) reported that vulnerability decreases with an increase in natural habitat. This study found that, on average, host species in maize fields were attacked by more parasitoid species in landscapes with a higher percentage of semi-natural patches and a larger proportion of semi-natural habitats, even in areas with significant agricultural land. Additionally, research by Murakami *et al*. (2008) indicated that vulnerability was greater in areas with high connectivity than in those with low connectivity. This suggests that spatial factors, including the dispersal frequency of parasitoid species, influence the regulation of parasitoid species per herbivore species. The findings also indicated that vulnerability decreased with habitat fragmentation, as evidenced by the increased crop patch numbers. A higher number of patches indicates greater landscape fragmentation (Rizali *et al*. 2022; Fletcher *et al*. 2023). Species loss tends to be most pronounced with an increase in small fragments (Pardini *et al*. 2010), thereby reducing vulnerability (Yang *et al*. 2021).

In conclusion, the introduction of flowering plants at the edges of maize fields significantly affected the structure of host-parasitoid food webs. However, at the landscape level, the composition of the landscape masked the effects of flowering plants and modified the food web structure within maize fields. Our findings highlight the role of landscape composition in shaping host-parasitoid food webs, with an increasing number of farmland patches leading to simplification of the food web. Supporting studies have emphasized the necessity of considering landscape composition as a key factor in food web ecology. Therefore, evaluating the benefits of flowering plants at the landscape scale is essential for optimizing habitat engineering practices and enhancing the complexity of food webs. This understanding can serve as the foundation for developing sustainable pest management strategies. From a conservation standpoint, our study underscores the role of flowering plants in enhancing parasitoid diversity within landscape-mediated host-parasitoid food webs. However, further research is necessary to consider additional factors, such as agricultural intensification, climate, and geographical conditions, to better comprehend the mechanisms that influence the success or failure of crop diversification strategies in biological pest control.

Acknowledgements

We extend our gratitude to Syngenta Indonesia, in partnership with the Indonesian Entomological Association (PEI) and the Indonesian Education Scholarship (BPI) from the Ministry of Education, Culture, Research and Technology of the Republic of Indonesia, facilitated by the Lembaga Pengelola Dana Pendidikan (LPDP) and Badan Pengkajian dan Penerapan Teknologi (BPPT), for their financial support of this research. Additionally, we appreciate the contributions of the team and laboratory assistants at the Biological Control Laboratory, Department of Plant Protection, Bogor Agricultural University, for their invaluable assistance in sample collection and identification throughout the study.

References

Abdala-Roberts, L., Puentes, A., Finke, D.L., Marquis, R.J., Montserrat, M., Poelman, E.H., Rasmann, S., Sentis, A., van Dam, N. M., Wimp, G., Mooney, K., Björkman, C., 2019. Tri-trophic interactions: bridging species, communities and ecosystems. *Ecology Letters*. 22, 2151-2167. https://doi.org/10.1111/ele.13392

Agrawal, A.A., 2000. Mechanisms, ecological consequences, and agricultural implications of tri-trophic interactions. *Current Opinion in Plant Biology*. 3, 329-335. https://doi.org/10.1016/S1369-5266(00)00089-3

Baggen, L.R., Gurr, G.M., Meats, A., 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomologia Experimentalis et Applicata*. 91, 155-161. https://doi.org/10.1046/J.1570-7458.1999.00478.X

Balmer, O., Pfiffner, L., Schied, J., Willareth, M., Leimgruber, A., Luka, H., Traugott, M., 2013. Noncrop flowering plants restore top-down herbivore control in agricultural fields. *Ecology and Evolution*. 3, 2634-2646. https://doi.org/10.1002/ece3.658

Begum, M., Gurr, G.M., Wratten, S.D., Nicol, H.I., 2004. Flower color affects tri-trophic-level biocontrol interactions. *Biological Control*. 30, 584-590. https://doi.org/10.1016/j.biocontrol.2004.03.005

Bersier, L.F., Banašek-Richter, C., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. *Ecology*. 83, 2394-2407. https://doi.org/10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2

Bonato, M., Martin, E.A., Cord, A.F., Seppelt, R., Beckmann, M., Strauch, M., 2023. Applying generic landscape-scale models of natural pest control to real data: Associations between crops, pests and biocontrol agents make the difference. *Agriculture, Ecosystems & Environment*. 342, 108215. https://doi.org/10.1016/j.agee.2022.108215

