

# Fallowing did not disrupt invertebrate fauna in Philippine low-pesticide irrigated rice fields

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## Summary

1. Fallowing, a type of rotation where no crop is grown, deprives insect pests of food. In tropical irrigated rice, it is not known whether fallow periods deplete natural enemy populations and reduce their pest control effectiveness in post-fallow crops. We tested the null hypothesis that small-scale synchronous cropping (embedded in asynchronously planted rice landscapes) does not significantly increase pest densities during post-fallow periods in the presence of a large, diverse natural enemy complex undisrupted by insecticides. We tested this null hypothesis by comparing the invertebrate fauna before and after fallowing.

2. In six molluscicide-only fields at the International Rice Research Institute (IRRI) in southern Luzon and at Zaragoza in central Luzon, Philippines, canopy and floodwater invertebrates were vacuum-sampled over two cropping seasons, dry and wet.

3. Thirty-three of the ubiquitous common taxa dominated the samples in both seasons at each site. Most species were natural enemies of rice pests and recyclers of organic matter in the floodwater and waterlogged sediments; some were rice pests.

4. Fallowing depleted populations of more ubiquitous taxa at Zaragoza (four natural enemies, one detritivore) than at IRRI (one herbivore, one natural enemy). At both sites, only green leafhoppers, *Nephotettix virescens* and *Nephotettix nigropictus*, had consistently higher post-fallow densities than pre-fallow densities.

5. At both sites, fallowing did not affect rice-invertebrate faunas differently between seasons with regard to community structure, trajectories and accumulation rates of guild members.

6. *Synthesis and applications.* In tropical irrigated rice fields, small-scale synchronous fallowing combined with low-pesticide inputs and pest-resistant rice varieties did not induce pest outbreaks or notably diminish populations of natural enemies when embedded in asynchronous cropping on larger, regional scales. Our results suggest that small-scale synchronous fallowing, when embedded in asynchronously planted landscapes, does little harm to biological regulation of the invertebrate faunal community and may be adopted as part of integrated pest management when it serves other purposes.

**Key-words:** asynchronous cropping, invertebrate oligarchy, natural enemies, rice-free fallow, synchronous cropping, tropical insect pest management, wet and dry seasons

## Introduction

Crop rotation is often practiced by growers to avoid crop disease and manage weeds (Peairs, Bean & Gossen 2005).

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Fallowing, a type of rotation where no crop is grown for at least one crop season, deprives pests of food, reduces weed seed banks and conserves soil moisture (Gliessman 2000; Norris, Caswell-Chen & Kogan 2003). For insect pest management, fallows must be long enough to ensure high pest mortality, usually more than one pest generation, and

area-wide synchronous fallowing requires enforcement by local governments or farmers' organizations to ensure that fields enter fallow at the same time. Fallowing has been practiced for insect pest control in annual field crops such as cotton, *Gossypium hirsutum* L. (Pearson 1958; Eveleens 1983; Masud *et al.* 1985; Allen 2008), wheat, *Triticum aestivum* L. (McColloch 1923) and sorghum, *Sorghum bicolor* (L.) Moench (Huddletson *et al.* 1972).

In tropical Asian rice cultivation, synchronous cropping creates a rice-free fallow of 1–3 months' duration, usually between the dry and wet seasons (DS, WS), and is a commonplace due to the need to conserve water in the DS. Fallowing reportedly disrupted insect pest life cycles (Dyck *et al.* 1979; Oka 1988; Loevinsohn, Bandong & Alviola 1993) and reduced leafhopper-transmitted disease (Wada & Nik 1992), but synchronous cropping promoted rapid buildup of green leafhopper (e.g. *Nephotettix virescens* [Distant]) and brown planthopper *Nilaparvata lugens* [Stål] populations in post-fallow, WS crops (Widiarta *et al.* 1990). Synchronous cropping may produce more frequent and intense pest outbreaks, and smaller and less diverse predator populations than asynchronous crops (Sawada *et al.* 1992; Wada & Nik 1992; Settle *et al.* 1996). Thus, a prolonged dry fallow between crop cycles could deplete natural enemy populations and reduce their effectiveness in the post-fallow crop.

In contrast, asynchronous cropping creates a mixture of cultivated and temporarily unused fields and is common where irrigation systems are less organized or have slower water delivery rates (Litsinger 2008). In their pest metapopulation model that incorporated both natural enemy and pest population movements, Ives & Settle (1997) found that asynchronous crops with predators migrating between fields lowered pest densities more than synchronous crops without migrating predators, particularly if predators rapidly colonized newly planted fields. It remains uncertain whether synchronous cropping on small spatial scales (Settle *et al.* 1996; Ives & Settle 1997), in the presence of an abundant and effective natural enemy complex (Settle *et al.* 1996; Schoenly *et al.* 1998), undisrupted by insecticides, can maintain low pest densities year round.

Previous studies of fallow effects in tropical rice ecosystems focused on selected insect pests and their principal natural enemies (Widiarta *et al.* 1990; Sawada *et al.* 1992; Wada & Nik 1992), not on entire complexes of pests, natural enemies of pests, and their alternate prey. These complexes may contain many invertebrate species. Philippine and Indonesian rice fields, for example, have more than 640 and 760 taxa of macroinvertebrates, respectively (Cohen *et al.* 1994; Settle *et al.* 1996). Biocontrol fauna, such as spiders and hymenopteran parasitoids, number up to 92 and 84 taxa, respectively, in Indian irrigated fields (Beevi & Lyla 2000; Sebastian *et al.* 2005).

To our knowledge, this is the first study to test empirically the prediction of Ives & Settle (1997) that small-scale synchronous cropping (embedded in asynchronously planted landscapes) does not significantly increase pest densities during post-fallow periods in the presence of a large, diverse natural enemy complex undisrupted by insecticides. We pre-

dicted that, at a similar crop age, synchronously planted fields grown under low-pesticide conditions in different seasons would have similar invertebrate faunal composition, community structure, time-specific trajectories and accumulation rates. We also predicted that, in fields with a longer and drier fallow, more taxa would have smaller post-fallow populations. To provide useful indicators to test the hypotheses of this study, we identified the commonest macroinvertebrate taxa found throughout the year at both study sites (referred to as an 'oligarchy' by Pitman *et al.* (2001)). The large scale of the sampling process in this study restricted the number of fields and sites that could be evaluated. No attempt was made to compare the presence or abundance of taxa in asynchronously fallowed fields. Because this study focused on the impact of synchronous fallowing on invertebrate composition and abundance, measurements of rice yields (to evaluate the economic impact of this cropping practice) were not evaluated. We discuss future studies that could remove these limitations.

