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RESEARCH ARTICLE

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Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems

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Abstract

1. Increasing landscape heterogeneity of agroecosystems can enhance natural enemy populations and promote biological control. However, little is known about the multiscale effects of landscape heterogeneity on arthropod communities in rice agroecosystems, especially in combination with trophic interactions.
2. We examined for the first time how landscape heterogeneity, measured by four independent metrics of landscape composition and configuration at three spatial scales, affected species abundance and species richness of rice arthropods within four functional groups and the abundance of the most common species at 28 sites in the Philippines. We additionally examined the influence of trophic interactions among these functional groups.
3. We found that both the compositional and configurational landscape heterogeneity in combination with trophic interactions determined the structure of rice-arthropod communities. Herbivore abundance decreased with increasing landscape diversity. The abundance of parasitoids and species richness of both parasitoids and predators increased with the structural connectivity of rice bunds. Fragmentation of the rice landscape had a clear negative effect on most arthropod groups, except for highly mobile predatory arthropods. Abundance of common predators and detritivore species decreased with increasing complexity in the shape of rice patches.
4. Trophic interactions, measured as the abundance of prey, outweighed the importance of landscape heterogeneity for predators. In contrast, parasitoids responded positively to configurational landscape heterogeneity but were unaffected by prey abundance.
5. *Synthesis and applications*. Our research shows how landscape heterogeneity and trophic interactions have different effects on different functional groups. While predator abundance was solely driven by the availability of prey, all other functional groups in the rice-arthropod community were significantly affected by the

composition and configuration of surrounding landscape features. Landscape management aiming to improve biodiversity and biological control in rice agroecosystems should promote a diversity of land uses and habitat types within 100–300 m radii to reduce the presence of pests. Management practices should also focus on maintaining smaller rice patches and the structural connectivity of rice bunds to enhance populations of the natural enemies of rice pests. Future research should focus on the temporal and spatial manipulation of rice fields to maximize the effects of biological control.

KEYWORDS

arthropods, biological control, farmland biodiversity, landscape heterogeneity, natural enemies, rice, trophic interactions

1 | INTRODUCTION

The importance of landscape heterogeneity in agricultural landscapes for the maintenance of regulatory ecosystem functions, including herbivore regulation, has often been discussed in the scientific literature (Altieri, 1999; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005; Way & Heong, 2009). Several authors suggest that monocultures are associated with declining regulatory services and consequent pest outbreaks (Altieri, 1999). As agroecosystems depend on a variety of ecosystem services, notably biological pest control (Bianchi, Booij, & Tscharntke, 2006; Losey & Vaughan, 2006), there has been an increased focus in recent years on methods such as “conservation biological control”, to maximize agricultural productivity (Bengtsson, Ahnstrom, & Weibull, 2005; Bianchi et al., 2006; Letourneau & Bothwell, 2008). Such approaches aim to enhance natural enemy populations by manipulating the habitat surrounding crops to provide alternative food sources, such as prey, pollen, and nectar, and a refuge from agricultural disturbances and thereby enhance the abundance and functional efficiency of natural enemies (Gurr, Wratten, & Altieri, 2004; Landis, Wratten, & Gurr, 2000).

The biodiversity present in rice landscapes in tropical Asia is often higher than in many natural ecosystems, as many of the species inhabiting rice fields are specialized, open grassland species (Dominik et al., 2017; Schoenly, Justo, Barrion, Harris, & Bottrell, 1998). Nevertheless, the intensification of rice cropping, in combination with the (over)use of insecticides, has led to disruptions in the interactions between herbivores and their natural enemies, resulting in often severe pest outbreaks (Heinrichs, Aquino, Chelliah, Valencia, & Reissig, 1982; Heinrichs & Mochida, 1984; Heong & Schoenly, 1998; Schoenly et al., 1996). Several studies have shown that unsprayed rice fields in less intensive farming systems have fewer pest problems and display little to no crop losses (Horgan et al., 2017; Kenmore, Carino, Perez, Dyck, & Gutierrez, 1984; Way & Heong, 2009). Settele, Biesmeijer, and Bommarco (2008) have called for a switch to conservation biological control (also called ecological engineering; see Gurr et al., 2004) in rice agroecosystems. However, to date only a few studies have focused on the potential benefits of landscape heterogeneity or habitat manipulation for the natural enemies of rice pests (Gurr et al., 2016; Horgan et al., 2017; Lin, You, Yang, & Chen, 2011; Yao, You, Vasseur, Yang, & Zheng, 2012).

Two aspects determine landscape heterogeneity: (a) landscape composition (diversity of landscape features and habitat types) and (b) landscape configuration (number, size, and connectivity of habitat patches; Seppelt et al., 2016). The composition of rice landscapes in tropical Asia is characterized by a mosaic of different habitats that include the rice crop itself, other crops, fallow fields, and natural vegetation. The diversity of habitat patches, neighboring the rice fields, may influence pests, natural enemies, and other biological components of the agroecosystem by modifying the extent of host and prey resources or the quality of microclimatic conditions (Landis et al., 2000; Pickett & Bugg, 1998). Since Asian rice farmers typically own small areas of land (often <2 ha), the configuration of rice landscapes is characterized by a relatively large number of small-sized habitat patches with varying degrees of connectivity. Habitat fragmentation is known to negatively affect natural enemies in temperate agricultural landscapes (i.e. parasitoids: Kruess & Tscharntke, 1994; Thies & Tscharntke, 1999; Tscharntke & Kruess, 1999; predators: Tscharntke & Kruess, 1999). However, rice fields are connected through an extensive network of bunds (levee of terrestrial area surrounding the fields), typically with sparse seminatural vegetation that can potentially offer alternative food resources or refugia to natural enemies (Way & Heong, 2009). The presence of bunds likely facilitates the ability of rice arthropods to move through the rice agroecosystem. For example, egg parasitoids of the genera *Anagrus* and *Oligosita* that cause high mortality of pest planthoppers such as *Nlugen lugens* and *Sogatella furcifera*, occur in wild grasses on rice bunds (Yu, Heong, Hu, & Barrion, 1996). Furthermore, the spider *Pardosa pseudoannulata*, which commonly inhabits bund vegetation, is known to be an early colonizer of newly established rice crops (Sigsgaard, 2000). However, the effects of rice bunds and their functional connectivity on the community composition of rice arthropods are still poorly understood at landscape scales.

In the tropical rice agroecosystems in the Philippines, regional-scale effects (e.g., the effects of elevation as a proxy for climate and other landscape factors) rather than fine-scale landscape heterogeneity explain much of the structure of the arthropod community (Dominik et al., 2017). However, the composition and spatial arrangement of habitat patches can also affect community structure at certain spatial scales (Pickett & Cadenasso, 1995; Roland & Taylor, 1997). Such scale effects are primarily driven by species mobility and thus vary across species (Horner-Devine, Daily, Ehrlich, & Boggs, 2003; Jackson & Fahrig, 2012; Ricketts, 2001).

There is growing evidence that predators and parasitoids are key to regulating herbivore densities in rice agroecosystems (Kenmore et al., 1984; Schoenly et al., 1996; Settle et al., 1996). Attributable to high arthropod diversity in many agro-ecosystems and particularly in tropical rice fields, taxa are often categorized into functional groups to condense information on the huge diversity and provide a research approach to study both food web complexity and community dynamics (Heong, Aquino, & Barrion, 1991, 1992; Settle et al., 1996). Functional groups are a useful descriptor for linking population and ecosystem processes, and for defining the functional differences between herbivores (pests when at high density), natural enemies (predators and parasitoids) and detritivores/tourists (i.e., nonpredatory species that have no direct association with the rice plant but which may be attracted to surrounding habitats; Moran & Southwood, 1982). However, less is known about the way in which trophic interactions have shaped arthropod communities at broader scales, and within the context of landscape heterogeneity. Wiens (2011) suggested that trophic interactions rarely play a role at the landscape scale, or that there are simply too few studies to fully explore the issue.

