

Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines

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Abstract

The above-water food webs of arthropod communities in irrigated rice fields on Luzon Island, Philippines, were studied over the growing season at five sites (Los Baños, Cabanatuan, Bayombong, Kiangan, Banaue) ranging in elevation from 22 m to 1524 m. Arthropod populations were vacuum-sampled at roughly weekly intervals from the date after seedlings were transplanted to flowering at each site. Site- and time-specific webs were constructed from a 687-taxa cumulative Philippines web and time-series of species present. Taxonomic composition, food web structure, and arthropod phenology were broadly similar across different sites. Arthropod abundance was inversely associated with altitude across the five sites, but numbers of taxa and links and six food web statistics showed no obvious increasing or decreasing trend with altitude. The rise of taxa, links and mean food chain length over the growing season at each site reflected an increase in plant size with age and, at some sites, an orderly accumulation of newly arriving herbivore, predator, parasitoid and omnivore species. At each site, herbivores built up faster than predators and parasitoids, and predators arrived faster than parasitoids; the difference between the latest and earliest sampling dates of first arrivals, averaged over the five sites, was 38, 63 and 73 days for herbivores, predators and parasitoids, respectively. Site-to-site consistencies in food web properties and first arrivals suggest that such patterns may be influenced more by crop age than by geography

or altitude. Sampled predator, parasitoid and omnivore taxa potentially encountered only a subset of their lifetime prey and predator species at any particular time in the rice field. Prey lists cumulated over time may underestimate the temporal specificity of predation by potential biological control agents. Research opportunities linking rice food webs and integrated pest management with East Indies biogeography are proposed.

Introduction

Rice is a staple food of roughly two-thirds of the human population and accounts for 5% or more of the national plant food supply grown or imported by 55% of the 146 countries listed by FAO (Prescott-Allen & Prescott-Allen, 1990). In a rice field, hundreds to thousands of different species of plants, insects, arachnids, fungi, nematodes, snails, vertebrates and other organisms are linked by a vast, intricate network of feeding relations called a food web. Food webs relate specific trophic resources and consumers to the structure and dynamics of ecological communities (Ricklefs, 1990; Pimm *et al.*, 1991; Cohen *et al.*, 1993).

Since 1977, entomologists of the International Rice Research Institute (IRRI) have been describing the food web of Philippine irrigated and rainfed rice fields at and above the water line (IRRI, 1980, 1983, 1984, 1985, 1986, 1987, 1988, 1989, 1990b). The present cumulative version of the IRRI web contains 687 taxa (pathogens, nematodes, mites, spiders, insects, snails, vertebrates) and over 10,000 trophic (consumer-resource) links, gathered from 23 sites in the Philippines. Mungbean is a popular crop grown in Asia before or after rice; its pest and predator species in the Philippines (Litsinger *et al.*, 1988) are also included in this 687-taxon cumulative web. Additional information on the food web of Philippine rice fields is available in Koch *et al.* (1990) and Settele *et al.* (1993). Way & Heong (1995) reviewed the roles of biodiversity in tropical rice integrated pest management (IPM).

Food webs of rice fields, like other food webs, vary in space and time. Schoenly & Cohen (1991) distinguished between cumulative and time-specific webs. A cumulative web is a web gathered over many occasions within specified spatial limits. A time-specific web is a web gathered over a single, relatively short time period (e.g. a specific crop growth stage). If the spatial limits include more than one site, then site-specific webs can be defined, one per site. Field studies have compared time- and site-specific webs of the same habitat type (Kitching, 1987; Winemiller, 1990), time-specific webs in different regions of the same habitat (Warren, 1989; Closs & Lake, 1994), and site-specific webs of the same habitat type in different locations (Beaver, 1985).

In this paper, we describe the rice-arthropod food web of Philippine rice fields at and above the water line at five sites along an elevational gradient. Our principal findings are that taxonomic composition and food web structure were broadly similar across sites. At each site, herbivores built up faster than predators and parasitoids, and predators arrived faster than parasitoids. Most sampled predator, parasitoid, and omnivore taxa potentially encountered only a subset of their lifetime prey and predator species at any particular time in the rice field. These observations have implications for biological pest control and for East Indies biogeography.

Natural history and growth stages of tropical rice

Asian rice (*Oryza sativa* Linnaeus) is an annual grass with hollow jointed culms, sessile leaf blades, and a terminal panicle (Chang & Bardenas, 1965). Like other members of tribe Oryzaceae, rice can grow in standing water, is wind-pollinated, and varies in height from 0.3 m (dwarf mutants) to 7 m (floating varieties). In tropical Asia, rice is either directly seeded or is transplanted into flooded fields as 9–11 or 16–20 day-old seedlings.

The development of a typical rice plant can be divided into three phases: vegetative (seedling germination to panicle initiation, 55 days or more), reproductive (panicle initiation to booting to flowering, ca. 35 days), and ripening (flowering to grain maturity and harvest, ca. 30 days). For tropical rice, the period from germination to harvest is 3–9 months, depending on the season, climate, and cultivar used. The vegetative stage is highly variable in duration between cultivars, while the reproductive and ripening stages for different cultivars vary less.

Field sites

The study was conducted in irrigated fields at five sites on Luzon Island, Philippines, ranging in elevation from 22 m to 1524 m. Farmers' fields were used at four sites (Cabanatuan, Bayombong, Kiangnan, Banaue). The fifth site was a standard experimental plot on the IRRI Central Farm in Los Baños. Except for Los Baños, the immediate surroundings of each site were dotted with an occasional farmhouse encircled by a small grove of coconut palm, banana and other vegetation. Figure 1 gives the location of each site. Because local weather data for Cabanatuan, Bayombong and Kiangnan are unavailable, climate summaries for only IRRI and the Agromet stations at Banaue and Guimba are shown in fig. 1.

These tropical sites have cool dry (November–April) and hot wet (May–October) seasons. This study began in the dry season when, generally, solar radiation is highest and relative humidity is lowest (IRRI Dryland longterm averages: 20.4 MJ m⁻² d⁻¹ and 74%, both in April; IRRI, 1990a). We now briefly describe each site.

Los Baños

This site is a lowland irrigated field on the Central Farm at IRRI in Los Baños, Laguna Province, in southern Luzon, 14°12'N, 121°15'E, 22 m elevation. At IRRI and along the flood plain bordering Laguna de Bay, rice is double cropped. Fieldwork was conducted on a standard IRRI plot of 25 m × 100 m. Rice seedlings were transplanted on 10 June and arthropod samples were collected from 23 June to 18 August on nine sampling dates; the average interval between consecutive sampling dates was 7.0 days (SD=0 days). Los Baños was slightly wetter during 1989 (2343 mm

