Heliyon 7 (2021) e07625

Contents lists available at ScienceDirect

Heliyon

journal homepage: www.cell.com/heliyon

Research article

CelPress

Composition of tropical agricultural landscape alters the structure of host-parasitoid food webs



Helivon

Tazkiyatul Syahidah^a, Akhmad Rizali^{b,*}, Lilik Budi Prasetyo^c, Pudjianto^a, Damayanti Buchori^{a, d}

^a Department of Plant Protection, IPB University, Kampus IPB Dramaga, Bogor, West Java, Indonesia

^b Department of Plant Pests and Diseases, Faculty of Agriculture, University of Brawijaya, Jl. Veteran, Malang, East Java, Indonesia

^c Department of Forest Resources Conservation and Ecotourism, Faculty of Forestry, IPB University, Dramaga, Bogor, West Java, Indonesia

^d Center for Transdisciplinary and Sustainability Science, IPB University, Jl. Pajajaran, Bogor, West Java, Indonesia

ARTICLE INFO

Keywords: Bogor Lepidopteran pest Landscape metric Semi-natural habitat

ABSTRACT

Land-use change and habitat fragmentation are well-known to affect host-parasitoid interactions. However, the study of the effects of landscape composition, as a result of habitat fragmentation, on host-parasitoid food webs is still limited especially in a tropical agricultural landscape. This research was aimed to study the effect of agricultural landscape composition on the structure of host-parasitoid food webs. Field research was conducted in sixteen long-bean fields located in Bogor Regency, West Java, Indonesia. In each long-bean field, sampling of insect pests and their parasitoids was carried out using direct observation within a plot size of 25 m \times 50 m. The collected insects were brought to the laboratory for rearing and observed for emerging parasitoids. Landscape composition of each long-bean field was measured by digitizing the whole patch within a radius of 500 m from the long-bean field as a center of landscape, and landscape parameters were then quantified by focusing on number of patches and class area of both semi-natural habitats and crop fields. In total, we found 51 morphospecies of insect pests and 110 morphospecies of associated parasitoids from all research locations. Lepidopteran pests are the most abundant and species-rich with 35 morphospecies and with 76 morphospecies of parasitoids. Based on the generalized linear models, landscape composition especially class area of natural habitat and crop field showed a positive relationship with host-parasitoid food-web structure especially on connectance and compartment diversity. In conclusion, landscape composition contributes to shaping the host-parasitoid foodwebs in a tropical agricultural landscape.

1. Introduction

In tropical regions, particularly in Southeast Asia, agricultural landscape has transformed mainly from traditional systems to intensive cropping systems since the Green Revolution (Rerkasem, 2005). Agricultural intensification with monoculture systems causes the increasing area of cropland at landscape scale and considerably influences the diversity, composition, and functioning of the remaining natural ecosystems (Tilman, 1999). In Indonesia, agricultural landscape is characterized as highly fragmented as a consequence of habitat transformation and decreasing amount of cropland per landowner. The last agricultural census by BPS-Statistics Indonesia (2013) reported that the average area per landowner is about 0.25 ha and is dominated by small farmers. This condition shapes the agricultural landscape into small or patchy cropland and in some regions still exist many patches of natural habitats of varying sizes scattered within the landscapes. For example, an urban agricultural landscape in Bogor Regency of West Java, where this study was conducted, has unique agricultural characteristics that are dominated by cropland but consist of dispersed semi-natural habitat remnant and surrounded by mountain areas (Widiatmaka et al., 2016).

Agricultural landscapes with the existence of semi-natural habitats have an important role to support biodiversity and other ecosystem services. The existence of semi-natural habitat in agricultural landscape is useful to preserve the occurrence of parasitoids, including sustaining diversity and frequency (Landis et al., 2000). A semi-natural habitat in the form of non-agricultural crops that are grown around agricultural ecosystems also has a positive effect on crops themselves (Thies et al., 2003). This non-agricultural crop is beneficial as a supplier of food sources, alternative host sources, refuges, and suitable habitat for parasitoids (Bianchi et al., 2006). However, biodiversity in agroecosystem is

E-mail address: arizali@ub.ac.id (A. Rizali).

https://doi.org/10.1016/j.heliyon.2021.e07625

Received 13 February 2021; Received in revised form 20 June 2021; Accepted 15 July 2021

^{*} Corresponding author.

^{2405-8440/© 2021} The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

not merely influenced by the presence of natural habitat, but also influenced by the composition of agricultural landscape. Landscape composition, in this case, the number and proportions of different habitat types in a landscape (Fahrig et al., 2011), revealed affects on biodiversity in agricultural landscapes. Previous studies in Bogor Regency showed that the composition of agricultural landscapes significantly affected the abundance and functional diversity of parasitoids (Ulina et al., 2019) and flower-visiting insects (Rizali et al., 2018).

