

Predator–prey interactions in rice ecosystems: effects of guild composition, trophic relationships, and land use changes — a model study exemplified for Philippine rice terraces

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Abstract

A model study is presented that investigates the effect of land use changes on arthropods in Philippine rice terraces. These changes include the increase of non-rice areas (vegetable fields and woodlots), the introduction of a second cropping season and the abandonment of the traditional synchrony in the cropping regimes over whole regions. Such changes are likely to have an effect on the balance between rice pests (plant and leaf hoppers, e.g. *Nilaparvata lugens* and *Sogatella furcifera*) and their natural enemies (spiders, predatory bugs and parasitoids), and therefore could be of considerable interest in the context of pest management. The model explicitly considers several arthropod species and their population dynamics in several rice fields with different cropping cycles. Thus various spatio-temporal land use regimes can be investigated and compared in their effect on pest abundance. According to the model results, a high proportion of vegetable fields reduces pest abundance. Whether synchronous cropping reduces pest abundance, depends on the interactions between their natural enemies, particular the feeding behaviour of the mirid bug *Cyrtorhinus lividipennis*. A cropping regime that minimises pest abundance in all circumstances, does not exist. Whether traditional farming practices are superior to modern ones or not, is very much influenced by the type of integration of different control strategies and tactics and the ecology of the species involved. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

1.1. Rationale

Due to global changes in demand for agricultural crops, drastic changes in land use systems can be observed. These changes take very different directions depending on the regional socio-economic conditions. In tropical countries population increase yields an increasing demand of food supply, which leads to cultivation of further areas (although oftentimes not suitable for agricultural production), changes in crop type and/or intensification of the already cultivated crop. On the contrary, in areas like Western Europe for example the phenomenon of so called ‘overproduction’ is the reason why many former agricultural areas are abandoned and extensification is subsidised.

We want to investigate the effects of these land use changes on arthropods with a focus on predator–prey interactions. We are especially interested in the effects on a regional scale (farming community), as this often is the reference level for land use planning. In pest management for instance we are especially concerned about potential insect pests and their population dynamics in order to keep their population densities at low levels. Thus it is important to understand the mutual interactions among the arthropod species in the system as well as the changes in habitat qualities and habitat area. As it is already quite complex to quantify effects on single species, the more this holds true for multi-species complexes. This suggests to use computer models which can integrate the many details of an agricultural system and derive the consequences for the whole.

We have developed a regional scale model, parameterised for predator–prey interactions in a rice dominated agricultural system in Ifugao (Philippines). Rice belongs to the world’s major food resources and rice farming is an important sector of Asian economy. A major threat to rice production in Asia are various insect pests, such as stemborers, plant- and leafhoppers. Methods to control these pests include the breeding of resistant varieties, spraying of insecticides and conservation of natural enemies, such as parasitoids or

predatory spiders and insects. These natural enemies account for more than 96% of insect pest mortalities (e.g. Shepard et al., 1987).

1.2. Changes in rice growing systems and their effects on arthropod population dynamics

In tropical regions most rice pests are not restricted by seasonal factors, thus they show up as soon as rice is planted (Loevinsohn et al., 1988). Modified rice growing systems with more seasons per year support mainly mono- or oligophagous species, while polyphagous ones are reduced in abundance, which can be seen e.g. by the reduced importance of leaf feeding species. Importance of the monophagous stem borer *Scirpophaga incertulas* is increasing while the polyphagous *Chilo suppressalis* remains constant (Loevinsohn et al., 1988). In addition, damage caused by the monophagous hoppers *Nephotettix virescens* (due to its role as a virus vector) and *Nilaparvata lugens* has become more severe. Differences in population densities of these species between peak periods of the growth period and the values at the start of a new growth season have decreased.

According to Loevinsohn et al. (1988) and Loevinsohn (1994), the two main factors responsible for changes are asynchrony (different planting times on neighbouring fields) and the growth of two or more crops per year. Both reduce the duration of fallow periods which have to be bridged by the pests. Most other reasons mentioned in literature, which are responsible for changes in pest abundance can be referred to activities during the growth period (fertilisers, pesticides) and not between them (Loevinsohn et al., 1988). In transplanted rice, according to Litsinger et al. (1987), pest densities increase if neighbouring farmers transplant with a certain staggering, because terrestrial rice pests then can easily move from early to late transplanted fields.

Loevinsohn et al. (1988), Oka (1988), and Loevinsohn (1994) recommend to go back to traditional systems, in which during the ‘tropical winter’ no rice is grown. Such fallow periods, to be efficient, would have to be synchronised in large scale, and thus would have to include many farmers. Exactly these conditions are found in the

traditional Ifugao land use system (Northern-Luzon, Philippines).

1.3. Hypothesis and modelling philosophy

Consequently, we hypothesise that the traditional land use, i.e. one cropping season per year, synchronised over whole regions, and only few vegetable fields, is better adapted to the environment than the modern farming practises, as measured by pest/prey abundance. This hypothesis is tested with the help of our simulation model.

The model explicitly considers the dominant arthropod species of the agricultural system and can simulate various types of land use. Based on this model, we intend to show the effects of intensification, i.e. an increase from one to two cropping periods per year, combined with increasing desynchronisation, and the impact of changes in land use on a regional scale (e.g. conversion of forest into vegetable fields) in our model land use system.