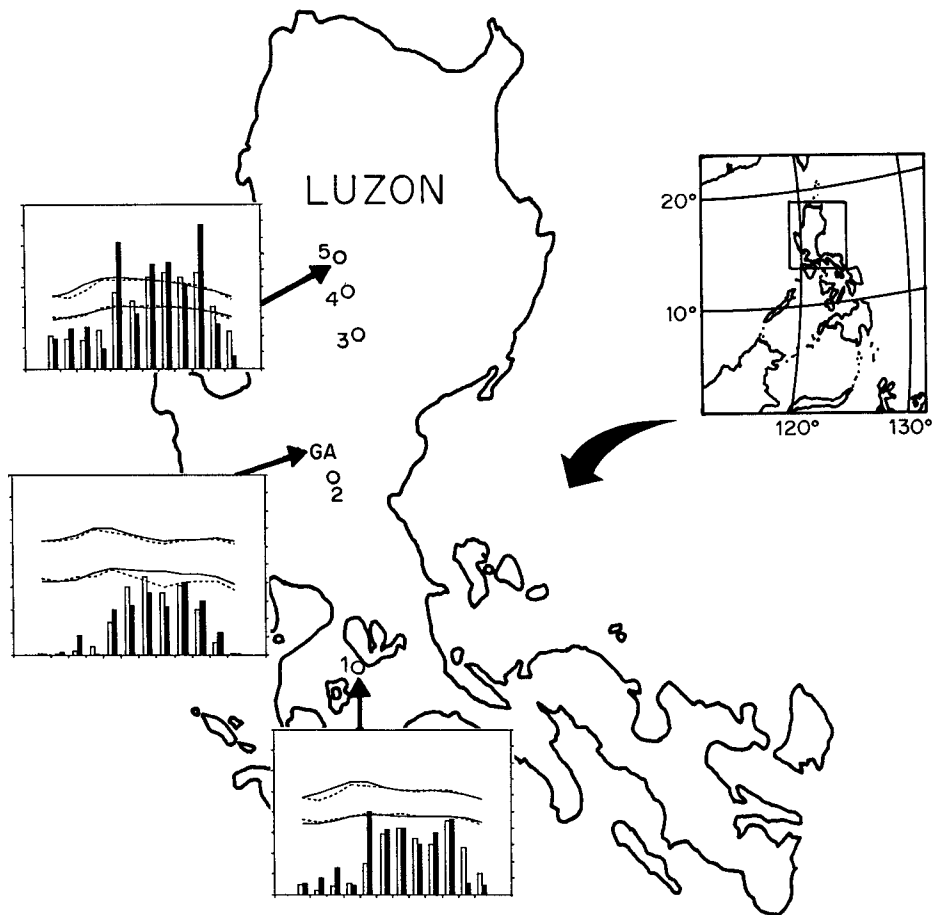


Fig. 1. Five rice-growing sites on Luzon Island, Philippines. 1, Los Baños; 2, Cabanatuan; 3, Bayombong; 4, Kiangnan; 5, Banaue; GA, Guimba Agrometeorological station. Values on each diagram are as follows: mean monthly precipitation in increments of 100 mm (left margin) for 1989 (black bars) and multiple years (white bars, see text), mean monthly temperatures (maximum and minimum) in increments of 5°C (right margin) for 1989 (dashed line) and multiple years (solid line, see text), and one month intervals beginning with January on the left (horizontal axis).

precipitation) than the annual longterm (1979–1991) average of 2113 mm for this site (fig. 1). During 1989, 11 tropical storms brought heavy monsoon rains to Los Baños (IRRI, 1990a).

Cabanatuan

This site is located in central Luzon, the heart of the Philippine 'rice bowl', in Nueva Ecija Province, 15°30'N, 121°15'E at 61 m elevation. Rice fields occupy over 95% of the land area and the typical cropping pattern is two crops with a fallow period in June. The observational plot was a rectangular field, 61 m average length × 52 m average width (approximate area: 3200 m²). Rice seedlings were transplanted on 9 February and arthropod samples were collected from 15 February to 29 April on eight sampling dates; the average interval between consecutive sampling dates was 10.3 days (SD=4.1 days). In 1989, rainfall for the Cabanatuan-Bayombong region (as registered at the Guimba Agromet) was 1649 mm, 36 mm lower than the annual longterm (1986–1991) average of 1685 mm (fig. 1).

Bayombong

This site is located in Nueva Vizcaya Province, 16°29'N, 121°09'E at 305 m elevation at the northernmost edge of Central Luzon's 'rice bowl'. Rice is cropped continuously throughout the year. The observational plot was a nearly square field, 31 m average length × 28 m average width (approximate area: 900 m²). Rice seedlings were transplanted on 5 January and arthropod samples were collected from 16 January to 8 April on 11 sampling dates; the average interval between consecutive sampling dates was 8.5 days (SD=3.6 days).

Kiangnan

This mountainous site is located in northern Luzon, in Ifugao Province, 16°47'N, 121°06'E at 800 m elevation. The typical cropping pattern is rice followed by mixed vegetables and legumes in terraced and unterraced fields on gradually sloping hillsides. The observational plot was an hourglass-shaped field 90 m × 37 m at its widest point

(approximate area: 2200 m²). Rice seedlings were transplanted on 2 March and arthropod samples were collected from 9 March to 31 May on 10 sampling dates; the average interval between consecutive sampling dates was 9.2 days (SD=3.4 days). The 1989 rainfall for the Kiangnan-Banaue region (as registered at the Banaue Agromet) was 3938 mm, nearly 300 mm higher than the annual longterm (1979–1991) average of 3634 mm (fig. 1).

Banaue

This mountainous site is located in Ifugao Province, 16°55'N, 121°05'E at 1524 m elevation. Banaue is a key site for testing cold-tolerant rice cultivars and is noted for its 2000-year-old rice terraces. Rice is cropped once per year with a 4-month fallow period. The observational plot enclosed two south-facing, crescent-shaped terraces of roughly equal area, one 3 m higher than the other, along steep mountain terrain. The terraces averaged 22 m × 4 m at their widest point (approximate combined area of both terraces: 200 m²). Rice seedlings were transplanted on 2 March and arthropod samples were collected from 9 March to 20 July on 13 sampling dates; the average interval between consecutive sampling dates was 11.0 days (SD=4.7 days).

Materials and methods

Land preparation and agronomic practice

Before planting, each field was ploughed and harrowed to puddle the soil, which was kept under standing water to lessen weed growth until transplanting of rice seedlings. At each site, 25-day-old rice seedlings of IR8866, a cold-tolerant, high-yielding cultivar, were transplanted by hand in the field. Due to differences in cultivation practice and regional water availability at the five sites, planting was not synchronized across sites. Planting was synchronized with planting in surrounding fields at each site except IRRi.

Standard agronomic practices followed at each site included planting 2–4 seedlings per hill in a regular spacing pattern (25 × 25 cm) with fertilizer applied at three stages of rice growth: basal, maximum tillering, and panicle initiation, at the rate of 120 kg N (as urea) per hectare. Handweeding was usually conducted at fortnightly intervals. Harvesting and threshing of the rice crop occurred approximately 100 days after transplanting (DT) at all sites except Banaue (see Results: Field problem).

Arthropod sampling

The sampling unit was a box enclosed by mylar sheeting (0.5 × 0.5 × 0.9 m high, planar area 0.25 m²). This framed barrier encloses four hills after transplanting but fewer hills as the plants reach maximum tillering. For each site and sampling date, ten randomly placed samples were taken. All organisms inside the enclosure were vacuumed using a portable FARMCOP suction device (Cariño *et al.*, 1979). The device is a hand-carried vacuum cleaner (National, Model HC-180) powered by two 12 volt rechargeable batteries with a capacity to suck 0.8 m³ of air per minute. Organisms and water were vacuumed through a rubber collection hose (1.5 cm internal diameter × 1.5 m long) into a plastic reservoir with a nylon mesh strainer. Collected

material was flushed into a glass vial containing 70% ethanol.

In Philippine rice communities, the numbers of arthropod species and individuals increase with crop age (Kenmore *et al.*, 1984; Heong *et al.*, 1991, 1992). Because FARMCOP's capture efficiency would decrease if sampling duration was fixed over the growing season, sampling duration was increased according to the following schedule: transplanted seedling to maximum tillering (2 min), maximum tillering to panicle development (3 min), panicle development to harvest (4 min).

The samples in each vial were sorted, counted and identified using a dissecting microscope and recorded on standard data sheets. Organisms were identified to the lowest possible taxon (family, genus or species), based on Barrion & Litsinger (1994), using the reference collections in the IRRi Entomology Division. The Division houses the world's largest reference collection of rice-associated arthropods (insects, spiders, mites). The collection has 2718 identified taxa belonging to 22 orders, 189 families and 540 genera.

These samples were previously analysed by Heong *et al.* (1991, 1992). Their analyses emphasized patterns of arthropod abundance of different feeding guilds over the growing season. In the present paper, revised estimates of total plot area (see above), based on direct field measurement, replace those of Heong *et al.* (1991, 1992) for all sites except Los Baños.

The Philippine rice food web

Trophic links of the cumulative Philippines web, i.e. species A eats or parasitizes species B, were determined using various field and laboratory methods. Herbivory was verified by laboratory and field rearings, not just presence of the species on the rice plant. Predation was determined by direct field observations and verified or supplemented by laboratory preference tests on selected sets of predators and prey. Parasite–host records were determined from laboratory rearings and from exposing potential hosts (egg, larval and pupal stages) in the field to collect immature parasitoids.

Laboratory methods for recording trophic links included: a) plastic bags containing D-vac populations of pest and enemy species for observation, b) 'cafeteria' experiments in glass cages (65 × 65 × 110 cm) containing different combinations and numbers of pest and enemy species, and c) arthropod dissections. Observations in b) were taken from 30–45-day-old rice plants over three, 3-h intervals (0700–0100, 1300–1600, 1830–2130 h). In c), 50 specimens of each life-cycle stage were taken from different rice growth stages (seedbed to harvest), dissected under a microscope, and recorded for parasites. IRRi researchers have logged approximately 700 trip-days and 2300 person-hours at Los Baños, Cabanatuan, Banaue and Kiangnan elucidating consumer-resource links of the rice paddy system (A.T. Barrion, unpublished data).

