

Hopper parasitoids do not significantly benefit from non-crop habitats in rice production landscapes



Christina Sann^{a,*}, Panagiotis Theodorou^{b,f}, Kong Luen Heong^c, Sylvia Villareal^d, Josef Settele^{d,e,f}, Stefan Vidal^a, Catrin Westphal^g

^a Agricultural Entomology, Department of Crop Sciences, University of Goettingen, Grisebachstraße 6, 37077 Goettingen, Germany

^b General Zoology, Institute for Biology, Martin Luther University Halle-Wittenberg, Hoher Weg 8, 06120 Halle, Germany

^c Institute of Insect Sciences, College of Agriculture and Biotechnology, Zhejiang University, Hangzhou, PR China

^d Institute of Biological Sciences, University of the Philippines, Los Banos, College, Laguna 4031, Philippines

^e Department of Community Ecology, Helmholtz-Centre for Environmental Research-UFZ, Theodor-Lieser-Straße 4, 06120 Halle, Germany

^f iDiv, German Centre for Integrative Biodiversity Research, Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

^g Agroecology, Department of Crop Sciences, University of Goettingen, 37077 Goettingen, Germany

ARTICLE INFO

Keywords:

Biological pest control
Hymenopteran parasitoids
Natural enemies
Nephotettix spp.
Nilaparvata lugens
Rice agroecosystem

ABSTRACT

Agricultural intensification threatens biodiversity and ecosystem functioning. Promoting ecosystem services, such as biological pest control, could help to reduce pesticide inputs while simultaneously sustaining a high productivity. The highly intensive rice production in Southeast Asia, where more than 20% of the world's rice yield is produced, is challenged by devastating losses each year due to rice hoppers. This poses a great threat to the more than 3.5 billion people depending on rice as staple food. Egg parasitoids are among the most important natural enemies of rice hoppers and might be promoted with effective habitat management. However, empirical studies that focus on the management of parasitoid populations to enhance biological pest control in rice agroecosystems are largely lacking. We therefore analysed the effects of the availability of diverse habitats on hopper parasitoid performance, parasitism rates and pest control services, hypothesising that egg parasitoid abundance and pest control is positively influenced by diverse non-crop areas, which provide food resources as well as retreat areas for the fallow season.

We experimentally tested the efficiency and abundance of egg parasitoids of *Nilaparvata lugens* and *Nephotettix* spp. in three study sites representing different levels of floral resources over the course of two rice growing seasons. We used mixed effect models to test whether habitat diversity positively influenced parasitoid abundance and subsequently reduces hatching rates of the hopper nymphs.

Nephotettix spp. eggs were parasitized by *Gonatocerus* spp. and *Paracentrobia* spp. by 92.5%; *Nilaparvata lugens* eggs were parasitized by *Oligosita* spp. and *Anagrus* spp. by 93%. In contrast to our hypothesis, we could demonstrate that additional floral resources do not significantly enhance parasitoid abundance and pest control in rice agroecosystems. Up to six times more parasitoids hatched from the bait plants exposed in the monoculture compared to the non-crop areas ($p < 0.05$). All parasitoid genera except *Anagrus* spp. were found in rice fields in triple or quadruple numbers compared to the non-crop habitats ($p < 0.05$). This was true also during the fallow period ($p < 0.05$), where only ratoon rice was available to sustain hopper populations.

In contrast to our hypotheses and findings from temperate production systems, we found higher parasitoid abundance during all crop stages and increased hatching rates in the monocultures than in the non-crop habitats. The structural and temporal heterogeneity of rice crops and ratoon rice within the production area seemed to be sufficient to sustain high densities of parasitoid populations. We conclude that ecological intensification schemes should implement asynchronous planting cycles in rice systems to maintain or enhance parasitoids populations and their biocontrol services. In combination with reduced pesticide inputs, these measures might help to avoid yield losses due to rice hoppers in the future.

* Corresponding author at: Grisebachstraße 6, 37077 Göttingen, Germany.

E-mail address: Christina.Sann@agr.uni-goettingen.de (C. Sann).

1. Introduction

Land-use change and agricultural intensification are considered as major threats to biodiversity and ecosystem functioning (Cardinale et al., 2012; Sala et al., 2000). The loss of non-crop habitats, habitat fragmentation and detrimental effects of pesticides on non-target organisms (Crowder and Harwood, 2014; Tschamtko et al., 2007) can cause declines of arthropod natural enemies leading to a reduction in biological pest control (Bianchi et al., 2006; Thies et al., 2011) which then might result in even higher inputs of pesticides.

Increasingly, scientists are promoting the benefits of ecological intensification in agriculture, which is targeting the improvement of ecosystem functions to sustain or improve yields (Foley et al., 2011; Garibaldi et al., 2017; Garnett et al., 2013; Godfray, 2015; Gurr et al., 2016; Kovács-Hostyánszki et al., 2017). Biological pest control represents one of these ecosystem functions. Natural enemies benefit from more complex landscapes surrounding agricultural fields or the availability of non-crop habitats. These can offer supplemental food resources (e.g. pollen and nectar) and retreat areas for natural enemies, enhancing their biocontrol services (Roschewitz et al., 2005; Thies et al., 2003). Parasitism rates, for example, have been shown to be higher in complex landscapes where non-crop habitats are available (Gardiner et al., 2009). To date, the majority of studies addressing the effect of land-use intensity and the availability of non-crop habitats on parasitoids have been conducted in the United States and European countries. However, little research has been conducted in one of the most important food production systems of the world: the rice production system of Asia (Gurr et al., 2016).

Since the Green Revolution of the 1960s, most of the traditional rice production systems have changed into intensively managed landscapes (Khush, 1997). Settle et al. (1996) stated that although natural enemies can abundantly be found in young rice fields, biological control is often disrupted by the application of insecticides and unfavourable landscape design. Despite the recommendations of Settle et al. (1996) the use of pesticides and fertilizers is still increasing (FAO, 2017). To promote and sustain high levels of biological control, more sustainable management options need to be developed, ideally based on participatory approaches that also involve the rice farmers and other stakeholders (Westphal et al., 2015). Homopterans are among the most devastating rice pests in Southeast Asia (Lin et al., 2011). The brown planthopper (BPH; *Nilaparvata lugens* Stål), and the green leafhoppers (GLH; including two species of *Nephotettix* spp.), are among the economically most important species. These pests can cause severe damage to rice plants by xylem sap feeding, resulting in wilting of the rice crops which subsequently die, a symptom described as 'hopper burn' (Heong et al., 2015; Heong and Hardy, 2009; Normile, 2013). In addition, both pests transmit destructive viruses, such as the rice tungro and the grassy and ragged stunt (Cabauatan et al., 2009). These hoppers are especially devastating as they can quickly re-colonize freshly transplanted rice fields, being able to migrate over long distances in their macropterous stages (Watanabe et al., 2009).

The introduction of rice varieties resistant to BPH and GLH has not been successful so far, as they rapidly adapt to specific traits in resistant cultivars (Catindig et al., 2009; Seo et al., 2009). The lack of sustainable control options requests a better understanding of the role of natural enemies in controlling hopper populations.

Among several generalists preying on the rice hoppers, egg parasitoids play an important role (Gurr et al., 2011). They can disperse over great distances (Antolin and Strong, 1987) and detect their hosts efficiently following plant volatiles and the chemical footprint of the host (Lou et al., 2005; Vet et al., 1990; Xiao et al., 2012). Therefore have the potential to recolonize rice fields as quickly as the hoppers. While the adults feed on pollen and nectar or the honeydew of their sap-feeding hosts, their larvae develop in the hopper eggs and disrupt the hoppers' life cycles at the earliest possible stage. Drechsler and Settele (2001) showed that parasitoids can play a major role in controlling

hoppers pests in rice agroecosystems, as, for instance, egg parasitism rates can range between 32% and 42% in Philippine rice fields (Cook and Perfect, 1989; Kenmore et al., 1984). Moreover, other studies found egg parasitism rates between 20% and 63% in Southeast-Asian rice fields (Fowler et al., 1991; Nishida et al., 1976; Watanabe et al., 1992), indicating high levels of biological control through egg parasitoids throughout Southeast Asia.

