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Research Article

Trophic Interaction of *Spodoptera frugiperda* and their Egg Parasitoids in Agricultural Landscape

Interaksi Trofik Spodoptera frugiperda dan Parasitoid Telur di Lanskap Pertanian

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Abstract: Trophic interactions between *Spodoptera frugiperda* and its parasitoids are crucial for effective biological control strategies. Understanding these interactions is essential for developing methods that mitigate pest impacts on crops while preserving agroecosystem balance. This study aims to (a) evaluate the interactions between *S. frugiperda* and its parasitoids, (b) explore the relationship between landscape composition and parasitism levels of *S. frugiperda*, and (c) analyze how landscape composition influences the food web metrics of *S. frugiperda* and its parasitoids. The findings identified three egg parasitoid species—*Telenomus* sp1, *Telenomus* sp2, and *Trichogramma* sp—parasitizing *S. frugiperda*, with *Telenomus* sp1 emerging as the dominant parasitoid and a potential biological control agent. Notably, landscape composition did not significantly affect the parasitization rate of *S. frugiperda* eggs. However, the age of maize plants positively influenced the parasitization rate, indicating that older plants may enhance the parasitization of *S. frugiperda* eggs. Landscape composition, particularly in agricultural contexts, positively influenced Shannon diversity while negatively affecting interaction evenness. In contrast, semi-natural habitats enhanced interaction evenness. These findings highlight the significance of landscape composition in understanding the complexity of the *S. frugiperda*-parasitoid food web, providing valuable insights for developing pest control strategies for *S. frugiperda* and conserving natural enemies.

Keywords: fall armyworm, food-webs metrics, landscape composition, maize.

Abstrak: Interaksi trofik antara *Spodoptera frugiperda* dan parasitoidnya sangat penting untuk strategi pengendalian hayati yang efektif. Memahami interaksi ini sangat penting untuk mengembangkan metode yang dapat mengurangi dampak hama pada tanaman sekaligus menjaga keseimbangan agroekosistem. Penelitian ini bertujuan untuk (a) mengevaluasi interaksi antara *S. frugiperda* dan parasitoidnya, (b) mengeksplorasi hubungan antara komposisi lanskap dan tingkat parasitisme *S. frugiperda*, dan (c) menganalisis bagaimana komposisi lanskap memengaruhi struktur jaring-jaring makanan *S. frugiperda* dan parasitoidnya. Temuan ini mengidentifikasi tiga spesies parasitoid telur - *Telenomus* sp1, *Telenomus* sp2, dan *Trichogramma* sp - yang memarasit *S. frugiperda*, dengan *Telenomus* sp1 muncul sebagai parasitoid yang dominan dan berpotensi sebagai agen pengendali hayati. Komposisi lanskap tidak secara signifikan mempengaruhi tingkat parasitisasi telur *S. frugiperda*. Namun, umur tanaman jagung berpengaruh positif terhadap tingkat parasitisasi, yang mengindikasikan bahwa tanaman yang lebih tua dapat meningkatkan parasitisasi telur *S. frugiperda*. Komposisi lanskap, khususnya dalam konteks pertanian, secara positif mempengaruhi keanekaragaman Shannon, sementara secara negatif mempengaruhi kemerataan interaksi. Sebaliknya, habitat semi-alami meningkatkan kemerataan interaksi. Temuan ini menyoroti pentingnya komposisi lanskap dalam memahami kompleksitas jaring makanan parasitoid *S. frugiperda*, memberikan wawasan yang berharga untuk mengembangkan strategi pengendalian hama *S. frugiperda* dan melestarikan musuh alami.

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Kata kunci: jagung, komposisi lanskap, metriks jaring makanan, ulat grayak

INTRODUCTION

The diversity and complexity of food webs are crucial for determining ecosystem function and stability, with changes in these webs influenced by trait-mediated interactions and species densities (Bukovinszky et al. 2008). Herbivores are an important link between plants at the bottom of the food chain and parasitoids above. In contrast, from the top down, parasitoids have long been considered the guardians of plants (Kaplan et al. 2016). Specific trophic interactions in plant-herbivorous-parasitoid food webs can spur "bottom-up" diversification if speciation in plants causes divergences driven by host displacement in herbivorous insects, and if the effects then flow to a third trophic level (Leppanen et al. 2013).