Construction of site- and time-specific webs

For each site, we constructed first a site-specific web and then used the web and the phenological data to construct a set of time-specific webs (Schoenly & Cohen, 1991). Table 1 shows the steps we followed to construct the five site-specific webs. Step 1 was sampling and counting the arthropods. The number of taxa sampled at the sites, over

Table 1. Steps in construction of site-specific food webs of five Philippine rice-field sites.

Step	Site (number of sampling dates)				
	Los Baños (9)	Cabanatuan (8)	Bayombong (11)	Kiangan (10)	Banaue (13)
1. Count of arthropods in time-specific samples					
a. taxa (number/sampling date)	143 (16)	87 (11)	90 (8)	113 (11)	120 (9)
b. individuals (number/sampling date)	21725 (2414)	15500 (1938)	11321 (1029)	8300 (830)	5808 (447)
2. Matches of sample taxa to cumulative web taxa					
a. unaggregated taxa	68	49	55	65	59
b. individuals in unaggregated taxa	14520	14618	8568	6892	4485
c. aggregated taxa	27	23	24	29	23
d. individuals in aggregated taxa	1311	614	1463	572	330
3. Count of arthropods in web					
a. taxa: 2a+2c (% of 1a)	95 (66%)	72 (83%)	79 (88%)	94 (83%)	82 (68%)
b. individuals: 2b+2d (% of 1b)	15831 (73%)	15232 (98%)	10031 (89%)	7464 (90%)	4815 (83%)
4. Count of isolated taxa*					
a. taxa (% of 3a)	5 (5%)	3 (4%)	3 (4%)	3 (3%)	1 (1%)
b. individuals (% of 3b)	136 (0.9%)	37 (0.2%)	72 (0.7%)	9 (0.1%)	8 (0.2%)
5. Final count or organisms in web					
a. taxa: 3a-4a+rice (% of 1a)	91 (64%)	70 (80%)	77 (86%)	92 (81%)	82 (68%)
b. individuals: 3b-4b (% of 1b)	15695 (72%)	15195 (98%)	9959 (88%)	7455 (90%)	4807 (83%)

*Organisms without known predators and prey at this site. See text.

all sampling dates, ranged from 87 at Cabanatuan to 143 at Los Baños (step 1a, table 1). The number of individual arthropods belonging to these taxa ranged from 5808 at Banaue to 21,725 at Los Baños (step 1b, table 1).

Step 2 in constructing the site-specific web was matching the taxa of the site-specific samples with the taxa of the cumulative Philippines web. Matching was straightforward for those taxa for which taxonomic resolution in the samples was identical to that of the Philippines web (unaggregated taxa, steps 2a–b, table 1). For other taxa, the samples had slightly coarser taxonomic resolution than the Philippines web (aggregated taxa, steps 2c–d, table 1). For example, in the Philippines web there are eight chrysomelid beetles, each identified to genus or to species; in the site samples, chrysomelids were lumped as a single (family-level) taxon. To match the taxa of the samples to those of the web, we resorted to taxonomic aggregation. Whenever a genus- or family-level taxon occurred in a site list, we searched the cumulative Philippines web for congeneric or confamilial members of that taxon and treated them as one. A species-by-site matrix containing 648 taxa (rows) of the cumulative Philippines web and 23 sites (columns) within the Philippines, including our five study sites, guided the choices of which taxa and how many to aggregate. The taxon with the lowest identification number in the matrix was arbitrarily chosen as the 'reference taxon' to which all site-specific taxa in the same genus or family would be aggregated. All prey and predator links of each taxon aggregated to a reference taxon were added to the prey and predator links, respectively, of the reference taxon. This process was repeated for each of the aggregated taxa at each site.

Step 3 summed the matching unaggregated and aggregated taxa. The percentages of matching taxa varied from 66% at Los Baños (95/143) to 88% at Bayombong (79/90). The percentage of matches was higher for individuals than for taxa at each site. The former ranged from 73% at Los Baños (15831/21725) to 98% at Cabanatuan (15232/15500).

Matching taxa included all species in the grazing, terrestrial and aquatic-surface portions of the rice food web.

Unmatched taxa included arthropods that ate detritus, species in the submerged lentic community, and taxa associated with vegetation other than rice. The percentage of unmatched taxa ranged from 12% at Bayombong to 34% at Los Baños.

In constructing site-specific webs from the matching taxa, we assumed that consumer A ate or parasitized resource B at a site, if, and only if, A ate or parasitized B in the cumulative Philippines web and species A and B occurred at this site (as in Schoenly & Cohen, 1991). Species A was recorded as eating or parasitizing species B, if at least one life-cycle stage of species A eats or parasitizes at least one life-cycle stage of species B.

Step 4 identified those taxa that were neither prey nor predator to any other species in the site-specific web. These 'isolated taxa' comprised 1–5% of the matching taxa and 0.1–0.9% of the matching individuals. They included orthopterans, *Velarifictorus aspersus* (Walker) (Gryllidae) and *Atractomorpha psittacina psittacina* (de Haan) (Pyrgomorphidae), thrips, dytiscids (*Bidessus* sp.), hydrophilids (*Berosus* sp.), and ceraphronid (*Ceraphron* sp.) and diapiiid wasps. The existence of isolated taxa indicates only that no predators and prey are known for these taxa at a site. Due to the low numbers of isolated taxa, we excluded them from each site-specific web. This procedure only marginally reduced the final counts of taxa and individuals (step 5a–b, table 1).

Time-specific webs for each site were constructed from the corresponding site-specific web and the phenological table for the site. An entry in a phenological table was the sampled abundance of the corresponding taxon (row) on the specified date (column). As with the site-specific webs, we assumed that consumer A ate or parasitized resource B in a time-specific web if and only if, in the site-specific web, species A ate or parasitized B and both occurred at the time of sampling. Because of differences in the time interval between samples and in the length of the growing season at different sites, the number of time-specific webs varied, ranging from eight (Cabanatuan) to 13 (Banaue) webs. A machine-readable version of the cumulative Philippines web and its species list, and cumulative site- and time-specific

webs from each of the five sites and their species lists have been deposited in the IRRI Entomology and Plant Pathology Division. The cumulative Philippines web will be described and analysed elsewhere (in preparation).

Community statistics

We assessed variation among sites and sampling dates by using nine statistics: one measure of community similarity (a), six measures of food web structure (b–g), and cumulative (over time) tallies of species and links (h–i).

The first statistic (a) used taxonomic data to determine community differences between pairs of sites:

(a) C_λ , degree of taxonomic similarity between two communities, formulated by Morisita (1959) for counts of individuals (see Krebs (1989) for equation and worked example). For each pair of sites, C_λ was calculated twice: once using individuals belonging to all the sampled taxa, and a second time using individuals belonging to the taxa only of the site-specific webs from each pair of sites. C_λ ranges from zero (no similarity) to 1.0 (complete similarity). According to Wolda (1981), Morisita's index is the best overall measure of ecological similarity (from Krebs, 1989).

The next six (b–g) statistics apply to both time-specific and site-specific webs:

(b) S , the number of taxa reported in the web.

(c) L , the number of consumer-resource links, including cannibalistic, interspecific, and loop-forming links (see below).

(d–f) B , the percentage of basal species in the web (i.e. 100 times the number of species with no reported prey, divided by S); I , the percentage of intermediate species (i.e. 100 times the number of species with both predators and prey, divided by S); and T , the percentage of top predators (i.e. 100 times the number of species with no reported predators, divided by S). Basal species here include rice and herbivores of plants other than rice in the rice field. Top predators are species without reported predators (some cannibalistic species were included as top predators). Because vertebrates were not collected in this study, top predators here are arthropod species without arthropod consumers.

(g) μ , the mean chain length of the web, i.e. the average length (counting links, not species) of all maximal food chains from a basal species to a top predator (Cohen, 1978). For each site- and time-specific web, μ was calculated using the long-way-up algorithm of Cohen & Luczak (1992).