Buffington, M.L., Forshage, M., Liljeblad, J., Tang, C.T., Van Noort, S., 2020. World cynipoidea (Hymenoptera): A key to higher-level groups. *Insect Systematics and Diversity*. 4, 1-69. https://doi.org/10.1093/isd/ixaa003

Bukovinszky, T., Van Veen, F.J.F., Jongema, Y., Dicke, M., 2008. Direct and indirect effects of resource quality on food web structure. *Science*. 319, 804-807. https://doi.org/10.1126/science.114831

Cagnolo, L., Valladares, G., Salvo, A., Cabido, M., Zak, M., 2009. Habitat fragmentation and species loss across three interacting trophic levels: Effects of life-history and food-web traits. *Conservation Biology*. 23, 1167-1175. https://doi.org/10.1111/J.1523-1739.2009.01214.X

CSIRO. 1990. *Insects of Australia, Volume 1: A Textbook for Students and Research Workers*, second ed. University Publishing, Melbourne.

CSIRO. 1991. *Insects of Australia, Volume 2: A Textbook for Students and Research Workers*, second ed. University Publishing, Melbourne.

Cuautle, M., Parra-Tabla, V., 2014. Describing a multitrophic plant-herbivore-parasitoid system at four spatial scales. *Acta Oecologica*. 55, 8-14. https://doi.org/10.1016/j.actao.2013.10.005

Cuny, M.A.C., Traine, J., Bustos-Segura, C., Benrey, B., 2019. Host density and parasitoid presence interact and shape the outcome of a tritrophic interaction on seeds of wild lima bean. *Scientific Reports*. 9, 1-9. https://doi.org/10.1038/s41598-019-55143-5

Damien, M., Le Lann, C., Desneux, N., Alford, L., Al Hassan, D., Georges, R., Van Baaren, J., 2017. Flowering cover crops in winter increase pest control but not trophic link diversity. *Agriculture, Ecosystems and Environment*. 247, 418-425. https://doi.org/10.1016/j.agee.2017.07.015

Demétrio, C.G.B., Hinde, J., Moral, R.A., 2014. Models for overdispersed data in entomology. In: Ferreira, C.P., Godoy, W.A. (Eds.). *Ecological modelling applied to entomology*, first edition. Springer Cham. pp. 219–259.

Dong, Z., Men, X., Liu, S., Zhang, Z., 2019. Food web structure of parasitoids in greenhouses is affected by surrounding landscape at different spatial scales. *Scientific Reports*. 9, 1-8. https://doi.org/10.1038/s41598-019-44857-1

Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: Analysing ecological networks. *R News*. 8, 8-11. https://doi.org/10.1159/000265935

Dormann, C. F., Frund, J., Bluthgen, N., Gruber, B., 2009. Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*. 2, 7-24. https://doi.org/10.2174/1874213000902010007

Dormann, C.F., Fruend, J., Gruber, B., Beckett, S., Devoto, M., Felix, G.M.F., Iriondo, M., Opsahl, T., Pinheiro, R.B.P., Diego, P.V., 2022. Visualising bipartite networks and calculating some (Ecological) indices. Comprehensive R Archive Network (CRAN).

Erythrina, E., Susilawati, S., Slameto, S., Resiani, N.M.D., Arianti, F.D., Jumakir, J., Fahri, A., Bhermana, A., Jannah, A., Sembiring, H., 2022. Yield advantage and economic performance of rice–maize, rice–soybean, and maize–soybean intercropping in rainfed areas of Western Indonesia with a wet climate. *Agronomy*. 12, 1-18. https://doi.org/10.3390/agronomy12102326

Fletcher, R.J., Smith, T.A.H., Kortessis, N., Bruna, E.M., Holt, R.D., 2023. Landscape experiments unlock relationships among habitat loss, fragmentation, and patch-size effects. *Ecology*. 104, e4037. https://doi.org/10.1002/ECY.4037

Gagic, V., Tscharntke, T., Dormann, C.F., Gruber, B., Wilstermann, A., Thies, C., 2011. Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *In: Proceedings of the Royal Society B: Biological Sciences*, pp. 2946-2953.

Gauld, I.D., 1984. *An introduction to the Ichneumonidae of Australia*. Bulletin of the British Museum (Natural History), British Museum (Natural History).

Gislason, P.O., Benediktsson, J.A., Sveinsson, J.R., 2006. Random forests for land cover classification. *Pattern Recognition Letters*. 27, 294-300. https://doi.org/10.1016/j.patrec.2005.08.011

Goulet, H., Huber, J.T., 1993. *Hymenoptera of the World: An Identification Guide to Families*. Centre for Land and Biological Resources Research, Ontario.