An increasing number of studies support an idea that the efficiency of natural enemies in regulating herbivores can be enhanced by increasing the structural and compositional diversity of rice-associated habitat (Gurr et al., 2016; Horgan et al., 2016, 2017). Most of this research has been conducted at field and plot scales without regard to the influence of natural vegetation outside and often distant from the experimental plots or fields. This could be an important oversight leading to variability in the success of interventions such as "ecological engineering" that manage rice bunds to enhance natural enemy habitat (e.g., see differences between results from Gurr et al., 2016; Yao et al., 2012; Yu et al., 1996; and those from Horgan et al., 2017 and Sann et al., 2018). Success might depend on the availability of suitable natural vegetation at scales hitherto omitted from research protocols or on the connectivity and form of rice bunds. Therefore, in this study, we compile a unique dataset on rice arthropods sampled from 28 field plots in tropical rice agroecosystems in the Philippines. For the first time, we quantify the heterogeneity of managed rice landscapes surrounding each sampling site based on high-resolution satellite imagery using four independent metrics of landscape composition and configuration. To our knowledge, this is the first study to separate the influences of associated habitat, rice bunds and the trophic composition of rice-associated arthropods on the biocontrol potential of rice landscape. Understanding the influence of such factors in rice is particularly valuable because of architectural restrictions in the design of rice landscapes that require scheduled flooding and draining. We examine the combined effects of landscape heterogeneity and trophic interactions on arthropod communities, particularly the natural enemies, and identify the spatial scales at which these effects are most pronounced. Specifically, we test the following hypotheses:

1. Landscape diversity has positive effects on the abundance and species richness of natural enemies.
2. The configuration of rice landscapes (size of habitat patches and connectivity of rice bunds) has positive effects on the abundance and species richness of natural enemies; and
3. The abundance of natural enemies responds to the abundance of prey.

2 | MATERIALS AND METHODS

2.1 | Study regions

The study was conducted within the project LEGATO (Settele et al., 2015) across three 15 × 15 km regions along an elevation gradient on the island of Luzon in the Philippines. The three regions were: (a) a rice landscape in the hilly lowlands of Laguna Province in southern Luzon (PH_1); (b) an intensively cultivated rice landscape in Nueva Ecija Province (PH_2) situated in central Luzon; and (c) a traditional terraced rice system in the mountainous Ifugao Province located in the north of Luzon (for details, see Dominik et al., 2017; Klotzbücher et al., 2015; Langerwisch, Václavík, von Bloh, Vetter, & Thonicke, 2017). Within each region, 10 "core sites" were selected, resulting in a total of 28 core sites (sampling could not be performed at two core sites in PH_2 because vegetables were planted instead of rice at the time of sampling) (Figure 1). The average distance between the nearest cores sites was ~369 m.

2.2 | Arthropod sampling

The arthropod communities present in the rice fields were sampled during the dry season of 2013 in PH_1 and PH_2 (double cropping is practiced in these regions; however, we only sampled during the dry season) and during the single cropping season of 2014 in PH_3 (which largely corresponded with the Luzon dry season). All samples were collected at the maximum tillering stage of the rice plant (50 days after transplanting) to ensure consistency of sampling; this stage is generally associated with a maximum abundance of arthropods (Heong et al., 1991; Wilby et al., 2006). Since the composition of arthropod communities can change with the development of the rice crop and between cropping seasons (wet and dry seasons: Heong et al., 1991), our analyses focused on the data obtained during the dry season only (January to June).

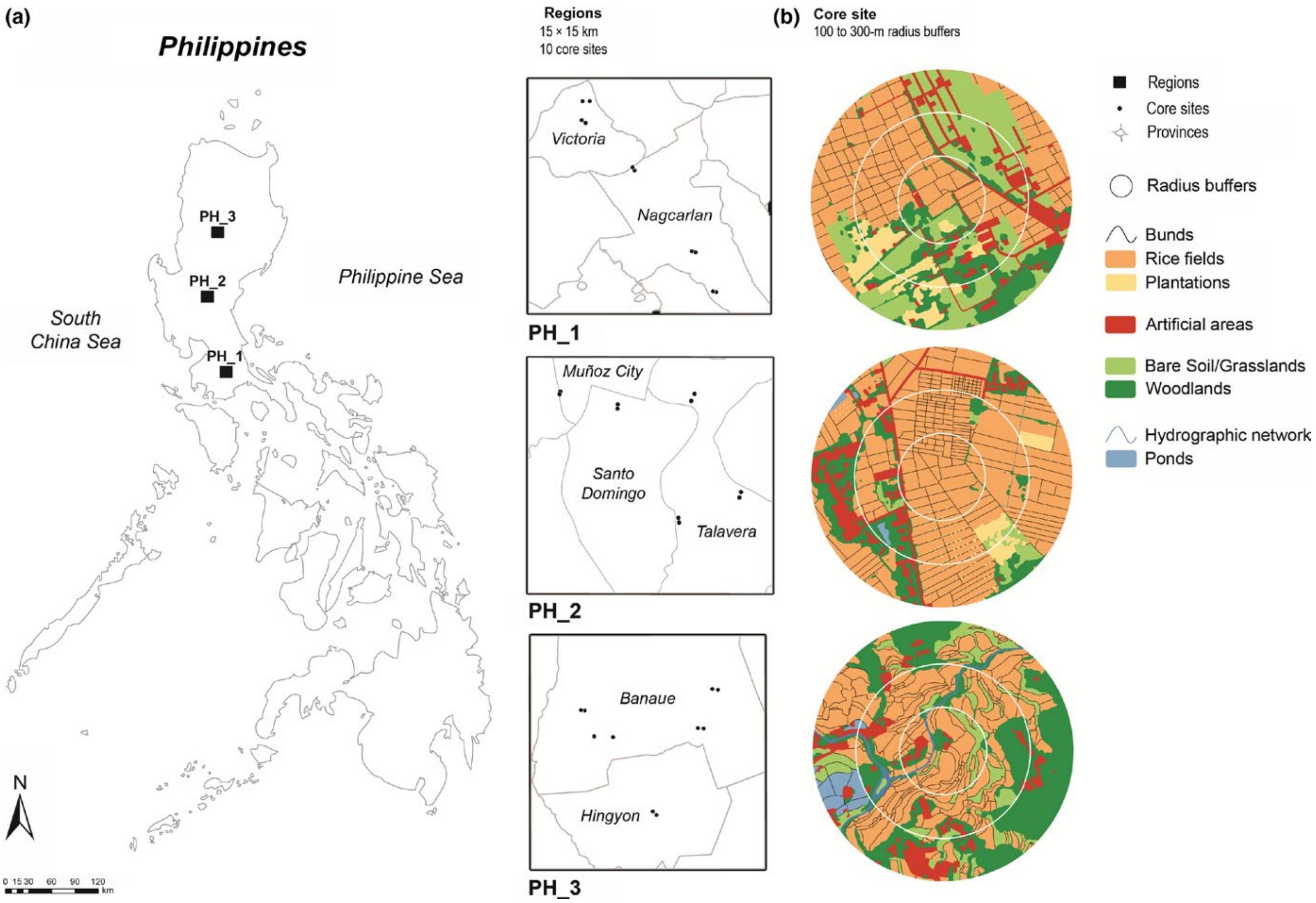

FIGURE 1 Study area on the island of Luzon in the Philippines. (a) Locations of the 15 × 15 km regions in Laguna (PH_1), Nueva Ecija (PH_2) and Ifugao (PH_3). (b) Examples of mapping land cover features within 100, 200 and 300 m radii buffers around core sites [Colour figure can be viewed at wileyonlinelibrary.com]

Arthropods were collected using a modified leaf blower-vacuum (as described by Arida & Heong, 1992). A sampling enclosure of about 1 m side length with a nylon mesh sleeve on the top was used to prevent the escape of mobile invertebrates. The enclosure was placed over four rice hills before suction sampling was performed and captured all arthropods present inside the enclosure. At each core site, five samples were taken at random locations near the centre of the field between 07.00 and 11.00 hr.