Although natural habitats may enhance species richness or the abundance of biodiversity, especially of parasitoids in cropland, their presence did not consistently enhance biological control in the agricultural landscape (Karp et al., 2018). Hence, understanding of agricultural landscape composition effects on biodiversity also needs to consider food web interactions (Miranda et al., 2013) that can explain the relationship between resource and consumer as well as within-guild competition (Dormann and Blüthgen, 2017; Batáry et al., 2021). Research on food webs has been developed in agricultural landscapes to investigate the effects of habitat fragmentation on food web interactions (Hagen et al., 2012) and also the relationship between diversity and food web structure (Rooney and McCann, 2012). In this research, we used quantitative food-web statistics (Bersier et al., 2002) to assess the effect of agricultural landscape composition on the structure of host-parasitoid food webs. The quantitative metrics of host-parasitoid food-webs include connectance, compartment diversity, nestedness, and interaction strength asymmetry, as the representation of network metrics that are important for the conservation of species interaction (Tylianakis et al., 2007, 2010).

The objectives of this research were (1) to study the diversity and abundance of parasitoids and their hosts in long-bean fields in different agricultural landscapes of Bogor and (2) to investigate the effect of landscape composition on the structure of host-parasitoid food webs. We hypothesized that the high proportion of natural habitat increases the interaction of host-parasitoid in the agricultural landscape. The research results will provide insight into the importance of agricultural landscape management on conserving species interaction networks.

2. Material and methods

2.1. Study area and site selection

The study area was located in urban agricultural landscapes in Bogor Regency, West Java, Indonesia (Figure 1). The landscapes are dominated by croplands and consist of patchily distributed fragments of seminatural habitats or non-crop vegetation (trees and shrubs) as well as settlements. Within the region, sixteen fields of long-bean (*Vigna sinensis*) were selected based on criteria including: cultivation technique without pesticide application, minimum field area of $25 \text{ m} \times 50 \text{ m}$, and distance between locations of at least 2 km apart to avoid overlapping landscapes as study units (Tischendorf and Fahrig, 2000). In this research, we used long bean fields that were cultivated by local farmers. Long beans were planted in a monoculture system within beds 120–150 cm wide and with a planting distance of 70 cm \times 30 cm.

2.2. Landscape characterization

The landscape of each long-bean field was characterized in a circle with a radius of 500 m centered on the long-bean field (adapted from Ulina et al., 2019) as the most appropriate scale to study the interaction between host and their parasitoids in the tropical region (Klein et al., 2006). Land-uses of each landscape were surveyed and marked based on digital maps from Google Earth and then manually digitalized using



Figure 1. Distribution of study sites located across Bogor Regency in West Java, Indonesia. The numbers indicate the location code: 1: Bojong, 2: Bojongjengkol, 3: Cemplang, 4: Ciangsana, 5: Ciawi, 6: Cibanteng, 7: Cibatok, 8: Cibeureum, 9: Cihideungudik, 10: Cikarawang, 11: Cimanggu, 12: Ciomas, 13: Laladon, 14: Nambo, 15: Petir, 16: Tapos.

ArcGIS software version 10. Land-uses were classified into six categories i.e. semi-natural habitat, cropland, settlement, open area, and other (road and water body). Landscape parameters included the class area (CA, i.e., the area in m2 of a particular category or "class" of habitat) and the number of patches (NP) of both natural and cropland habitats. These parameters were calculated using Patch Analyst version 5.2.0.16, extension for ArcGIS (Rempel et al., 2012).

2.3. Sampling of long-bean pests and their parasitoids

Samplings were done from June 2017-July 2018. The sampling of long-bean pests and their parasitoids was carried out using direct observation within the long-bean field with a plot size of $25 \text{ m} \times 50 \text{ m}$ (Vaissière et al., 2011). Observations were conducted across different ages of plants ranging from 7-49 days after planting. The sampling of pests and their parasitoids was carried out at 06.00 am within a transect with 100 long-bean plants per transect. In each transect, insect pests were counted and collected using hand or plastic, while small insects such as

ants and trips are collected directly using a brush. The live insect pests were brought to the laboratory for rearing and observed for emerging parasitoids. Specimens both of insect pests and parasitoids were stored in alcohol 70% for later identifications.

The insect specimens were initially sorted and identified to morphospecies level using relevant taxonomic literature (e.g. Goulet and Huber, 1993; Borror et al., 1996) and the reference collection of Zoological Museum, LIPI, Indonesia. The specimens were deposited in the Laboratory of Biological Control, Department of Plant Protection, IPB University.