Flower-rich non-crop areas have been suggested as ecological engineering measures in rice production systems to enhance levels of biological control, as known from temperate regions. However, research so far has only focused on a single parasitoid genus, *Anagrus* spp. Whether this practice helps to promote the whole parasitoid community associated with egg parasitism and hopper control is still unknown.

With regard to promoting more sustainable rice production in Southeast Asia we analysed the effects of the availability of resource-rich non-crop habitats on the performance of rice hopper parasitoids, parasitism rates and their pest control services. The following hypotheses were tested:

1. Egg parasitoid abundance is higher in non-crop and diverse habitats compared to monocultures, because of the availability of floral resources and retreat areas.
2. Parasitoids are abundant in the paddy fields during the rice growing season and migrate to retreat areas during the fallow period.
3. The hatching rate of parasitoids in diverse and non-crop habitats is higher compared to the monocultures.

We chose three study sites representing different levels of habitat complexity (i.e. availability of food and retreat areas) which were located in eight paddy rice production landscapes on the main island of the Philippines (Luzon). The selected paddy rice production landscapes were representative for smallholder paddy rice production areas throughout Southeast Asia. Egg parasitoid communities of BPH and GLH were sampled with standardized bait plants during rice growing and fallow seasons in two years.

2. Materials and methods

2.1. Study region and experimental design

The study was conducted in the rice-dominated agricultural landscape of the Laguna province, Philippines. The Laguna province is located in the south of Luzon and covers 1.760 km² of land. 34.5% of this area is managed for agriculture with rice being the principal crop. All rice grown in Laguna is rainfed or irrigated lowland rice. Across the study area two rice crops are grown per year, one during the dry season from December to April and the other one during the wet season from June to October. During the dry season all rice fields are regularly irrigated. Depending on the location of the field and the water availability, planting time between different farmers varies up to 6 weeks.

Post-harvest crop residues generally remain on the fields during the fallow season and are incorporated into the soil when preparing the paddies for the next rice crop. Fields are not irrigated during the fallow and a high variety of herbs emerge between the ratoon rice plants. Few farmers use the fallow season to plant crops like mustard and onions. Bunds between the fields are generally not managed but are trimmed and repaired after every rice cropping season.

Eight study landscapes were selected throughout the Laguna province. Each study landscape comprised a set of three study sites (triplets) differing in resource availability and representing characteristic land-use types within Asian rice agriculture systems (Fig. A1 in Appendix in Supplementary material). All the paddy rice fields included in our study, regarding agrochemical inputs and fertilizer administration, were managed by the farmers according to the common practices in this area. The least intensively managed study sites were represented by diverse agroforests with various main crops, for instance coconut

trees, bananas and different fruit trees and vegetables. As they were extensively managed and often only entered during the harvesting season, they also contained a high diversity of herbs, grasses and shrubs which were partially cleared once or twice a year. These areas harboured a diverse array of nectar resources for the parasitoids as well as grasses for the hoppers and were considered as potential non-crop habitats for parasitoid wasps. We exposed bait plants randomly and well detectable within grassy areas in these agroforests (hereafter referred to as **agroforest**) with a minimum distance of 5 m and a maximum distance of 15 m to the border of the adjacent study rice fields (see Material and Methods 2.2. *Standard sampling with bait plants*).

Rice fields with a common border to their respective agroforests sites represented intensively managed habitats which were closely connected to the diverse agroforests and thus spill over processes between both habitats could easily take place (Rand et al., 2006; Woodcock et al., 2016) due to the great mobility of parasitoids (Antolin and Strong, 1987). These sites will hereafter be referred to as ‘rice fields embedded in structurally diverse surroundings (**diverse**)’. The bait plants were exposed with at least 1 m distance to the borders of the bunds of the rice fields to avoid edge effects.

Thirdly study sites of the triplets was represented by a rice field, which was completely surrounded by other rice fields representing the typical rice monoculture and intensively managed habitat in the rice production systems of the Philippines. These structurally poor sites were located at a distance of at least 300 m to the diverse sites. They will be referred to as the ‘rice fields embedded in rice monocultures (**mono**)’. Again the bait plants were exposed with at least 1 m distance to the borders of the bunds of the rice fields.

2.2. Standardised sampling with bait plants

Sampling took place in the fallow period of the dry season in 2012 and in the rice growing and fallow period of the dry season in 2013 using the bait plant method. Watanabe et al. (1992) have shown that this method reflects the actual state of parasitism in these habitats. We therefore argue that this standardized method is suitable to test our hypotheses.

Rice plants (variety Taichung Native (1) (TN (1))) were grown in small terracotta pots, with a volume of 0.23 l, in a greenhouse for six weeks without any chemical treatments. Thereafter, plants were trimmed to three tillers per pot. The remaining plants were covered with a small plastic cage with a diameter of 6 cm and a height of 50 cm. Greenhouse cultures of BPH (*Nilaparvata lugens*) and GLH (*Nephotettix* spp.) were reared on rice plants of the same variety using the standard method as described by Heinrichs et al. (1985). Four gravid females (20–25 days old) of either BPH or GLH were released into each cage. After 48 h the hoppers were removed. Eight plants per treatment were held back and dissected to calculate the average amount of eggs laid per run. The remaining plants were transferred to the rice fields and agroforests by car while still covered. Three plants infested with BPH eggs and three plants infested with GLH eggs were randomly placed within the rice fields and on grassy areas in the agroforests and thereafter cages were removed. Parasitoids are able to locate hopper infested plants easily as they are attracted to volatiles released from the plants and insects (Lou et al., 2005; Vet et al., 1990; Xiao et al., 2012). In total, three runs were executed in 2012 and four in 2013. Every four weeks we randomly placed the six plants within each rice field and agroforest and exposed them to the parasitoids for 72 h. We collected the plants in the same order they were placed in the fields to standardise the 72 h exposition time. When removed from the fields, the plants were immediately covered by a cage again to ensure that the plants would not be attacked by other herbivorous insects and that all hatching insects would be confined to their plant. Hopper nymphs typically hatch between 5 and 8 days after the egg laying. They were manually collected from the plants 10 days after the last day of infestation. Thereafter plants were placed back into their cages and the cages were additionally

covered by a black cloth sleeve preventing any light to seep through. The parasitoid adults typically hatch 13–17 days after female oviposition. Due to positive phototaxis, parasitoids aggregated in little glass vials which were firmly connected inversely on top of the sleeve cages and which were not covered by cloth. Parasitoid specimens were collected daily in the early afternoon and killed immediately by freezing. The hatched parasitoids were identified to genera level with the help of a taxonomist, noting whether they hatched from BPH or GLH plants and on which day after the exposure.

All plants were dissected afterwards to count the remaining parasitized and non-parasitized eggs. At this stage parasitoids still left in the eggs were developed far enough to distinguish the different genera. The data used for analyses include the parasitized and non-parasitized eggs found when dissecting the plants.

2.3. Data analysis

We analysed the data according to growth stages because the rice fields were not planted synchronously. The different growth stages were grouped into five ‘rice stages’ according to the plant age (see Table A1 and Fig. A2 in Appendix in Supplementary material). The 5th stage represents the rice fields in the 2–3 weeks period when the paddies are prepared for the next season and no vegetation can be found on the fields. We calculated an average of eggs laid per plant per hopper species (see Table A2 in Appendix in Supplementary material) for the analysis.

All analyses were performed in R 3.2.2 statistical software (R Development Core Team, 2013). We fitted our data to mixed effects models to account for the spatial and temporal component of our sampling design (Zuur et al., 2009).