Parasitoid diversity is crucial for the complexity and functionality of food webs. Interactions between processes at various levels can influence food web dynamics (Pedroso et al. 2021). Changes in land use and agricultural intensification adversely affect natural enemy communities, including parasitoids, and the ecosystem services they provide, such as biological pest control (Yang et al. 2021). The interactions between pests and parasitoids in agricultural fields are shaped by cultivation practices, habitat conditions such as crop diversity and the age of the plants (Nugraha et al. 2014). In addition, Midega et al (2014) reported that cropping systems affected egg parasitism most strongly under simple landscape conditions. Research indicates that agricultural intensification may enhance the complexity of tick-parasitoid food webs, challenging the assumption that organic farming practices are essential for maintaining species richness and food-web complexity (Lohaus et al. 2013).

Host-parasitoid communities serve as effective models for studying quantitative food webs due to the straightforward establishment and quantification of trophic interactions between hosts and their parasitoids (Lewis et al. 2002). Quantitative food webs serve as a valuable resource for formulating and evaluating hypotheses regarding the dynamic processes that shape natural communities of herbivorous insects (Morris et al. 2004). They also shed light on the effects of human activities, including the introduction of non-native species (Henneman & Memmott 2001), and the degradation of tropical forest ecosystems (Tylianakis et al. 2007). Numerous parasitoid quantitative food webs have been documented, enhancing our understanding of these ecological relationships (Dong et al. 2019; Syahidah et al. 2021; Yang et al. 2021). The characteristics of food web structure offer valuable insights into ecosystem stability and can inform effective ecosystem management strategies (Tylianakis et al. 2010; Calizza et al. 2015).

Agricultural land use poses a threat to ecosystem services, particularly biological control by natural enemies, due to habitat simplification and increased disturbance from agrochemical inputs (Jonsson et al. 2012). The low levels of pest parasitism in agricultural fields are often linked to a scarcity of parasitoid resources in simplified landscapes; however, this relationship is complicated by the consistent association between landscape complexity and the extent of intensively cultivated crops (Hawro et al. 2017). The prevailing explanation for the influence of landscape complexity on biological control is that intricate landscapes offer parasitoids essential resources, such as nectar (Tscharntke et al. 2007).

Spodoptera frugiperda, a significant pest of maize and other crops globally, is often managed through biological control agents like parasitoids to mitigate its populations (Navik et al. 2023). The trophic interactions between *S. frugiperda* and its parasitoids are essential to biological control strategies. Grasping these interactions is critical for formulating effective biological control methods that reduce pest impacts on crops while preserving the ecological balance of agroecosystems. Parasitoid species of this pest have been previously reported (*e.g.,* Herlinda et al. 2023; Nurkomar et al. 2024). However, their relationship with landscape composition has not been widely documented. This study investigated the interactions between *S. frugiperda* and its parasitoids. We analyzed the effect of landscape composition on the food web structure (Shannon diversity and interaction evenness) of *S. frugiperda* and its parasitoids. We hypothesized that landscape composition influences the complexity of *S. frugiperda*-parastioid food webs.

RESEARCH METHODS

Study site

This study was conducted on farmland in Nipa Kalemoa and Malik Village, Bualemo District, Banggai Regency (Figure 1), from December 2023 to February 2024. A preliminary survey confirmed the land's suitability for research, followed by the preparation of necessary materials. Four fields, each approximately 1.5 hectares, were observed, with each field divided into five plots measuring 2x2 meters. A total of 200 plants per field were sampled, with 40 plants randomly selected from each plot.