## Materials and methods

### FIELD SITES AND CLIMATE

To test the null hypothesis that small-scale synchronous cropping does not significantly increase pest densities during post-fallow periods, canopy and floodwater invertebrates were vacuum-sampled over two cropping seasons, dry (DS) and wet (WS). Macroinvertebrates were sampled in 1992–1993 in three irrigated researcher fields at International Rice Research Institute (IRRI) (14° 12' N, 121° 15' E) in Laguna Province and three fields of one farmer in Zaragoza (15° 30' N, 120° 40' E) in Nueva Ecija Province, both on Luzon Island, Philippines. The two cropping seasons were interrupted by a shorter, wet fallow at IRRI and a longer, dry fallow at Zaragoza. Asynchronous, year-round cropping has been the norm on the 182 ha experimental farm at IRRI in southern Luzon at least since the 1970s (Way & Heong 1994). Similarly, cultivation at Zaragoza is asynchronous, at least since the 1970s, due to uncoordinated releases of irrigation water (Loevinsohn *et al.* 1993); elsewhere within Nueva Ecija, however, the majority of rice fields are synchronously planted (Cabunagan *et al.* 2001).

At each site and season, planting was earlier than in most surrounding fields. At IRRI, we used three adjacent plots on the Institute's experimental farm (averaging 24 × 89 m). At Zaragoza, we used three adjacent fields on one farm (averaging 28 × 42 m). At each site, fields were separated from each other by earthen levees or bunds. Wild vegetation bordering rice fields provided refugia for certain rice pests and their natural enemies (e.g. Yu *et al.* 1996). Vegetables were important secondary crops in Nueva Ecija, especially during the DS (Heong, Lazaro & Norton 1997).

At each site, two rice crops were planted, one in the DS (14 January 1992 at IRRI, 10 February 1993 at Zaragoza) and the other in the WS (14 July 1992 at IRRI, 9 August 1992 at Zaragoza). Mean monthly temperatures varied by 4–5 °C in the DS and only 1–2 °C in the WS (12-month mean ± SE: 27.0 ± 0.4 °C for both sites). The 1992 rainfall for IRRI was 1808 mm, nearly 300 mm lower than the 1979–1982 average of 2091 mm (12-month mean ± SE: 150 ± 39.8 mm; IRRI 1993). The 1992–1993 rainfall for Zaragoza, registered at the nearby PhilRice agrometeorological

station (15° 45' N, 120° 56' E), was 1246 mm, nearly 350 mm lower than the 1985–1992 average of 1581 mm (12-month mean  $\pm$  SE: 117  $\pm$  45.1 mm; IIRRI 1993). The 6-week fallow at IIRRI, which fell between the 1992 DS and WS (30 May to 13 July), was wet (daily precipitation averaged 3.1 mm). The 12-week fallow at Zaragoza between the 1992 WS and 1993 DS (7 November to 9 February) was much drier (daily average: 0.2 mm).

#### LAND PREPARATION AND AGRONOMIC METHODS

Before planting, each field was ploughed and harrowed to puddle the soil, which was kept under standing water to lessen weed growth until rice seedlings were transplanted. Two to four seedlings per hill were transplanted by hand (25  $\times$  25 cm spacing). The seedlings were 20 days old (variety IR72 at IIRRI) or 25 days old (variety IR60 at Zaragoza). IR60 and IR72 are modern, high-yielding varieties with resistance to several rice diseases and insect pests (i.e. bacterial blight, grassy stunt, tungro, brown planthopper, green leafhopper; Khush 1989). Fertilizer was applied during the basal, maximum tillering and panicle initiation stages (see De Datta 1981 for details of stages of development) at both sites at a total rate of 120 kg ha<sup>-1</sup> N (Planters Urea 46). Metaldehyde (in 6% pellets) was broadcast at 0.5 kg a.i. ha<sup>-1</sup> 1 week before transplanting to control the golden apple snail *Pomacea canaliculata* [Lamarck] and was the only pesticide used at both sites. Except for differences in cultivar and age of rice seedlings, plot size and length of the growing season, agronomic practices were similar at both sites.

#### INVERTEBRATE SAMPLING

Canopy and floodwater invertebrates were sampled weekly at each site. The shorter growing seasons at Zaragoza permitted 12 weekly samples compared with 15 at IIRRI. Comparisons were based on the first 12 weekly samples. At IIRRI, the first samples were collected on 23 January 1992 [nine days after transplanting (DT) in DS] and 21 July 1992 (seven DT in WS). At Zaragoza, the first samples were collected on 20 August 1992 (11 DT in WS) and 18 February 1993 (8 DT in DS). Thus, sampling dates differed between seasons by 2 days of crop age at IIRRI and 3 days at Zaragoza.

Invertebrate sampling followed the technique used by Arida & Heong (1992) in irrigated rice fields. The sampling enclosure was a plastic barrel that measured 45 cm in diameter (0.16 m<sup>2</sup> planar area) and 54 cm high with its bottom removed and its top fitted with a muslin sleeve to prevent escape of mobile species. The enclosure covered four rice hills during the vegetative stage and 2–3 hills afterward. At each season and site, 60 samples randomly placed were taken from three adjacent fields at weekly intervals for a total of 3300 samples. Fresh sites were randomly selected each week. Sampling commenced at 07:00 h but varied with crop age: 2 min from seedling to maximum tillering, 3 min from maximum tillering to panicle initiation and 4 min from panicle initiation to harvest (due to increase in foliage that led to canopy closure). Thus, increasing sampling intensity over the cropping season improved the comparability of samples between sampling dates and seasons and compensated for increases in species richness and abundance of targeted invertebrates (see Appendix S1, Supporting information).

#### INVERTEBRATE IDENTIFICATIONS AND FEEDING GUILDS

Collected invertebrates (immatures, adults) were preserved in 70% ethanol and sorted and counted under a binocular microscope with

500 $\times$  magnification. Specimens were identified to the species or genus level using taxonomic keys of Barrion & Litsinger (1994) and to the family level for more difficult taxa. Taxa were grouped into functional guilds described by Schoenly & Zhang (1999): (i) detritivores (i.e. feeders on suspended particles, submerged rice straw, sediments) and tourists (i.e. non-predatory species with no known functional association with rice except for transit, shelter, sun-basking or sexual display; Moran & Southwood 1982); (ii) herbivores (i.e. feeders on rice, aquatic plants, plankton); (iii) invertebrate predators; and (iv) parasitoids and blood-feeding parasites. Each guild included the members found in the rice canopy (terrestrial) and floodwater (aquatic) zones. Guild assignments were straightforward for all but 18 taxa; as these taxa made up only 4% of the total species richness and 0.07% of the total invertebrate abundance, we discarded them from the analysis.

#### DATA ANALYSIS

Differences between sampling dates, growing seasons and sites were assessed using graphical and statistical measures: (i) triangle graphs, (ii) matched rank-abundance plots (Longino & Colwell 1997), (iii) the Morisita–Horn–Wolda (MHW) index of community similarity (Morisita 1959; Horn 1966; Wolda 1981) which weights abundant species more than rare species and returns high values when abundant species occur in both samples (Krebs 1999); (iv) Spearman's rank-correlation test ( $R_s$ ), adjusted for ties (Daniel 1990); and (v) Mann–Whitney test for medians (Daniel 1990). All statistical tests were judged at the nominal level of significance ( $P = 0.05$ ). Bonferroni or sequential Bonferroni adjustment was deemed inappropriate in this analysis because only a small fraction of the comparisons tested under the null hypothesis, i.e. that adjusted median densities for WS taxa were similar to median densities of DS taxa, was rejected. Consequently, Bonferroni or sequential Bonferroni adjustment would only have strengthened this conclusion by reducing the number of nominally significant results.