Cannibalism occurred in nearly all site- and time-specific webs. All reported cases of cannibalism occurred among spiders. Mutual predation occurred in only a few site- and time-specific webs. Tetragnathid spiders (e.g. *Dyschiriognatha* sp., *Tetragnatha maxillosa* (Thorell)) and ichneumonid wasps (*Amauromorpha accepta metathoracica* (Ashmead)) formed 2-cycle links (i.e. A eats or parasitizes B, and B eats or parasitizes A). Trichogrammatid wasps (*Trichogramma japonicum* Ashmead), tetragnathid spiders (*Dyschiriognatha* sp., *T. maxillosa*) and sciomyzid flies (*Sepeidon* spp.) formed 3-cycle links (i.e. A eats or parasitizes B, and B eats or parasitizes C, and C eats or parasitizes A). Because of inconsistencies between field workers in the reporting of cannibalism and mutual predation, we excluded all cannibalistic and mutual predation links before calculating μ (following Pimm, 1982; Cohen *et al.*, 1990; Schoenly *et al.*, 1991; Schoenly & Cohen, 1991).

The last two (h–i) statistics pertain only to time-specific webs:

(h–i) the cumulative numbers of taxa and links, defined as the sums of the number of taxa and links in the previous time-specific web and the number of taxa and links in the present time-specific web that were not observed in any previous time-specific web. For the first time-specific web, the cumulative numbers of taxa and links are defined to equal its numbers of taxa and links.

Results

Yield-effort curves

To gauge completeness of sampling, yield-effort curves for cumulative numbers of taxa and for trophic links were plotted for each site (fig. 2A–B). Although 95% of the sampled arthropod taxa and 93% of recorded links were recorded before the last sampling date at each site, curves for taxa and links at each of the five sites failed to level off. Last sampling dates at each site collected taxa that were not captured in earlier samples. Among the late arrivals at these sites were *Cotesia* sp. (Hymenoptera: Braconidae), *Eysarcoris ventralis* (Westwood) (Hemiptera: Pentatomidae), and *Megaselia scalaris* (Loew) (Diptera: Phoridae). The chrysomelid *Monolepta bifasciata* (Hornstedt), being a pollen feeder, appeared late at Los Baños and Kiangán. *M. bifasciata* and *E. ventralis* normally arrive during the flowering and ripening stages, respectively; however, the timing of *Cotesia*

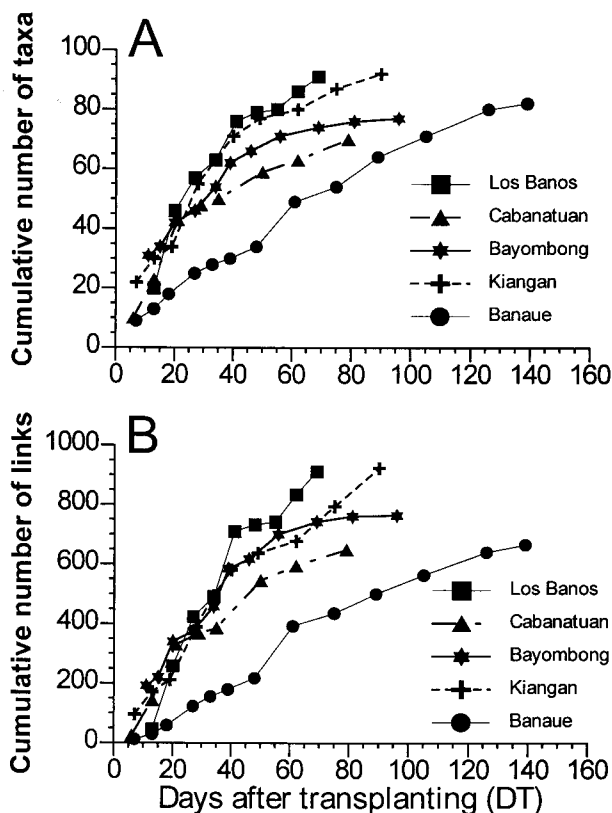


Fig. 2A–B. Cumulative number of (A) taxa and (B) links for each site.

Table 2. Properties of site-specific webs at five rice-growing sites in the Philippines.

Property*	Site (elevation)				
	Los Baños (22 m)	Cabanatuan (61 m)	Bayombong (305 m)	Kiangan (800 m)	Banaue (1524 m)
<i>S</i>	91	70	77	92	82
<i>L</i>	912	650	764	924	666
<i>B</i>	5.5	15.7	7.8	7.6	6.1
<i>I</i>	75.8	57.1	67.5	78.3	78.0
<i>T</i>	18.7	27.2	24.7	14.1	15.9
μ	4.28	3.77	4.07	4.12	4.11
<i>S/sd</i>	10	9	7	9	6
<i>Ind/sd</i>	1744	1899	905	746	370

Morisita's taxonomic similarity between sites†					
	Los Baños	Cabanatuan	Bayombong	Kiangan	Banaue
Los Baños	—	0.5400	0.6252	0.6071	0.6220
Cabanatuan	0.6874	—	0.7369	0.3128	0.2520
Bayombong	0.7620	0.7908	—	0.3903	0.3108
Kiangan	0.7438	0.3248	0.3737	—	0.8239
Banaue	0.7489	0.2785	0.3268	0.8817	—

**S*=number of food web taxa; *L*=number of trophic links in the web; *B*, *I* and *T* the percentages of basal species, intermediate species, and top predators, respectively, in the web; μ =the mean chain length of the web; *S/sd* and *Ind/sd*=number of species and individual arthropods in the web, respectively, per sampling date, each rounded to the nearest integer.

†Numbers in the triangle above the diagonal are between-site similarities of sample taxa and individuals (food-web taxa plus non-food-web taxa, row 1b, table 1); numbers below the diagonal are between-site similarities of food-web taxa and individuals (row 5b, table 1).

sp. and *M. scalaris* depend on whether their prey, particularly the striped stem borer (*Chilo suppressalis* Walker) (Lepidoptera: Pyralidae), are present. In each yield-effort curve for links, a steep rise in cumulative number of links coincided with the arrival of polyphagous predators, especially spiders.

Taxonomic variation between sites

Table 2 describes some numerical and taxonomic properties of the five site-specific webs. The numbers of taxa (*S*), links (*L*), the three fractions of basal, intermediate and top trophic species (*B*, *I*, *T*), and the mean chain length (μ) showed no obvious increasing or decreasing trend with elevation. The counts of arthropods in the samples and the webs (steps 1b and 5b, table 1) diminished as altitude increased. Except for Cabanatuan, the number of web individuals taken per sampling date dropped with increasing altitude, from 1744 individuals per sampling date at Los Baños to 370 individuals at Banaue (table 2).

Of the 115 taxa in the site-specific webs, 26 are herbivores, 47 are predators, 40 are parasitoids, and two are omnivores (the tettigoniid *Conococephalus longipennis* (de Haan) and the mirid *Cyrtorhinus lividipennis* Reuter). Each omnivore is insectivorous and also eats the rice plant: *C. lividipennis* and *C. longipennis* eat rice at the vegetative and booting stages, respectively.