2.4. Food webs construction

Quantitative host-parasitoid food webs were compiled for each long-bean landscape. Based on data from the rearing and the emerged parasitoids, we constructed trophic interactions between insect pests (lower bars) and their parasitoids (upper bars). Trophic interaction networks of insect pests and their parasitoids for each long-bean landscape were quantified by using the bipartite package version

Table 1. Landscape composition (class area (CA.nat) and number of patches (NP.nat) of natural habitat, class area (CA.crop) and number of patches (NP.crop) of crop fields) for the 16 study sites and species richness (S) and abundance (N) of insect pests and parasitoids of each study site.

No	Landscape	Landscape composition				Insect pests		Parasitoids	
		CA.nat (ha)	NP.nat	CA.crop (ha)	NP.crop	s	Ν	s	Ν
1.	Bojong	17.9	19	29.2	117	26	2,345	37	313
2.	Bojongjengkol	17.3	12	33.9	68	25	4,065	45	1,174
3.	Cemplang	8.0	11	41.9	122	30	1,747	27	859
4.	Ciangsana	26.9	20	26.2	37	25	3,859	41	872
5.	Ciawi	14.1	20	18,3	28	26	2,143	35	434
6.	Cibanteng	22.4	9	30.7	58	24	1,938	27	420
7.	Cibatok	8.6	7	40.6	98	23	1,685	31	389
8.	Cibeureum	25.6	13	27.4	73	20	2,267	33	531
9.	Cihideungudik	15.8	11	52.3	88	19	1,591	29	339
10.	Cikarawang	21.6	30	40.9	100	24	4,188	31	1,180
11.	Cimanggu	28.1	4	35.0	84	20	2,512	20	379
12.	Ciomas	11.1	13	37.2	63	26	5,117	47	1,145
13.	Laladon	1.8	7	32.1	117	22	3,268	29	428
14.	Nambo	33.1	22	14.7	44	27	5,516	45	1,120
15.	Petir	21.3	16	43.1	78	19	2,857	15	211
16.	Tapos	3.2	3	21.2	74	22	3,948	34	872



Figure 2. Landscape composition of study sites. Site codes are based on Figure 1 and depicted in order of increasing semi-natural habitat (dark green) land cover. Other major land cover classes include cropland (light green), settlement (red), and open area (grey). Other land cover (light brown) consisted of water body and street.

Table 2. Species richness (S) and abundance (N) of insect pests based on insect order and their parasitoids.

2.11 (Dormann et al., 2009) of the R statistical software (R Core Team, 2020).

2.5. Data analysis

No Insect pests Parasitoids Order s S Ν N 13 101 1. Coleoptera 1 2 2. Diptera 5 9,576 36 2,377 3. Hemiptera 10 25,419 42 3,603 4. Lepidoptera 35 14,038 76 4,564 9 21 5. Unidentified 3 Total 51 49,055 110 10.666

We selected the parameter of host-parasitoid food-webs i.e. connectance, compartment diversity, nestedness, and interaction strength asymmetry (adapted from Tylianakis et al., 2010) to study the relationship with landscape composition. The effect of landscape composition on the abundance of insect pests and their parasitoids was analyzed by fitting a generalized linear model (GLM) without interactions (Zuur et al., 2009) and using a gaussian distribution. Explanatory variables included number of patches (NP.nat) and class area (CA.nat) of semi-natural



(caption on next page)

habitat and number of patches (NP.crop) and class area (CA.crop) of crop fields. Based on the correlation analysis, we did not find auto-correlations among explanatory variables (P > 0.05).

The GLM without interactions was also used to analyze the effect of landscape composition on host-parasitoid food webs, using a gaussian distribution. We used the same explanatory variables i.e. NP.nat, CA.nat, NP.crop, and CA.crop. The significance level All analyses were performed using the R statistical software.

3. Results

3.1. Landscape characteristic of long-bean fields and the diversity of insect pests and their parasitoids

Agricultural landscapes surrounding each long-bean field in a radius of 500 m were dominated by cropland (13.78%–75.78%) with the area of cropland on each landscape ranging from 12.80 to 53.83 ha (Table 1). The proportion of semi-natural habitat in the study area varied between 1.49% and 31.71% (Figure 2). The highest proportion of semi-natural habitat was found in Nambo and the lowest proportion in Laladon. In addition, the highest proportion of crop fields was found in Cihideungudik and the lowest proportion in Nambo. The composition of the crop plants that are cultivated on each agricultural landscape differs but is dominated by rice plants.

As the result of insect sampling from all long-bean fields, we found 49,055 individuals and 51 morphospecies of insect pests and 10,666 individuals, and 110 morphospecies of parasitoids (Table 2). The most abundant Order, with the highest species richness, was Lepidoptera. The highest species richness of insect pests was found in Cemplang with 30 morphospecies and 1,747 individuals, while the lowest in Cihideungudik with 19 morphospecies and 1,591 individuals (Table 1). While for parasitoids, the highest species richness was found in Ciomas with 47 morphospecies and 1,145 individuals, and the lowest in Petir with 15 morphospecies and 211 individuals.