The response of parasitism to the three different study sites (agroforest, diverse and mono; see Material and Methods for details) during the different developmental stages of the rice crop was analysed using generalised linear mixed models (GLMMs) with a negative binomial error structure using the R package “glmmADMB” (Fournier et al., 2012). We used a negative binomial error structure due to overdispersion, tested using the R package “RVAideMemoire” (Hervé, 2016). The response variables were (i) number of all hatched parasitoids, (ii) number of hatched parasitoids at genera level and (iii) number of hatched hopper nymphs. The fixed effects were the study site and the developmental stage of the rice plants. The study landscape, run, site and single plants were included as random effects to account for the nested experimental design and the temporal pattern of the data. Further, Tukey post-hoc tests were used for pairwise comparisons between study sites in each rice field stage, using the R package “multcomp” (Hothorn et al., 2008).

Moreover, we analysed the effect of study site on the ratio of hatched parasitoids and hopper nymphs using linear mixed effect models (LMMs) implemented with the R package “lme4” (Bates et al., 2015). Variables were log-transformed when necessary to meet homogeneity of variance and normality assumptions. The response variables were (i) proportion of hatched parasitoids and (ii) proportion of hatched hopper nymphs. The study landscape, run, site and single plants were again included as random effects and further Tukey post-hoc tests were used for pairwise comparisons between the study sites in each rice field stage.

3. Results

Within the three days of exposure the three GLH females laid an average of 108.67 ± 5.24 (SE) eggs per plant with a minimum of 77.45 ± 3.81 (SE) and a maximum of 132.33 ± 12.98 (SE) eggs per plant. The three BPH females laid an average of 225.48 ± 8.51 (SE) eggs per plant with a minimum of 162.75 ± 11.33 (SE) and a maximum of 229.33 ± 8.13 (SE) eggs per plant within the three days of exposure. Of all the parasitoids that hatched from GLH eggs,

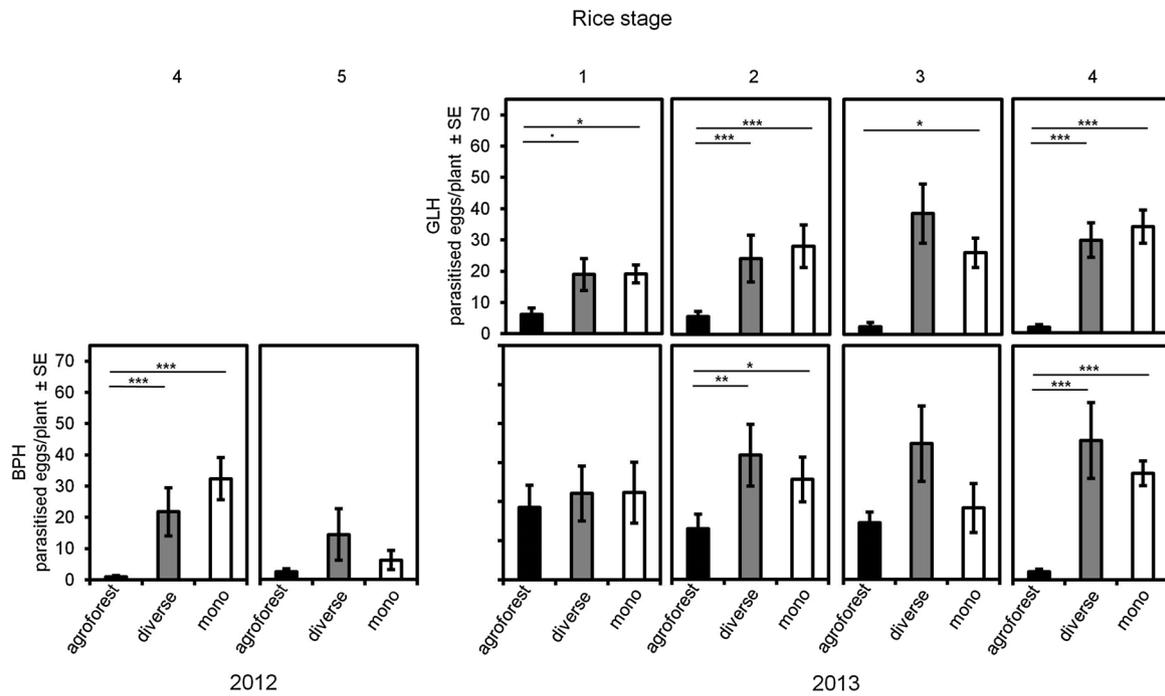


Fig. 1. Effects of study site on egg parasitism.

Effects of rice stages on egg parasitism: Number of parasitized eggs per host species (GLH or BPH; mean ± SE) in a fallow season 2012 and during one rice growing season in 2013. Black columns show abundance in agroforests, grey columns show abundance in rice fields embedded in diverse surroundings (diverse) and empty columns show abundance in rice fields embedded in rice monocultures (mono). Significant differences between * P < 0.05, ** P < 0.001, *** P < 0.001.

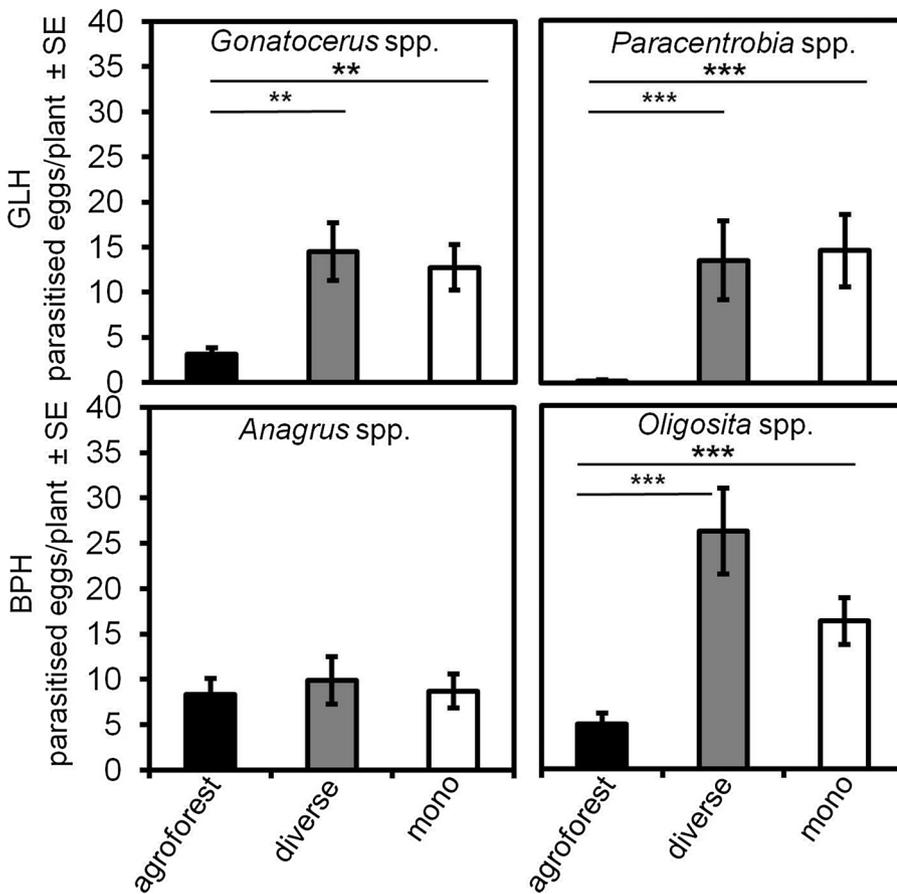


Fig. 2. Effects of study site on parasitoid genera.

Parasitism rates (mean ± SE) of the four parasitoid genera within the different study sites. Black columns: agroforests; grey columns: rice fields embedded in diverse surroundings (diverse); empty columns: rice fields embedded in rice monocultures (mono), * P < 0.05, ** P < 0.001, *** P < 0.001.

Paracentrobia spp. (Chalcidoidea: Trichogrammatidae) and *Gonatocerus* spp. (Chalcidoidea: Mymaridae) were the most dominant genera. Of all the parasitoids that hatched from the BPH eggs, most parasitoids belonged to the genera *Anagrus* spp. (Chalcidoidea: Mymaridae) and *Oligosita* spp. (Chalcidoidea: Trichogrammatidae).