The paper will concentrate on important mechanisms and processes to gain a better understanding of the arthropod system and the problems to be discussed. We do not intend to make quantitative predictions either for particular species or for special guilds. Therefore our model will be of ‘intermediate complexity’ in the sense of Godfray and Waage (1991), who distinguish between simple and complex models. The aim of the simple models (e.g. Hassell, 1978) is to gain general insight into the dynamics of populations. They are usually abstract and cannot be applied to specific problems. The complex models (e.g. Carter et al., 1982) are used for predictions in specific situations. Their drawback is however, that they need a lot of data. Godfray and Waage (1991) favour models of ‘intermediate complexity’ which consider the most important factors but need only a minimum of data, such as fecundity rates, developmental and mortality rates, and attack rates to describe pest–enemy interaction. Such models can usually not be used to make exact quantitative predictions but are able to qualitatively investigate the essential processes in the system.

2. Materials and methods

2.1. Land use in the model system

In central areas of the impressive irrigated rice terraces of the mountain areas of Northern-Luzon (Ifugao Province, Philippines) irrigated rice traditionally is grown once a year. Land use is highly synchronised. Additional to rice, sweet potato is grown as a security crop and small woodlots are used for example for the growth of fruit and timber trees (for a detailed description see Conklin (1980) and Voggesberger (1988)). Changing socio-economic conditions however resulted in new agricultural practices, like the introduction of a second rice crop based on new rice varieties, partly desynchronised rice growing and increased vegetable production (for a summary of the major changes see Settele (1998)). Thus, in addition to vegetable fields (mainly swiddens; i.e. sweet potato fields and their early fallow stages) and forests (mainly woodlots and secondary growth forest), we distinguish between traditional (old varieties, one crop per year) and modern rice fields (new varieties, two crops per year). The proportions of different land use compartments show considerable variability in space and time (compare Conklin, 1980; Herzmann et al., 1998). In Settele et al. (1998) further literature and field data on the particular system of our case study have been compiled.

As representative examples for differences in present day land use we have chosen conditions as can be observed in the two Ifugao municipalities of Banaue and Kiangan, with a landscape dominated by traditional land use around the former and with a more or less even mix of modern and traditional systems around the latter (compare Settele, 1992).

2.2. Spatial and temporal model structure

For the model the spatially structured landscape is divided into four compartments (traditional and modern rice fields, vegetable fields, and forest patches). The traditional rice fields have one cropping season per year, the modern rice fields have two seasons. Each of the two rice

compartments is further divided into three sub-compartments (leading to a total of six rice compartments). This allows the consideration of asynchronous cropping where not all rice fields are transplanted at the same time. We call the difference between the transplanting times of different rice compartments the staggering time. A staggering time of zero for modern rice compartments, e.g. means that all modern rice compartments are managed in synchrony, i.e. have the same transplanting times. A large staggering time of 60 days in modern rice compartments, e.g. means that the early modern rice compartment is transplanted 60 days before the median compartment which in turn is 60 days ahead of the late compartment. Similar can be done with the three traditional rice compartments, which normally however are transplanted within a very short time period in late February/early March. This is approximated by setting the staggering time to zero (simplified e.g. as 1st of March in our model).

As a modern rice field has two seasons, each with a length of about 4 months (compare Fig. 3), a staggering time of 60 days in modern rice leads to a more or less ‘continuous’ form of land use where there is an overlap of early, median and late rice fields. Here the landscape always contains rice plants and arthropods can always find another rice field when their field of origin is harvested.

Next to the staggering time, the model considers three other land use parameters, which are the proportion of modern rice fields, the proportion of non-rice areas in the system and the proportion of vegetable fields within the non-rice areas. The plausible ranges of the four land use parameters are given in Table 1. Any other aspects of spatial structure, i.e. mainly geographical arrangement,

are ignored, because the relevant species are considered good dispersers and thus should be able to easily reach any of the land use compartments of the entire landscape (Perfect et al., 1985; Riley et al., 1987).

The model considers three different time scales. The basic time scale of the simulation is one day and reproduction and death of individuals are simulated on a daily basis. Predation and parasitization are modelled every hour. The population dynamics are affected by the described annual cycle of agricultural activities in the area. Two climatic seasons are distinguished. The ‘warm’ season (mean daily temperature $T = 23^{\circ}\text{C}$) starts on 1st March and the ‘cold’ season (mean daily temperature $T = 21^{\circ}\text{C}$) on 1st September.

Below we will give a brief overview of the model which should be sufficient to follow the model analysis and understand the results. A more detailed description of the model, including the parameterisation, is given in the Appendix A.

2.3. *The main arthropods and their ecological classification in the model*

For the modelling and analysis of our system we need detailed data on the ecology of the important arthropod species involved. Fortunately, many of the data on the dominating Asian rice arthropod species are available due to intensive research at the IRRI (International Rice Research Institute; Los Banos, Philippines). For an overview of the important rice arthropods see, for instance, van Vreden and Abdul Latif (1986).

According to Settele (1992), Heong et al. (1992) Barrion et al. (1994), leaf and planthoppers are the dominating groups of pest arthropods in the Ifugao system (as in most Asian rice systems).