## Results

#### THE FAUNA

More than 340 000 invertebrate specimens, belonging to at least 24 orders, 147 families and 444 genera or species (after excluding the 18 unclassified taxa mentioned in 'Materials and methods'), were identified from the two field sites. Invertebrate abundances were 2–2.8 times higher in the dry season than the wet season (Table 1). Of the 444 taxa, 33% occurred in both seasons at both sites; these shared taxa included 87% of the > 340 000 individuals, indicating that the shared taxa were most abundant. Regardless of season or site, detritivores and planktonic feeders (e.g. chironomid and mosquito larvae, ostracods, springtails), collected mostly from the water column and sediments, were the most abundant guild, followed by natural enemies (i.e. arthropod predators, insect parasitoids) and herbivores, both of which came mostly from the canopy (Table 1). Predatory taxa outnumbered parasitic and herbivorous taxa in both seasons at IIRRI and the WS at Zaragoza (Table 1).

For the 198 taxa recorded in both seasons at IIRRI and the 194 taxa recorded in both seasons at Zaragoza, rank of

**Table 1.** Invertebrate fauna in the IRRI and Zaragoza irrigated rice fields in pre- and post-fallow crop seasons

Group	IRRI Research Farm		Zaragoza Farmers' Fields	
	Pre-fallow (DS 1992)	Post-fallow (WS 1992)	Pre-fallow (WS 1992)	Post-fallow (DS 1993)
Total No. organisms	96 258	47 983	52 854	146 981
Total No. taxa	306	248	241	250
No. terrestrial organisms	54 908 (264)	28 036 (215)	33 131 (207)	81 081 (215)
No. aquatic organisms	41 350 (42)	19 947 (33)	19 723 (34)	65 900 (35)
No. herbivores	25 052 (82)	9750 (70)	14 927 (71)	32 509 (88)
No. predators	30 080 (99)	16 428 (93)	16 321 (87)	31 560 (84)
No. parasitoids or parasites	3986 (78)	2546 (51)	2742 (46)	5830 (38)
No. detritivores or tourists	37 140 (47)	19 259 (34)	18 864 (37)	77 082 (40)

For each habitat and feeding guild, the number of taxa appears in parentheses.

abundance in one season was positively correlated with rank of abundance in the other season, according to Spearman rank-correlation tests (IRRI:  $R_s = 0.751$ ,  $P \leq 0.01$ ; Zaragoza:  $R_s = 0.697$ ,  $P \leq 0.01$ ). Because this is a nonparametric test of ranks, the numerical abundances of the most abundant taxa at each site (i.e. chironomids at IRRI and sminthurid collembolans at Zaragoza) had no quantitative effect on the correlations. Species that were locally abundant in one sample tended to be collected in many samples and on most sampling dates. Positive correlations between local abundance and spatial frequency (defined as the total number of samples in which the taxon occurred) were highly significant for each pairwise comparison of sites and seasons (range of Spearman  $R_s = 0.981$ – $0.988$ ,  $P < 0.01$ ). Correlations between local abundance and temporal frequency (defined as the number of sampling dates over the season in which that taxon appears) were also positive and significant for each comparison of seasons and sites (range of Spearman  $R_s = 0.884$ – $0.916$ ,  $P < 0.01$ ).

#### OLIGARCHY TAXA

Because of the very large number of taxa in the invertebrate fauna, we decided to use the commonest species as indicators of the faunal impact (or lack thereof) of fallowing, season and site. In tropical irrigated rice, the common invertebrate taxa often include the most serious insect pests, their most effective natural enemies (i.e. arthropod predators, insect parasitoids) and detritivores living in paddy sediments (e.g. Settle *et al.* 1996; Schoenly *et al.* 1998). Distinguishing common species from rare species required setting arbitrary thresholds (Rabinowitz 1981; Hubbell & Foster 1986; Pitman *et al.* 2001). Using local abundance, spatial frequency and temporal frequency (as described above), we identified three thresholds applicable to both seasons at IRRI and Zaragoza. These thresholds picked out 33 common taxa and sorted them by decreasing total abundance: (i) group 1 (eight taxa):  $\geq 1\%$  of total abundance within sites,  $\geq 30\%$  of samples within sites and  $\geq 83\%$  sample dates within sites; (ii) group 2 (four taxa):  $\geq 0.50\%$  of total abundance,  $\geq 18\%$  of samples and  $\geq 58\%$  of sample dates; and (iii) group 3 (21 taxa):  $\geq 0.1\%$  of total abundance,  $\geq 4\%$  of samples and  $\geq 13\%$  of sample dates (Table 2). Of these 33 taxa, the majority were commonly reported natural enemies living in the

canopy (e.g. spiders, mirid bugs, ladybird beetles, parasitoids), followed by several pest species (the white-backed planthopper, *Sogatella furcifera* [Horvath], the zig-zagged leafhopper, *Recilia dorsalis* [Motschulsky], green leafhoppers, *N. virescens*, *N. nigropictus* [Stål], and the rice brown planthopper, *N. lugens*), and a taxonomically diverse group of insects living at or near the water surface (i.e. Veliidae, Hydrometridae, Smynthuridae, Entomobryidae, Isotomidae, Culicidae) or in paddy sediments (i.e. chironomids, Baetidae, Ceratopogonidae). Most of the 33 taxa also occur widely in wetland (irrigated and rainfed) rice elsewhere on Luzon Island in the Philippines (Schoenly *et al.* 1996; Appendix S2, Supporting information).

#### EFFECTS OF FALLOW

Fallowing did not randomize the order of abundance of common taxa. For the 33 oligarchy taxa detected in both seasons at both sites, the rank of abundance in one season was positively correlated with the rank of abundance in the other season (IRRI: Spearman's  $R_s = 0.765$ ,  $P < 0.01$ ; Zaragoza:  $R_s = 0.717$ ,  $P < 0.01$ ).

Before analysing individual taxa for seasonal differences in their median densities, WS counts were multiplied by 2.0 and 2.8 for each IRRI and Zaragoza taxon, respectively, to make them comparable to DS taxa (see 'The Fauna'). Adjusted median densities for WS taxa were found to be similar to medians of DS taxa for all but nine taxa at IRRI and seven taxa at Zaragoza (Fig. 1).