Based on the host-parasitoid food webs (Figure 3), we found that Braconidae sp04, Encyrtidae sp02, Eulophidae sp04, and Scelionidae sp01 were the most abundant parasitoids in the long-bean fields, while the most parasitized pests were *Liriomyza* sp, *Nezara viridula, Chrysodeixis chalcities*, and *Spodoptera litura*. The host-parasitoid food-webs of lepidopteran pests (Figure 3b) were more complex than hemipteran pests (Figure 3c). The GLM results showed that landscape composition especially class area and number of patches of natural habitat affected the abundance of lepidopteran parasitoids, and not affected the abundance of their host (lepidopteran pests) (Table 3). We did not find an effect of landscape composition on the abundance of all insect pests as well as all parasitoids (Table 3).

3.2. Effect of landscape composition on the structure of host-parasitoid food-webs

Based on the GLM, landscape composition affected the structure of host-parasitoid food-webs for all insect pests and not for specific pests such as lepidopteran pests (Table 4). Class area of crop field affected the connectance (P = 0.072), while class area of semi-natural habitat affected the compartment diversity (P = 0.099) of host-parasitoid food-webs although with marginal significance. Increasing class area of crop fields causes increasing the connectance ($R^2 = 0.285$, P = 0.033; Figure 4a) and increasing class area of semi-natural habitat cause increasing the compartment diversity ($R^2 = 0.278$, P = 0.036; Figure 4b). We did not find an effect of landscape composition on nestedness and interaction strength asymmetry of host-parasitoid food webs (Table 4).

4. Discussion

Our results found that the diversity of insect pests and their parasitoids varied between agricultural landscapes. The composition of agricultural landscapes, especially the proportion of semi-natural habitat, affected the abundance of lepidopteran parasitoids but not their hosts. It supports the hypothesis that the presence of semi-natural habitats in agricultural landscapes can maintain the presence of parasitoids in longbean fields. Several studies in Indonesia revealed the important role of semi-natural habitat in maintaining the diversity of insects including natural enemies in crop fields (e.g. Settle et al., 1996; Rizali et al., 2002). However, the diversity of parasitoids may also track the changes in host diversity at each phase of crop plant growth (Heinrichs et al., 1994). In this research, an effect of semi-natural habitat was only found for parasitoids of lepidopteran pests, arguably due to parasitoid abundance following the abundance of the dominant (lepidopteran) pests or hosts in long-bean fields.