Haro, M.M., Silveira, L.C.P., Wilby, A., 2018. Stability lies in flowers: Plant diversification mediating shifts in arthropod food webs. *PLoS ONE*. 13, 1-18. https://doi.org/10.1371/journal.pone.0193045

Hawro, V., Ceryngier, P., Tscharntke, T., Thies, C., Gagic, V., Bengtsson, J., Bommarco, R., Winqvist, C., Weisser, W. W., Clement, L.W., Japoshvili, G., Ulrich, W., 2015. Landscape complexity is not a major trigger of species richness and food web structure of European cereal aphid parasitoids. *BioControl*. 60, 451-461. https://doi.org/10.1007/s10526-015-9660-9

Hutasoit, R.T., Kalqutny, S.H., Widiarta, I.N., 2020. Spatial distribution pattern, bionomic, and demographic parameters of a new invasive species of armyworm *Spodoptera frugiperda* (Lepidoptera; Noctuidae) in maize of South Sumatra, Indonesia. *Biodiversitas Journal of Biological Diversity*. 21, 3576-3582. https://doi.org/https://doi.org/10.13057/biodiv/d210821

Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. *Journal of Applied Ecology*. 49, 706-714. https://doi.org/10.1111/j.1365-2664.2012.02130.x

Kawatsu, K., Ushio, M., van Veen, F.J.F., Kondoh, M., 2021. Are networks of trophic interactions sufficient for understanding the dynamics of multi-trophic communities? Analysis of a tri-trophic insect food-web time-series. *Ecology Letters*. 24, 543-552. https://doi.org/10.1111/ele.13672

Kenis, M., du Plessis, H., Van den Berg, J., Ba, M.N., Goergen, G., Kwadjo, K.E., Baoua, I., Tefera, T., Buddie, A., Cafà, G., Offord, L., Rwomushana, I., Polaszek, A., 2019. *Telenomus remus*, a candidate parasitoid for the biological control of *Spodoptera frugiperda* in Africa, is already present on the continent. *Insects*. 10, 92. https://doi.org/10.3390/insects10040092

Kruess, A., 2003. Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography*. 26, 283-290. https://doi.org/10.1034/j.1600-0587.2003.03402.x

Kumar, P., Dobriyal, M., Kale, A., Pandey, A.K., 2021. Temporal dynamics change of land use/land cover in Jhansi district of Utter Pradesh over past 20 years using LANDSAT TM, ETM+ and OLI sensors. *Remote Sensing Applications: Society and Environment.* 23, 1-9. https://doi.org/10.1016/j.rsase.2021.100579

Laminou, S.A., Ba, M.N., Karimoune, L., Doumma, A., Muniappan, R., 2020. Parasitism of locally recruited egg parasitoids of the fall armyworm in Africa. *Insects*. 11, 430. https://doi.org/10.3390/insects11070430

Laminou, S.A., Ba, M.N., Karimoune, L., Doumma, A., Muniappan, R., 2023. Parasitism of *Telenomus remus* Nixon on *Spodoptera frugiperda* J.E. Smith and acceptability of *Spodoptera littoralis* Boisduval as factitious host. *Biological Control*. 183, 105242. https://doi.org/10.1016/j.biocontrol.2023.105242

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*. 45, 175-201. https://doi.org/10.1146/annurev.ento.45.1.175

Laterza, I., Dioli, P., Tamburini, G., 2023. Semi-natural habitats support populations of stink bug pests in agricultural landscapes. *Agriculture, Ecosystems and Environment*. 342, 1-7. https://doi.org/10.1016/j.agee.2022.108223

Letourneau, D.K., Allen, S.G.B., Kula, R.R., Sharkey, M.J., Stireman, J.O., 2015. Habitat eradication and cropland intensification may reduce parasitoid diversity and natural pest control services in annual crop fields. *Elementa*. 3, 69. https://doi.org/10.12952/journal.elementa.000069

Lohaus, K., Vidal, S., Thies, C., 2013. Farming practices change food web structures in cereal aphid-parasitoid-hyperparasitoid communities. *Oecologia*. 171, 249-259. https://doi.org/10.1007/s00442-012-2387-8