The contrasting fallows at IRRI (short and wet) and Zaragoza (long and dry) affected the oligarchy taxa in opposite ways. At IRRI, seven of the nine taxa increased in post-fallow crops, compared to only two of the seven Zaragoza taxa. The taxa that decreased significantly in post-fallow crops included two aquatic bugs, *Hydrometra lineata* Say and *Micronecta quadristrigata* Breddin, both at IRRI, and four natural enemies (spiders: *Pardosa* spp. and *Dyschiriognatha* sp., the shining flower beetle, *Stilbus* sp., and the fly, *Drapetis* sp.) and culicine mosquitoes (*Aedes* sp.), all at Zaragoza. At both sites, only green leafhoppers (*N. virescens*, *N. nigropictus*) had consistently larger post-fallow densities than pre-fallow densities, averaging five- and sevenfold increase over the two seasons at IRRI and Zaragoza, respectively. These observations

**Table 2.** Most abundant taxa common to both IRRI and Zaragoza irrigated rice fields during both pre- and post-fallow growing seasons (i.e. oligarchy taxa)

Order: Family	Genus or species	Functional group <sup>1</sup>	Habitat zone <sup>2</sup>
Group 1: ≥1% total abundance, ≥30% of the samples and ≥83% of the sample dates			
Diptera: Chironomidae	<i>Chironomus</i> spp./ <i>Cryptochironomus</i> spp. (1)	D, T	B, T
Hemiptera: Veliidae	<i>Microvelia douglasi atrolineata</i> (2)	Pr	N
Araneae: Lycosidae	<i>Pardosa</i> spp. (3)	Pr	T
Hemiptera: Delphacidae	<i>Sogatella furcifera</i> (4)	H	T
Collembola: Sminthuridae	<i>Sminthurus</i> sp. (5)	D	N
Araneae: Linyphiidae	<i>Atypena formosana</i> (6)	Pr	T
Hemiptera: Cicadellidae	<i>Recilia dorsalis</i> (7)	H	T
Collembola: Entomobryidae	<i>Sinella</i> sp. (8)	D	N
Group 2: ≥0.5% of total abundance, ≥18% of samples and ≥58% of sampling dates			
Ephemeroptera: Baetidae	<i>Baetis</i> sp. (9)	D, T	B, T
Hemiptera: Miridae	<i>Cyrtorhinus lividipennis</i> (10)	H, Pr	T
Ostracoda: Cyprididae	<i>Cyprinotus venusi</i> (11)	D	P
Diptera: Culicidae	<i>Aedes</i> sp. (12)	D, Pa	P, T
Group 3: ≥0.1% of total abundance, ≥3.8% of samples and ≥13.3% of sampling dates			
Collembola: Isotomidae	Unspecified genus and species (13)	D	N
Coleoptera: Coccinellidae	<i>Micraspis crocea</i> (14)	Pr	T
Araneae: Tetragnathidae	<i>Dyschiriognatha</i> spp. (15)	Pr	T
Hemiptera: Delphacidae	<i>Nilaparvata lugens</i> (16)	H	T
Hemiptera: Corixidae	<i>Micronecta quadristrigata</i> (17)	H	P
Coleoptera: Phalacridae	<i>Stilbus</i> sp. (18)	Pr	T
Hemiptera: Cicadellidae	<i>Nephotettix virescens</i> (19)	H	T
Hemiptera: Cicadellidae	<i>Nephotettix nigropictus</i> (20)	H	T
Ampullaroida: Ampullariidae	<i>Pomacea canaliculata</i> (21)	H	B
Diptera: Ceratopogonidae	Unspecified genus and species (22)	Pr	B, T
Diptera: Chloropidae	<i>Mepachymerus ensifer</i> (23)	H, D	T
Araneae: Tetragnathidae	<i>Tetragnatha</i> sp. (24)	Pr	T
Hemiptera: Hydrometridae	<i>Hydrometra lineata</i> (25)	Pr	N
Diptera: Ephydriidae	<i>Notiphila</i> sp. (26)	H	N
Acari: Oribatellidae	<i>Domatorina plantivaga</i> (27)	D	T
Araneae: Araneidae	<i>Araneus</i> sp. (28)	Pr	T
Coleoptera: Hydrophilidae	<i>Sternolopus</i> sp. (29)	Pr, H	P
Orthoptera: Gryllidae	<i>Anaxipha</i> sp. (30)	Pr	T
Diptera: Empididae	<i>Drapetis</i> sp. (31)	Pr	T
Coleoptera: Dytiscidae	Unknown genus and species (32)	Pr	P
Hymenoptera: Trichogrammatidae	<i>Oligosita</i> sp. (33)	Pa	T

Identification number of each taxon in parentheses.

<sup>1</sup>H, herbivore; Pr, predator; Pa, parasitoid or blood feeder; D, detritivore; T, tourist. Functional guilds of immatures and adults, if known, are shown separately.

<sup>2</sup>T, terrestrial (canopy); N, neustonic (at or near water surface); P, planktonic (water column); B, benthic (mud dweller). Habitat associations for immatures and adults are shown separately.

were the only evidence we saw that synchronous small-scale fallowing increased the abundance of an important rice pest. Fallowing depleted post-fallow populations in more Zaragoza taxa than IRRI taxa.

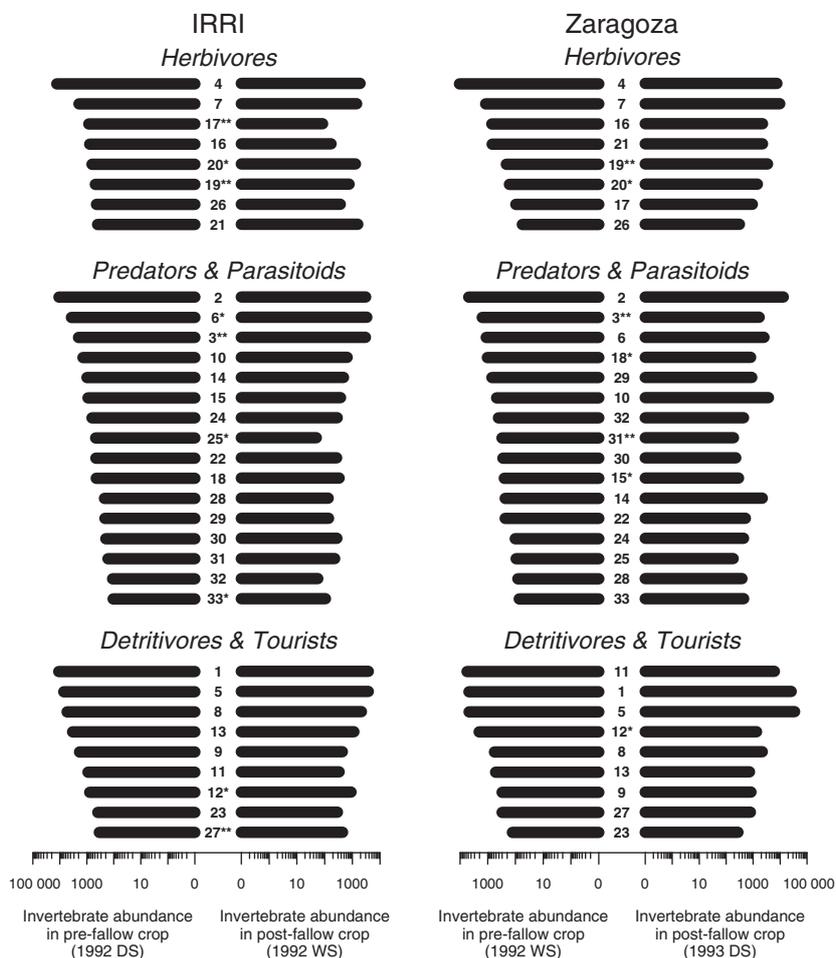
#### GUILD TEMPORAL DYNAMICS AND ACCUMULATION RATES

At the start of each growing season at both sites, detritivores and plankton feeders contributed up to 96% of the sampled individuals (Fig. 2a–d). Of the 23 common detritivore taxa, half were present in the first samples (Fig. 3g–h), compared to 30% for predators (Fig. 3c,d), 28% for herbivores (Fig. 3a,b) and 19% for parasitoids and parasites (Fig. 3e,f). Over the next several weeks,