3.1. Effects of study site on egg parasitism

The study site had overall a significant influence on the total numbers of parasitized eggs (GLMMs, GLH: $\chi^2 = 64.73$, $p < 0.001$; BPH: $\chi^2 = 36.96$, $p < 0.001$). Generally, parasitoids of both hosts, GLH and BPH, were found in significantly smaller numbers in the agroforests than in the rice fields during rice cultivation (stage 1, 2, 3; Tukey post-hoc test: $p < 0.05$; Fig. 1, see Table A3a in Appendix in Supplementary material) and the fallow season (stage 4; Tukey post-hoc test: $P < 0.05$; Fig. 1, see Table A3a in Appendix in Supplementary material).

We did not find a significant interaction between the study site and the growth stages of the rice plants for GLH egg parasitism (GLMM, $\chi^2 = 12.18$, $p = 0.06$). 170%–580% more parasitoid specimens hatched from the plants exposed in both rice field sites compared to the agroforest (Tukey post-hoc test: $p < 0.05$; Fig. 1, see Table A3a in Appendix in Supplementary material).

A significant interaction between study site and the developmental stages of the rice crop was observed for BPH egg parasitism (GLMM, $\chi^2 = 25.02$, $p < 0.001$). During stage 1, at the beginning of the rice growing season, no significant differences between the numbers of parasitized eggs could be found between the different study sites for BPH (Tukey post-hoc test: $p > 0.05$; Fig. 1, see Table A3a in Appendix in Supplementary material). However, we found an increasing trend of parasitoids being more abundant in the rice fields compared to the agroforest for the later stages (Tukey post-hoc test: $p < 0.05$ for 2nd and 4th stage; see Table A3a in Appendix in Supplementary material).

In detail, we found significantly higher levels of egg parasitism in both mono and diverse rice fields compare to the agroforest for three of the four genera. *Gonatocerus* (GLH) numbers were 323–330% higher in the rice fields compared to the agroforest, *Paracentrobia* (GLH) and *Oligosita* (BPH) numbers were 383–473% higher in the rice fields compared to the agroforest. (Tukey post-hoc test: $p < 0.05$; Fig. 2, see Table A3b in Appendix in Supplementary material).

In contrast, the genus *Anagrus* (BPH) exhibited similar levels of egg

Table 1

Proportion of the four egg parasitoid genera in relation to total parasitoid emergence, separated by host species (green leafhoppers (GLH) and brown planthopper (BPH)) and rice stages.

		rice stage			
		1	2	3	4
GLH	<i>Anagrus</i> spp.	4.6%	14.6%	13.8%	0.3%
	<i>Oligosita</i> spp.	6.7%	7.6%	2.6%	4.9%
	<i>Paracentrobia</i> spp.	6.4%	11.4%	16.8%	70.3%
	<i>Gonatocerus</i> spp.	80.7%	64.3%	61.1%	24.3%
BPH	<i>Anagrus</i> spp.	40.4%	48.8%	40.1%	14.6%
	<i>Oligosita</i> spp.	54.0%	44.3%	46.7%	78.6%
	<i>Paracentrobia</i> spp.	0.0%	0.3%	0.2%	5.5%
	<i>Gonatocerus</i> spp.	2.6%	5.5%	12.2%	0.2%

parasitism in all three study sites (Tukey post-hoc test: $p > 0.05$; Fig. 2, see Table A3b in Appendix in Supplementary material).

3.2. Effect of rice stages on overall parasitism

Generally, the relative abundance of all four parasitoid genera changed over the course of the rice growing season (rice stages 1–4), following different patterns (Fig. 3), though only for *Gonatocerus* spp. and *Paracentrobia* spp. the relationship was found to be statistical significant (GLMMs; *Gonatocerus* spp.: $\chi^2 = 22.18$, $p < 0.001$; *Paracentrobia* spp.: $\chi^2 = 28.29$, $p < 0.001$).

For the GLH eggs, we found ten times more *Gonatocerus* spp. compared to *Paracentrobia* spp. during the 1st rice stage (Tukey post-hoc test: $p < 0.05$; Fig. 3a, see Table A4 in Appendix in Supplementary material). During the 2nd and 3rd rice stage the abundance of *Gonatocerus* spp. was still higher, though not statistically significant (Tukey post-hoc test: $p > 0.05$; Fig. 3a, see Table A4 in Appendix in Supplementary material). In the fallow season this ratio was inverted. Only 3.2% of the parasitoids found were *Gonatocerus* spp. (Tukey post-hoc test: $p < 0.05$; Fig. 3a, see Table A4 in Appendix in Supplementary material). The abundance of *Anagrus* spp. and *Oligosita* spp. was not modelled due to small sample sizes (Table 1).

For BPH eggs, *Oligosita* spp. and *Anagrus* spp. were equally present during rice stage 1–3 (Fig. 3b, see Table A4 in Appendix in Supplementary material) with 90% of all parasitoids found on BPH plants

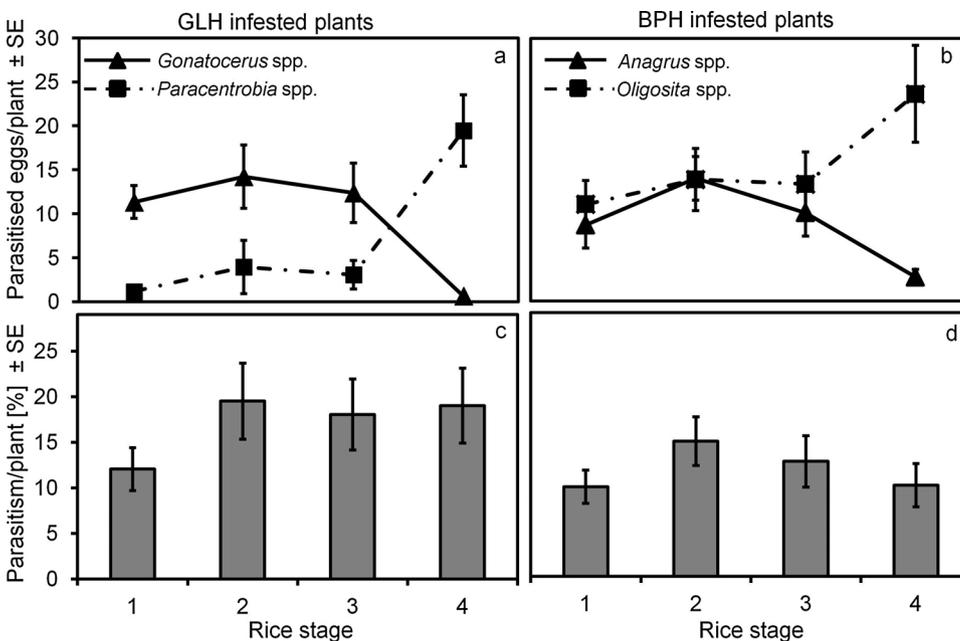


Fig. 3. Effect of rice stages on over all parasitism. (a) Percent parasitism of *Paracentrobia* spp. and *Gonatocerus* spp. and *Anagrus* spp. and (b) *Oligosita* spp. during one rice growing season. In (c) and (d) the overall respective parasitism rates are shown.