Figure 3. Trophic interactions between insect pests (lower bars) and their parasitoids (upper bars) were recorded from sixteen long-bean fields in Bogor. (a) all insect pests and their parasitoids, (b) lepidopteran pests and their parasitoids, and (c) hemipteran pests and their parasitoids. Parasitoids: p001: Tachinidae sp01, p002: Tachinidae sp02, p003: Tachinidae sp03, p004: Aphelinidae sp01, p005: Aphelinidae sp02, p006: Aphelinidae sp03, p007: Aphelinidae sp04, p008: Braconidae sp01, p009: Braconidae sp02, p010: Braconidae sp03, p011: Braconidae sp04, p012: Braconidae sp05, p013: Braconidae sp06, p014: Braconidae sp07, p015: Braconidae sp08, p016: Braconidae sp09, p017: Braconidae sp10, p018: Braconidae sp11, p019: Braconidae sp13, p020: Braconidae sp14, p021: Braconidae sp15, p022: Microplitis manilae, p023: Therobillus marucae, p024: Chalcididae sp01, p025: Chalcididae sp02, p026: Elasmidae sp01, p027: Elasmidae sp02, p028: Elasmidae sp03, p029: Elasmidae sp04, p030: Encyrtidae sp01, p031: Encyrtidae sp02, p032: Encyrtidae sp03, p033: Encyrtidae sp04, p034: Encyrtidae sp05, p035: Encyrtidae sp06, p036: Encyrtidae sp07, p037: Encyrtidae sp08, p038: Encyrtidae sp09, p039: Encyrtidae sp10, p040: Eucoilidae sp01, p041: Eulophidae sp01, p042: Eulophidae sp02, p043: Eulophidae sp03, p044: Eulophidae sp04, p045: Eulophidae sp05, p046: Eulophidae sp06, p047: Eulophidae sp07, p048: Eulophidae sp08, p049: Eulophidae sp09, p050: Eulophidae sp10, p051: Eulophidae sp11, p052: Eulophidae sp12, p053: Eulophidae sp13, p054: Eulophidae sp15, p055: Eulophidae sp16, p056: Eulophidae sp18, p057: Eulophidae sp19, p058: Eulophidae sp20, p059: Eulophidae sp21, p060: Eulophidae sp22, p061: Eulophidae sp23, p062: Eulophidae sp25, p063: Eulophidae sp26, p064: Neochrysocharis formosa, p065: Quadrastichus liriomyza, p066: Eupelmidae sp01, p067: Eupelmidae sp03, p068: Hymenoptera sp01, p069: Hymenoptera sp10, p070: Hymenoptera sp20, p071: Ichneumonidae sp02, p072: Ichneumonidae sp03, p073: Ichneumonidae sp04, p074: Ichneumonidae sp05, p075: Ichneumonidae sp07, p076: Ichneumonidae sp09, p077: Ichneumonidae sp10, p078: Megaspilidae sp01, p079: Megaspilidae sp02, p080: Mymaridae sp01, p081: Mymaridae sp02, p082: Mymaridae sp03, p083: Mymaridae sp04, p084: Mymaridae sp05, p085: Mymaridae sp06, p086: Mymaridae sp07, p087: Mymaridae sp08, p088: Mymaridae sp09, p089: Platygastridae sp01, p090: Platygastridae sp02, p091: Platygastridae sp03, p092: Platygastridae sp04, p093: Pteromalidae sp01, p094: Scelionidae sp01, p095: Scelionidae sp02, p096: Scelionidae sp03, p097: Scelionidae sp04, p098: Scelionidae sp05, p099: Scelionidae sp06, p100: Scelionidae sp07, p101: Torymidae sp01, p102: Torymidae sp02, p103: Trichogrammatidae sp01, p104: Trichogrammatidae sp02, p105: Trichogrammatidae sp03, p106: Trichogrammatidae sp04, p107: Trichogrammatidae sp05, p108: Trichogrammatidae sp06, p109: Trichogrammatidae sp07, p110: Trichogrammatidae sp10. Insect pests: h01: Coccinellidae sp1, h02: Agromyzidae sp2, h03: Drosophilidae sp1, h04: Liriomyza sp, h05: Phytomyza sp, h06: Syrphidae sp1, h07: Aleyrodidae sp1, h08: Alydidae sp1, h09: Aphis craccivora, h10: Aphis gossypii, h11: Coreidae sp1, h12: Empoasca sp, h13: Nezara viridula, h14: Penacoccus sp1, h15: Pentatomidae sp2, h16: Pseudococcidae sp1, h17: Arctiidae sp1, h18: Chrysodeixis chalcities, h19: Crambidae sp1, h20: Crambidae sp2, h21: Diapania indica, h22: Doleschallia bisaltide, h23: Geometridae sp1, h24: Geometridae sp2, h25: Geometridae sp3, h26: Geometridae sp4, h27: Hesperiidae sp1, h28: Hesperiidae sp2, h29: Lycaenidae sp1, h30: Lycaenidae sp2, h31: Lymantridae sp1, h32: Lymantridae sp2, h33: Lymantridae sp3, h34: Lymantridae sp5, h35: Maruca vitrata, h36: Microlepidoptera sp1, h37: Microlepidoptera sp2, h38: Noctuidae sp2, h39: Noctuidae sp3, h40: Noctuidae sp4, h41: Psychidae sp1, h42: Psychidae sp2, h43: Pyralidae sp1, h44: Pyralidae sp2, h45: Pyralidae sp3, h46: Pyralidae sp4, h47: Satyridae sp1, h48: Sphingidae sp1, h49: Spodoptera exigua, h50: Spodoptera litura, h51: Totricidae sp1, h52: Unidentified.

Table 3. Generalized linear models relating the abundance of insects pests and their parasitoids (both all insects and lepidopteran) to class area (CA.nat) and number of patches (NP.nat) of natural habitat, as well as class area (CA.crop) and number of patches (NP.crop) of crop fields as predictors. Significance level: *P < 0.10, **P < 0.05.

Variable	All pests		All parasitoids		Lepidopteran pests		Lepidopteran parasitoids	
	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value
(Intercept)	8.342	0.000	6.869	0.000	7.127	0.000	5.850	0.000
CA.nat	-0.004	0.800	-0.015	0.501	-0.012	0.481	-0.052	0.052*
NP.nat	0.017	0.321	0.025	0.317	0.016	0.418	0.064	0.038**
CA.crop	-0.013	0.336	-0.011	0.572	-0.003	0.861	0.010	0.663
NP.crop	-0.002	0.737	-0.003	0.684	-0.005	0.435	-0.010	0.270

Table 4. Generalized linear models relating the structure of host-parasitoid food webs (connectance, compartment diversity, nestedness, and interaction strength asymmetry) to class area (CA.nat) and number of patches (NP.nat) of natural habitat, as well as class area (CA.crop) and number of patches (NP.crop) of crop fields as predictors. Significance level: *P < 0.10.