detritivores declined monotonically while percentages of herbivores and their natural enemies (arthropod predators and insect parasitoids) increased (Fig. 2a–d). At each site and season, herbivores peaked earlier than their natural enemies, by as many as 35 days; however, natural enemies outnumbered herbivores on 78% of the sampling dates. Within 1 month of harvest at each season and site, detritivores reached a second smaller peak (Fig. 2a–d), due mostly to increases in springtails.

#### FAUNAL SIMILARITY BETWEEN SEASONS

IRRI and Zaragoza revealed similar temporal trends in taxonomic similarity between seasons for some but not all guilds, as revealed by MHW similarity. At the start of the growing



**Fig. 1.** Matched rank-abundance plots of the 33 oligarchy taxa before and after fallow at IRRI and Zaragoza. At each site, the left-most plot (with its taxa sorted by decreasing total abundance within each of the three major guilds) represents the pre-fallow crop against which the post-fallow crop is compared. The identity of each taxon, listed by its ID number (shown between the plots of each graph), is listed in Table 1. Asterisks beside taxon ID numbers indicate that the two seasonal medians are significantly different, based on Mann–Whitney nonparametric tests (\* $P < 0.05$ , \*\* $P < 0.01$ ). Before analysis, wet season abundances were multiplied by 2.0 and 2.8 for each IRRI and Zaragoza taxon, respectively, to make them more comparable to dry season abundances.

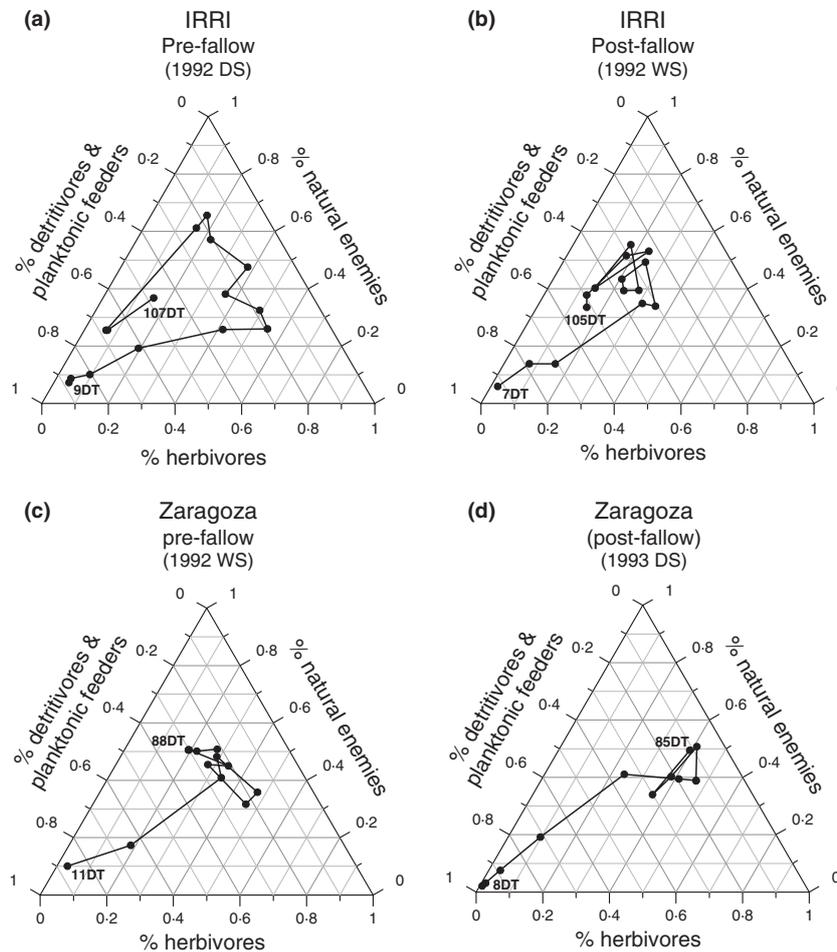
season, DS and WS faunas shared few abundant species, regardless of guild. Only herbivore similarity between DS and WS fauna rose over time at both sites, exceeding 90% MHW similarity on the last sampling dates. Unlike the other guilds, parasitoids and detritivores at both sites revealed two distinct peaks of high between-season similarity (at 15–36 DT and 64–106 DT). Over the growing season, predators yielded the highest between-season similarities (two-site mean: 55%), followed by herbivores (52%), detritivores and planktonic feeders (49%), and parasitoids and parasites (32%).

For taxa reported in both seasons at each site, abundance ranks were positively and significantly correlated between pre- and post-fallow crops on 93% of the sampling dates for predators, 67% for herbivores, 63% for detritivores and plankton feeders, and 33% for parasitoids and parasites, according to Spearman rank-correlation tests. Therefore, on most sampling dates over the growing season, taxa that were recorded in both seasons had similar abundance ranks in all guilds except parasitoids and parasites.

## Discussion

To our knowledge, this is the first field study to test empirically the prediction of Ives & Settle (1997) that small-scale synchronous cropping of tropical irrigated rice, embedded in asynchronously cropped landscapes, maintains low pest densities year round. We found that fallowing did not notably affect invertebrate faunal composition (Tables 1 and 2), guild and community structure (Fig. 1), time-specific trajectories (Fig. 2) and accumulation rates (Fig. 3) between seasons at either site.