Mahdianpari, M., Salehi, B., Mohammadimanesh, F., Brisco, B., Homayouni, S., Gill, E., DeLancey, E.R., Bourgeau-Chavez, L., 2020. Big data for a big country: The first generation of Canadian wetland inventory map at a spatial resolution of 10-m using sentinel-1 and sentinel-2 data on the google earth engine cloud computing platform. *Canadian Journal of Remote Sensing*. 46, 15-33. https://doi.org/10.1080/07038992.2019.1711366

Maunsell, S.C., Kitching, R.L., Burwell, C.J., Morris, R.J., 2015. Changes in host-parasitoid food web structure with elevation. *Journal of Animal Ecology*. 84, 353-363. https://doi.org/10.1111/1365-2656.12285

Michereff, M.F.F., Magalhães, D.M., Hassemer, M.J., Laumann, R.A., Zhou, J.J., Ribeiro, P.E.d.A., Viana, P.A., Guimarães, P.E.d.O., Schimmelpfeng, P.H.C., Borges, M., Pickett, J.A., Birkett, M.A., Blassioli-Moraes, M.C., 2019. Variability in herbivore-induced defence signalling across different maize genotypes impacts significantly on natural enemy foraging behaviour. *Journal of Pest Science*. 92, 723-736. https://doi.org/10.1007/s10340-018-1033-6

Montoya, J.M., Pimm, S.L., Solé, R.V., 2006. Ecological networks and their fragility. *Nature*. 442, 259-264. https://doi.org/10.1038/nature04927

Murakami, M., Hirao, T., Kasei, A., 2008. Effects of habitat configuration on host–parasitoid food web structure. *Ecological Research*. 23, 1039-1049. https://doi.org/10.1007/S11284-008-0478-0

Nagaraja, H., Nagarkatti, S., 1969. Three new species of Trichogramma [Hymenoptera: Trichogrammatidae] from India. *Entomophaga*. 14, 393-400. https://doi.org/10.1007/BF02390544

Nilsson, L., Klatt, B.K., Smith, H.G., 2021. Effects of flower-enriched ecological focus areas on functional diversity across scales. *Frontiers in Ecology and Evolution*. 9, 1-12. https://doi.org/10.3389/fevo.2021.629124

Nitschke, N., Allan, E., Zwölfer, H., Wagner, L., Creutzburg, S., Baur, H., Schmidt, S., Weisser, W.W., 2017. Plant diversity has contrasting effects on herbivore and parasitoid abundance in *Centaurea jacea* flower heads. *Ecology and Evolution*. 7, 9319-9332. https://doi.org/10.1002/ECE3.3142

Nixon, G.E.J., 1937. Some asiatic telenominae (Hymenoptera: Proctotrupoidea). *Annals and Magazine of Natural History*. 20, 444-475. https://doi.org/10.1080/00222933708655367

Nixon, G.E., 1970. A revision of the N.W. European species of Microplitis Forster (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History). *Entomology*. 25, 1-30.

Noi Phan, T., Kuch, V., Lehnert, L.W., 2020. Land cover classification using google earth engine and random forest classifier-the role of image composition. *Remote Sensing*. 12, 1-22. https://doi.org/10.3390/RS12152411

Nurkomar, I., Putra, I.L.I., Buchori, D., Setiawan, F., 2024. Association of a global invasive pest *Spodoptera frugiperda* (Lepidoptera: Noctuidae) with local parasitoids: Prospects for a new approach in selecting biological control agents. *Insects*. 15, 1-16. https://doi.org/10.3390/insects15030205

O'Gorman, E.J., Emmerson, M.C., 2009. Perturbations to trophic interactions and the stability of complex food webs. Proceedings of the National Academy of Sciences of the United States of America. 106, 13393-13398. https://doi.org/10.1073/pnas.0903682106

Pardini, R., de Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: Regime shifts in biodiversity across fragmented landscapes. *PLoS ONE*. 5, 1-10. https://doi.org/10.1371/journal.pone.0013666

Pascual, S., Rescia, A.J., Ondul, B.A., Paul, C., Ortega, M., 2022. Effects of landscape structure on abundance and family richness of hymenopteran parasitoids in the olive agroecosystem. *Agriculture, Ecosystems & Environment*. 332, 107914. https://doi.org/10.1016/j.agee.2022.107914

Peñaflor, M.F.G.V., Erb, M., Miranda, L.A., Werneburg, A.G., Bento, J.M.S., 2011. Herbivore-induced plant volatiles can serve as host location cues for a generalist and a specialist egg parasitoid. *Journal of Chemical Ecology*. 37, 1304-1313. https://doi.org/10.1007/s10886-011-0047-9