Variable	Connectance		Compartment d	Compartment diversity		Nestedness		Interaction strength asymmetry	
	Estimate	P value	Estimate	P value	Estimate	P value	Estimate	P value	
All species									
(Intercept)	0.085	0.001	1.111	0.665	12.982	0.100	0.314	0.059	
CA.nat	0.000	0.910	0.120	0.099*	0.097	0.625	0.004	0.379	
NP.nat	-0.001	0.297	0.042	0.596	-0.185	0.420	-0.001	0.868	
CA.crop	0.001	0.072*	0.007	0.914	0.145	0.420	0.001	0.870	
NP.crop	0.000	0.611	0.014	0.562	-0.009	0.899	0.000	0.969	
Lepidopteran									
(Intercept)	0.101	0.088	4.289	0.016	1.864	0.898	0.285	0.162	
CA.nat	0.000	0.852	0.037	0.384	0.101	0.794	0.005	0.323	
NP.nat	0.002	0.352	-0.016	0.743	0.565	0.219	-0.004	0.454	
CA.crop	0.001	0.443	-0.017	0.658	0.196	0.576	-0.001	0.767	
NP.crop	0.000	0.648	-0.005	0.731	0.167	0.228	0.001	0.690	

The composition of agricultural landscapes, especially the relative areas of semi-natural habitat and cropland, also influenced the structure of host-parasitoid food webs. Increasing the proportion of seminatural habitat had a positive effect on increasing compartment diversity of host-parasitoid food webs. Agricultural landscapes with a high proportion of semi-natural habitat tend to have stabile interaction networks (Krause et al., 2003) as well as lower rates of disturbance as resource species are compartmentalized across habitats (Rooney et al., 2008). Surprisingly, increasing the proportion of cropland had a positive effect on increasing the connectance or interaction diversity of hostparasitoid food webs. Connectance is related to the stability of ecosystem processes and the stability of food webs (Tylianakis et al., 2010; Hagen et al., 2012). These results contradict the hypothesis that it is the proportion of cropland rather than the proportion of semi-natural habitat that affects interaction diversity. This may be due to a lot of generalist parasitoids in long bean fields act as important factors that affect the increase of connectance with increasing the proportion of



Figure 4. Relationship between food-web structure and landscape composition. (a) connectance and class area of crop (CA.crop) ($R^2 = 0.285$, P = 0.033), and (b) compartment diversity and class area of natural habitat (CA.nat) ($R^2 = 0.278$, P = 0.036).

cropland. A recent study by Batáry et al. (2021) also found that food web interaction diversity was more affected by patch connectivity than the proportion of patches in agricultural landscapes.

In addition, we did not find effects of landscape composition on nestedness or interaction strength asymmetry. This is perhaps due to host-parasitoid food webs in long bean fields being dominated by generalist parasitoids. Nestedness that is also related to interaction asymmetries is more associated with specialist species than with generalists (Tylianakis et al., 2010). While landscape composition has effects on more specialized parasitoids, as have been shown on lepidopteran parasitoids (Elzinga et al., 2007). In addition, different pest species within the same cropping system can have different responses to landscape composition (Perez-Alvarez et al., 2018), which may cause nestedness and interaction asymmetries that were not affected by the composition of agricultural landscape.

In conclusion, agricultural landscape composition cannot be related to the structure of host-parasitoid food webs due to the interaction complexity is not only affected by the proportion of patches but also other factors. Besides food webs, other multitrophic systems may be used to investigate the effects of fragmentation or landscape composition (Kruess, 2003) or even compare landscape composition and food webs on affecting communities in agricultural landscape (e.g. Dominik et al., 2018). Small spatial scale also needs to be considered that can affect food webs in agricultural landscapes. Research by Haro et al. (2018) revealed that species richness and abundance of natural enemies, as well as food webs interaction, were particularly affected by the presence of flowers in an agroecosystem. However, more research is needed to investigate the effects of fragmentation or landscape composition on host-parasitoid food webs (Hagen et al., 2012). The results will enhance our understanding of the characteristics of food webs that provide stability and function for conserving species interaction networks in agricultural landscapes.

Declarations

Author contribution statement

Tazkiyatul Syahidah: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Akhmad Rizali: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

Lilik Budi Prasetyo: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data.

Pudjianto: Conceived and designed the experiments.

Damayanti Buchori: Conceived and designed the experiments; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Funding statement

This research was supported by IPB University, Indonesia and The Ministry of Research Technology and Higher Education, Indonesia under PMDSU Research Grant No. 136/SP2H/LT/DRPM/IV/2017 and PMDSU Research Grant No. 129/SP2H/PTNBH/DRPM/2018.