Table 1
Plausible ranges of the land use parameters

	Minimum	Median	Maximum
Temporal staggering of transplanting times (in days)	0 (synchrony)	20	60
Proportion of modern rice fields in the system	0	0.5	1.0
Proportion of non-rice areas	0.625	0.7	0.75
Proportion of vegetable fields within non-rice areas	0.072	0.286	0.722

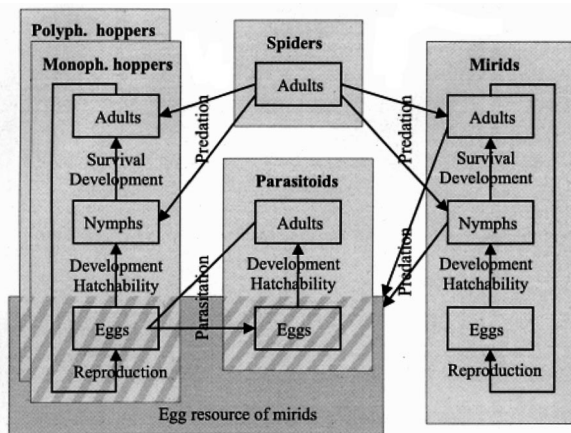


Fig. 1. Interactions in the arthropod species complex. For simplicity, predation and parasitization of polyphagous hoppers are not depicted in this figure.

Main species are the planthoppers *Sogatella furcifera* (white-backed planthopper: WBPH), *Nilaparvata lugens* (brown planthopper: BPH) and the leafhoppers *Nephotettix* spp. (green leafhoppers: GLH), *Cofana spectra* (white leafhopper), and *Recilia dorsalis* (zigzag leafhopper).

The main groups of hopper parasitoids are the Trichogrammatid genera *Anagrus*, *Oligosita* and *Paracentrobia* and the Mymarid genus *Gonatocerus*. Major predators are the wolf spider *Pardosa pseudoannulata*, web building spiders of the family Tetragnathidae, and the predatory mirid bug *Cyrtorhinus lividipennis*.

To keep the model tractable, all relevant species are summarised into six different groups. These groups are: (1) monophagous rice hoppers (e.g. BPH); (2) polyphagous rice hoppers (e.g. WBPH and some GLH); (3) parasitoids; (4) mirid bugs; (5) hunting spiders (*Pardosa pseudoannulata*); and (6) web building spiders (Tetragnathidae). The model does not distinguish between the species within each group but considers each group as a single entity. Within the species of an individual group there will be variability in model parameters, such as the oviposition rate. Here we assume that the group oviposition rate is given by the average of the species values. The highest and the lowest species values are used as bounds on the group average (see Appendix A).

Although hopper species (for simplicity we summarise planthoppers and leaf hoppers under the label 'hoppers') differ in their life traits, we could not find evidence in the literature for a systematic difference between the traits of monophagous and polyphagous hoppers in the sense that e.g. one group has higher dispersal ability or fecundity than the other. Therefore, in this study monophagous hoppers and polyphagous hoppers are assumed to have the same attributes except of course that the former occur only in rice. Hoppers not feeding on rice and their parasitoids are ignored at this stage of the study. In each of the two hopper groups and in the mirids we consider three stages ((a) eggs of various ages; (b) nymphs of various ages; and (c) adults) in the parasitoids we have eggs of various ages and adults. In the spiders only adults are considered.

The model does not distinguish between sexes. In the hoppers and the mirids we consider the total number of adults assuming a constant and even sex ratio. In the parasitoids we consider females only. An uneven sex ratio in the offspring of parasitoids is considered in the parameters of female reproduction (3:1 towards the females). The model structure is shown in Fig. 1.

2.4. Model component summary

2.4.1. Reproduction of hoppers

Each model day starts with the reproduction of hoppers. The number of eggs laid each day depends on the quality of the habitat and is negatively related to hopper density (Appendix A1; Fig. 6). Parameters are the daily oviposition rate, a density exponent measuring the strength of density dependence, and a habitat quality factor which in rice fields depends on the developmental stage of the crop (Fig. 3). In non-rice fields habitat quality is constant and lower than in rice fields and in forest it is lower than in vegetable fields (compare also Yu et al., 1996).

2.4.2. General parasitization and predation, and reproduction of mirids

The reproduction of hoppers is followed by parasitization and predation which are modelled

on a time scale of hours (Appendix A2). Each hour a number of hopper eggs is parasitised depending on the density of hopper eggs and parasitoids. Parasitization of hopper eggs depends on egg and parasitoid abundance and can be described by a Holling Type-II functional response (compare Chantarasana et al., 1984; Cronin and Strong, 1994) which is characterised by the saturation level and the half saturation density (Fig. 7).

Parasitoids usually do not lay all their eggs on one day and therefore we have to keep track of the parasitoid eggs not yet laid. The maximum number of eggs a parasitoid female can lay during its life time is denoted as *parasitoid fecundity*. The relevant parasitoid species have partly complementary, partly overlapping ranges of host species. As we consider a mix of species, we consider the whole group of parasitoids to be polyphagous on all hopper species, assuming that each day a parasitoid may switch from one hopper species to another with a certain switching probability, denoted as *switchiness*.