Total invertebrate abundance was at least twice higher in the DS than the WS (Table 1); this trend is consistent with the two-thirds higher rice yields Philippine farmers achieve in the DS than that in the WS in the same fields under low-pesticide conditions (Islam & Heong 1997). Most invertebrate individuals belonged to 33 taxa (Table 2). Despite the longer and drier fallow at Zaragoza, these abundant taxa had neither more frequent nor wider differences in pre- and post-fallow densities than at IRRI (Fig. 1). However, more taxa at

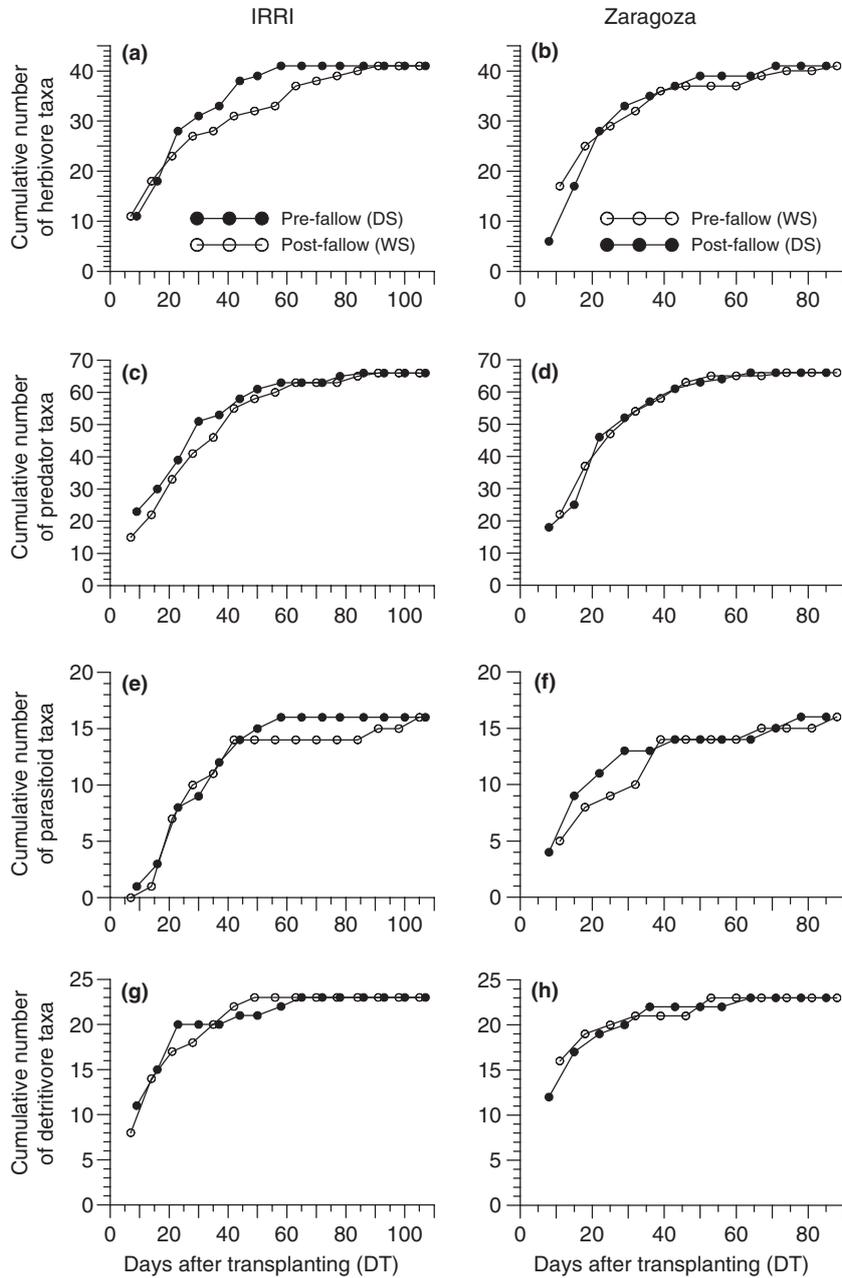


**Fig. 2.** Temporal variation in percentage abundances of herbivores (%H), natural enemies of herbivores (%E), and detritivores and planktonic feeders (%D & PF), as proportions of the sum of the abundances of these three guilds, sampled on 15 dates from IRRI (a, b) and 12 dates from Zaragoza (c, d) during the pre-fallow (a, c) and post-fallow seasons (b, d). Numbers in each graph are days after transplanting (DT) for the first and last sampling dates. For example, 9 DT in the lower left corner of (a) means that most individuals were detritivores and planktonic feeders 9 days after transplanting; on subsequent sampling dates, %D & PF fell while %H and %E rose. Percentages are based on invertebrate counts per 60 samples per sampling date.

Zaragoza than at IRRI had smaller densities in post-fallow crops, including four natural enemies (*Pardosa* spp., *Stilbus* sp., *Drapetis* sp., *Dyschiriognatha* sp.). Except for significantly higher green leafhopper populations (*N. virescens*, *N. nigropictus*) in post-fallow crops, as Widiarta *et al.* (1990) reported in WS crops, our results showed that, when embedded in large-scale asynchronous planting, small-scale synchronous planting in molluscicide-only fields using pest- and disease-resistant rice varieties (IR60, IR72) did not notably increase pest densities in post-fallow crops. This finding upheld the prediction of Ives & Settle (1997).

In asynchronously cropped tropical rice landscapes, several mechanisms and practices ensure between-field and between-season exchanges of rice-invertebrate populations that can preserve post-fallow faunas. Wind-assisted migration (Rosenberg 1981; Hokyo & Norton 1996) ensures insect exchanges locally (between fields) and regionally (between islands). Vegetation bordering rice fields provides year-round refugia for certain rice pests and their natural enemies. For example, the egg parasitoids *Anagrus* spp. and *Oligosita* spp. of rice leafhoppers

and planthoppers live in nearby *Echinochloa*- and *Leptochloa*-rich habitats, respectively, while parasitizing other leaf- and planthopper species there (Yu *et al.* 1996). Other grasses bordering the crop (e.g. *Paspalum* spp.) support sizeable populations of gryllid crickets (e.g. *Anaxipha longipennis* [Serville], *Metioche vittaticollis* [Stål]) that are efficient predators of rice leafhopper eggs (de Kraker 1995). Fallow fields harbour spiders that live in soil crevices or on levees and remain there or migrate to non-rice habitats (Arida & Heong 1994). Nearby water sources (i.e. irrigation canals, drainage ditches, rivers and streams) harbour aquatic taxa that recolonize rice fields and may influence species accumulation rates (Fig. 3g–h), species richness (Roger 1996) and vector management (Mogi & Miyagi 1990), especially during the WS. Finally, practices that conserve and enhance natural enemy populations may potentially reduce the rates at which pests adapt to and overwhelm pest-resistant rice (Heinrichs 1992; Gallagher, Kenmore & Sogawa 1994). In sum, when embedded in asynchronous cropping on larger, regional scales, small-scale synchronous planting with low-pesticide inputs and pest-resistant varieties



**Fig. 3.** Cumulative number of herbivore (a, b), predator (c, d), parasitoid or parasite (e, f) and detritivore or planktonic or tourist (g, h) taxa, common to both seasons and sites, as a function of days after transplanting (DT). The pre- and post-fallow curves are notably similar.

need not induce pest outbreaks or notably diminish populations of natural enemies.

Future field studies on this topic should measure rice yields in otherwise comparable replicated sets of small fields, some of which are planted synchronously while others are planted asynchronously (controls), in addition to following the invertebrate communities. Our use of different rice varieties at different sites (IR60, IR72) did not allow us to test for the effect of varietal differences on the invertebrate community. Beyond differences in architecture, colour and phenology, rice varieties may produce different volatile chemicals that may affect interactions between pests and natural enemies (e.g. Bottrell, Barb-

osa & Gould 1998). Consequently, another question for the future is whether varietal differences impact invertebrate faunal composition, guild and community structure, time-specific trajectories, or accumulation rates. To get around the prodigious amount of taxonomic labour required for the present study, future studies could focus on the ubiquitous invertebrate taxa identified here or the equivalent dominant species in other settings (see Appendix S2, Supporting information).