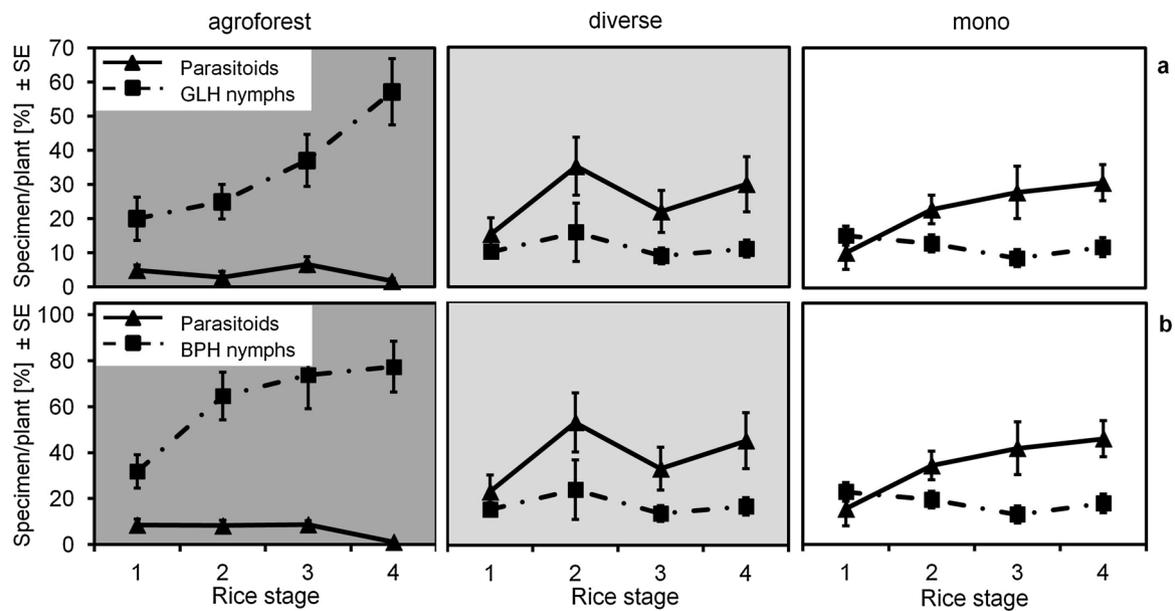


Fig. 4. Influence of study site on hatching rates.

Hatching rates (mean \pm SE) of hoppers and parasitoids in (a) GLH infested plants and (b) BPH infested plants in different study sites during one rice growing season. The dashed line shows the percentage of hopper nymphs hatched the bold line the percentage of parasitoids hatched from the original amount of eggs per plant.

being *Oligosita* spp. (Tukey post-hoc test: $p < 0.05$; Fig. 3b, see Table A4 in Appendix in Supplementary material). The effects of rice stages on the abundance of *Gonatocerus* spp. and *Paracentrobias* spp. could not be analysed due to the small samplesizes (Table 1).

The overall parasitism rates of BPH were generally lower compared to GLH infested plants (LMM, $\chi^2 = 20.63$, $p < 0.001$). The parasitism rates for either hopper species did not differ between the rice field stages, although there was a tendency of lower parasitism during the first rice stage (Tukey post-hoc test: $p > 0.05$; Fig. 3c and d; see Table A4 in Appendix in Supplementary material).

3.3. Influence of study site on hatching rates

On the plants exposed in the agroforests the hatching rates of hopper nymphs were 360%–510% higher than the hatching rates of the parasitoids (Tukey post-hoc test: $p < 0.05$; Fig. 4a and b; see Table A5 in Appendix in Supplementary material). This pattern was not observed in the rice fields, with similar hatching rates of both hopper nymphs and parasitoids (Tukey post-hoc test: $p > 0.05$; Fig. 4a and b; see Table A5 in Appendix in Supplementary material).

4. Discussion

Surprisingly and in contrast to our first hypothesis, the availability of non-crop habitats providing additional nectar resources and retreat areas did not increase the abundance of hopper egg parasitoids in rice production landscapes. Contrasting to several recent studies (Baggen et al., 1999; Balzan and Wäckers, 2013; Lu et al., 2014), we found that egg parasitoids of rice hoppers were able to maintain high population densities in rice monocultures. The high levels of egg parasitism in both rice types indicate that the temporal and spatial variation of rice crops and ratoon rice is more important to sustain vital parasitoids populations than the availability of nectar-rich floral resources in non-crop habitats, such as agroforests.

Temperate agricultural systems, on which we based our hypotheses, are characterised by seasonal crop cycles with winter breaks, whereas seasonal changes in tropical productions systems are less fluctuant and vegetation can grow all year-round. Plant- and leafhoppers and their parasitoids in temperate systems have to overwinter and parasitoids often have to switch to alternative prey for a certain amount of time

(Chantarasa-ard et al., 1984; Moya-Raygoza and Becerra-Chiron, 2014). In tropical rice agroecosystems however, rice hoppers can complete their entire lifecycle year-round (Dyck et al., 1979; Kiritani, 1979) and thus provide a continuous food source for all stages of the parasitoid's life cycle, inside the rice fields, throughout the entire year. Parasitoids do not have to disperse or search for alternative hosts and are therefore likely to be specialised on their rice hopper hosts.

This specialisation on the rice hoppers inside the rice fields could be enhanced by the parasitoids' feeding habits. The rice hoppers are sap-feeding insects and therefore produce honeydew. This can have beneficial effects on life history traits of parasitoids (Lenaerts et al., 2016; Tena et al., 2016; Wäckers et al., 2008). Irvin et al. (2007) showed that honeydew, when saturated with sufficient glucose and fructose can considerably increase the life span of the egg parasitoid *Gonatocerus* spp. Our findings therefore indicate that egg parasitoids could make use of the continuous availability of honeydew produced by their hosts, rather than using floral food resources outside the rice fields. This makes rice monocultures as attractive for them as more diverse landscapes. Although, Lee et al. (2004) showed that the life span of parasitoids is increased when exploiting pollen and nectar instead of honeydew, it has recently been shown that this does not necessarily have to be true for parasitoids of honeydew producing insects (Lenaerts et al., 2016). As their hosts can only be found in low numbers outside the rice fields, the adjacent habitats are less attractive for the parasitoids, even if they provide high quality food resources.

Looking at the four parasitoid genera separately we found that three of the four parasitoids genera found to parasitize eggs of the hopper species investigated were present in higher numbers in both the rice field types 'mono' and 'diverse' compared to the agroforests. The only genus which did not exhibit a clear habitat preference was *Anagrus* spp., which was found in equal numbers in all habitats. We assume that species of the genus *Anagrus* spp. are less specialised than the other three parasitoid genera and may switch between alternative hopper species found in the nectar rich agroforests (Zheng et al., 2017, 2003). Most studies investigating effects of non-crop habitats in rice agroecosystems have been conducted solely on *Anagrus* spp. indicating positive responses to additional resources (Li and He, 1991; Yu, 2001; Zhu et al., 2013).

In contrast to the findings regarding *Anagrus* spp. response to flower resources, we found variable responses to flower-rich non-crop habitats