Consumption of hopper eggs by the mirid bug *Cyrtorhinus lividipennis* (a polyphagous predator of rice hopper eggs) exhibits a Type-II functional response (cf. Heong et al., 1990; Qingcai and Kwon, 1991; Laba and Heong, 1996) (cf. Fig. 7). We have no evidence that mirids avoid parasitized eggs and as a default we assume that they eat parasitized and unparasitized eggs at the same rates, showing no preference for either type. To assess the effect of this assumption on the model results we also consider scenarios with the mirid only eating unparasitized eggs. For each female mirid the number of eggs laid is calculated depending on the number of eggs consumed (Chua and Mikil, 1989; Appendix A2, Fig. 8).

The most important species of spiders preying on hopper and mirid adults and nymphs are the wolf spider *Pardosa pseudoannulata* and species of the family Tetragnathidae which are all generalists. Consumption by hunting spiders follows a Holling Type-II relationship, too (Heong and Rubia, 1989; Döbel and Denno, 1994). A parameter called *attention factor* is used to take account of the fact that hunting spiders are generalists and their diet includes other species, as well. The

attention factor measures how much attention the hunting spiders pay to hoppers and mirids. In contrast, the web building Tetragnathidae show no functional response. We assume that they impose a constant *mortality* on hoppers and mirids (compare Reddy and Heong, 1991a). The dynamics of the generalist spiders are not coupled to the dynamics of the hoppers and mirids. They rather depend on the total number of prey which we relate to the developmental stage of the crop in the rice field (Fig. 3). The ratio of hunting to web building spiders is measured by a parameter called *spider ratio* (see below and Appendix A6).

2.4.3. Ageing and development of eggs and nymphs

Now the eggs and nymphs of all species age and develop into the next stage (nymphs or adults, respectively). In the hoppers and the parasitoids we consider species groups, each containing a number of species with different developmental periods. We cannot expect distinct generations in any of these groups, because generations of different species will overlap. Overlapping generations can be obtained by considering constant developmental rates. However, this approach ignores that each individual of each species needs some minimum number of days to develop. This is valid in a species group, as well, and we assume that development from one stage to the next takes at least a number of d_{\min} days and from then on takes place at a constant daily rate of $(d_{\text{ave}} - d_{\min})^{-1}$. This ensures that on average development takes exactly d_{ave} days. The developmental times, d_{\min} and d_{ave} , in each species group depend on the developmental times of the individual species included and temperature ('cold' or 'warm' season: see above).

2.4.4. Hatching of eggs and death of nymphs and adults

Eggs that have developed and are viable hatch. Nymphs and adults may die due to starvation or age. The hatchability of hopper eggs is temperature-dependent and therefore differs between the warm and the cold season (e.g. Mochida, 1982). Hopper nymphal survival (from hatching to adulthood) is nearly constant (Mochida, 1982).

However, it is reduced at high densities (Denno et al., 1994). The life time of adult hoppers is assumed density independent. Their daily mortality rate is given by the inverse of their life time (see Appendix A4.1).

In the absence of better data, we model the hatchability of mirid eggs as temperature-independent. The survival of mirid nymphs and the life time of mirid adults depends on the number of eggs consumed (Chua and Mikil, 1989; Appendix A4.2, Fig. 9).

The hatchability of parasitoid eggs and the life time of adults are assumed to be independent of density and temperature. Note that if a parasitoid hatches from a particular type of hopper egg (monophagous or polyphagous), it will parasitize the same type of eggs preferentially but may switch to the other type of eggs as described above. Parasitized or unparasitized eggs that do not hatch at the end of their development may still be available as a resource to the mirids for some time. These unviable eggs decay at a constant rate (compare Appendix A4.3).

2.4.5. *Migration and dispersal*

After these local processes adults of all species may immigrate into the system, disperse to other habitats, or emigrate from the system. The mirids and most of the relevant rice hoppers are very good migrants (Riley et al., 1987) and may immigrate at any time of the year (Perfect et al., 1985). We assume constant daily *immigration rates* for hoppers and mirids from outside the system (compare Lim, 1978; Ooi, 1979; Denno and Roderick, 1990; Kisimoto and Rosenberg, 1994). Immigration of all species is proportional to the area of the habitat. In addition, hopper immigration is proportional to habitat quality (see above).

Hopper emigration from rice-fields is correlated to hopper abundance but also depends on the time of the season (e.g. Dyck et al., 1978). From the non-rice habitats where the conditions are constant, we assume that each day a certain proportion of all (polyphagous) hoppers emigrates (*non-rice emigration*). From the rice fields we assume no emigration early in the season

and a linear increase with time (called *rice emigration*) until some maximum is reached at the end of the season (cf. Cheng and Holt, 1990). If a ratoon period follows, emigration drops to zero and then increases to its maximum again, reached at the end of the ratoon season. Even in an old rice or ratoon field, habitat quality is still higher than that in non-rice habitats. Therefore, emigration from rice fields is always below emigration from non-rice habitats.

Mirids are found less frequently at the end of the rice season or in ratoon (IRRI, 1988; Settele, 1992). We assume that emigration of mirids increases linearly as the crop ages until a maximum is reached at the end of the season. If a ratoon season follows, emigration remains on that level. The daily emigration rate of parasitoids is assumed to be constant and identical in all habitats. To model dispersal within the system, all these emigrants are now distributed on the landscape components. The share of dispersers each component receives is proportional to its size. Mirids and monophagous hoppers immigrate only into rice fields. Altogether, we have modelled a net movement of individuals from high density and/or low quality habitats to low density and/or high quality habitats.