Land use classification from high-resolution Sentinel-2 satellite imagery sources using Google Earth Engine. The acquisition of image data was adjusted to the research time, by using cloud-masked median-based pixelwise imageries from November 2023 to February 2024. The channels (bands) used are channels that have a spatial resolution of 10 and 20 m, including bands 2, 4, 5, 6, 7, 8, 8A, 11 and 12. The classification of land use is made into seven classes, including build-up area, water body, agriculture, plantations, shrubs, trees, and bare land. Land uses were classified using supervised classification with random forest machine learning algorithm (Breiman 2001), which resulting in a kappa coefficient value of > 0.70. The results of land use classification in the form of raster data were converted to polygon using ArcGIS 10.8 software. The determination of landscape composition was analyzed by buffering the maize field area within a radius of 500 m from the midpoint of the observation plot (Ulina et al. 2019; Syahidah et al. 2021) using the buffer tool in ArcGIS 10.8 software, then verified by observing the vegetation conditions around the observation plot. The landscape parameters used are class area (CA) of agricultural land and semi-natural habitats (shrubs and trees).

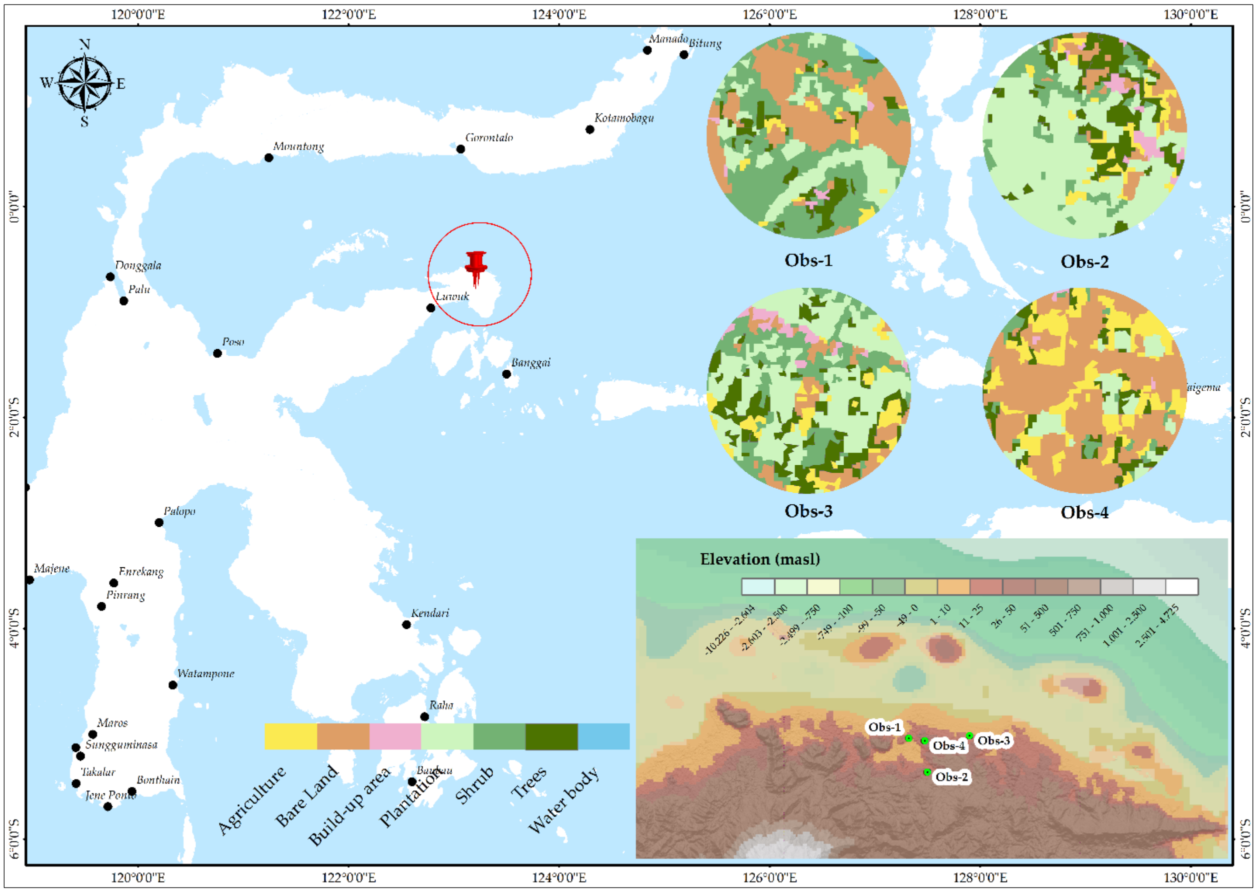

Figure 1. Map of study location depicting topographic and landuse conditions. Obs 1 - Obs 4 indicate sampling locations