Collected arthropods were preserved in 70% ethanol, sorted and identified to species level (or to morphospecies where specimens could not be adequately identified to species level) using a binocular microscope and the taxonomic keys of Barrion and Litsinger (1994). Morphological similarity at the pre-adult stages and quality of the samples limited the identification of arachnids, dipterans and collembolans to family level. Additionally, arthropods were grouped into functional guilds as follows: (a) herbivores; (b) predators; (c) parasitoids; and (d) detritivores and tourists.

2.3 | Mapping and landscape metrics

All landscape features were identified and mapped within a 300-m radius around each sampling site using heads-up digitizing in a geographic information system (ArcGIS 10.3, ESRI) based on high-resolution SPOT-5 DIMAP images (2.5 m). In addition, we collected ground-truth data in June 2014 to verify the photo-interpretation using Collector for ArcGIS (version 9.3, ESRI). We randomly attributed 10 ground-truth locations within each 300 m buffer, verified the land cover in the field and if necessary corrected the digitized maps. Land cover features were classified at a consistent scale of 1:1,000 into eight final categories: rice fields, woodlands, grasslands, artificial areas, plantations, rice bunds, hydrographic network, and ponds (Figure 1b).

To quantify landscape heterogeneity around sampling sites, we calculated four independent metrics of landscape composition and configuration within three buffer distances (100, 200 and 300 m radii) using Fragstats 3.3 (McGarigal & Marks, 1995). As a measure of compositional landscape heterogeneity, we used the Shannon's Diversity Index (SHDI) calculated at the landscape level with all eight land cover categories. Three metrics of configurational landscape heterogeneity focused on the rice landscape and quantified the connectivity, number/size and shape complexity of rice habitat patches. The rice agroecosystem is usually composed of several rice fields (typically 1–3 ha in size) interconnected by a network of terrestrial levees (bunds). Therefore, we calculated the patch cohesion index

(COH) to quantify the structural connectivity of rice bunds and the number of patches (NP) to represent the degree of rice habitat fragmentation (higher numbers representing more fragmented habitat with smaller mean patch size). Finally, we measured the shape complexity of each rice field using the fractal dimension index (FRAC) because the shape of habitat patches may affect the arthropod communities via edge effects, e.g., influencing host finding due to the way that plant odors are emitted from habitat patches (Stanton, 1983). We selected these landscape metrics because (a) they were not correlated with each other, (b) they allowed easy interpretation and (c) they described unique characteristics of landscape heterogeneity (diversity, connectivity, size, and shape).

2.4 | Statistical analyses

The responses of rice-arthropod communities to landscape heterogeneity were analysed using linear mixed-effect models for each response variable and each spatial scale (100, 200, and 300 m). The response variables were (a) the species richness within functional groups, (b) the abundance within functional groups, and (c) the abundance of the most common species (present in at least 20% of the total samples and representing at least 10% of all collected organisms in any sample). The abundance of all arthropods was log-transformed prior to analyses to meet the assumptions of normality (Pinheiro, Bates, DebRoy, Sarkar & R Team, 2014). Since each region has relatively distinct arthropod assemblages and rice management practices (Dominik et al., 2017), subsamples nested within "region" (PH_1, PH_2 and PH_3) were assigned as a random effect. The four metrics of compositional and configurational landscape heterogeneity (i.e. SHDI, NP, COHESION and FRAC) were assigned as fixed effects. Although the main focus of our study was to test the effects of landscape heterogeneity, we included elevation as another predictor because this variable, being a proxy for regional-scale climatic conditions and land-use intensity, has been previously shown to determine the arthropod community composition in our study areas (Dominik et al., 2017). Climate data were obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) V2 at a 30-m resolution (https://lpdaac.usgs.gov/). A stepwise regression procedure was used together with testing all variable combinations to determine the best-fitting model based on the lowest $\mathrm{AIC_c}$ score. The procedure was repeated separately for each response variable and spatial scale.

To account for trophic interactions, additional fixed effects were added to the full models when testing the responses of abundance of individual functional groups. As we expected predator–prey interactions between natural enemies and other functional groups, especially herbivores, the abundance of both predators and parasitoids were added to the model for herbivores and, similarly, the abundance of detritivores/tourists and herbivores were added to the model for predators. Detritivores act as a primary source of food during the early stages of the rice plant for many generalist predators (Gurr et al., 2016; Settele, 1992; Settle et al., 1996). However, interactions between parasitoids and other groups (except for herbivores) have not been documented, thus only the abundance of herbivores was added to the model for parasitoids. Finally, the abundance of predators was included when testing responses in the abundance of detritivores/tourists. Again, the best-fitting models were determined across all spatial scales by selecting the models with the minimal AICc scores.

All statistical analyses were conducted using the *lme* function in the *nlme* package (Pinheiro et al., 2014) in R version 3.1.1 (R Development Core Team, 2016).

3 | RESULTS

In total, we collected 8,547 individuals and identified 113 different arthropod morphospecies across the three study regions. Herbivores accounted for 36.8% of the total arthropods collected and were dominated by the Whitebacked Planthopper (*S. furcifera*), the Brown Planthopper (*N. lugens*), and Green Leafhoppers (*Nephottetix* spp). Predators contributed 26.9% of the total abundance and were mostly represented by dwarf spiders (Linyphiidae), wolf spiders (Lycosidae), long-jawed orb weavers (Tetragnathidae), lady beetles of the genus *Micraspis*, and the mirid bug *Cyrtorhinus lividipennis*. The detritivores/tourists guild represented 29.6% of the total arthropod abundance and was mainly composed of chironomids and collembolans (Isomotidae, Sminthuridae, and Entomidae). Finally, parasitoids accounted for 6.7% of the total abundance and were mainly represented by *Gonatocerus* spp and *Oligosita* spp.

3.1 | Landscape heterogeneity

All best models included the combined effects of compositional or configurational landscape heterogeneity and trophic interactions. However, each functional group and more common species responded differently to landscape heterogeneity (Figure 2). Elevation explained only the abundance of parasitoids (t = 2.766, p = 0.011) and the predator *C. lividipennis* (t = 3.278, p = 0.003).

The abundance of herbivores, including the more common species, declined with increasing landscape diversity (SHDI) (t = −3.383, p = 0.003; Figure 2a). The scale at which herbivores species responded to landscape diversity varied from one species to the next but the best model for herbivores was based on habitat characteristics defined at 300 m (Table 1). Additionally, landscape diversity was negatively correlated with the abundance of Sminthuridae (t = −2.769, p = 0.010), a family of detritivores. We found no effect of landscape diversity on the abundance or species richness of predators and parasitoids.