After dispersal, a certain proportion of hoppers and mirids leaves the system altogether. Their emigration is modelled in the same way as the 'local emigration' above (see Appendix A5).

2.4.6. *Spiders*

The spiders are generalists and have generation lengths of several months (Shepard et al., 1987). Therefore, their number will not depend strongly on the fluctuations of hoppers and mirids. However, in the rice fields their abundance will depend on the age of the crop. At the beginning of the season spiders immigrate from surrounding habitats and their number will reach a maximum around the middle of the season when conditions are optimal. Towards the end of the season when the field is harvested, the spiders are disturbed and leave the field, leading to decreasing abundance. In all, spider abundance is roughly proportional to the habitat quality factor (Fig. 3).

2.5. Model procedure

2.5.1. General procedure

Every model day is simulated by passing through the events described above (reproduction, feeding, ageing, etc.). All model parameters are set at the median of their plausible ranges (see Appendix A). The simulation of the population dynamics starts at 1 January. The initial population sizes are zero in all fields except for the vegetable fields with 50 polyphagous hoppers and 50 parasitoids per m². The dynamics are modelled for 6 years and the abundance of hoppers, mirids and parasitoids are recorded for each day and each habitat compartment (six rice compartments, vegetable fields and forest). The dynamics in the first year slightly depend on the initial conditions. Therefore only from the population trajectories of years 2–6 and the average and peak densities are calculated.

2.5.2. Understanding predator–prey interactions

To obtain a first understanding of the modelled arthropod interaction, we perform the following simulation experiment. We start with a situation where only hoppers but no enemies are present (scenario 1). Then we add one enemy group in turn, either spiders, mirids or parasitoids (scenarios 2–4). To these scenarios, we add another enemy group (scenarios 5–7: spiders + mirids, spiders + parasitoids, mirids + parasitoids) and finally we consider all three enemies (scenario 8).

As basic conditions we take a constant ratio of rice field area to the areas of vegetable fields and forests of 3:2:5. This is oriented at the present situation around the village of Banaue/Ifugao (compare Herzmann et al., 1998). We assume an even mix of modern and traditional rice fields, oriented at the situation in Kiangan/Ifugao (compare Settele, 1992).

2.5.3. Ecological and land use scenarios

2.5.3.1. Ecological parameters. We are interested in the effects of different forms of land use on the abundance of hoppers (we consider the sum of monophagous and polyphagous hoppers), and in how these effects depend on the ecological

parameters. As ecological parameters we denote all model parameters except those four describing the land use. The ecological parameters determine growth and the interactions of the species in the model.

In particular we consider the temporal averages of the arthropod abundances. For this we take the means of the daily abundances over the 5 years. In the rice fields between the cropping seasons, abundances are zero. These zero values are not considered in the temporal averages to reflect only infestation in the crop itself.

2.5.3.2. Sensitivity analysis, ecological scenarios, and land use scenarios. The analysis is carried out in two steps. First we perform a sensitivity analysis to establish which of the ecological parameters have the strongest effect on the temporal averages of hopper abundance (for simplicity we consider the mean of traditional and modern rice fields). From the results of the sensitivity analysis eight ‘ecological scenarios’ are formed which reflect different assumptions about the ecological conditions. In a second step, for each of the ecological scenarios various land use scenarios are tested.

The first step of the sensitivity analysis starts from a standard scenario where all ecological and all land use parameters are set at their median values with respect to their plausible ranges. Then the ecological parameters are varied in turn to their upper and lower plausible limits which leads to pairs of parameter combinations. In each pair all ecological parameters are at their median values except the one of interest which is either at its upper or at its lower bound. For each pair of parameter combinations we calculate the relative change in hopper abundance when the ecological parameter of interest is varied from its lower to its upper bound. We call this relative difference a sensitivity coefficient, because it describes how strongly the ecological parameter affects hopper abundance.

To identify the most important ecological parameters, we sum the absolute values of all sensitivity coefficients. Then we exclude those sensitivity coefficients with the smallest absolute values one by one until the sum of the absolute values of the remaining sensitivity coefficients is

reduced to 80% of the original value. The remaining parameters then produce 80% of the variation in hopper abundance and are used to construct the eight ecological scenarios.

Most of this variation can be encompassed by eight ecological scenarios (A–G and A'; see below). For each of these we investigate 13 different forms of land use (Table 2). In the first nine land use scenarios the proportions of non-rice areas (vegetable fields and forest) are fixed at median levels and the proportion of modern rice fields and the staggering time are varied systematically. In the last four scenarios the proportion of modern rice fields and the staggering time are fixed and the proportions of non-rice habitats are varied. The abundance values are compared among the 13 land use scenarios to establish which scenario leads to the lowest hopper abundance.