Insect Sampling and Identification

The eggs of *S. frugiperda* were collected from the maize plant by direct hand collection, ages 2 to 11 weeks after planting (WAP). Eggs sampling was carried out on all parts of the maize plantation by hand collection. Eggs of *S. frugiperda* collected from each observation site were categorized by observation time and placed in labeled plastic containers according to their location and timing. All eggs were subsequently transported to the laboratory for rearing.

The parasitoids that emerged from *S. frugiperda* eggs were sorted and identified to the morphospecies level. This identification was performed based on their morphological traits, using identification keys from Hymenoptera of the World (Goulet and Huber 1993), Nagaraja and Nagarkatti (1969), and Nixon (1937).

Data Analyses

Trophic interactions between *S. frugiperda* and its parasitoids were analyzed using the `bipartite` package version 2.19 (Dormann et al. 2023) specifically employing the `networklevel` function (Dormann et al. 2008). The food web structure employed in this analysis included Shannon diversity, which quantifies the number of host and parasitoid species within each compartment (Murakami et al. 2008), and interaction evenness, which assesses the distribution of interactions among species in the network (Tylianakis et al. 2007). The parasitization rate was calculated based on Keerthi et al. (2023) with the formula:

$$\%\ \text{parasitization rate} = \frac{number\ of\ parasitised\ hosts}{number\ of\ hosts\ observed}\, x\ 100$$

To assess the influence of maize age, host abundance, and landscape composition on parasitization rates and food web structure, Generalized Linear Mixed Models with negative binomial family were employed through the `glmmTMB` package version 1.1.9 (Brooks et al. 2024). Model evaluation was conducted using the Akaike Information Criterion (AIC), along with marginal (R^2m) and conditional (R^2c) R-squared values, utilizing the `MuMIn` package version 1.47.5 (Barton. 2024). All analyses were performed using R statistical software version 4.3.0 (R Core Team 2023).

RESULT AND DISCUSSION

Overall, individuals of parasitoids were found to parasitize *S. frugiperda* eggs, comprising 1,832 individuals of *Telenomus* sp1, 803 individuals of *Telenomus* sp2, and 181 individuals of *Trichogramma* sp. (Figure 2). The highest abundance of parasitoids was recorded in observation field 2, with a total of 1,006 individuals, while the lowest was observed in field 3, which contained 414 individuals.