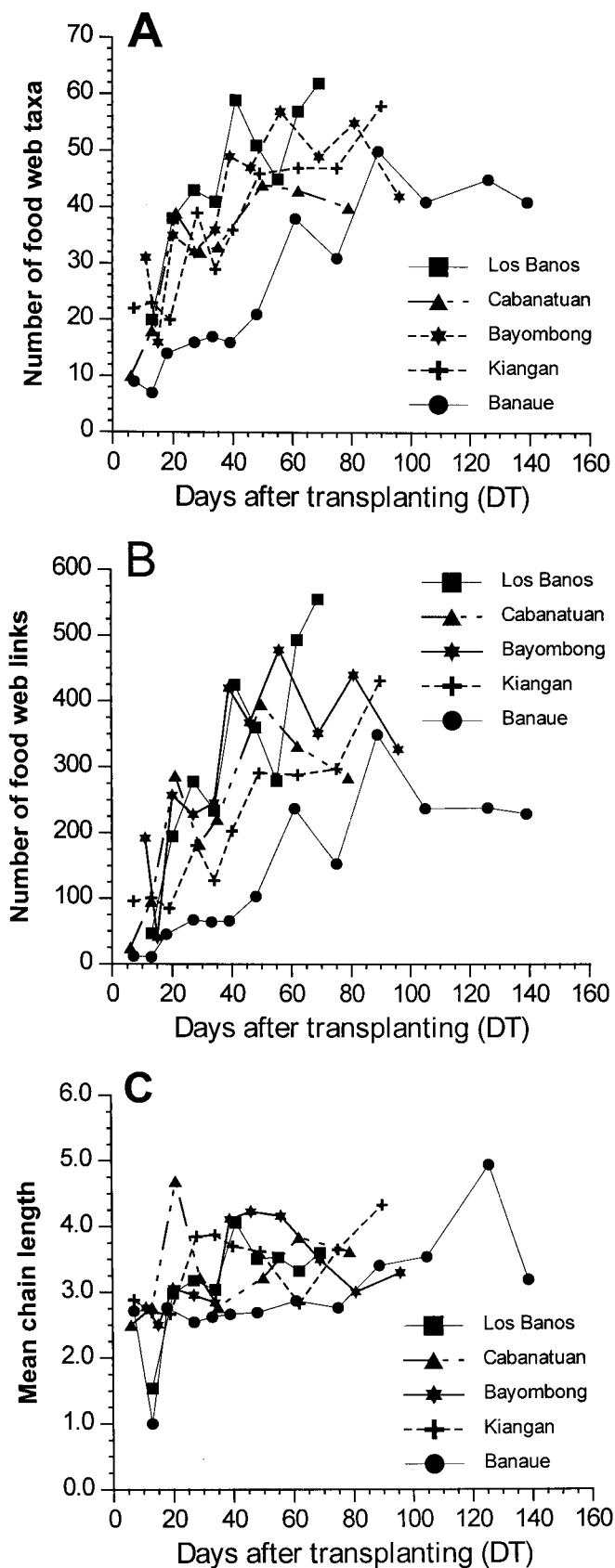
Among the 26 herbivore taxa, 13 occurred at all five sites (tables 3 and 6). Of these 13, seven have been classified by Reissig *et al.* (1986) as major pests of tropical rice: *Hydrellia philippina* Ferino (rice whorl maggot), *Nilaparvata lugens* (Stål) (rice brown planthopper), *Sogatella furcifera* (Horváth) (whitebacked planthopper), *Recilia dorsalis* (Motschulsky) (zigzag leafhopper), *Nephotettix virescens* (Distant), *N. malayanus* Ishihara & Kawase, and *N. nigropictus*

(Stål) (green leaf-hoppers). *Nephotettix* spp. and *R. dorsalis* are not pests unless they transmit tungro virus to the rice plant. Four other joint taxa were classified by Reissig *et al.* (1986) as minor pests or non-pests of tropical rice: *Notiphila latigenis* Hendel, *N. similis* de Meijere, *N. spinosa* Cresson (Diptera: Ephydriidae) and *Tagosodes pusanus* (Distant) (Homoptera: Delphacidae). The assignment of pest or non-pest status was based on a combination of severity of economic loss caused by the pest, its frequency of occurrence and area of occupied habitat, and its ease of control (Reissig *et al.*, 1986).

Of the 49 predator and omnivore taxa collected at the five sites, 23 (including 21 predators) occurred at all five sites (tables 4 and 6). Many of these predators eat leafhoppers, planthoppers and other pests. Three species, *Pardosa pseudoannulata* (Boesenberg Strand) (Araneae: Lycosidae), *C. lividipennis* and *Microvelia douglasi atrolineata* (Bergroth) (Hemiptera: Veliidae) are key pest control agents and candidates for manipulation in tropical rice (Dyck *et al.*, 1979; Kenmore *et al.*, 1984; Cook & Perfect, 1989; Heong *et al.*, 1992).

Of the 40 parasitoid taxa collected at the five sites, 12 occurred at all five sites (tables 5–6). Among the most commonly sampled of these 12 parasitoids were mymarid wasps (*Gonatocerus* spp.), scelionids (*Telenomus* spp.), various diapiid wasps, a braconid wasp (*Opius barrioni* Fischer), trichogrammatid wasps (*Oligosita* spp.), and a eulophid wasp (*Tetrastichus* sp.). All the above parasitoids have been reported as putative biocontrol agents of tropical rice pests (Van Vneden & Ahmadzabidi, 1986; Shepard *et al.*, 1987; Fowler *et al.*, 1991).

Table 2 shows the matrix of Morisita's similarities using all sampled individuals (upper triangle) and using only food web individuals (lower triangle) for each pair of sites. Using sampled individuals, the two mountainous sites, Kiangan and Banaue, were most taxonomically similar (82%), and



Cabanatuan and Banaue were least taxonomically similar (25%). These same pairs of sites yielded the largest and smallest similarities when web individuals were used (88% vs 28%, table 2). The ranking of similarities using sampled individuals was nearly identical to the ranking using web individuals (Spearman rank correlation coefficient $r_s=0.988$, 8 df, $P < 0.01$). We conclude that enough elements of the samples were contained in the webs to reflect between-site differences in taxonomic composition.

Temporal patterns in web properties and in food web taxa

Temporal patterns in food web properties will be described in qualitative terms, without attaching levels of statistical significance to the data in figs 3A–C, because successive data points of each trend line for each site are not statistically independent (Schoenly & Cohen, 1991). Numbers of food web taxa (fig. 3A), links (fig. 3B) and mean chain length μ (fig. 3C) generally increased over the growing season at each site, particularly during the first 50 days, though there were substantial fluctuations. The rise of taxa, links and mean chain length reflects, first, an increase in plant size with age, which enlarged the habitat for pests and their natural enemies to feed, and second, the relatively orderly, and sometimes rapid, accumulation of newly arriving taxa.

Some of the 48 taxa common to all five sites first arrived at these sites in an orderly way (tables 3–5). We deal first with broad patterns among three trophic groups (herbivores, predators and omnivores, parasitoids), and then with specific patterns among related taxa within each trophic group. Because of differences in the time interval between samples and in the length of the growing season at the five sites we resorted to a nonparametric procedure (Kendall's concordance test) to compare ranks of first arrival times. The significance test for Kendall's coefficient, W , is the Chi-square statistic (Sokal & Rohlf, 1981).

At each site, herbivores built up faster than predators and parasitoids, and predators arrived faster than parasitoids. The difference between the latest and the earliest sampling dates of first arrivals, averaged over the five sites, was 38.2 ($SE_{\bar{x}}=5.6$), 62.8 (14.5) and 73.4 (15.2) days for herbivores, predators, and parasitoids, respectively (tables 3–5).

A transient is a species collected on only one sampling date. Of the 48 jointly occurring taxa, one-fifth were transients. On the whole, transients were limited to species represented by four or fewer individuals. Such taxa occurred from 20 to 126 DT (tables 3–5) and included one herbivore (table 3), three predator (table 4) and six parasitoid taxa (table 5). The low frequency of transient taxa did not suggest any correlation with altitude or geography.

For the 13 herbivore taxa found at all five sites (table 3), the rank order of first arrivals was significantly associated ($W=0.22$, 4 df, $P < 0.05$). At all sites except Cabanatuan, the early vegetative pests, such as whorl maggots (*H. philippina*) and whitebacked planthoppers (*S. furcifera*), either preceded the others or came with the green leafhoppers

Fig. 3. Temporal and site-specific variation in food web structure at five rice-growing sites in the Philippines. (A), number of food web taxa; (B), number of links; and (C), mean chain lengths as functions of time.

Table 3. First arrival times of 13 herbivore taxa that occurred at all five Philippine sites.*

Los Baños	Cabanatuan	Bayombong	Kiangan	Banaue
1,2,3,4,5,6,7, 8(20DT)	4,10,13(6DT)	2,3,4,5,6,7,8 9,10(11DT)	2,3,6,7,8,10 (7DT)	2,7(7DT)
9,10,11,12 (27DT)	2,3,5,7,11 (13DT)	13(15DT)	1,11,12(13DT)	1,3,10(18DT)
13(48DT)	1,6,12(21DT)	11(20DT)	13(19DT)	5(27DT)
	9(29DT)	1,12(34DT)	4(28DT)	6,9(33DT)
	8(50DT)		5(34DT)	4,13(39DT)
			9(49DT)	8+,11,12(61DT)

*Taxa listed are: 1=chrysomelids, 2=*Hydrellia philippina*, 3=*Nephotettix nigropictus*, 4=*Nilaparvata lugens*, 5=*Notiphila similis*, 6=*N. spinosa*, 7=*Sogatella furcifera*, 8=*Tagosodes pusanus*, 9=*Nephotettix malayanus*, 10=*N. virescens*, 11=*Recilia dorsalis*, 12=thrips, 13=*Notiphila latigenis*. DT=days after transplanting.

†transient species (see text).