In agreement with our second hypothesis, the structural connectivity of the rice bunds (COH) increased the abundance and species richness of most natural enemies, particularly the parasitoids. The abundance (t = 5.753, p = 0.000) and number of parasitoid species (t = 3.528, p = 0.002) were strongly correlated with the structural connectivity of rice bunds at the scale of 300 m (Figure 2b). The connectivity of rice bunds also best explained the abundance of *Oligosita* spp (t = 4.628,

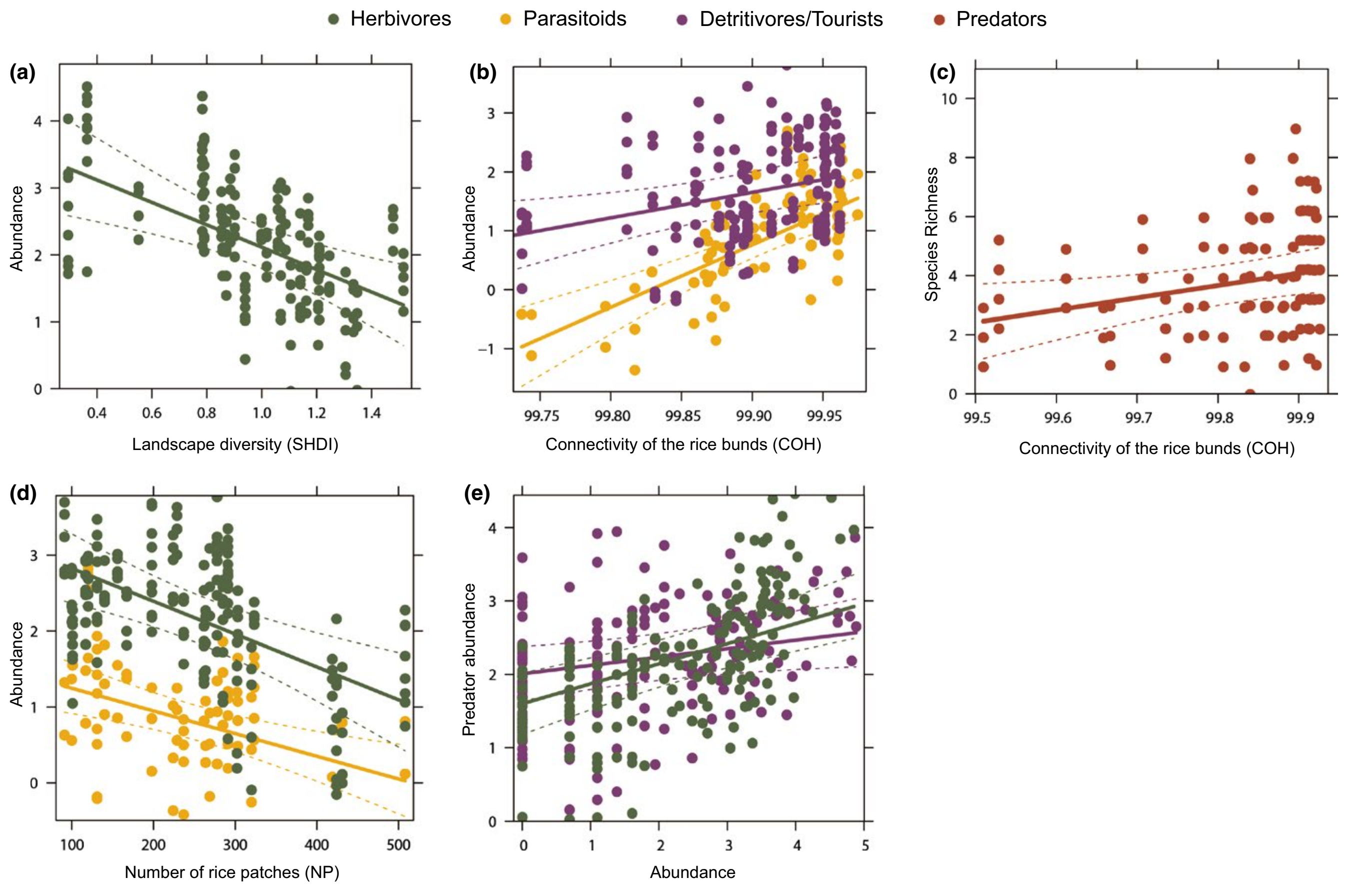

FIGURE 2 Linear mixed effects models representing relationships between (a) landscape diversity (SHDI) and abundance of herbivores, (b) structural connectivity of the rice bunds (COH) and abundance of detritivores/tourists and parasitoids, (c) structural connectivity of the rice bunds (COH) and species richness of predators, (d) number of rice patches (NP) and abundance of both herbivores and parasitoids, and (e) trophic interactions between predators, herbivores, and detritivores/tourists. All abundance data were log-transformed [Colour figure can be viewed at wileyonlinelibrary.com]

$p < 0.001$) and *Gonatocerus* spp ($t = 2.458$, $p = 0.022$). The structural connectivity of rice bunds was also the only landscape metric, which explained the species richness of predators. The abundance of long-jawed orb weaver spiders (Tetragnathidae) was also positively correlated with the structural connectivity of rice bunds ($t = 3.596$, $p < 0.002$). The same effect was found for the abundance of detritivores/tourists ($t = 2.762$, $p = 0.011$) and chironomids ($t = 2.360$, $p = 0.027$) (Figure 2b).

The fragmentation of the rice landscape to smaller patches, represented by the number of rice patches (NP), negatively influenced arthropod communities. The abundance of both herbivores ($t = -4.002$, $p < 0.001$) and parasitoids ($t = -3.930$, $p < 0.001$) declined with increasing number of rice patches, measured at 300 m radii (Figure 2c). Similarly, the same pattern emerged with the number of parasitoid species ($t = -2.381$, $p = 0.026$). At the species level, the more common species of all guilds were negatively correlated with the number of rice patches (Table 1). Surprisingly, only the abundance of the predatory Coccinellidae *Micraspis* spp increased significantly with the number of rice patches ($t = 3.299$, $p < 0.003$).

The shape complexity of the rice fields (FRAC) did not influence the total abundance or species richness of the functional groups. However, the shape complexity of the rice fields negatively influenced the abundance of some common species such as spiders from the Linyphiidae family ($t = -2.356$, $p = 0.016$), ladybugs of the genus *Micraspis* ($t = -2.268$, $p = 0.033$), and chironomids ($t = -2.158$, $p = 0.042$). In contrast, the parasitoids *Oligosita* spp. responded positively to the shape complexity of the rice fields ($t = 2.688$, $p = 0.013$).

The scale at which the arthropods responded to landscape heterogeneity varied between functional groups and between species. By comparing the AICs score among the models, the largest scale was constantly favoured when arthropods responded to two or more scales. The detritivores/tourists guild responded to landscape heterogeneity at a smaller scale than the other guilds (200 m and below). Highly mobile arthropods such as parasitoids were typically influenced by landscape heterogeneity at the largest scale (300 m).