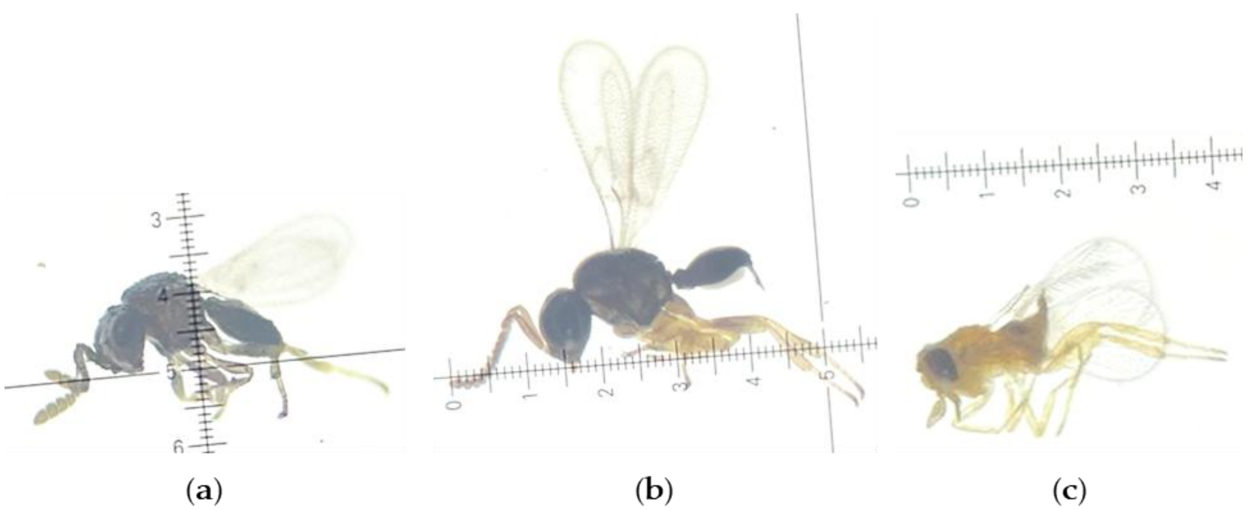

Figure 2. Parasitoid species on *S. frugiperda*; a = *Telenomus sp1*; b = *Telenomus sp2*; c = *Trichogramma sp*