Nephotettix nigropictus and *N. virescens* during the vegetative phase. Another leafhopper, *N. malayanus*, arrived either with its sister taxa or later at each site (table 3). Later arrivals included two ephydriids (*Notiphila spinosa*, *N. similis*) and chrysomelid beetles during the vegetative and reproductive phases. No consistent order of arrivals was evident for the plant hoppers (*T. pusanus* and *Nilaparvata lugens*), thrips, the cicadellid (*R. dorsalis*), and the third ephydriid (*Notiphila latigenis*; table 3). Except for *T. pusanus*, all herbivores had large populations, particularly *Nephotettix virescens*, *S. furcifera* and *Nilaparvata lugens*.

For the eight predaceous bugs found at all five sites (taxa 17, 19, 20, 21, 25, 27, 33, 36 in table 4), the rank order of first arrivals was not significantly associated ($W=0.14$, 4 df, $P > 0.05$). A large number of ties of first arrival times

could influence the lack of statistical significance in this test; however, some consistent trends were observed (table 4). At every site, the veliid *Microvelia douglasi atrolineata* was an early and prominent colonist. At Los Baños, Bayombong and Banaue, *M. douglasi atrolineata* arrived with *Mesovelia vittigera* (= *orientalis*) (Horváth) (Hemiptera: Mesoveliidae), another semi-aquatic bug (table 4). The omnivorous mirid *C. lividipennis* usually arrived early, sometimes with *M. douglasi atrolineata* and *M. vittigera*. These three bugs arrived during the vegetative phase and were numerically the most dominant arthropod predators at each site. Another three bugs, all semi-aquatic, joined the other three at three or more sites: Gerrids (*Limnogonus fossarum* (Fabricius)), corixids (*Micronecta quadristrigata* Breddin), and hydrometrids (*Hydrometra lineata* Eschscholtz). A second terrestrial bug *Polytoxus*

Table 4. First arrival times of 23 predator and omnivore taxa that occurred at all five Philippine sites.*

Los Baños	Cabanatuan	Bayombong	Kiangan	Banaue
14,15,16,17,18, 19,20,21,22,23, 24(13DT)	20,21,24,29,31 (6DT)	16,17,19,20,22, 23,24,25,26,27, 28,29,32(11DT)	17,20,22,24,25, 29,32,33(7DT)	19,20,22,27 (7DT)
25,26,27,28,29 (20DT)	22,23,25,30,33 (13DT)	33(15DT)	16,19,23(13DT)	24,29,32,33 (13DT)
30,31,32(27DT)	15,16,19,26,27, 32,35(21DT)	15,21,30(20DT)	26,28(19DT)	28(18DT)
33(34DT)	17(29DT)	14,18,36(34DT)	14,15,18,27 (28DT)	23,25,26,30 (27DT)
34,35(41DT)	14,18,28(50DT)	31,35(39DT)	30,34(34DT)	35(33DT)
36(62DT)	34,36†(62DT)	34(46DT)	31,35†(40DT)	16(48DT)
			36(49DT)	14,17,18(61DT)
			21†(62DT)	15(75DT)
				31†,36†(105DT)
				21,34(126DT)

*Taxa listed are: 14=*Agriocnemis femina femina*, 15=*A. pygmaea*, 16=*Atypena* (= *Callitrichia*) *formosana*, 17=*Hydrometra lineata*, 18=hydrophilids, 19=*Mesovelia vittigera*, 20=*Microvelia douglasi atrolineata*, 21=*Anisops* sp., 22=*Pardosa pseudoannulata*, 23=*Tetragnatha javana*, 24=*T. virescens*, 25=*Cyrtorhinus lividipennis*, 26=*Dyschirognatha* sp., 27=*Micronecta quadristrigata*, 28=*Solenopsis geminata*, 29=*T. maxillosa*, 30=*Clubiona japonicola*, 31=*Ophionea nigrofasciata*, 32=*Theridion* sp., 33=*Limnogonus fossarum*, 34=*Conocephalus longipennis*, 35=*Micraspis* spp., 36=*Polytoxus fuscovittatus*. DT=days after transplanting. †transient species (see text).

Table 5. First arrival times of 12 parasitoid taxa that occurred at all five Philippine sites.*

Los Baños	Cabanatuan	Bayombong	Kiangan	Banaue
37,38,39(13DT)	37(13DT)	37,38(11DT)	39(7DT)	37(7DT)
40,41,42†,43 (20DT)	38,39,40,41,42, 43†,45,47†,48 (21DT)	39(15DT)	38(13DT)	42(18DT)
44(34DT)	46(29DT)	42,48(20DT)	42(19DT)	38,44(48DT)
45,46(41DT)	44†(79DT)	40,45(27DT)	37,40,41,45,46, 48(28DT)	40(61DT)
47†(55DT)		44(34DT)	47(40DT)	41,46(89DT)
48†(69DT)		46(39DT)	44(49DT)	39†(105DT)
		41,43†47(56DT)	43(75DT)	47†,48(126DT)
				43,45(139DT)

*Taxa listed are: 37=diapriids, 38=*Opius barrioni*, 39=*Tetrastichus* sp., 40=*Gonatocerus* sp., 41=*Oligosita* sp., 42=*Telenomus rowani*, 43=*Telenomus* sp., 44=*Trichomalopsis* sp., 45=*Anagrus* sp., 46=*Sepedon* sp., 47=*Elasmus* sp., 48=*Trichogramma japonicum*. DT=days after transplanting.

†Transient species (see text).

fuscovittatus Stål) (Hemiptera: Reduviidae) arrived either last or next-to-last during the reproductive stage at all sites except Bayombong. No consistent order of arrival was evident for notonectids (*Anisops* spp.; table 4).

Like herbivores, spiders in table 4 (taxa 16, 22, 23, 24, 26, 29, 30, 32) had consistent first arrival times across the five sites ($W=0.30$, 4 df, $P < 0.05$). Unlike herbivores and predaceous bugs, no transient spiders were found. The lycosid *P. pseudoannulata* and the tetragnathid *Tetragnatha virescens* always arrived early (table 4) and developed sizeable populations during the vegetative stage. Another tetragnathid (*T. maxillosa*) joined *P. pseudoannulata* or *T. virescens* at four of the five sites. A third tetragnathid (*T. javana* (Thorell)) and a theridid spider (*Theridion* sp.) joined the other three at three sites. At four sites, another tetragnathid (*Dyschiriognatha* sp.) and the linyphiid *Atypena* (= *Callitrichia*) *formosana* (Oi) each joined the other five spiders. The clubionid *Clubiona japonicola* (Boesenberg & Strand) arrived either last or was among the last spiders to arrive at four of the five sites during the vegetative and reproductive stages (table 4).

The remaining seven predators (taxa 14, 15, 18, 28, 31, 34, 35 in table 4) had diverse first arrival patterns. Ants (*Solenopsis geminata* Fabricius) arrived early at all sites except Cabanatuan; tettigoniids (*C. longipennis*) arrived last or late at these sites. Various beetles (hydrophilids, *Micraspis* sp. and *Ophionea nigrofasciata* (Schmidt-Goebel)) and coenagrionid (*Agriocnemis femina femina* (Brauer) and *A. pygmaea* (Rambur)) displayed no systematic trend in their order of arrival. Except for *O. nigrofasciata*, these predators maintained small but sustained populations at each site.

For the 12 parasitoid taxa found at all five sites (table 5), the rank order of first arrivals was significantly associated ($W=0.34$, 4 df, $P < 0.01$). At the five sites, 85% of the parasitoid taxa had sustained populations. Except for Kiangan, diapriid wasps either arrived first or were among the first arrivals. The braconid (*O. barrioni*) and certain scelionid wasps (*Telenomus rowani* (Gahan)) joined or followed diapriids at all sites except Kiangan. Four chalcidoid wasps (*Gonatocerus* sp., *Tetrastichus* sp., *Oligosita* sp., *T. japonicum*) joined or preceded the other three at three or more sites. Some early arrivals maintained sizeable

populations (*Gonatocerus* sp. and *Oligosita* sp.) while others became transients (*T. rowani* and *Tetrastichus* sp.). A mymarid wasp (*Anagrus* sp.), a sciomyzid fly (*Sepedon* sp.) and a pteromalid (*Trichomalopsis* sp.) each arrived during mid-season at most sites. One parasitoid, *Telenomus* sp., was the latest or among the latest arrivals at three of the five sites (table 5).