Data availability statement

Data will be made available on request.

Declaration of interests statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

Acknowledgements

We are grateful to the sixteen cucumber farmers for providing access to their fields for this study. We also thank Samuel W Skinner and Christopher Bennett for language checking before submitting this manuscript.

References

Batáry, P., Rösch, V., Dormann, C.F., Tscharntke, T., 2021. Increasing connectivity enhances habitat specialists but simplifies plant-insect food webs. Oecologia 195, 539–546.

- Bersier, L.-F., Banasek-Richter, C., Cattin, M.-F., 2002. Quantitative descriptors of foodweb matrices. Ecology 83, 2394–2407.
- Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc. Biol. Sci. 273, 1715–1727.
- Borror, D., Triplehorn, C.H., Johnson, N.F., 1996. An Introduction to the Study of Insects. Saunders College Publishing, Philadelphia, USA.
- BPS-Statistics Indonesia, 2013. Census of Agriculture 2013. BPS-Statistics Indonesia, Jakarta.
- Dominik, C., Seppelt, R., Horgan, F.G., Settele, J., Václavík, T., 2018. Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. J. Appl. Ecol. 55, 2461–2472.
- Dormann, C.F., Blüthgen, N., 2017. Food webs versus interaction networks: principles, pitfalls and perspectives. In: Moore, J.C., de Ruiter, P.C., McCann, K.S., Wolters, V. (Eds.), Adaptive Food Webs: Stability and Transitions of Real and Model Ecosystems. Cambridge University Press, Cambridge, pp. 1–11.
- Dormann, C.F., Fruend, J., Bluethgen, N., Gruber, B., 2009. Indices, graphs and null models: analyzing bipartite ecological networks. Open Ecol. J. 2, 7–24.
- Elzinga, J.A., van Nouhuys, S., van Leeuwen, D.-J., Biere, A., 2007. Distribution and colonisation ability of three parasitoids and their herbivorous host in a fragmented landscape. Basic Appl. Ecol. 8, 75–88.
- Fahrig, L., Baudry, J., Brotons, L., Burel, F.G., Crist, T.O., Fuller, R.J., Sirami, C., Siriwardena, G.M., Martin, J.-L., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112.
- Goulet, H., Huber, J.T., 1993. Hymenoptera of the World: an Identification Guide to Families. Canada Communication Group - Publishing, Ottawa.
- Hagen, M., Kissling, W.D., Rasmussen, C., De Aguiar, M.A.M., Brown, L.E.,
 Carstensen, D.W., Alves-Dos-Santos, I., Dupont, Y.L., Edwards, F.K., Genini, J.,
 Guimarães, P.R., Jenkins, G.B., Jordano, P., Kaiser-Bunbury, C.N., Ledger, M.E.,
 Maia, K.P., Marquitti, F.M.D., Mclaughlin, Ó., Morellato, L.P.C., O'Gorman, E.J.,
 Trøjelsgaard, K., Tylianakis, J.M., Vidal, M.M., Woodward, G., Olesen, J.M., 2012.
 Biodiversity, species interactions and ecological networks in a fragmented world.
 Adv. Ecol. Res. 46, 89–120.
- 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, e019304.
- Heinrichs, E.A., Aguda, R.M., Barrion, A.T., Bharathi, M., Chelliah, S., Dalle, D., Gallagher, K.O., Kritani, K., Litsinger, J.A., Loevinsohn, M.E., Naba, K., Ooi, P.A.C., Parada, O., Roberts, D.W., Rombach, M.C., Shepard, B.M., Smith, C.M., Weber, G., 1994. Biology and Management of Rice Insects. International Rice Research Institute - Willey Eastern, New Delhi, India.
- Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martinez-Salinas, A., O'Rourke, M.E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J.A., Schellhorn, N.A., Tscharntke, T., Wratten, S.D., Zhang, W., Iverson, A.L., Adler, L.S., Albrecht, M., Alignier, A., Angelella, G.M., Zubair Anjum, M., Avelino, J., Batary, P., Baveco, J.M., Bianchi, F., Birkhofer, K., Bohnenblust, E.W., Bommarco, R., Brewer, M.J., Caballero-Lopez, B., Carriere, Y., Carvalheiro, L.G., Cayuela, L., Centrella, M., Cetkovic, A., Henri, D.C., Chabert, A., Costamagna, A.C., De la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekotter, T., Dormann, C.F., Eckberg, J.O., Entling, M.H., Fiedler, D., Franck, P., Frank van Veen, F.J., Frank, T., Gagic, V., Garratt, M.P.D., Getachew, A., Gonthier, D.J., Goodell, P.B., Graziosi, I., Groves, R.L., Gurr, G.M., Hajian-Forooshani, Z., Heimpel, G.E., Herrmann, J.D., Huseth, A.S., Inclan, D.J., Ingrao, A.J., Iv, P., Jacot, K., Johnson, G.A., Jones, L., Kaiser, M., Kaser, J.M., Keasar, T., Kim, T.N., Kishinevsky, M., Landis, D.A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D.K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K. Madeira, F., Mader, V., Cortesero, A.M., Marini, L., Martinez, E., Martinson, H.M., Menozzi, P., Mitchell, M.G.E., Miyashita, T., Molina, G.A.R., Molina-Montenegro, M.A., O'Neal, M.E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Ostman, O., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perovic, D.J., Peterson, J.A., Petit, S., Philpott, S.M., Plantegenest, M., Plecas, M., Pluess, T., Pons, X., Potts, S.G., Pywell, R.F., Ragsdale, D.W., Rand, T.A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.P., Saulais, J., Schackermann, J., Schmidt, N.P., Schneider, G., Schuepp, C., Sivakoff, F.S., Smith, H.G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M.B., Taki, H., Tamburini, G., Thomson, L.J., Tricault, Y. Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K.T., Werling, B.P., Wickens, J.B., Wickens, V.J., Woodcock, B.A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., Zou, Y., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. Proc. Natl. Acad. Sci. 115, E7863-E7870.