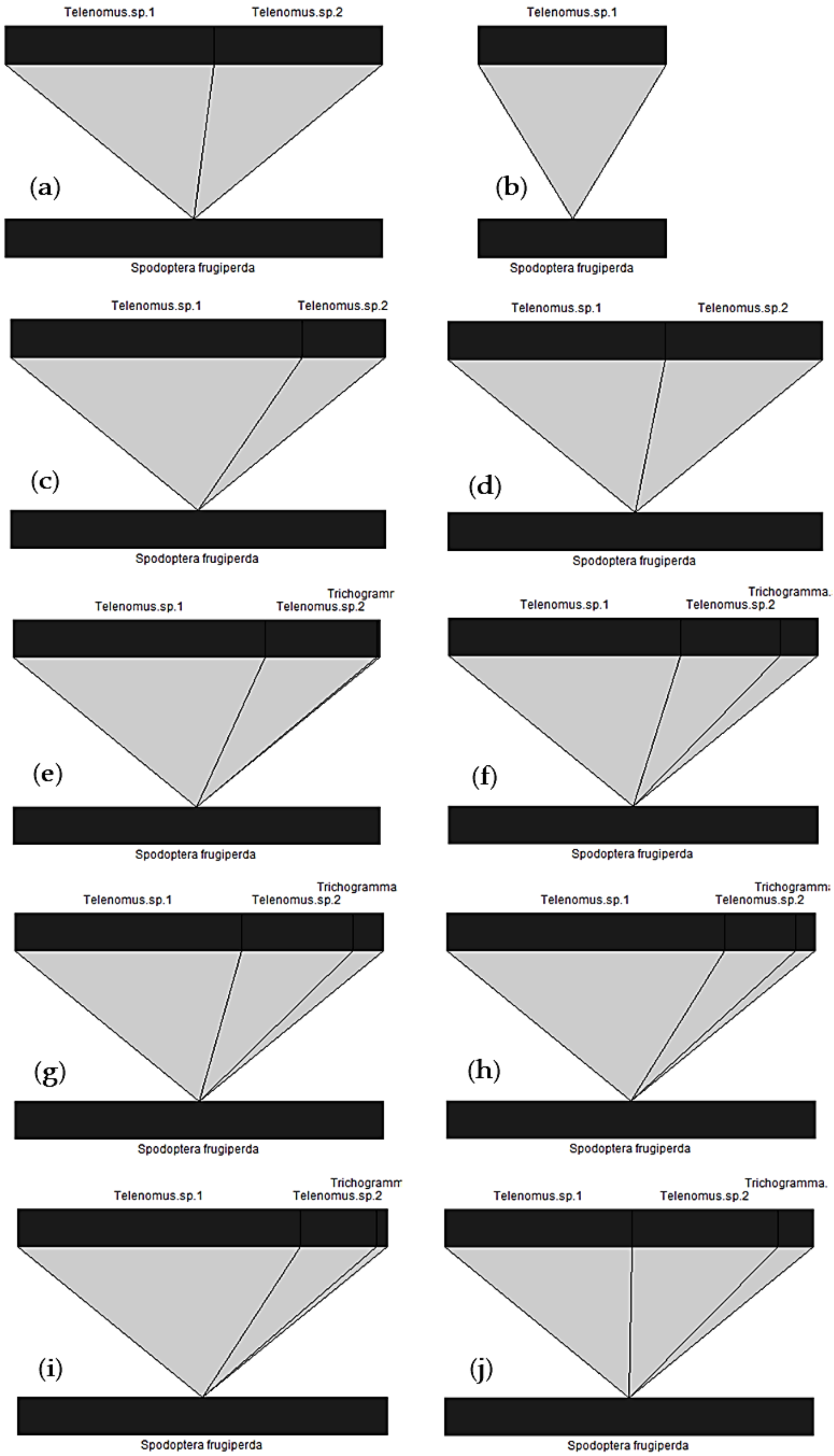

Figure 3. Trophic interaction of *S. frugiperda* and parasitoids based on maize age. Observation at 2 WAP (a), 3 WAP (b), 4 WAP (c), 5 WAP (d), 6 WAP (e), 7 WAP (f), 8 WAP (g), 9 WAP (h), 10 WAP (i), 11 WAP (j)

The trophic interactions between *S. frugiperda* and its parasitoids revealed two parasitoid species present in the food web at 2 to 5 weeks after planting (WAP), increasing to three species at 6 to 11 WAP (Figure 3). The parasitoid *Telenomus* sp1 emerged as the dominant species within the food web, indicating its potential as a biological control agent for *S. frugiperda*. These findings suggest that the age of maize influences the trophic interactions between *S. frugiperda* and its parasitoids. The findings of this study indicate that the parasitoid *Telenomus* sp. serves as a natural enemy of *S. frugiperda* eggs. With a diminutive body size of approximately 0.8 mm (de Almeida et al. 2015), *Telenomus* sp. is characterized by its black coloration and hindwings, which feature a single small hook and are smaller than the forewings. This parasitoid possesses elbowed or geniculate antennae comprising 10 to 11 segments. Notably, *Telenomus* sp. is a specific egg parasitoid, primarily targeting Lepidopteran hosts (Susiawan & Yuliarti 2011), and is recognized as a promising natural enemy due to its ease of rearing. Female *Telenomus* sp. adults invade colonies of *S. frugiperda* eggs, preventing the hatching of larvae and instead facilitating the development of their own larvae (Sari et al. 2020).

Effect of Landscape on Parasitization Rate of *S. frugiperda* eggs.

The composition of the landscape did not influence the parasitization rates of *S. frugiperda* eggs. Instead, the age of the maize plants had a significant positive effect on parasitization rates, indicating that older maize plants were associated with increased parasitization of *S. frugiperda* eggs (Table 1). The findings indicate that maize age significantly influenced the parasitization rate of *S. frugiperda* eggs. Understanding the relationship between maize age and parasitization rates is crucial for comprehending the dynamics of biological control in agricultural systems (Zhang et al. 2020). Additionally, research by Li et al (2023) highlighted that *S. frugiperda* is a significant pest affecting various crops, with management strategies often relying on parasitoid wasps that deposit their eggs within the host eggs. The age of a plant significantly influenced the diversity and abundance of pests in vegetable fields, as well as the trophic interactions between these pests and their parasitoids. As plants mature, the associated organism community tended to stabilize, resulting in increased rates of parasitism (Nugraha et al. 2014).

Table 1. Relationship of parasitization rates with the maize age, number of hosts, class area of agriculture (CA. Agriculture) and class area of semi-natural (CA. Semi-natural) as a predictor. Significance level: *$P < 0.05$.