Site-specific webs vs. time-specific webs

Each site-specific web is the cumulative web of the time-specific webs for that site. If a site-specific number of prey or enemies of a given set of taxa (herbivores, predators, parasitoids or omnivores) falls above the corresponding range for the time-specific webs, then we shall say that the site-specific web for this set of taxa overstates the time-specific data. If the site-specific value falls below that of the time-specific webs, we shall say the site-specific web understates. We now compare numbers of prey and enemy taxa of the 48 taxa found at all sites, in time- and site-specific webs.

The site-specific web overstates the number of enemies of 11 herbivore taxa for all five sites (table 6). For example, for herbivores at Los Baños, a mean of 30 enemy taxa was reported in the site-specific web; in the time-specific webs at Los Baños, a range of 14 to 24 enemies for herbivores was found. The site-specific webs overstate the numbers of enemies of predator, parasitoid and omnivore taxa for all sites except Banaue (for predators) and Bayombong (for parasitoids). Most of the 48 taxa never encountered their full range of enemy species on any given day.

The site-specific webs overstate the mean numbers of prey taxa of the sets of predator, parasitoid and omnivore taxa in the time-specific webs for all five sites except Cabanatuan (for parasitoids). Based on our samples, most taxa potentially encountered only a subset of their lifetime prey species on any given day.

The lower a species feeds in the food chain, the more enemy taxa and fewer prey or host taxa it will have in both time- and site-specific webs (table 6). The mean number of enemy taxa was highest for herbivores in site- and time-specific webs (25–31 and 8–24 taxa, respectively), followed

Table 6. Mean numbers of potential prey and enemy taxa of each trophic group at all five sites. The value for the site-specific web is followed by the range in variation in the time-specific webs. Mean numbers of prey and enemy taxa are rounded to the nearest integer.

Trophic Group (number of taxa)	Los Baños		Cabatuan		Bayombong		Kiangnan		Banaue	
	No. of species of Prey*	No. of species of Enemy	No. of species of Prey	No. of species of Enemy	No. of species of Prey	No. of species of Enemy	No. of species of Prey	No. of species of Enemy	No. of species of Prey	No. of species of Enemy
Herbivores (11)†	23,7-16	30,14-24	19,8-14	26,8-20	21,8-16	29,11-23	22,6-15	31,10-21	22,4-15	25,8-16
Predators (21)	44,14-30	6,3-5	38,13-25	5,2-4	42,19-31	5,2-4	44,11-28	5,2-4	44,6-28	3,2-3
Spiders (8)	9,2-8	2,1-2	7,4-7	2,1-2	8,3-7	2,1-2	8,4-7	3,1-2	9,2-7	2,1-2
Bugs (8)	10,3-8	6,3-6	7,4-6	5,2-5	9,5-8	5,1-5	10,3-7	6,2-4	10,4-7	3,1-3
Others (5)	4,2-3	10,4-9	3,2-3	8,4-7	4,2-3	8,5-7	5,2-3	8,4-6	5,2-3	5,3-4
Parasitoids (12)	13,7-9	9,5-8	9,7-8	8,5-6	11,6-8	7,5-7	13,4-10	12,5-9	12,6-9	6,3-4
Omnivores (2)		13,6-12		11,6-9		11,7-10				9,4-6

*Because rice is the only prey of herbivores in both site- and time-specific webs, the column 'No. of species of Prey' in the herbivore block was intentionally left blank.

†Because rice is not a reported prey of 2 of the 13 herbivores (chrysomelids, thrips) in all site- and time-specific webs, means were calculated from the remaining 11 taxa.

by omnivores (9-13 and 4-12 taxa), parasitoids (6-9 and 3-8), and predators (3-6 and 2-5; table 6). The mean number of prey or host taxa was highest for predators, in site- and time-specific webs (19-23 and 4-16 taxa, respectively), followed by omnivores (9-13 and 4-10), and parasitoids (3-5 and 2-3; table 6). At each site, little or no overlap was found in the ranges of numbers of prey and enemy taxa belonging to different trophic groups.

Field problem

An unexpected field problem limited the comparisons we could make between sites, but also provided a natural experiment. The rice crop at Banaue failed to flower. We therefore limited comparisons between sites to the vegetative and reproductive phases.

Although the Banaue crop failed to flower, Banaue revealed no obvious differences from the other four sites during the vegetative and reproductive stages. Thus the loss of the ripening stage is not reflected in earlier differences between Banaue and the other four sites. As in the other four webs, the numbers of taxa and links and the average food chain length of the Banaue web each increased over the growing season. Except for more transient taxa (tables 3-5) and later periods of peak abundance of *N. virescens* and *S. furcifera* populations at Banaue, the first arrival times at Banaue were similar to those at the other four sites.

Discussion

The Philippine rice food web at and above the water line is described with a high degree of taxonomic refinement in all trophic categories except detritivores and planktonic taxa. Our emphasis on describing populations to genus and to species differs from element-cycling studies on conventional and no-till managed agroecosystems (e.g. Hendrix *et al.*, 1986; Mueller *et al.*, 1990; Beare *et al.*, 1992) and the many guild-focused studies of soil-arthropod communities in natural and agricultural ecosystems (e.g. Witkamp & Crossley, 1966; Santos & Whitford, 1981; Whitford *et al.*, 1982; Ingham *et al.*, 1985; Freckman & Mankau, 1986; Groffman *et al.*, 1986; Palmalee & Alston, 1986; Hunt *et al.*, 1987; Walter *et al.*, 1988). Studies of stocks and flows of essential nutrients like carbon and nitrogen provide useful quantitative descriptions of agroecosystem structure and function (Risser, 1986). When functional groups are included in such studies, high-resolution food web data may not be essential for understanding plant litter decomposition (Beare *et al.*, 1992). However, for biological pest management, the identity, life-history and population dynamics of individual species matter strongly to IPM practitioners because of the importance of population-based economic thresholds, diagnosing pest outbreaks, and interactions between populations of specific pests and their natural enemies.

This paper compares food webs from five rice fields in Luzon that differ in elevation (22-1524 m), size (200-3200 m²), geometry (nearly square, 4:1 rectangular, two disjoint crescents), timing of planting compared to surrounding fields (synchronous except IRR1), average annual precipitation (1649-3938 mm), and other respects. Any or all of these factors could influence web structure. For example, area is well-known to influence species richness (e.g. Conner & McCoy, 1979). Geometry also matters: long

narrow rectangles are likely to include a wider range of biological variation (such as species or communities) and habitat heterogeneity than square or circular regions of equal area (e.g. Williamson, 1987; Krebs, 1989). Timing of planting affects whether surrounding fields are initially cleared like the study site, or are at different stages of the growing cycle and able to serve as sources of colonization for the study site (Way & Heong, 1995).

Because the study sites vary in so many respects, the quantitative information about food webs presented in this paper could hardly show whether any differences between sites are due to one factor (e.g. elevation) or some other factor, singly or in combination. However, if the food webs of all sites displayed similar structure and dynamics, it would appear that the many respects in which the sites differed were not associated with major changes in the food webs present.

In the data analysed here, the five site-specific webs are not very different from each other, at least by the six web statistics in table 2. There are at least three explanations. First, the field practices, sampling programme and methods used to define species and links in this study were standardized across sites. All site-specific webs are subwebs of the same cumulative Philippines web and would be expected to have similar internal structure. Comparable results were achieved by Beaver (1985), Sprules & Bowerman (1988), Kitching (1987), Warren (1989), Winemiller (1990), Havens (1992), Locke & Sprules (1994) and Closs & Lake (1994) when they used the same set of methods for multiple times or sites. Second, the measures may have limited sensitivity because they rely on qualitative (presence/absence) information on species and links (not on abundance of species or strength of web links). Third, the five site-specific webs were taxonomically similar, in part, because sampling was conducted in irrigated fields during daylight hours.

Environmental correlates of web structure

Population and community structure is strongly influenced by environmental gradients and habitat structure (e.g. Bell *et al.*, 1991; Holland *et al.*, 1991). For example, Stevens (1992) found that species richness decreases with increasing altitude in several different groups of organisms (trees, mammals, birds, reptiles, orthopterous insects, amphibians). In the present study, however, total numbers of arthropod taxa in the samples and in the webs showed no obvious decreasing trend with altitude across the five rice-growing sites. This result prevailed irrespective of whether species richness was based on raw numbers of taxa per site or numbers per sampling date (tables 1 and 2). In this study, the only notable associations with altitude were a decline in numbers of individuals in the samples and the webs (tables 1 and 2).