T. Syahidah et al.

Klein, A.M., Steffan-Dewenter, I., Tscharntke, T., 2006. Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. J. Anim. Ecol. 75, 315–323.

- Krause, A.E., Frank, K.A., Mason, D.M., Ulanowicz, R.E., Taylor, W.W., 2003. Compartments revealed in food-web structure. Nature 426, 282–285.
- Kruess, A., 2003. Effects of landscape structure and habitat type on a plant-herbivoreparasitoid community. Ecography 26, 283–290.
- Landis, D.A., Wratten, S.D., Gurr, G., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45, 175–201.
- Miranda, M., Parrini, F., Dalerum, F., 2013. A categorization of recent network approaches to analyse trophic interactions. Methods Ecol. Evol. 4, 897–905.Perez-Alvarez, R., Nault, B.A., Poveda, K., 2018. Contrasting effects of landscape
- composition on crop yield mediated by specialist herbivores Ecol. Appl. 1–12, 0. R Core Team, 2020. R: A Language and Environment for Statistical Computing. R
- Foundation for Statistical Computing, Vienna, Austria. Rempel, R.S., Kaukinen, D., Carr, A.P., 2012. Patch Analyst and Patch Grid. Ontario Ministry of Natural Resources. Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario.
- Rerkasem, B., 2005. Transforming subsistence cropping in Asia. Plant Prod. Sci. 8, 275–287.
- Rizali, A., Buchori, D., Susilawati, S., Pudjianto, P., Clough, Y., 2018. Does landscape complexity and semi-natural habitat structure affect diversity of flower-visiting insects in cucumber fields? AGRIVITA J. Agri. Sci. 40, 107–117.
- Rizali, A., Buchori, D., Triwidodo, H., 2002. Insect diversity at the forest margin-rice field interface: indicator for a healthy ecosystem. HAYATI J. Biosci. 9, 41–48.
- Rooney, N., McCann, K.S., 2012. Integrating food web diversity, structure and stability. Trends Ecol. Evol. 27, 40–45.

- Rooney, N., McCann, K.S., Moore, J.C., 2008. A landscape theory for food web architecture. Ecol. Lett. 11, 867–881.
- Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A.S., 1996. Pajarningsih and Sartanto, Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. Ecology 77, 1975–1988.
- Thies, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. Oikos 101, 18–25.
- Tilman, D., 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. Proc. Natl. Acad. Sci. Unit. States Am. 96, 5995–6000.
- Tischendorf, L., Fahrig, L., 2000. On the usage and measurement of landscape connectivity. Oikos 90, 7–19.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. Biol. Conserv. 143, 2270–2279.
- Tylianakis, J.M., Tscharntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. Nature 445, 202–205.
- 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? Agric. For. Entomol. 21, 318–325.
- Vaissière, B.E., Freitas, B.M., Gemmill-Herren, B., 2011. Protocol to Detect and Assess Pollination Deficits in Crops: a Handbook for its Use. the Food and Agriculture Organization of the United Nations (FAO), Rome.
- Widiatmaka, W., Ambarwulan, W., Sudarsono, 2016. Spatial multi-criteria decision making for delineating agricultural land in Jakarta metropolitan area's hinterland: case study of Bogor regency, West Java. AGRIVITA J. Agri. Sci. 38, 105–115.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.