Only tentative management recommendations can be derived from our work because observations of the effects on rice yield of small-scale synchronous following are still needed. Our results suggest that small-scale synchronous following,

when embedded in asynchronously planted landscapes, does little harm to biological regulation of the invertebrate faunal community and may be adopted as part of integrated pest management when it serves other purposes.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Results of the sensitivity analysis of the invertebrate sampling programme and the suction device.

**Appendix S2.** Invertebrate oligarchies in Philippine wetland rice.

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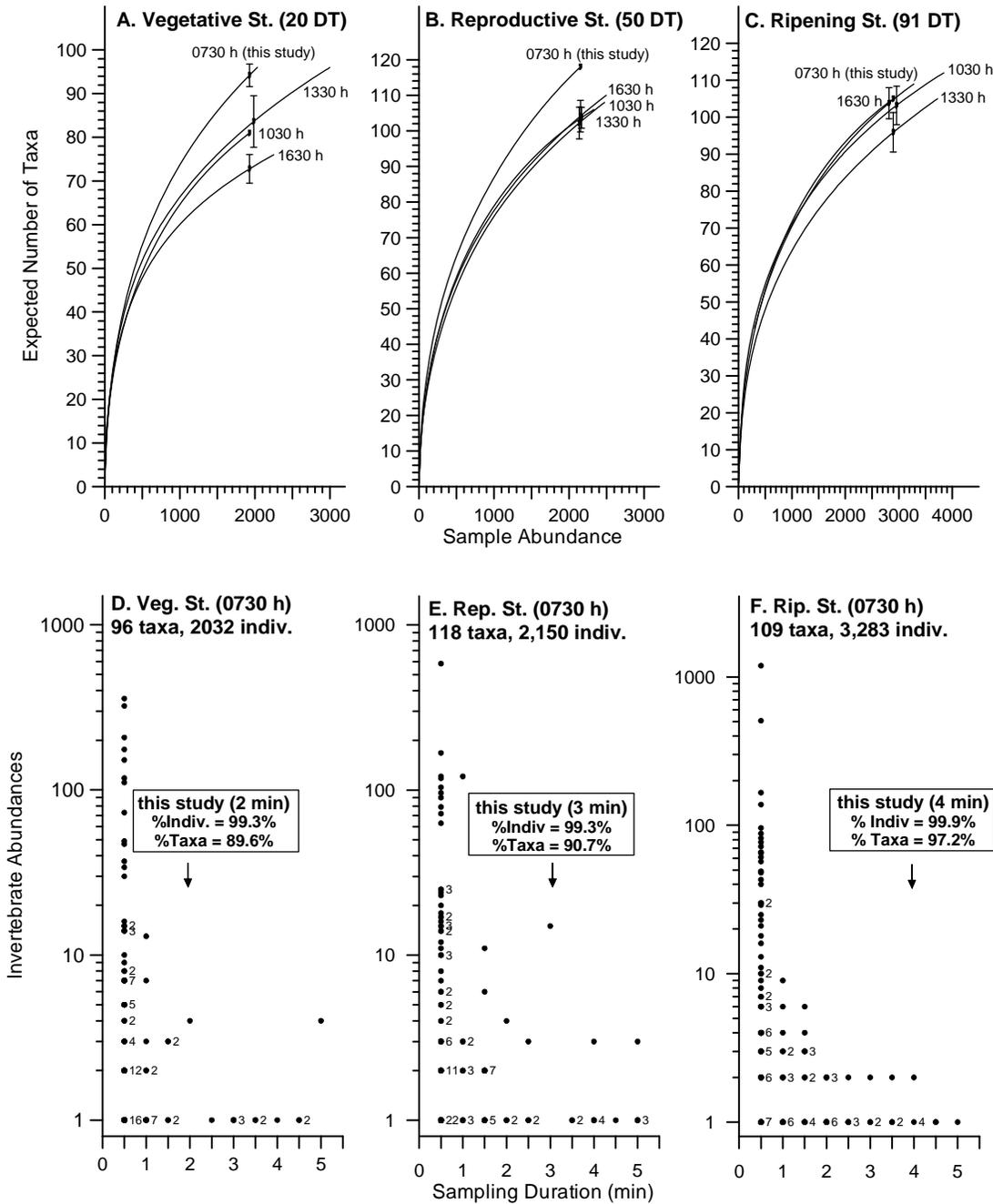
**Appendix S1.** Results of the sensitivity analysis of the invertebrate sampling programme and the suction device.

Kenneth G. Schoenly, Joel E. Cohen, K.L. Heong, James A. Litsinger, Alberto T. Barrion, and Gertrudo S. Arida. Fallowing did not disrupt invertebrate fauna in Philippine low-pesticide irrigated rice fields

Performance tests of the sampling programme and suction device were conducted at IRRI Farm during WS 1998. In these tests, 10 sites were sampled in the same field at 4 different times of day (0730, 1030, 1330, 1630 h) during each of three crop stages: vegetative (20 DT), reproductive (50 DT) and ripening (91 DT) (De Datta 1981). After standardizing (rarefying) invertebrate abundances to a common size, samples taken in the early morning (0730 h) were found to contain significantly more invertebrate species than those taken later in the day, at least during the vegetative and reproductive stages (Fig. S1A-B). After canopy closure (i.e. ripening stage), samples yielded nearly identical counts of taxa, regardless of time of day (Fig. S1C).

Results from the 0730 h samples showed that the most abundant taxa were captured within the first minute of sampling (Fig. S1D-F). By two minutes, 90, 87 and 86% of the taxa were captured during the vegetative stage, reproductive and ripening stages, respectively, justifying the need to increase sampling intensity over the growing season. By the end of three minutes at the reproductive stage and four minutes at the ripening stage – the sampling intensities used in the present study – percentages of taxa (91% and 97%) nearly bracketed those of the vegetative stage at two minutes. Thus, increasing sampling intensity over the cropping season compensated for increases in species richness and abundance, at least up to the reproductive stage, and improved the comparability of samples between sampling dates and seasons.

**Figure S1.** Panels A-C are rarefaction curves (mean  $\pm$  2SD) for rice invertebrates suction-sampled from 10 sites four times during the day (0700, 1030, 1330, 1630 h) at the vegetative (20 DT), reproductive (50 DT), and ripening (91 DT) stages at IRRI Farm during DS 1998. Panels D-F show the effect of sampling intensity on the invertebrate catch at 0730 h in which vials were replaced every 30 sec over a 5-min sampling period. Numbers besides data points are the number of taxa with the same abundance.