3. Results

3.1. Understanding the modelled predator–prey interactions

3.1.1. Effect of single and combined predator guilds

The peak densities of hoppers, mirids, and par-

asitoids for the scenarios 1–8 are shown in Fig. 2 (similar results are found for the seasonal averages; not shown). One can see that when adding a single enemy, the parasitoids are most effective (peak density of hoppers reduced from 22 000 to 290 per m²), followed by the spiders and the mirids (of course the effect of the spiders strongly depends on their assumed densities). When adding two enemies, the most effective control is achieved by the spiders and the parasitoids (peak density of hoppers reduced to 200 per m²). Four times more hoppers are found when the mirid is added together with the spiders or the parasitoids. Interestingly, when adding mirids and parasitoids (Scenario 7), hopper density is higher than with parasitoids alone (No. 4). At the same time the density of parasitoids is reduced by the mirids from 970 to 130 per m². The same can be observed when adding mirids to the spider–parasitoid–hopper system (cf. Nos. 6 and 8 in Fig. 2). The density of hoppers increases and that of parasitoids is reduced which represents a drastic change in species composition.

In contrast, adding spiders to a mirid–hopper or to a mirid–parasitoid–hopper system alters the species composition only slightly: the densities of *all* species are reduced. Adding parasitoids to the system leads to a strong reduction in hoppers and moderate reduction in mirids. This means a moderate change in species composition.

Table 2

The 13 land use scenarios. Scenario three represents traditional farming, as in Banaue^a

Scenario	Staggering	% Modern rice	% Non-rice area	% Vegetable fields
1	Max	Min	Med	Med
2	Med	Min	Med	Med
3	Min	Min	Med	Med
4	Max	Med	Med	Med
5	Med	Med	Med	Med
6	Min	Med	Med	Med
7	Max	Max	Med	Med
8	Med	Max	Med	Med
9	Min	Max	Med	Med
10	Med	Med	Max	Max
11	Med	Med	Max	Min
12	Med	Med	Min	Max
13	Med	Med	Min	Min

^a scenario five represents a mix of traditional and modern farming, as in Kiangan.

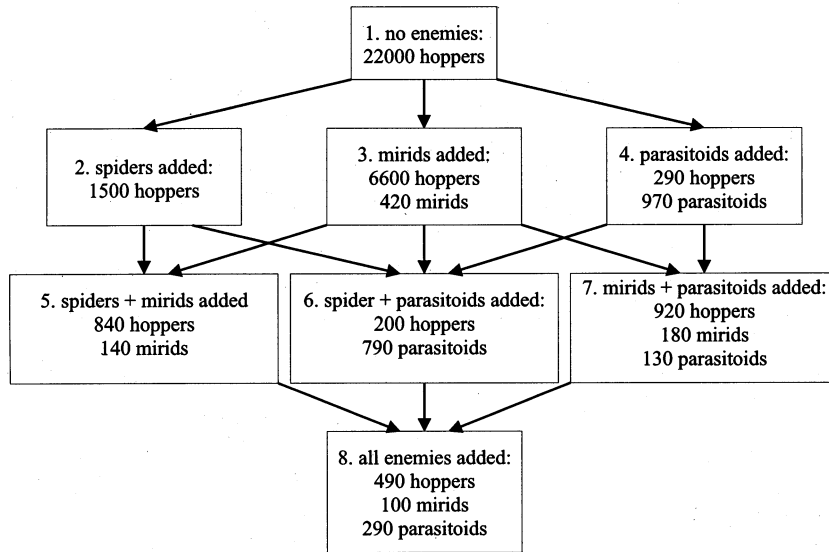


Fig. 2. Peak density of arthropods (individuals/m²), depending on the presence of enemies. Top: no enemy, second row: one enemy group, third row: two enemy groups, bottom: three enemy groups.

3.1.2. The role of spiders

Spiders were not modelled explicitly, but their numbers were correlated to habitat quality. The spiders impose a more or less time-independent — though density-dependent — mortality on the hoppers (Ooi, 1980; Reddy and Heong, 1991a,b). Within the ranges considered in the model, the parameters describing the spiders do not seem to affect the model results considerably (Table 3). Therefore below we will concentrate on the effects of mirids and parasitoids only.

3.1.3. Role of the mirid *Cyrtorhinus lividipennis*

The effects of spiders and parasitoids on the system follow our expectations. Both enemies only attack hoppers (adults, nymphs and eggs, respectively) reducing hopper growth and abundance. This of course will have an adverse effect on other enemies dependent on hoppers as a resource, thus reducing their densities as well. More surprising on first sight is that introducing the mirid into the system increases hopper abundance, which is most unwanted from a prey control perspective. This effect can be explained by the following reasons. First, as the mirids eat both parasitized and unparasitized eggs, they reduce

the parasitoids' 'resource' for egg production and also parasitoid egg survival. Second, as parasitoids have a higher attack rate (higher saturation level and lower half saturation density) than the mirids. They also have a higher reproduction rate. From each egg attacked by a parasitoid 0.2–0.4 parasitoids hatch after about 12 days. For each egg consumed, a female mirid lays about 0.25 eggs which produces less than about 0.1 adult mirids within 3 weeks.