when including multiple parasitoid genera. Hence, future studies on the restoration of biological pest control in rice should take multiple parasitoid genera into account to develop efficient management schemes. Besides the clear preference of the parasitoids for the rice fields during the growing season, we found that, in contrast to our second hypothesis, the parasitoids were prevalent in the rice fields also during the fallow season. We assume that the ratoon rice in the fallow paddies provided sufficient food plants to sustain small hopper populations (Chakravarthy, 1987). Hence, the dry paddy fields remained an attractive habitat for the parasitoids, but simultaneously did not promote high hopper populations in the post fallow crop (Schoenly et al., 2010). Myrmarids and Trichogrammatids are quite mobile (Antolin and Strong, 1987; Hendricks, 1967) and can disperse quickly from ratoon rice fields to freshly transplanted fields. Here they have the possibility to respond to the quickly increasing hopper populations (Heong et al., 1992) and reduce the hopper pest populations already at the start of the season. In contrast to temperate agroecosystems, non-crop habitats seem to play a minor role as foraging or retreat habitats for the egg parasitoids after harvest due to their high specialisation. We further investigated the role of the four parasitoid genera in controlling the hoppers in the rice fields and the agroforest, over the course of the rice growing season. For the parasitoids of the green leafhopper (GLH), *Gonatocerus* spp. was dominating in rice stages 1–3, when only rice was growing in the paddies. In the fallow season however *Paracentrobia* spp. increased in numbers whereas numbers of *Gonatocerus* spp. declined. Their combined parasitism rate was slightly lower in rice stage 1 and remained at around 20% for rice stages 2–4, although the composition of the parasitoids changed dramatically in the 4th rice stage. Fowler et al. (1991) observed, that while GLH egg batches were attacked by one or the other parasitoid genera only, BPH egg batches were attacked by both *Anagrus* spp. and *Oligosita* spp. and concluded, that *Paracentrobia* spp. and *Gonatocerus* spp. might be competing for these resources. GLH comprises two species (*Nephotettix virescens* (Distant), *Nephotettix nigropictus* (Stål)), which can only be determined to species level by the genitalia of the males, which was beyond the scope of this study possibilities in this study. A more refined analysis of the host selection pattern by the two parasitoid species might have revealed that the increase of *Paracentrobia* spp. during the fallow season was due to a switch towards a species of GLH better adapted to the ratoon rice fields. *Oligosita* spp. and *Anagrus* spp. parasitized BPH eggs in almost equal amounts during rice stages 1–3. In the fallow season, however, numbers of eggs parasitized by *Anagrus* spp. declined while those of *Oligosita* spp. increased. The overall parasitism levels were highest during the 2nd rice stage when the sum of eggs parasitized on the bait plants by both parasitoid genera was also the highest. BPH, in contrast to GLH, encompasses only one species, *Nilaparvata lugens*. The changes in the abundance of the two parasitoid species can therefore not be accounted for by a potential change of the hopper species. Instead, as functional responses differ in egg parasitoid species (Fowler et al., 1991) *Oligosita* spp. seems to be better adapted to cope with decreasing host densities compared to *Anagrus* spp. when hopper numbers decline during the fallow season. The temporal changes in hopper parasitism rates by the four genera show that for a successful hopper control, more than one parasitoid genus is needed. We also found significantly more nymphs hatching from the plants exposed in the agroforests compared to the plants exposed in the two rice field types. Knowing that the parasitoid population in the agroforests was much smaller than in the rice fields, this implies that the presence of egg parasitoids can significantly reduce the hatching success of hopper nymphs. This is in line with findings from Lam (2002) and Watanabe et al. (1992) who found that egg parasitism in rice fields can range from 20% up to 95% indicating their immense biological pest control potential.

Additionally, we could show that this potential is not dependent on diversified landscapes. While the rice fields showed great differences to the agroforest, no differences could be found between the rice fields. That means the parasitoids didn't even profit in the diverse rice field

from the availability of floral resources in the close proximity. We also documented the predators we found on the rice plants after the exposure in the rice fields, but could not find differences between the two rice field types and the agroforest, and their numbers were generally very low.

Although rice parasitoids don't seem to be dependent on diverse non-crop habitats, it is known that they are highly susceptible to pesticides and would benefit from a less intense management (Bottrell and Schoenly, 2012; Gurr et al., 2016; Heong et al., 2007; Jonsson et al., 2012; Wang et al., 2008). As the fields we worked in were regularly treated with agrochemicals it is to be expected that the parasitism rate could have been much higher in their absence.

5. Conclusion

Our results show for the first time that the hopper parasitoid communities in rice fields are independent of the availability of non-crop habitats providing additional nectar resources and retreat areas. These parasitoid species seem to be very well adapted to the spatial and temporal heterogeneity in the traditional paddy rice production areas of Southeast Asia. Hence, high population densities can be sustained by slightly altering planting and harvesting times of the many smallholder farmers as well as providing ratoon rice during the dry fallow periods. In contrast to temperate host-parasitoid systems, we need to be aware that rice hopper parasitoids have evolved in a rice monoculture system that offers sufficient resources within the spatially and temporally heterogeneous environment that is created by traditional smallholder farms. Hence, to reduce pesticide inputs and to conserve high levels of biological pest control, management schemes need to be developed that are based on the smallholder farmers who maintain the heterogeneity within the system.

Additionally, the rice crop should be monitored carefully and the prophylactic use of pesticides should be avoided. However, insect pests are not the only challenge that rice farmers have to deal with. As plant pathogens also play an important and prevailing role in rice fields, recommendations for sustainable production systems need to be adapted to specific scenarios and local conditions. A combination of sustainable measures targeting both the main pest and disease complex would help to increase the quality of life and health of many rice farmers in Southeast Asia and beyond.

Funding

This work was supported by the LEGATO project (Settele et al., 2015), which is part of the BMBF (German Federal Ministry of Education and Research) Framework Programme Research for Sustainable Development (FONA, FKZ: 01LL0917A & 01LL0917N).

Acknowledgements

We thank Joe Catindig for her support in species identification and Antonio Salamatin and Deomedez Izon for their help and knowledge in the greenhouse and field at the International Rice Research Institute (IRRI).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.agee.2017.11.035>.

References

- Antolin, M.F., Strong, D.R., 1987. Long-distance dispersal by a parasitoid (*Anagrus deli-catus*, Mymaridae) and its host. *Oecologia* 73, 288–292.
- Baggen, L.R., Gurr, G.M., Meats, A., 1999. Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological

- control. *Entomol. Exp. Appl.* 91, 155–161.
- Balzan, M.V., Wäckers, F.L., 2013. Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by *Tuta absoluta* and its parasitoid *Necremnus arynes*. *Biol. Control* 67, 21–31. <http://dx.doi.org/10.1016/j.biocontrol.2013.06.006>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67. <http://dx.doi.org/10.18637/jss.v067.i01>.
- Bianchi, F.J., Booi, C.J., Tschamrke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. B Biol. Sci.* 273, 1715–1727. <http://dx.doi.org/10.1098/rspb.2006.3530>.
- Bottrell, D.G., Schoenly, K.G., 2012. Resurrecting the ghost of green revolutions past: the brown planthopper as a recurring threat to high-yielding rice production in tropical Asia. *J. Asia-Pac. Entomol.* 15, 122–140. <http://dx.doi.org/10.1016/j.aspen.2011.09.004>.
- Cabauatan, P.Q., Cabunagan, R.C., Choi, I.-R., 2009. Rice viruses transmitted by the brown planthopper *Nilaparvata lugens* Stal. *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia*. International Rice Research Institute, Los Banos, Philippines, pp. 357–368.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B., Larigauder, A., Srivastava, D.S., Naem, S., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67. <http://dx.doi.org/10.1038/nature11148>.
- Catindig, J.L., Arida, G.S., Baehaki, S.E., Bentur, J.S., Cuong, L.Q., Norowi, M., Rattanakarn, W., Sriratanasak, W., Xia, J., Lu, Z., 2009. Situations of planthoppers in Asia. *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia*. International Rice Research Institute, Los Banos, Philippines, pp. 191–220.
- Chakravathy, A.K., 1987. Insect pests on main and ratoon rice. *Int. Rice Res. Newsl.* 12, 35–36.
- Chantarasa-ard, S., Hirashima, Y., Hirao, J., 1984. Host range and host suitability of *Anagrus incarnatus* Haliday (Hymenoptera: Mymaridae), an egg parasitoid of delphacid planthoppers. *Appl. Entomol. Zool.* 19, 491–497.
- Cook, A.G., Perfect, T.J., 1989. The population characteristics of the brown plant hopper, *Nilaparvata lugens*, in the Philippines. *Ecol. Entomol.* 14, 1–9. <http://dx.doi.org/10.1111/j.1365-2311.1989.tb00746.x>.
- Crowder, D.W., Harwood, J.D., 2014. Promoting biological control in a rapidly changing world. *Biol. Control* 75, 1–7. <http://dx.doi.org/10.1016/j.biocontrol.2014.04.009>.
- Drechsler, M., Settele, J., 2001. Predator–prey interactions in rice ecosystems: effects of guild composition, trophic relationships, and land use changes — a model study exemplified for Philippine rice terraces. *Ecol. Model.* 137, 135–159. [http://dx.doi.org/10.1016/S0304-3800\(00\)00423-3](http://dx.doi.org/10.1016/S0304-3800(00)00423-3).
- Dyck, V.A., Misra, B.C., Alum, S., Chen, C.N., Hsieh, C.Y., Rejesus, R.S., 1979. Ecology of the brown planthopper in the tropics. *Brown Planthopper Threat to the Rice Production in Asia*. International Rice Research Institute, Los Banos, Philippines, pp. 61–98.
- FAO, 2017. WWW Document]. URL <http://www.fao.org/faostat/en/#home>. (Accessed 30 March 2017).
- Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M., 2011. Solutions for a cultivated planet. *Nature* 478, 337–342. <http://dx.doi.org/10.1038/nature10452>.
- Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M.N., Nielsen, A., Sibert, J., 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optim. Methods Softw.* 27, 233–249. <http://dx.doi.org/10.1080/10556788.2011.597854>.
- Fowler, S.V., Claridge, M.F., Morgan, J.C., Peries, I.D.R., Nugaliyadde, L., 1991. Egg mortality of the brown planthopper, *Nilaparvata lugens* (Homoptera: delphacidae) and green leafhoppers, *Nephotettix* spp. (Homoptera: cicadellidae), on rice in Sri Lanka. *Bull. Entomol. Res.* 81, 161–167.
- Gardiner, M.M., Landis, D.A., Gratton, C., DiFonzo, C.D., O'Neal, M., Chacon, J.M., Wayo, M.T., Schmidt, N.P., Mueller, E.E., Heimpel, G.E., 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol. Appl. Publ. Ecol. Soc. Am.* 19, 143–154.
- Garibaldi, L.A., Gemmill-Herren, B., D'Annolfo, R., Graebur, B.E., Cunningham, S.A., Breeze, T.D., 2017. Farming approaches for greater biodiversity, livelihoods, and food security. *Trends Ecol. Evol.* 32, 68–80. <http://dx.doi.org/10.1016/j.tree.2016.10.001>.
- Garnett, T., Appleby, M.C., Balmford, A., Bateman, I.J., Benton, T.G., Bloomer, P., Burlingame, B., Dawkins, M., Dolan, L., Fraser, D., Herrero, M., Hoffmann, I., Smith, P., Thornton, P.K., Toulmin, C., Vermeulen, S.J., Godfray, H.C.J., 2013. Sustainable intensification in agriculture: premises and policies. *Science* 341, 33–34. <http://dx.doi.org/10.1126/science.1234485>.
- Godfray, H.C.J., 2015. The debate over sustainable intensification. *Food Secur.* 7, 199–208. <http://dx.doi.org/10.1007/s12571-015-0424-2>.
- Gurr, G.M., Liu, J., Read, D.M.Y., Catindig, J.L.A., Cheng, J.A., Lan, L.P., Heong, K.L., 2011. Parasitoids of Asian rice planthopper (Hemiptera: delphacidae) pests and prospects for enhancing biological control by ecological engineering. *Ann. Appl. Biol.* 158, 149–176. <http://dx.doi.org/10.1111/j.1744-7348.2010.00455.x>.
- Gurr, G.M., Lu, Z., Zheng, X., Xu, H., Zhu, P., Chen, G., Yao, X., Cheng, J., Zhu, Z., Catindig, J.L., Villareal, S., Van Chien, H., Cuong, L.Q., Channoo, C., Chengwattana, N., Lan, L.P., Hai, L.H., Chaiwong, J., Nicol, H.I., Perovic, D.J., Wratten, S.D., Heong, K.L., 2016. Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nat. Plants* 2, 16014. <http://dx.doi.org/10.1038/nplants.2016.14>.
- Heinrichs, E.A., Medrano, F.G., Rapusas, H.R., 1985. Genetic Evaluation for Insect in Rice. International Rice Research Institute, Los Banos, Philippines.
- Hendricks, D.E., 1967. Effect of wind on dispersal of *Trichogramma semifumatum*. *J. Econ. Entomol.* 60, 1367–1373. <http://dx.doi.org/10.1093/jee/60.5.1367>.
- Heong, K.L., Hardy, B., 2009. *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia*. International Rice Research Institute, Los Banos, Philippines.
- 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 Prot.* 11, 371–379.
- Heong, K.L., Manza, A., Catindig, J., Villareal, S., Jacobsen, T., 2007. Changes in pesticide use and arthropod biodiversity in the IRR1 research farm. *Outlooks Pest Manage.* 18, 229–233. <http://dx.doi.org/10.1564/18oct11>.
- Heong, K.L., Cheng, J., Escalada, M.M. (Eds.), 2015. *Rice Planthoppers*. Springer, Netherlands, Dordrecht. <http://dx.doi.org/10.1007/978-94-017-9535-7>.
- Hervé, Maxime, 2016. RVAideMemoire: Diverse Basic Statistical and Graphical Functions. R Package Version 0. pp. 9–62. <https://CRAN.R-project.org/package=RVAideMemoire>.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biom. J.* 50, 346–363. <http://dx.doi.org/10.1002/bimj.200810425>.
- Irvin, N.A., Hoddle, M.S., Castle, S.J., 2007. The effect of resource provisioning and sugar composition of foods on longevity of three *Gonatocerus* spp., egg parasitoids of *Homalodisca vitripennis*. *Biol. Control* 40, 69–79. <http://dx.doi.org/10.1016/j.biocontrol.2006.09.005>.
- Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. *J. Appl. Ecol.* 49, 706–714. <http://dx.doi.org/10.1111/j.1365-2664.2012.02130.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* Stal) within rice fields in the Philippines. *J. Plant Prot Trop.* 1, 19–37.
- Khush, G.S., 1997. Origin, dispersal, cultivation and variation of rice. In: Sasaki, T., Moore, G. (Eds.), *Oryza: From Molecule to Plant*. Springer, Netherlands, pp. 25–34. http://dx.doi.org/10.1007/978-94-011-5794-0_3.
- Kiritani, K., 1979. Pest management in rice. *Annu. Rev. Entomol.* 24, 279–312.
- Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A.J., Settele, J., Kremen, C., Dicks, L.V., 2017. Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecol. Lett.* 20, 673–689. <http://dx.doi.org/10.1111/ele.12762>.
- Lam, P.V., 2002. Findings on collecting and identifying natural enemies of key pests on economic crops in Vietnam. *Natural Enemy-Resources of Pests: Studies and Implementation*. Agriculture Publishing House, Hanoi, Vietnam, pp. 7–57.
- Lee, J.C., Heimpel, G.E., Leibe, G.L., 2004. Comparing floral nectar and aphid honeydew diets on the longevity and nutrient levels of a parasitoid wasp. *Entomol. Exp. Appl.* 111, 189–199. <http://dx.doi.org/10.1111/j.0013-8703.2004.00165.x>.
- Lenaerts, M., Abid, L., Paulussen, C., Goelen, T., Wäckers, F., Jacquemyn, H., Lievens, B., 2016. Adult parasitoids of honeydew-producing insects prefer honeydew sugars to cover their energetic needs. *J. Chem. Ecol.* 42, 1028–1036. <http://dx.doi.org/10.1007/s10886-016-0764-1>.
- Li, B.C., He, J.X., 1991. The investigation of fluctuation on numbers of three species of Mymaridae parasitising the eggs of planthoppers and their protection and utilization. *Nat. Enemies Insects* 13, 156–161.
- Lin, S., You, M.S., Yang, G., Chen, L.L., 2011. Can polycultural manipulation effectively control rice planthoppers in rice-based ecosystems? *Crop Prot.* 30, 279–284. <http://dx.doi.org/10.1016/j.cropro.2010.11.013>.
- Lou, Y.-G., Ma, B., Cheng, J.-A., 2005. Attraction of the parasitoid *Anagrus nilaparvatae* to rice volatiles induced by the rice brown planthopper *Nilaparvata lugens*. *J. Chem. Ecol.* 31, 2357–2372. <http://dx.doi.org/10.1007/s10886-005-7106-z>.
- Lu, Z.-X., Zhu, P.-Y., Gurr, G.M., Zheng, X.-S., Read, D.M.Y., Heong, K.-L., Yang, Y.-J., Xu, H.-X., 2014. Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: prospects for enhanced use in agriculture: flowering plants benefit natural enemies. *Insect Sci.* 21, 1–12. <http://dx.doi.org/10.1111/1744-7917.12000>.
- Moya-Raygoza, G., Becerra-Chiron, I.M., 2014. Overwintering biology of egg parasitoids of *Dalbulus maidis* (Hemiptera: cicadellidae) on perennial grasses, volunteer maize, stubble, and drip-irrigated maize. *Ann. Entomol. Soc. Am.* 107, 926–932. <http://dx.doi.org/10.1603/AN14003>.
- Nishida, T., Wongsiri, T., Wongsiri, N., 1976. Species composition, population trends and egg parasitism of planthopper and leafhopper rice pests of Thailand. *Plant Prot. Bull. FAO* 24, 22–26.
- Normile, D., 2013. Vietnam turns back a tsunami of pesticides. *Science* 341, 737–738. <http://dx.doi.org/10.1126/science.341.6147.737>.
- R Development Core Team, 2013. *The R Foundation for Statistical Computing*, Ver 3.0.2. Vienna University of Technology, Vienna, Austria Available at: <http://www.r-project.org/>.
- Rand, T.A., Tylianakis, J.M., Tschamrke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* 9, 603–614. <http://dx.doi.org/10.1111/j.1461-0248.2006.00911.x>.
- Roschewitz, I., Hücker, M., Tschamrke, T., Thies, C., 2005. The influence of landscape context and farming practices on parasitism of cereal aphids. *Agric. Ecosyst. Environ.* 108, 218–227. <http://dx.doi.org/10.1016/j.agee.2005.02.005>.
- Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A.P., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. *Science* 287, 1770–1774.
- 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. *J. Appl. Ecol.* 47, 593–602. <http://dx.doi.org/10.1111/j.1365-2664.2010>