3.2 | Trophic interactions

In addition to the effects of landscape heterogeneity, we found significant trophic interactions between herbivores, predators and detritivores/tourists (Table 2). The abundance of predators was highly

TABLE 1 Results of the best-fitting linear mixed-effect models (based on the lowest AIC_c): the effects of elevation (DEM), landscape diversity (SHDI), structural connectivity (COH), fragmentation of the rice landscape (NP), and shape complexity of the rice patches (FRAC) on the abundance (log-transformed) and species richness of functional groups and more common species. The scale at which the effect of landscape heterogeneity was most pronounced (landscape metric entered the best model) is shown as: 100, 200, 300 m, and NA when the scale is undetermined

		Elevation DEM		Landscape diversity SHDI		Connectivity COH		Fragmentation NP		Shape FRAC	
	Scale	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Abundance											
All herbivores	300 m			−3.383	0.003			−4.002	0.001		
Sogatella furcifera	300 m			−3.941	0.001			−3.009	0.006		
Nilaparvata lugens	NA										
Nephotettix spp	200 m			−3.808	0.001						
All predators	NA										
Cyrtorhinus lividipennis	NA	3.278	0.003								
Linyphiidae	300 m									−2.356	0.016
Lycosidae	NA										
Tetragnathidae	300 m					3.596	0.002	−4.394	0		
Micraspis spp	300 m							3.299	0.003	−2.268	0.033
All parasitoids	300 m	2.766	0.011			5.753	0	−3.93	0.001		
Gonatocerus spp	NA					2.458	0.022				
Oligosita spp	300 m					4.628	0	−4.575	0	2.688	0.033
All detritivores	200 m					2.762	0.011				
Chironomidae	200 m					2.36	0.027			−2.158	0.042
Isomotidae	NA										
Sminthuridae	100 m			−2.769	0.01						
Entomidae	NA										
Richness											
All herbivores	300 m							−2.069	0.049		
All predators	100 m					2.42	0.023				
All parasitoids	300 m					3.528	0.002	−2.381	0.026		
All detritivores	NA										

TABLE 2 Results of linear mixed model analyses on the effects of trophic interactions (abundance) between herbivores, predators, parasitoids, and detritivores

	Trophic interactions							
	Herbivores		Predators		Parasitoids		Detritivores	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Abundance								
All herbivores			3.841	0.000				
All predators	4.587	0.000					2.037	0.043
All parasitoids								
All detritivores			2.379	0.019			2.037	0.043

dependent on the abundance of herbivores ($t = 3.841$, $p < 0.001$). Althoughno effects of landscape composition were found on the abundance of predators, both the abundance of herbivores ($t = 4.587$, $p < 0.001$) and detritivores ($t = 2.037$, $p = 0.043$) explained the abundance of predators (Figure 2d). We found no effects of trophic interaction on the abundance of parasitoids.

4 | DISCUSSION

The responses of arthropod communities to the effects of landscape heterogeneity and trophic interactions greatly differed from one functional group to the next. Although landscape diversity did reduce the abundance of herbivores, it had no effects on the population of natural enemies. The abundance of parasitoids was better explained by the structural connectivity of the rice bunds, rather than by trophic interactions. In contrast, the abundance of predators was solely explained by the availability of prey, showing no significant response to any form of landscape heterogeneity.

4.1 | Landscape heterogeneity

Our analyses did not support our first hypothesis that landscape diversity has a positive effect on the abundance and species richness of the natural enemies of rice herbivores. However, we found that landscape diversity reduced the abundance of the herbivore guild as well as the abundance of two common herbivore genera *Sogatella* and *Nephottetix*. This is potentially explained by the fact that increasing landscape diversity reduces the amount of crop habitat, i.e., the primary area where herbivores thrive. While heterogeneous landscapes with a diversity of habitat types generally increase biodiversity and ecosystem services in agricultural systems, natural noncrop habitats do not always have significant effects on pest control (Sann et al., 2018; Tscharntke et al., 2016). The absence of landscape diversity effects on natural enemy populations may be due to the fact that, even for natural enemies, crops represent more important food and habitat resource than other surrounding habitat types. In our study regions, asynchronous cropping creates a mosaic of cultivated and temporarily unused fields that provide a continuous supply of resources for predators and parasitoids over space and time, helping them to avoid spatial and temporal bottlenecks (Schoenly et al., 2010). In contrast, synchronous cropping could promote more frequent and intense pest outbreaks of green leafhopper (*Nephottetix* spp.) and brown planthopper (*N. lugens*) populations (Sawada, Subroto, Suwardiwijaya, Mustaghfirin, & Kusmayadi, 1992; Widiarta, Suzuki, Sawada, & Nakasuji, 1990). Wilby et al. (2006) showed that local landscape heterogeneity (measured as different crop, crop stage and habitat types) could influence rice-arthropod communities at different stages of the rice plant.

Our observation of strong positive effects of the structural connectivity of bunds on the abundance and species richness of parasitoids is in agreement with Yu et al. (1996), who demonstrated that the egg parasitoids of *Anagrus* spp. and *Oligosita* spp. consumed eggs of nonpest planthoppers in wild grasses on rice bunds during fallow periods when fields were without a rice crop. In our case, the structural connectivity also positively influenced the detritivore/tourist populations. In general, field margins have greater arthropod abundance and diversity than the agricultural fields (Botero-Garcés & Isaacs, 2004; Denys & Tscharntke, 2002) and can provide potential refuge and food resources for flower-visiting, non-pest insects and predatory arthropods (Lagerlöf & Wallin, 1993). The suitability of these field margins as habitat for natural enemies can also depend on the width of the margin and the way margin vegetation is managed. With regard to pest management in rice, new ideas such as ecological engineering aim to manipulate the habitat on rice bunds to enhance biological control (Gurr et al., 2004; Horgan et al., 2016). By increasing the diversity and density of nectar flowering plants along the rice bunds, the fecundity and longevity of many predators and parasitoids potentially increase because they find alternative food resources such as pollen and nectar (Landis et al., 2000; Pickett & Bugg, 1998). The application of ecological engineering at the farm scale has been associated with higher abundances of predators and parasitoids across sites in China, Thailand and Vietnam (Gurr et al., 2016). However, several authors have also indicated that some plants that are commonly used in flowering strips fail to promote natural enemy populations at the field scale (Horgan et al., 2017; Lin et al., 2011; Yao et al., 2012). Additionally, parasitoids were found to be more abundant in rice habitats than in agroforests (Sann et al., 2018). Our results indicate that discrepancies between the results of previous studies could be related to factors such as bund connectivity and field size. We found that the effects of connectivity were most pronounced when measured at the scale of 200–300 m. This suggests that the structural connectivity of bunds surrounding rice fields can potentially contribute to the functional connectivity of highly mobile arthropods such as parasitoids, and that interventions to increase the connectivity of field margins should focus on larger scales, e.g., at least several hundreds of meters.

The arthropod communities in our study strongly responded to the number of rice patches within the defined buffers around sampling sites. Patch area and fragmentation have often been associated with the richness of arthropods (Kruess & Tscharntke, 1994; Steffan-Dewenter, Munzenberg, Burger, Thies, & Tscharntke, 2002). Habitat fragmentation can lead to disruption of the food chain and trophic structure, with predators being generally more vulnerable to fragmentation than their prey. Our study shows that the fragmentation of rice fields negatively influences the richness and abundance of parasitoids but also of herbivores. Specialists such as rice herbivores (e.g., *N. lugens* and *S. furcifera*) are more likely to show a positive density-area relationship in their feeding habitat type than are habitat generalists (i.e., Hambäck et al., 2007). Additionally, parasitoids are often less effective in searching for food resources when in fragmented landscapes (Kruess & Tscharntke, 1994; Tscharntke & Brandl, 2004). However, we did not find the expected negative correlation between fragmentation of the rice landscape and the predator guild. On the contrary, the abundance of a predatory ladybird (*Micraspis* spp) increased with the number of rice patches. Ladybirds of the genus *Micraspis* feed on the eggs, nymphs and adults of a variety of pest insects. They are more abundant during outbreaks of *N. lugens* and during rice flowering when they also feed on rice pollen (Pathak & Khan, 1994). In asynchronous cropping systems, fragmentation of the rice landscape can increase the occurrence of rice crops at different stages (e.g., flowering stage vs. temporarily unused fields), thus smaller rice habitat patches coupled with asynchronous rice fields could enhance mobile predator populations such as *Micraspis* spp. Indeed, it has been shown that arthropods can better colonize rice fields when the rice landscape is a mix of different rice crop stages or interspersed with other crops (Wilby et al., 2006). Mobile predators migrating between fields decreased pest densities more in asynchronous fields than synchronous ones, particularly if predators rapidly colonized newly planted rice fields (Ives & Settle, 1997). For example, the lycosid *P. pseudoannulata*, that inhabits rice bunds during fallow periods, is one of the first natural enemies found in newly established rice crops (Sigsgaard, 2000). In contrast, long-jawed orb-weaver spiders (family Tetragnathidae), which require tall foliage to suspend their webs, cannot rapidly recolonize rice fields (Barrion & Litsinger, 1994). This is also supported by our data where orb-weaver spiders were the only predator species negatively impacted by fragmentation of rice landscape in our study.