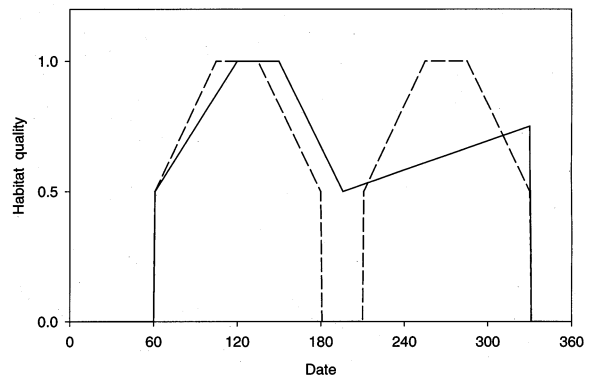


Fig. 3. Annual dynamics of the habitat quality factor in traditional (solid line) and modern (dashed line) rice fields.

Table 3
Sensitivity coefficients of the ecological parameters^a

<i>Spiders</i>		<i>Reproduction of mirids</i>	
Spider abundance	−0.02	Oviposition rate	1.00
Spider ratio	0.00		
Quality of non-rice habitats for spiders:		<i>Survival of hoppers</i>	
<i>Pardosa pseudoannulata</i>	0.00	Hatchability of eggs	0.05
<i>Tetragnatha</i> spp.	0.00	Adult life time	0.07
<i>Reproduction of hoppers</i>		<i>Survival of mirids</i>	
Oviposition rate	0.18	Hatchability of eggs	0.42
Density dependence	−0.17	Nymphal survival	0.31
Non-rice habitat quality	−0.66	Adult survival	0.14
<i>Parasitization</i>		<i>Survival of parasitoids</i>	
Saturation level	−0.68	Hatchability of eggs	−0.98
Half saturation density	1.06	Adult survival	−1.20
Parasitoid fecundity	−0.60		
Parasitoid switchiness	−0.19	<i>Decay rate of 'dead' eggs</i>	−0.03
<i>Eggs eaten by female mirids</i>		<i>Migration and dispersal rates</i>	
Saturation level	0.73	Immigration of hoppers	0.14
Half saturation density	−0.82	Immigration of mirids	0.52
		Hopper emigration from non-rice	−0.09
		Hopper emigration from rice fields	−0.35
		Mirid emigration from rice fields	−0.51
		Parasitoid emigration (any habitat)	−0.09
<i>Consumption by spiders</i>		<i>Development times</i>	
<i>Pardosa pseudoannulata</i> :		Hopper eggs	−0.22
Saturation level (hoppers)	0.00	Hopper nymphs	−0.05
Half saturation density	0.00	Mirid eggs	−0.09
Saturation level (mirids)	0.00	Mirid nymphs	0.00
Half saturation density	0.00	Parasitoid eggs	0.44
Attention factor	0.26		
<i>Tetragnathidae</i> :			
Hopper and mirid mortality	−0.03		

^a The bold-faced parameters produce 80% of the variation in hopper density (see text). A positive (negative) sensitivity coefficient means that hopper abundance increases (decreases) when the ecological parameter is increased. The parameters *saturation level* and *half saturation density* characterise the shape of the Type-II functional response of predator (or parasitoid) on prey (or host). With increasing prey (host) density the feeding (parasitization) rate increases and at high prey (host) densities saturates at the *saturation level*. The *half saturation density* is the prey (host) density where half the saturation level is reached.

Because of the first reason the parasitoids are inferior competitors to the mirids and because of the second reason they are the more effective control agents. Therefore in our system *the inferior competitors (the parasitoids) are the superior control agent*. In two-parasitoid-host systems, Briggs (1993) found that in such a situation the introduction of the superior competitor increases host abundance. Although our system is a host-parasitoid–predator system, the results of Briggs (1993) seem to apply as well, as the mirid is a superior competitor to the parasitoid.

We tested this hypothesis in two simulation experiments. First we made the assumption that the mirid does not eat parasitised eggs, thus reducing its competitive superiority. Alternatively we increased the mirid's attack rate and reduced that of the parasitoids. This reduced the parasitoids' superiority as control agents. According to Briggs (1993), both these changes should reduce the mirid's adverse effect (from the perspective of prey control) or even turn it to positive, which we could indeed confirm in our simulation experiments.

3.2. Sensitivity analysis and ecological scenarios

The result of the sensitivity analysis is shown in Table 3. One can see that the most important ecological parameters (bold faced) are those describing the living conditions for mirids (feeding rate, reproduction, survival and immigration), the living conditions for the parasitoids (parasitization rate, reproduction and survival) and the suitability of non-rice habitats for hoppers ('non-rice habitat quality'). In particular we find:

(1) Hopper abundance is positively related to the mirid's living conditions, as mirids inhibit the parasitoids (assuming they eat parasitised eggs), which are more efficient control agents than mirids (see above).

(2) Abundance of hoppers increases with deteriorating conditions for the parasitoids (see Table 3), as poor conditions mean low parasitoid abundance and fewer enemies to keep hopper numbers low.

(3) The abundance of hoppers in rice fields decreases if the suitability of non-rice habitats for hoppers is increased, which is due to the fact that habitat quality determines the immigration rate of hoppers (see model description). If the quality of non-rice habitats is increased more hoppers will immigrate into these habitats. As the mirid is not present in non-rice habitats (Settele, 1992), parasitised eggs are relatively safe there and para-

sitoids exploit the hopper eggs more efficiently than in rice fields where the mirid is present. This leads to a higher ratio of parasitoid numbers to hopper numbers in non-rice habitats. The non-rice habitats then act as traps that appear to be suitable to hoppers but are not really because of the high parasitoid abundance (compare Yu et al., 1996). The higher the apparent suitability of non-rice habitats to hoppers the stronger that trapping effect and the less hoppers are found in rice fields.