R Core Team. 2024. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rizali, A., Oktaviyani, Putri, S.D.P.S., Doananda, M., Linggani, A., 2021. Invasion of fall armyworm *Spodoptera frugiperda*, a new invasive pest, alters native herbivore attack intensity and natural enemy diversity. *Biodiversitas Journal of Biological Diversity*. 22, 3482-3488. https://doi.org/10.13057/biodiv/d220847

Rizali, A., Himawan, T., Yuniasari, N., Yuliastanti, N., Bachtiar, M. A., Rafid, E.D.R., 2022. Contribution of agricultural landscape composition on shaping the interaction between pests and natural enemies in cacao agroforestry. *AGRIVITA Journal of Agricultural Science*. 44, 479-489. https://doi.org/10.17503/agrivita.v44i3.3388

Rizali, A., Karindah, S., Ainy, N., Luthfie, M., Meiadi, T., Tawakkal, I., Rahardjo, B.T., Buchori, D., 2023. Long-term changes as oil palm plantation age simplify the structure of host-parasitoid food webs. *PLoS ONE*. 18, 1-16. https://doi.org/10.1371/journal.pone.0292607

Rizali, A., Buchori, D., 2024. Host–parasitoid food webs in oil palm plantations in Asia. *Current Opinion in Insect Science*. 66, 101272. https://doi.org/10.1016/j.cois.2024.101272

Root, R.B., 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of Collards (*Brassica oleracea*). *Ecological Monographs*. 43, 95-124. https://doi.org/10.2307/1942161

Sari, A., Buchori, D., Nurkomar, I., 2020. The potential of *Telenomus remus* Nixon (Hymenoptera: Scelinoidae) as biocontrol agent for the new fall armyworm *S. frugiperda* (Lepidoptera: Noctuidae) in Indonesia. *Planta Tropika: Journal of Agro Science*. 8, 69-74. https://doi.org/10.18196/PT.2020.116.69-74

Sarkar, S.C., Wang, E., Wu, S., Lei, Z., 2018. Application of trap cropping as companion plants for the management of agricultural pests: A review. *Insects*. 9, 1-16. https://doi.org/10.3390/insects9040128

Sartiami, D., Dadang, Harahap, I.S., Kusumah, Y.M., Anwar, R., 2020. First record of fall armyworm (*Spodoptera frugiperda*) in Indonesia and its occurence in three provinces. *IOP Conference Series: Earth and Environmental Science*. 468, 012021. https://doi.org/10.1088/1755-1315/468/1/012021

Sirami, C., Gross, N., Baillod, A.B., Bertrand, C., Carrié, R., Hass, A., Henckel, L., Miguet, P., Vuillot, C., Alignier, A., Girard, J., Batáry, P., Clough, Y., Violle, C., Giralt, D., Bota, G., Badenhausser, I., Lefebvre, G., Gauffre, B., … Fahrig, L., 2019. Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. *Proceedings of the National Academy of Sciences of the United States of America*. 116, 16442-16447. https://doi.org/10.1073/pnas.1906419116

Sisay, B., Simiyu, J., Mendesil, E., Likhayo, P., Ayalew, G., Mohamed, S., Subramanian, S., Tefera, T., 2019. Fall armyworm, *Spodoptera frugiperda* infestations in East Africa: Assessment of damage and parasitism. *Insects*. 10, 1-10. https://doi.org/10.3390/insects10070195

Song, Y., Yang, X., Li, H., Wu, K., 2023. The invasive Spodoptera frugiperda (J.E. Smith) has displaced *Ostrinia furnacalis* (Guenée) as the dominant maize pest in the border area of southwestern China. *Pest Management Science*. 79, 3354-3363. https://doi.org/10.1002/ps.7524

Staab, M., Blüthgen, N., Klein, A.M., 2015. Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. *Oikos*. 124, 827-834. https://doi.org/10.1111/OIK.01723

Sullivan, D.J., Völkl, W., 1999. Hyperparasitism: Multitrophic ecology and behavior. *Annual Review of Entomology*. 44, 291-315. https://doi.org/10.1146/annurev.ento.44.1.291

Syahidah, T., Rizali, A., Prasetyo, L.B., Pudjianto., Buchori, D., 2021. Composition of tropical agricultural landscape alters the structure of host-parasitoid food webs. *Heliyon*. 7, e07625. https://doi.org/10.1016/j.heliyon.2021.e07625