Complexity in the shapes of crop patches has rarely been addressed in studies focusing on arthropods. Although patch shape can influence host finding for herbivores (Stanton, 1983), we found no significant relationships between herbivores and shape complexity in our study. On the other hand, the abundance of highly mobile predators and chironomids declined when the shapes of rice patches increased in complexity. As patches become more irregular, the perimeter-area relation of the patches changes considerably. For example, Grez and Prado (2000) showed that coccinellids in Chile emigrated less from square patches (simple shape with a low perimeter-area ratio) than rectangular patches (more complex shape with a high perimeter-area ratio) of wild cabbages. It was suggested that coccinellids are more likely to emigrate and abandon the more complex shapes because of the accessibility of alternative habitats and prey. In contrast, in our study the parasitoids from the genus *Oligosita* were more abundant in complex patch shapes where the perimeter-area ratio was higher, suggesting that the edge effect of field margins is important for parasitoids in rice fields. Such a factor could also determine the success of interventions such as ecological engineering.

The scale at which arthropods responded best to the landscape metrics varied among functional groups and species and partly reflected their dispersal abilities. Detritivores/tourists and predator guilds mostly live at the base of the rice plants and are either wingless (collembolans, spiders) or limited in flight (chironomids). Thus, the scale at which they responded (100 and 200 m) is expected to be lower than for highly mobile flying arthropods such as parasitoids (300 m). Some rice herbivores such as delphacids exhibit a physical dimorphism with a fully winged "macropterous" form and a truncate-winged "brachypterous" form (Heong & Hardy, 2009). The macropterous delphacids can colonize and disperse to multiple habitat patches and thus could be the reason why herbivores responded to the landscape metrics at a larger scale (300 m). While the long-jawed orb-weaver spider (Tetragnathidae) has low mobility, it still responded to the number of patches at a broad scale (300 m). However, a buffer of 100 m might not be enough to capture the fragmentation of the rice landscape, and thus, arthropods may respond to this landscape metric at broader scales only.

4.2 | Trophic interactions

The predator guild showed a strong numerical response to prey density. The abundances of predators were associated with a higher abundance of both herbivores and detritivores/tourists. In our study, spiders represented most of the predator guild and have been noted to respond numerically to prey density (Kenmore et al., 1984; Riechert & Lockley, 1984). In the early stages of the rice plant, when the abundance of herbivores is low, detritivores act as an alternative prey for generalist predators (Gurr et al., 2016; Settle et al., 1996). Kenmore et al. (1984) suggested that a greater availability of food for predators could lead to an increase in the predators' fitness leading to more offspring, lower competition, and higher survival of smaller individuals. The absence of a density-dependent relationship between parasitoids and herbivores can be explained by the sampling methods we used in our study. In a previous study, Horgan et al. (2017) showed that despite the lack of numerical response of parasitoids to herbivores in rice fields, egg parasitism was still density-dependent. Our sampling method did not measure egg abundance as a determinant of parasitoid abundance (i.e., parasitoid individuals remaining in larval stages inside the eggs or larvae of herbivores), and thus parasitoids sampled at the adult life stage may not have responded to prey the same way as generalist predators. Indeed, predator populations were largely driven by the availability of prey, likely masking any effects of landscape heterogeneity.

4.3 | Synthesis and applications

Our study shows, for the first time, that the combined effects of landscape heterogeneity and trophic interactions shape arthropod communities in rice agroecosystems. Fragmentation of the rice-production habitat is expected to increase production costs particularly since it constrains mechanization (Kawasaki, 2010); however, it can be beneficial for farmers, as it limits the risks of pest outbreaks, particularly if the production costs are not considerably higher than the ecosystem services it provides (i.e., weed and herbivore control). Our study provides evidence that increasing the landscape diversity surrounding rice fields and increasing the number of rice patches can result in lower herbivore abundance. The bunds interconnecting rice fields are an important feature for parasitoids and predators, and more studies should focus on the potential functional connectivity of bunds in enhancing natural enemies particularly as a factor in the success of interventions such as crop diversification and ecological engineering. Manipulating the landscape to create a mosaic of rice fields with different temporal and spatial compositions and configurations could also provide natural enemies with a continuous availability of food. Arthropods with low dispersal ability such as spiders may benefit from the high availability of prey in the neighboring patches at a small scale, while flying arthropods with high dispersal ability such as parasitoids may benefit from the configuration of the landscape at larger scales. Based on these findings we recommend that landscape management to improve biodiversity and biological pest control in rice agroecosystems should promote a diversity of land uses and habitat types within at least 100–300 m radii, maintain smaller rice patches and enhance the structural connectivity of rice bunds.

Our study was conducted in a real agricultural setting in which land management factors, such as pesticide input or cropping synchrony, were not controlled. Management practices and to a larger extent the use of insecticides can potentially disrupt the predator–prey relationships and the food web structure, ultimately leading to the loss of arthropod biodiversity and the reduction in the agro-ecosystem resilience to pest outbreaks (Heong et al., 1991; Horgan & Crisol, 2013; Kenmore et al., 1984; Way & Heong, 2009). In a previous study (Dominik et al., 2017), we have shown that management effects are potentially important in determining the arthropod composition in our study areas but that they vary between regions, while being relatively homogeneous within regions. Although these regional-scale effects cannot be fully disentangled from the effects of landscape heterogeneity, in this study we indirectly accounted for them by the nested design of our analyses. To further unravel the effects of landscape heterogeneity on arthropod communities, future research should directly address management practices and land-use intensity as additional factors potentially shaping rice arthropod communities. In addition, future research should focus on the effects of temporal and spatial manipulation of the rice landscape, and on the potential benefits of coupling small rice patches with large ones to better understand the effects of fragmentation in rice agroecosystems.

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AUTHORS’ CONTRIBUTIONS

C.D., R.S., T.V., and J.S. conceived the idea and designed methodology; C.D. and F.G.H. collected the data; C.D. analysed the data; C.D. and T.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.6mv5372 (Dominik, Seppelt, Horgan, Settele, & Václavík, 2018).

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REFERENCES

Altieri, M. A. (1999). The ecological role of biodiversity in agroecosystems. *Agriculture Ecosystems & Environment*, *74*, 19–31. https://doi.org/10.1016/S0167-8809(99)00028-6

Arida, G., & Heong, K. L. (1992). Blow-vac: A new suction apparatus for sampling rice arthropods. *International Rice Research Notes*, *17*, 30–31.

Barrion, A. T., & Litsinger, J. A. (1994). Taxonomy of rice insect pests and their arthropod parasites and predators. In E. A. Heinrichs (Ed.), *Biology and management of rice insects* (pp. 13–359). New Delhi, India: Wiley Eastern Limited.