In tropical rice ecosystems, species richness may not correlate well with altitude because rice-associated species are strongly influenced by the area and composition of surrounding non-rice habitats (Loevinsohn, 1984). For example, Los Baños possesses the highest vegetational richness of the five sites due to its proximity to agricultural fields, gardens and greenhouses and experimental farms of the UP-Los Baños campus. At the other extreme, Bayombong has a nearly pure rice flora. When the five sites were arranged in order of decreasing vegetational diversity,

decreased numbers of sampled arthropod taxa per sampling date were found: Los Baños (16 taxa), Cabanatuan (11 taxa), Kiangnan and Banaue (11 and 9 taxa, respectively) and Bayombong (8 taxa, row 1a; table 1). Vegetation surrounding ricefields likely provides alternate food sources, reproductive sites and prey refugia for local species (e.g. Menge & Sutherland, 1976; Bell *et al.*, 1991) that help to sustain high arthropod richness in the paddy ecosystem.

Temporal developments in webs and among jointly occurring taxa

The first arrival times of the 48 taxa present at all five sites showed some consistent trends across the five sites (tables 3–5). Herbivores built up sustained populations faster than predators and parasitoids, and predators arrived faster than parasitoids. The patterns in first arrivals influenced the increases in numbers of taxa, numbers of links and mean chain lengths over time (fig. 3A–C). These consistencies suggest that assembly rules might exist for successional communities (Lawton, 1989), a topic that has received little attention among insect ecologists (e.g. Southwood *et al.*, 1979; Brown & Southwood, 1983; Law & Morton, 1993).

Second, 20% of the 48 jointly occurring taxa, mostly parasitoids and predators, were transients, taxa observed on only one sampling date. Sometimes the same parasitoid or predator taxon was a transient at more than one site. These patterns in food web properties and first arrival times may be influenced more by crop age than by geography.

Site- vs time-specific webs and choices of biocontrol agents

At each site, species consistently encountered fewer enemy taxa and fewer prey taxa at any one time than were encountered over the course of the growing season. Species that appeared to be polyphagous from site lists (cumulated over time) were actually oligophagous or monophagous in time-specific webs from the same site. This pattern of variation parallels that in earlier comparative studies of site- and time-specific webs (Schoenly & Cohen, 1991) and local or regional spatial scales (Fox & Morrow, 1981).

This observation has implications for biological pest control. Historically, natural enemies have been chosen as biocontrol agents based on host or prey specificity, time of contact with the target prey or host, high searching capacity, synchronization with its prey or host and its habitat, and other criteria (e.g. Doutt & DeBach, 1964; Huffaker *et al.*, 1977; van den Bosch *et al.*, 1982; Stiling, 1993). Because site-specific webs tend to overestimate numbers of prey per enemy at the sites studied here, predators that are identified as polyphagous from site lists may be dismissed prematurely from consideration for biocontrol campaigns. For example, the polyphagy of spiders is one reason why they are less favored than parasitoids as potential biocontrol species for many cropping systems (Dent, 1991).

In this study, the potential prey of sampled spiders and parasitoids averaged 42 and 4 taxa, respectively, in the five site-specific webs; however, in the time-specific versions, average ranges of prey taxa of spiders and parasitoids dropped to 33–69% (13–28) and 25–50% (2–3), respectively, of the site-specific values (table 6). Time-specific webs are more sensitive than site-specific webs in revealing prey or host ranges and enemy–prey synchronization in the

habitat. Concentration on time-specific webs may be useful in planning biological control programmes that involve introduction, augmentation or conservation of natural enemies.

Limitations of the data

The 687-taxa cumulative Philippines web of taxa and links at and above the water line in irrigated rice presently includes the grazer- and terrestrial-based components and some lentic (surface-active) taxa, but ignores members of the detrital food web, many submerged taxa and species associated with vegetation other than rice and mungbean. Although many submerged and detritivorous taxa are known, the food and consumers of these groups are incomplete. Because the cumulative web excludes the detrital and (non-rice) grazer-based webs of the paddy ecosystem, the present version represents a source (not a community) web of rice (in the sense of Cohen, 1978).

Our sampling methods did not capture paddy-frequenting toads, frogs, lizards, snakes, bats, rats, and birds. The significance of vertebrates in the rice paddy ecosystem awaits further investigation. Unlike web studies based on vertebrates, the high degree of taxonomic refinement for arthropods in the Philippine web allows a detailed study of predator-prey interactions at lower trophic levels where pest species and many of their natural enemies feed.

It would be desirable to identify the predator-prey links of species that are omitted, determine the pathways that link them to the rice web, and evaluate their importance for biological control. Yasumatsu *et al.* (1981) postulated that accumulations of dead organic matter cause outbreaks of chironomid populations in flooded fields and trigger prey-switching by predators; predators that otherwise control rice insect pests switch to chironomids because chironomids are more numerous and easier to capture than pests. To our knowledge, this hypothesis has not been field tested. Heckman (1974, 1979) studied aquatic communities of irrigated rice paddies in Laos and Thailand, but did not elucidate specific predator-prey relationships.

A second limitation of our food web data is that site-specific webs incorporated only 64–86% of the sampled taxa (line 5a, table 1) because specific prey or enemies of many taxa are still unknown. This failing, however, is not limited to the Philippines or the Old World tropics. Tropical arthropod communities from natural and agricultural systems remain some of the least understood ecosystems (e.g. Elton, 1973; Young, 1982; Penny & Arias, 1982; Gliessman, 1990; Janzen, 1991). Our results nevertheless suggest that data on rice–arthropod food webs, although far from complete, may reveal some general patterns.

A third limitation of our data is that we assumed that if taxon A eats taxon B in a particular site-specific web, then A eats B in all time-specific webs at this site when both are present. This assumption may not be realistic (Schoenly & Cohen, 1991). Havens (1992) claimed this assumption is robust for pelagic lake webs. However, Zerba & Collins (1992) showed that the diets of tiger salamander larvae varied notably among natural ponds, and Kling *et al.* (1992) showed that there are different food web structures in similar lakes that contain the same species. Tests of this assumption are needed for tropical rice ecosystems.

Future opportunities

The approach taken in this paper could be applied to other major crops and to important questions of biogeography. Published studies give species lists and some relationships of the pests, predators and parasitoids of sugar cane (Box, 1953), cotton (Whitcomb & Bell, 1964), coffee (Le Pelley, 1968), soybean (Dietz *et al.*, 1980), muscadine grapes (McGiffen & Neunzig, 1985) and cassava (Neuenschwander *et al.*, 1987). These and other studies have not been organized into site- and time-specific food webs nor analysed in a coherent, systematic way with the taxonomic resolution we illustrate here for tropical rice. Similar analyses could be done with data for many other crop systems.

The islands of the East Indies, of which the Philippines are part, divide two great zoogeographical divisions, the Oriental and Australian faunas (Mayr, 1944; Simpson, 1977; Brown & Gibson, 1983). Vane-Wright (1990) recognized six biogeographical regions within the Philippines alone and concluded that the region played a major role in the development of the Wallacean biota, at least its butterfly and mammal fauna, during the geologically recent past. Future studies of rice food webs for the Philippine islands and other East Indian islands could test predictions about these faunas. For example, Simpson (1977) and others have claimed that all faunas and islands to the west of Huxley's (1868) line (e.g. Bornea, Palawan, Java, Sumatra) belong to the Oriental Region and all faunas and islands to the east of Lydekker's (1896) line (e.g. New Guinea, Waigeo) belong to the Australian Region. Faunas and islands that lie between Huxley's and Lydekker's lines contain admixtures of Oriental and Australian faunas. For East Indies biogeography at least, further division of this transitional zone by additional lines serves no useful purpose (Simpson, 1977; Brown & Gibson, 1983).

Classical biogeographical theory would predict that the faunal lists for rice fields of Palawan and Vietnam would be more similar to one another than either would be to the faunal list of a rice field in New Guinea, for example, because New Guinea's fauna would contain more Australian elements than either Palawan or Vietnam. Comparison of these lists, one faunal group at a time (e.g. beetles, spiders, parasitoids, herbivores), could supplement between-site comparisons of entire faunas. Pairwise comparison of web statistics for these sites would provide an independent test of biogeographic claims and would integrate food webs and agroecology with classical biogeography.

Biogeographical analyses could also prove useful to integrated pest management. For example, if the fauna and food webs of Palawan and Vietnam were indeed more similar to one another than to corresponding data from other sites, then a biocontrol measure effective in one of these two sites might be expected to be effective in the other because of the similarity between them in both species composition and trophic structure.

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