Thies, C., Roschewitz, I., Tscharntke, T., 2005. The landscape context of cereal aphidparasitoid interactions. *Proceedings of the Royal Society B: Biological Sciences*. 272, 203-210. https://doi.org/10.1098/RSPB.2004.2902

Thompson, R.M., Brose, U., Dunne, J.A., Hall, R.O., Hladyz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T. N., Stouffer, D.B., Tylianakis, J.M., 2012. Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*. 27, 689-697. https://doi.org/10.1016/j.tree.2012.08.005

Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Hunt, L., Ives, A., Jonsson, M., Larsen, A., Martin, E.A., Martínez-Salinas, A., Meehan, T. D., O'Rourke, M., Poveda, K., Rosenheim, J.A., Rusch, A., Schellhorn, N., Wanger, T.C., Wratten, S., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. *Biological Conservation*. 204, 449-458. https://doi.org/10.1016/j.biocon.2016.10.001

Tylianakis, J.M., Tscharntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature*. 445, 202-205. https://doi.org/10.1038/nature05429

Tylianakis, J.M., Binzer, A., 2014. Effects of global environmental changes on parasitoid–host food webs and biological control. *Biological Control*. 75, 77-86. https://doi.org/10.1016/j.biocontrol.2013.10.003

Ubaidillah, R., 2003. Parasitoid wasps of Eulophinae (Hymenoptera: Eulophidae) in Nusa Tenggara Timur, Indonesia. *Treubia*. 33, 43-70. https://doi.org/10.14203/treubia.v33i1.563

Ubaidillah, R., 2007. A contribution to the knowledge of the parasitic wasps subfamily Eulophinae (Hymenoptera: Eulophidae) of Java, Indonesia. *Treubia*. 35, 1-98. https://doi.org/10.14203/treubia.v35i0.105

Ulina, E.S., Rizali, A., Manuwoto, S., Pudjianto, Buchori, D., 2019. Does composition of tropical agricultural landscape affect parasitoid diversity and their host–parasitoid interactions?. *Agricultural and Forest Entomology*. 21, 318-325. https://doi.org/https://doi.org/10.1111/AFE.12334

Van-Achterberg, C., 1993. Illustrated key to the subfamilies of the Braconidae (Hymenoptera: Ichneumonoidea). *Zoologische Verhandelingen*. 283, 1-189.

Van De Koppel, J., Bardgett, R.D., Bengtsson, J., Rodriguez-Barrueco, C., Rietkerk, M., Wassen, M.J., Wolters, V., 2005. The effects of spatial scale on trophic interactions. *Ecosystem*. 8, 801-807. https://doi.org/10.1007/S10021-005-0134-2

Wang, M.-Q., Guo, S.-K., Guo, P.-F., Yang, J.-J., Chen, G.-A., Chesters, D., Orr, M., Niu, Z.-Q., Staab, M., Chen, J.-T., Li, Y., Zhou, Q.-S., Fornoff, F., Shi, X., Li, S., Martini, M., Klein, A.-M., Schuldt, A., Liu, X., … Zhu, C.-D., 2024. Multi-dimensionality of tree communities structure host-parasitoid networks and their phylogenetic composition. *ELife*, 13. https://doi.org/10.7554/ELIFE.100202.1

Wang, S., Brose, U., 2018. Biodiversity and ecosystem functioning in food webs: the vertical diversity hypothesis. *Ecology Letters*. 21, 9-20. https://doi.org/10.1111/ele.12865

Wengrat, A.P.G.S., Coelho Junior, A., Parra, J.R.P., Takahashi, T.A., Foerster, L.A., Corrêa, A.S., Polaszek, A., Johnson, N.F., Costa, V.A., Zucchi, R.A., 2021. Integrative taxonomy and phylogeography of *Telenomus remus* (Scelionidae), with the first record of natural parasitism of Spodoptera spp. in Brazil. *Scientific Reports*. 11, 1-9. https://doi.org/10.1038/s41598-021-93510-3

Yang, F., Liu, B., Zhu, Y., Wyckhuys, K.A.G., van der Werf, W., Lu, Y., 2021. Species diversity and food web structure jointly shape natural biological control in agricultural landscapes. *Communications Biology*. 4, 1-11. https://doi.org/10.1038/s42003-021-02509-z

Zhang, Y., Huang, D., 2004). A review and an illustrated key to genera of Encyrtidae (Hymenoptera : Chalcidoidea) from China, Science Press, China.