Bengtsson, J., Ahnstrom, J., & Weibull, A. C. (2005). The effects of organic agriculture on biodiversity and abundance: A meta-analysis. *Journal of Applied Ecology*, *42*, 261–269. https://doi.org/10.1111/j.1365-2664.2005.01005.x

Bianchi, F. J., Booij, C. J., & Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proceedings. Biological Sciences*, *273*, 1715–1727. https://doi.org/10.1098/rspb.2006.3530

Botero-Garcés, N., & Isaacs, R. (2004). Movement of the grape berry moth, Endopiza viteana: Displacement distance and direction. *Physiological Entomology*, *29*, 443–452. https://doi.org/10.1111/j.0307-6962.2004.00415.x

Denys, C., & Tscharntke, T. (2002). Plant-insect communities and predator-prey ratios in field margin strips, adjacent crop fields, and fallows. *Oecologia*, *130*, 315–324. https://doi.org/10.1007/s004420100796

Dominik, C., Seppelt, R., Horgan, F. G., Marquez, L., Settele, J., & Václavík, T. (2017). Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities. *Agriculture, Ecosystems & Environment*, *246*, 269–278. https://doi.org/10.1016/j.agee.2017.06.011

Dominik, C., Seppelt, R., Horgan, F. G., Settele, J., & Václavík, T. (2018). Data from: Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.6mv5372

Grez, A. A., & Prado, E. (2000). Effect of plant patch shape and surrounding vegetation on the dynamics of predatory coccinellids and their prey *Brevicoryne brassicae* (Hemiptera: Aphididae). *Environmental Entomology*, *29*, 1244–1250. https://doi.org/10.1603/0046-225X-29.6.1244

Gurr, G. M., Lu, Z., Zheng, X., Xu, H., Zhu, P., Chen, G., … Heong, K. L. (2016). Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nature Plants*, *2*(3), 16014. https://doi.org/10.1038/nplants.2016.14

Gurr, G. M., Wratten, S. D., & Altieri, M. A. (2004). Ecological engineering: A new direction for agricultural pest management. *AFBM Journal*, *1*, 28–35.

Hambäck, P. A., Summerville, K. S., Steffan-Dewenter, I., Krauss, J., Englund, G., & Crist, T. O. (2007). Habitat specialization, body size, and family identity explain lepidopteran density-area relationships in a cross-continental comparison. *Proceedings of the National Academy of Sciences of United States of America*, *104*, 8368–8373. https://doi.org/10.1073/pnas.0611462104

Heinrichs, E. A., Aquino, G. B., Chelliah, S., Valencia, S. L., & Reissig, W. H. (1982). Resurgence of *Nilaparvata lugens* (Stål) populations as influenced by method and timing of insecticide applications in lowland rice. *Environmental Entomology*, *11*, 78–84. https://doi.org/10.1093/ee/11.1.78

Heinrichs, E. A., & Mochida, O. (1984). From secondary to major pest status: The case of insecticide-induced rice brown planthopper, *Nilaparvata lugens*, resurgence. *Protection Ecology*, *7*(2/3), 201–218.

Heong, K. L., Aquino, G. B., & Barrion, A. T. (1991). Arthropod community structures of rice ecosystems in the Philippines. *Bulletin of Entomological Research*, *81*, 407–416. https://doi.org/10.1017/S0007485300031977

Heong, K. L., Aquino, G. B., & Barrion, A. T. (1992). Population dynamics of plant- and leafhoppers and their natural enemies in rice ecosystems in the Philippines. *Crop Protection*, *11*, 371–379. https://doi.org/10.1016/0261-2194(92)90066-E

Heong, K. L., & Hardy, B. (2009). Planthoppers: New threats to the sustainability of intensive rice production systems in Asia. International Rice Research Institute (IRRI), Los Banos, Philippines.

Heong, K. L., & Schoenly, K. G. (1998). Impact of insecticides on herbivore-natural enemy communities in tropical rice ecosystems. In P. T. Haskell, & P. McEwen (Eds.), *Ecotoxicology: Pesticides and beneficial organisms* (pp. 381–403). Boston, MA: Springer. https://doi.org/10.1007/978-1-4615-5791-3

Horgan, F. G., & Crisol, E. (2013). Hybrid rice and insect herbivores in Asia. *Entomologia Experimentalis et Applicata*, *148*, 1–19. https://doi.org/10.1111/eea.12080

Horgan, F. G., Ramal, A. F., Bernal, C. C., Villegas, J. M., Stuart, A. M., & Almazan, M. L. (2016). Applying ecological engineering for sustainable and resilient rice production systems. *Procedia Food Science*, *6*, 7–15. https://doi.org/10.1016/j.profoo.2016.02.002

Horgan, F. G., Ramal, A. F., Villegas, J. M., Jamoralin, A., Bernal, C. C., Perez, M. O., … Almazan, M. L. P. (2017). Effects of bund crops and insecticide treatments on arthropod diversity and herbivore regulation in tropical rice fields. *Journal of Applied Entomology*, *141*, 587–599. https://doi.org/10.1111/jen.12383

Horner-Devine, M. C., Daily, G. C., Ehrlich, P. R., & Boggs, C. L. (2003). Countryside biogeography of tropical butterflies. *Conservation Biology*, *17*, 168–177. https://doi.org/10.1046/j.1523-1739.2003.01310.x

Ives, A. R., & Settle, W. H. (1997). Metapopulation dynamics and pest control in agricultural systems. *American Naturalist*, *149*, 220–246. https://doi.org/10.1086/285988

Jackson, H. B., & Fahrig, L. (2012). What size is a biologically relevant landscape? *Landscape Ecology*, *27*, 929–941. https://doi.org/10.1007/s10980-012-9757-9

Kawasaki, K. (2010). The costs and benefits of land fragmentation of rice farms in Japan. *Australian Journal of Agricultural and Resource Economics*, *54*(4), 509–526. https://doi.org/10.1111/j.1467-8489.2010.00509.x

Kenmore, P. E., Carino, F. O., Perez, C. A., Dyck, V. A., & Gutierrez, A. P. (1984). Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stål) within rice fields in the Philippines. *Journal of Plant Protection in the Tropics*, *1*(1), 19–37.

Klotzbücher, T., Marxen, A., Vetterlein, D., Schneiker, J., Türke, M., van Sinh, N., … Jahn, R. (2015). Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. *Basic and Applied Ecology*, *16*(8), 665–673. https://doi.org/10.1016/j.baae.2014.08.002

Kruess, A., & Tscharntke, T. (1994). Habitat fragmentation, species loss, and biological control. *Science*, *264*, 1581–1584. https://doi.org/10.1126/science.264.5165.1581

Lagerlöf, J., & Wallin, H. (1993). The abundance of arthropods along two field margins with different types of vegetation composition: An experimental study. *Agriculture, Ecosystems & Environment*, *43*, 141–154. https://doi.org/10.1016/0167-8809(93)90116-7

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

Langerwisch, F., Václavík, T., von Bloh, W., Vetter, T., & Thonicke, K. (2017). Combined effects of climate and land-use change on the provision of ecosystem services in rice agro-ecosystems. *Environmental Research Letters*, *13*, 015003. https://doi.org/10.1088/1748-9326/aa954d

Letourneau, D. K., & Bothwell, S. G. (2008). Comparison of organic and conventional farms: Challenging ecologists to make biodiversity functional. *Frontiers in Ecology and the Environment*, *6*, 430–438. https://doi.org/10.1890/070081

Lin, S., You, M. S., Yang, G., & Chen, L. L. (2011). Can polycultural manipulation effectively control rice planthoppers in rice-based ecosystems? *Crop Protection*, *30*, 279–284. https://doi.org/10.1016/j.cropro.2010.11.013

Losey, J. E., & Vaughan, M. (2006). The economic value of ecological services provided by insects. *BioScience*, *56*, 311–323. https://doi.org/10.1641/0006-3568(2006) 56[311:TEVOES]2.0.CO;2

McGarigal, K., & Marks, B. (1995). FRAGSTATS conceptual background. FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. United States Forestry Services General Technical Report PNW GTR-351. Pacific Northwest Research Station, Portland OR.