The suction apparatus used in this study sampled the canopy with greater efficiency than the floodwater (Schoenly & Domingo 1998, Schoenly et al. 2003) and probably undersampled the aquatic fauna. Although some rice ecologists have used separate devices to sample the terrestrial and aquatic faunas (Settle et al. 1996, Schoenly et al. 1998), up to 90% of the invertebrate fauna during the DS can come from the floodwater and waterlogged sediments (Schoenly et al. 1998). If this proportion held for both seasons and both sites, then the suction sampler may have undersampled the aquatic fauna by as much as 50% (Table 1). Since taking these samples in 1992-93, we field-tested a modified version of the area sampler (Takahashi et al. 1982) for collecting aquatic invertebrates in tropical irrigated rice. The modified area sampler yielded 2-5 times more organisms and taxa than our suction sampler, depending on crop stage. However, after standardizing (rarefying) abundances to a common sample size, both methods gave statistically comparable species richness regardless of crop stage (Schoenly and Domingo 1998). Thus if aquatic populations were undersampled by the suction sampler, species richness may have been unaffected, for the given sample size.

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**Appendix S2.** Invertebrate oligarchies in Philippine wetland rice.

Kenneth G. Schoenly, Joel E. Cohen, K.L. Heong, James A. Litsinger, Alberto T. Barrion, and Gertrudo S. Arida. Fallowing did not disrupt invertebrate fauna in Philippine low-pesticide irrigated rice fields

In this study, most invertebrate abundance came from 33 taxa, whose large local abundances and high spatiotemporal frequency in the samples formed an “oligarchy” (Pitman et al. 2001) reported year round at both sites. These taxa affected rice production and ecological processes as pests of rice, natural enemies of rice pests (i.e., arthropod predators, insect parasitoids), and nutrient recyclers.

This invertebrate oligarchy occurs widely in Philippine wetland (irrigated and rainfed) rice (Table S2.1). A species-by-site matrix, originally containing 648 taxa (rows) and 13 sites (columns) representing 7 provinces on 2 islands, was constructed in 1992. Cells of the matrix specified each species’ presence or absence. Rows included terrestrial (canopy) taxa and some aquatic (i.e., neustonic, planktonic, benthic) taxa. Of the 33 “oligarchy” taxa, 22 were included in the matrix below (Table S2.2). After the two study sites were deleted from the matrix, 20 of the 22 oligarchy taxa were present at all 11 of the remaining sites. The remaining two oligarchy taxa were present at 5 or fewer sites. The 22 oligarchy members were widespread across many rice-growing areas that spanned thousands of square kilometers. Whether they comprised the dominant 0.1% or more of the total invertebrate catch at these sites awaits further investigation.

**Table S2.1.** Presence/absence matrix of the 22 oligarchy taxa at 13 Philippine sites.

## Legend of 13 Philippine Sites

- |                                 |                                   |
|---------------------------------|-----------------------------------|
| A. IRRI Farm, Laguna Province   | G. Cabanatuan, N. Ecija Province  |
| B. Manaoag, Pangasinan Province | H. Zaragoza, N. Ecija Province    |
| C. Santa Maria, Laguna Province | I. Bayombong, N. Vizcaya Province |
| D. Victoria, Laguna Province    | J. Banaue, Mountain Province      |
| E. Bay, Laguna Province         | K. Kiangon, Mountain Province     |
| F. Guimba, N. Ecija Province    | L. Solana, Cagayan Province       |
|                                 | M. Oton, Iloilo                   |

**Table S2.2.** Twenty-two oligarchy taxa by 11 site matrix (presence = 1, absence = 0). The two sites of the study, IRRI (A) and Zaragoza (H), were excluded from the matrix.

Taxon	Sites										
	B	C	D	E	F	G	I	J	K	L	M
<i>Pomacea canaliculata</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Microvelia douglasi atrolineata</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Sogatella furcifera</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Atypena (=Callitrichia) formosana</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Recilia dorsalis</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Pardosa spp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Cyrtorhinus lividipennis</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Micraspis crocea</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Dyschiriognatha spp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Nilaparvata lugens</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Nephotettix nigropictus</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Tetragnatha sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Nephotettix virescens</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Stilbus sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Araneus sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Drapetis sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Oligosita sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Notiphila sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Hydrometra lineata</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Sternolophus sp.</i>	1	0	1	1	0	1	0	0	0	0	1
<i>Anaxipha sp.</i>	1	1	1	1	1	1	1	1	1	1	1
<i>Sminthurus sp.</i>	0	0	0	0	0	1	0	0	1	0	0

Three of the most abundant oligarchy taxa – midges, ostracods and snails – browse on epipellic algae at the soil-water interface and, together with protozoans and rotifers, recycle nutrients from decaying plant and animal sources (Roger 1996). These organisms and oligochaetes increase in abundance when N-fertilizer, pesticides, and green and animal manure

are applied (Simpson et al. 1993a, 1994a, b; Settle et al. 1996). Although chironomids feed mostly on sediments, a few genera (e.g., *Chironomus* and *Cricotopus*), also feed on roots and sometimes shoots of young rice seedlings (Stevens et al. 2006). Midges have also been documented as significant rice pests in temperate rice-growing countries (Jones 1968; Ferrarese 1992; Stevens et al. 2000). Because chironomids may be eaten by early-arriving predators of rice pests (e.g., spiders), Yasumatsu et al. (1979) warns that ignoring midges “may give unreliable information on the development of integrated rice pest control”. Ostracods are so ubiquitous in temperate and tropical rice fields (Roger 1996) that their high local dominance and widespread spatiotemporal distributions (Victor & Fernando 1980; cited by Roger 1996) make them ideal surrogates of the entire floodwater fauna (Schoenly et al. 1998). The golden apple snail (*P. canaliculata*), introduced to the Philippines from South America as a potential livelihood project (Naylor 1996), became a significant pest of irrigated and rainfed rice throughout southeast Asia in the 1980s (Joshi & Sebastian 2006). In non-rice ecosystems, this snail transforms macrophyte-dominated, clear-water wetlands to turbid, algae-dominated states, altering both ecosystem function (Carlsson, Bronmark & Hansson 2004) and the value of ecological services the wetland provides (Jeppesen et al. 1998).

The rice brown planthopper, *Nilaparvata lugens* (BPH), the most serious acute insect pest of tropical Asian rice (Kenmore et al. 1984), averaged only 973 individuals per season per site and occurred in only 33% of samples per season per site (Table 2, Group 3). Its principal natural enemies, also present in Table 2, especially wolf spiders (*Pardosa* spp.), veliid bugs (*Microvelia douglasi atrolineata* Bergroth), and mirid bugs (*Cyrtorhinus lividipennis* Reuter), are important agents in the biological control of BPH (e.g., Heinrichs & Mochida 1984; Kenmore et al. 1984). Because our study was conducted in low pesticide fields, the omission of BPH from Groups 1

and 2 in Table 2 was expected, however, its presence in the Group 3 list suggests that its densities remain high despite high predation pressure on BPH-resistant varieties (IR60 and IR72).

The details of Table S2 should be interpreted cautiously because not all of the sites may have used the same sampling plan and, while all the included sites were wetland (irrigated and rainfed) rice, they may have differed in other ecological attributes. That the sites were so similar in the ubiquitous species reported indicates the robustness of this invertebrate oligarchy.

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