- 01799.x.
- Seo, B.Y., Jung, J.K., Choi, B.-R., Park, H.M., Lee, B.H., 2009. Resistance-breaking ability and feeding behavior of the brown planthopper *Nilaparvata lugens*, recently collected in Korea. *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia*. International Rice Research Institute, Los Banos, Philippines, pp. 303–314.
- Settele, J., Spangenberg, J.H., Heong, K.L., Burkhard, B., Bustamante, J.V., Cabbigat, J., Van Chien, H., Escalada, M., Grescho, V., Hai, L.H., Harpke, A., Horgan, F.G., Hotes, S., Jahn, R., Kühn, I., Marquez, L., Schädler, M., Tekken, V., Vetterlein, D., Villareal, S., Bong, Westphal, C., Wiemers, M., 2015. Agricultural landscapes and ecosystem services in South-East Asia—the LEGATO-Project. *Basic Appl. Ecol.* 16, 661–664. <http://dx.doi.org/10.1016/j.baae.2015.10.003>.
- Settle, W.H., Ariawan, H., Astuti, E.T., Cahyana, W., Hakim, A.L., Hindayana, D., Lestari, A.S., 1996. Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology* 77, 1975–1988.
- Tena, A., Wäckers, F.L., Heimpel, G.E., Urbaneja, A., Pekas, A., 2016. Parasitoid nutritional ecology in a community context: the importance of honeydew and implications for biological control. *Curr. Opin. Insect Sci.* 14, 100–104. <http://dx.doi.org/10.1016/j.cois.2016.02.008>.
- Thies, C., Steffan-Dewenter, I., Tscharntke, T., 2003. Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101, 18–25.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W.W., Winqvist, C., Tscharntke, T., 2011. The relationship between agricultural intensification and biological control: experimental tests across Europe. *Ecol. Appl. Publ. Ecol. Soc. Am.* 21, 2187–2196.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., Nohuys, S., van Vidal, S., 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43, 294–309. <http://dx.doi.org/10.1016/j.biocontrol.2007.08.006>.
- Vet, L.E.M., Dicke, M., Wäckers, F.L., 1990. How to hunt for hiding hosts: the reliability-Detectability problem in foraging parasitoids. *Neth. J. Zool.* 41, 202–213. <http://dx.doi.org/10.1163/156854291X00144>.
- Wäckers, F.L., van Rijn, P.C.J., Heimpel, G.E., 2008. Honeydew as a food source for natural enemies: making the best of a bad meal? *Biol. Control* 45, 176–184. <http://dx.doi.org/10.1016/j.biocontrol.2008.01.007>.
- Wang, H.Y., Yang, Y., Su, J.Y., Shen, J.L., Gao, C.F., Zhu, Y.C., 2008. Assessment of the impact of insecticides on *Anagrus nilaparvatae* (Pang et Wang) (Hymenoptera: mymaridae), an egg parasitoid of the rice planthopper, *Nilaparvata lugens* (Hemiptera: delphacidae). *Crop Prot.* 27, 514–522. <http://dx.doi.org/10.1016/j.cropro.2007.08.004>.
- Watanabe, T., Wada, T., Salleh, N.M.N., Bin, N., 1992. Parasitic activities of egg parasitoids on the rice planthoppers, *Nilaparvata lugens* (Stal) and *Sogatella furcifera* (Horvath) (Homoptera: delphacidae), in the muda area, peninsular Malaysia. *Appl. Entomol. Zool.* 27, 205–211.
- Watanabe, T., Matsumura, M., Otuka, A., 2009. Recent occurrences of long-distance migratory planthoppers and factors causing outbreaks in Japan. *Planthoppers: New Threats to the Sustainability of Intensive Rice Production Systems in Asia*. International Rice Research Institute, Los Banos, Philippines, pp. 179–190.
- Westphal, C., Vidal, S., Horgan, F.G., Gurr, G.M., Escalada, M., Van Chien, H., Tscharntke, T., Heong, K.L., Settele, J., 2015. Promoting multiple ecosystem services with flower strips and participatory approaches in rice production landscapes. *Basic Appl. Ecol.* 16, 681–689. <http://dx.doi.org/10.1016/j.baae.2015.10.004>.
- Woodcock, B., Bullock, J., McCracken, M., Chapman, R., Ball, S., Edwards, M., Nowakowski, M., Pywell, R., 2016. Spill-over of pest control and pollination services into arable crops. *Agric. Ecosyst. Environ.* 231, 15–23. <http://dx.doi.org/10.1016/j.agee.2016.06.023>.
- Xiao, Y., Wang, Q., Erb, M., Turlings, T.C.J., Ge, L., Hu, L., Li, J., Han, X., Zhang, T., Lu, J., Zhang, G., Lou, Y., 2012. Specific herbivore-induced volatiles defend plants and determine insect community composition in the field. *Ecol. Lett.* 15, 1130–1139. <http://dx.doi.org/10.1111/j.1461-0248.2012.01835.x>.
- Yu, X.P., 2001. Role of *Saccharosydne procerus* on *Zizania caduciflora* as an alternate host for *Anagrus nilaparvatae*, the egg parasitoid of the brown planthopper *Nilaparvata lugens*, which attacks temperate rice. In: *Proceedings of the Impact Symposium on Exploiting Biodiversity for Sustainable Pest Management*. International Rice Research Institute, Los Banos, Philippines, pp. 15–22.
- Zheng, X., Yu, X., Lu, Z., Chen, J., Xu, H., Ju, R., 2003. Parasitization adaptability of *Anagrus optabilis* on *Nilaparvata lugens*. *Chin. J. Biol. Control* 19, 136–138.
- Zheng, X., Lu, Y., Zhu, P., Zhang, F., Tian, J., Xu, H., Chen, G., Nansen, C., Lu, Z., 2017. Use of banker plant system for sustainable management of the most important insect pest in rice fields in China. *Sci. Rep.* 7, 45581. <http://dx.doi.org/10.1038/srep45581>.
- Zhu, P., Gurr, G.M., Lu, Z., Heong, K., Chen, G., Zheng, X., Xu, H., Yang, Y., 2013. Laboratory screening supports the selection of sesame (*Sesamum indicum*) to enhance *Anagrus* spp. parasitoids (Hymenoptera: mymaridae) of rice planthoppers. *Biol. Control* 64, 83–89. <http://dx.doi.org/10.1016/j.biocontrol.2012.09.014>.
- Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, USA.