Moran, V. C., & Southwood, T. R. E. (1982). The guild composition of arthropod communities in trees. *Journal of Animal Ecology*, *51*, 289–306. https://doi.org/10.2307/4325

Pathak, M., & Khan, Z. (1994). *Insect pests of rice*. Manila, Philippines: International Rice Research Institute.

Pickett, C. H., & Bugg, R. L. (Eds.). (1998). Enhancing biological control: Habitat management to promote natural enemies of agricultural pests. University of California Press.

Pickett, S. T., & Cadenasso, M. L. (1995). Landscape ecology: Spatial heterogeneity in ecological systems. *Science*, *269*, 331–334. https://doi.org/10.1126/science.269.5222.331

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & Team, R. C. (2014). *nlme: linear and nonlinear mixed effects models. R package version 3.1-118*. Vienna, Austria: R Project for Statistical Computing.

R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Ricketts, T. H. (2001). The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist*, *158*, 87–99. https://doi.org/10.1086/320863

Riechert, S. E., & Lockley, T. (1984). Spiders as biological-control agents. *Annual Review of Entomology*, *29*, 299–320. https://doi.org/10.1146/annurev.en.29.010184.001503

Roland, J., & Taylor, P. D. (1997). Insect parasitoid species respond to forest structure at different spatial scales. *Nature*, *386*, 710–713. https://doi.org/10.1038/386710a0

Sann, C., Theodorou, P., Heong, K. L., Villareal, S., Settele, J., Vidal, S., & Westphal, C. (2018). Hopper parasitoids do not significantly benefit from non-crop habitats in rice production landscapes. *Agriculture, Ecosystems & Environment*, *254*, 224–232. https://doi.org/10.1016/j.agee.2017.11.035

Sawada, H., Subroto, S. G., Suwardiwijaya, E., Mustaghfirin, K. A., & Kusmayadi, A. (1992). Population-dynamics of the brown planthopper in the coastal lowland of West-Java, Indonesia. *Japan Agricultural Research Quarterly*, *26*, 88–97.

Schoenly, K. G., Cohen, J. E., Heong, K. L., Litsinger, J. A., Aquino, G. B., Barrion, A. T., & Arida, G. S. (1996). Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines. *Bulletin of Entomological Research*, *86*, 451–466. https://doi.org/10.1017/S0007485300035033

Schoenly, K. G., Cohen, J. E., Heong, K. L., Litsinger, J. A., Barrion, A. T., & Arida, G. S. (2010). Fallowing did not disrupt invertebrate fauna in Philippine low-pesticide irrigated rice fields. *Journal of Applied Ecology*, *47*, 593–602. https://doi.org/10.1111/j.1365-2664.2010.01799.x

Schoenly, K. G., Justo, H. D., Barrion, A. T., Harris, M. K., & Bottrell, D. G. (1998). Analysis of invertebrate biodiversity in a Philippine farmer's irrigated rice field. *Environmental Entomology*, *27*, 1125–1136. https://doi.org/10.1093/ee/27.5.1125

Seppelt, R., Beckmann, M., Ceauşu, S., Cord, A. F., Gerstner, K., Gurevitch, J., … Powell, K. (2016). Harmonizing biodiversity conservation and productivity in the context of increasing demands on landscapes. *BioScience*, *66*(10), 890–896. https://doi.org/10.1093/biosci/biw004

Settele, J. (1992). Auswirkungen der Intensivierung des Naßreisanbaus auf die terrestrischen Arthropodengemeinschaften philippinischer Reisterrassen (Doctoral dissertation, Margraf).

Settele, J., Biesmeijer, J., & Bommarco, R. (2008). Switch to ecological engineering would aid independence. *Nature*, *456*, 570. https://doi.org/10.1038/456570a

Settele, J., Spangenberg, J. H., Heong, K. L., Burkhard, B., Bustamante, J. V., Cabbigat, J., & Wiemers, M. (2015). Agricultural landscapes and ecosystem services in South-East Asia—The LEGATO-Project. *Basic and Applied Ecology*, *8*(16), 661–664. https://doi.org/10.1016/j.baae.2015.10.003

Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., Hindayana, D., & Sri Lestari A. (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology*, *77*, 1975–1988. https://doi.org/10.2307/2265694

Sigsgaard, L. (2000). Early season natural biological control of insect pests in rice by spiders-and some factors in the management of the cropping system that may affect this control. *European Arachnology*, *2000*, 57–64.

Stanton, M. L. (1983). *Spatial patterns in the plant community and their effects upon insect search (vol. 125)*. New York, NY: Academic Press.

Steffan-Dewenter, I., Munzenberg, U., Burger, C., Thies, C., & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, *83*, 1421–1432. https://doi.org/10.1890/0012-9658(2002) 083[1421:SDEOLC]2.0.CO;2

Thies, C., & Tscharntke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, *285*, 893–895. https://doi.org/10.1126/science.285.5429.893

Tscharntke, T., & Brandl, R. (2004). Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology*, *49*, 405–430. https://doi.org/10.1146/annurev.ento.49.061802.123339

Tscharntke, T., Karp, D. S., Chaplin-Kramer, R., Batary, P., DeClerck, F., Gratton, C., … 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

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, *8*, 857–874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tscharntke, T., & Kruess, A. (1999). Habitat fragmentation and biological control. In B. A. Hawkins, & H. V. Cornell (Eds.), *Theoretical approaches to biological control* (pp. 190–205). Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511542077

Way, M. J., & Heong, K. L. (2009). Significance of the tropical fire ant *Solenopsis geminata* (hymenoptera: formicidae) as part of the natural enemy complex responsible for successful biological control of many tropical irrigated rice pests. *Bulletin of Entomological Research*, *99*, 503–512. https://doi.org/10.1017/S0007485308006524

Widiarta, I. N., Suzuki, Y., Sawada, H., & Nakasuji, F. (1990). Population dynamics of the green leafhopper, *Nephotettix virescens* Distant (Hemiptera: Cicadellidae) in synchronized and staggered transplanting areas of paddy fields in Indonesia. *Researches on Population Ecology*, *32*, 319–328. https://doi.org/10.1007/BF02512566

Wiens, J. J. (2011). The niche, biogeography and species interactions. *Philosophical Transactions of the Royal Society London B Biological Sciences*, *366*, 2336–2350. https://doi.org/10.1098/rstb.2011.0059

Wilby, A., Lan, L. P., Heong, K. L., Huyen, N. P. D., Quang, N. H., Minh, N. V., & Thomas, M. B. (2006). Arthropod diversity and community structure in relation to land use in the Mekong Delta, Vietnam. *Ecosystems*, *9*, 538–549. https://doi.org/10.1007/s10021-006-0131-0

Yao, F. L., You, M. S., Vasseur, L., Yang, G., & Zheng, Y. K. (2012). Polycultural manipulation for better regulation of planthopper populations in irrigated rice-based ecosystems. *Crop Protection*, *34*, 104–111. https://doi.org/10.1016/j.cropro.2011.12.003

Yu, X., Heong, K. L., Hu, C., & Barrion, A. T. (1996). Role of non-rice habitats for conserving egg parasitoids of rice planthoppers and leafhoppers. In N. Hokyo & G. Norton (Eds.), *International Workshop on Pest Management Strategies in Asian Monsoon Agroecosystems* (pp. 63–67). Kumamoto, Japan: Kyushu National Agricultural Experiment Station.

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