Variable	Estimate	Std. Error	P	R^2m	R^2c
(Intercept)	1.159	1.589	0.466	0.44	0.44
Maize age	0.334	0.136	0.014*		
Number of hosts	0.000	0.001	0.822		
CA. Agriculture	0.005	0.023	0.815		
CA. Semi-natural	-0.011	0.027	0.694		

Effect of Landscape Composition on *S. frugiperda*-Parasitoid Food Web Structure

We observed significant impacts of landscape composition on the structure of the *S. frugiperda*-parasitoid food web (Table 2). Notably, the agriculture class area (CA Agriculture) exhibited a positive correlation with Shannon diversity (P = 0.019) while negatively affecting interaction evenness (P < 0.001). Conversely, the semi-natural class area (CA semi-natural) positively influenced interaction evenness (P < 0.001). We found no significant effect of maize age and number of hosts on Shannon diversity and interaction evenness within the *S. frugiperda*-parasitoid food webs.

Table 2. Relationship of food web structure (Shannon diversity and Interaction evenness) *S. frugiperda*-parasitoid with maize age, number of hosts, class area of agriculture (CA. Agriculture) and class area of semi-natural (CA. Semi-natural) as a predictor. Level of significance: *P < 0.05; **P < 0.01; ***P < 0.001

Variable	Estimate	Std. Error	P	R^2m	R^2c
Shannon diversity					
(Intercept)	-1.464	0.976	0.134	0.38	0.59
Maize age	-0.026	0.030	0.395		
Number of hosts	-0.000	0.000	0.409		
CA. Agriculture	0.040	0.017	0.019*		
CA. Semi-natural	0.006	0.027	0.829		
Interaction evenness					
(Intercept)	-0.348	0.489	0.476	0.57	0.57
Maize age	0.009	0.032	0.768		
Number of hosts	0.000	0.001	0.786		
CA. Agriculture	-0.029	0.008	0.000***		
CA. Semi-natural	0.037	0.011	0.000***		

Our findings indicate that landscape composition significantly influences the structure of host-parasitoid food webs. This aligns with previous research that has emphasized the role of landscape composition in shaping these interactions (Hawro et al. 2015; Dong et al. 2019; Syahidah et al. 2021). Surprisingly, our study showed that increasing CA Agriculture had a significant impact on enhancing Shannon diversity. This phenomenon may arose due to the prevalence of *S. frugiperda* in landscapes dominated by agriculture area, which could enhance parasitoid diversity. The presence of generalist parasitoids in broad crop fields significantly influenced the structure of food webs along the increase of the proportion of agricultural area (Syahidah et al. 2021). Response of natural enemy populations to agriculture area and landscape composition can vary, exhibiting positive, negative, or neutral effects. The natural enemies' life history and behavioural traits influence these variabilities (Haan et al. 2020).

Our study indicated that the class areas of semi-natural significantly influences interaction evenness, with an increase in semi-natural class area leading to a positive enhancement of interaction evenness. Higher interaction evenness indicates a more balanced distribution of relationships (Dong et al. 2019). Landscapes characterized by semi-natural habitats exhibit high connectivity, which can enhance the interaction evenness within those ecosystems (Murakami et al. 2008). In contrast, Kaartinen and Roslin (2011) suggested that factors such as interaction evenness do not affect these dynamics within a landscape context. An increase in the agricultural area leads to a reduction in interaction evenness. Research by Tylianakis et al (2007) demonstrated that interaction evenness within host-parasitoid food webs is lower in intensively managed agricultural environments. This is because an increase in the amount of agricultural habitat is associated with an increase in the frequency of pesticide applications (Jonsson et al. 2012), which in turn leads to a decrease in pest-parasitoid interactions (Schindler et al. 2022).

CONCLUSION

This study demonstrated the potential use of *Telenomus* sp., a specific egg parasitoid of Lepidopteran hosts for biological control agent for *S frugiperda* which was emerged as the dominant species in the food web. While the composition of the landscape did not influence parasitization rates, the trophic interactions between *S. frugiperda* and its parasitoids, including *Telenomus* sp., were significantly affected by maize age. Our study highlights that landscape composition significantly shapes *S. frugiperda*-parasitoid food webs, with agricultural areas increasing Shannon diversity but reducing interaction evenness, while semi-natural areas enhance evenness. Our study emphasizes the critical role of crop phenology in shaping food web structures and optimizing pest management strategies, as well as the critical role of landscape structure in influencing food web dynamics and guiding sustainable pest management strategies

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