From this we form eight different ecological scenarios (Table 4). Scenario A is the standard scenario where all ecological parameters are median. In scenarios B and C the living conditions for the mirids are varied to optimal (B) and pessimal (C). In scenarios D and E the living conditions for the parasitoids are varied to optimal and pessimal and in scenarios F and G the suitability of non-rice habitat is varied to maximal and minimal. Comparison of scenarios B and C, e.g. reveals the effect of the mirid's living conditions on hopper abundance. Lastly we consider a scenario A' which is identical to the standard scenario A, but in contrast we assume that mirids do not eat parasitised eggs. It is not known whether mirids eat parasitised eggs or not and it has been shown further above that this question sensitively affects the arthropod community. Therefore both alternatives are encompassed by scenarios A and A'.

Table 4

The eight ecological scenarios. Scenario A' is identical to the standard scenario A except that mirids do not eat parasitised hopper eggs (see text)^a

Scenario	Conditions for mirids	Conditions for parasitoids	Suitability of non-rice habitat for hoppers
A	Med	Med	Med
A'	Med	Med	Med
B	Opt	Med	Med
C	Pes	Med	Med
D	Med	Opt	Med
E	Med	Pes	Med
F	Med	Med	Opt
G	Med	Med	Pes

^a The terms 'optimal' and 'pessimal conditions' for mirids and parasitoids are defined in the text.

Table 5

Temporal average values of arthropod density (individuals per m²) for the first four ecological scenarios and the 13 land use scenarios^a

	A. Standard scenario				A'. Parasitised eggs not eaten				Optimal mirid conditions				C. Pessimil mirid conditions			
	HT	HM	MR	PR	HT	HM	MR	PR	HT	HM	MR	PR	HT	HM	MR	PR
1	152	0	55	114	33	0	23	276B	68	0	89	26	38	0	12	281
2	145	0	49	132	35	0	21	275	75	0	82	27	41	0	11	281
3	123	0	37	196	44	0	15	332	89	0	77	28	48	0	8	337
4	175	164	67	97	33	40	25	309	65	75	97	26	38	47	14	319
5	153	189	56	127	36	47	23	206	70	78	88	26	42	54	12	313
6	137	121	40	186	47	59	16	379	83	86	80	26	52	65	9	287
7	0	219	86	67	0	40	29	344	0	72	108	26	0	48	16	354
8	0	199	72	93	0	55	28	348	0	73	99	26	0	65	16	358
9	0	128	42	163	0	72	17	445	0	83	80	26	0	79	10	450
10	133	143	59	122	36	46	27	308	51	56	90	35	43	54	15	317
11	201	210	67	93	42	56	27	312	76	86	97	23	49	64	15	319
12	101	110	42	179	31	40	18	305	65	71	80	32	36	45	10	313
13	147	158	48	153	37	47	18	306	89	100	87	20	41	52	10	311

^a HT: hoppers in traditional rice fields; HM: hoppers in modern rice fields; MR: mirids in rice fields (average of modern and traditional); PR: parasitoids in rice fields. In each group of four or three lines (scenarios 1–3, 4–6, 7–9, 10–13), the bold-faced numbers give minimum hopper density.

Table 6

Temporal average values of arthropod density (individuals per m²) for the second four ecological scenarios and the 13 land use scenarios (see Table 5)

	D. Optimal parasitoid conditions				E. Pessimil parasitoid conditions				F. Optimal non-rice habitat				G. Pessimil non-rice habitat			
	HT	HM	MR	PR	HT	HM	MR	PR	HT	HM	MR	PR	HT	HM	MR	PR
1	11	0	29	139	496	0	81	14	119	0	51	127	219	0	62	89
2	12	0	25	145	517	0	74	16	112	0	45	150	219	0	57	103
3	12	0	20	169	555	0	68	20	102	0	35	200	172	0	42	182
4	11	13	32	145	479	481	93	13	135	146	61	115	248	269	76	65
5	12	14	28	156	503	492	83	14	116	126	51	145	237	246	65	92
6	12	15	22	186	542	478	72	18	112	99	38	190	191	168	45	173
7	0	14	39	142	0	453	106	12	0	176	79	88	0	290	94	36
8	0	20	38	160	0	466	94	13	0	155	66	116	0	275	80	56
9	0	21	26	204	0	458	72	20	0	104	309	168	0	173	46	151
10	10	12	33	146	466	457	87	29	96	104	53	139	225	234	70	83
11	16	19	35	146	520	510	88	6	163	172	62	108	268	280	74	68
12	8	9	21	167	486	476	77	26	78	85	39	186	169	181	52	142
13	12	14	23	170	533	521	78	5	118	128	45	170	223	234	57	116

3.3. Land use scenarios

For each of the eight ecological scenarios and

each of the 13 land use scenarios (Table 2 and Table 4) the temporal averages of hopper, mirid and parasitoid abundances in traditional and

modern rice fields are given in Table 5 and Table 6 (for mirids and parasitoids the average of traditional and modern rice fields is given). For each

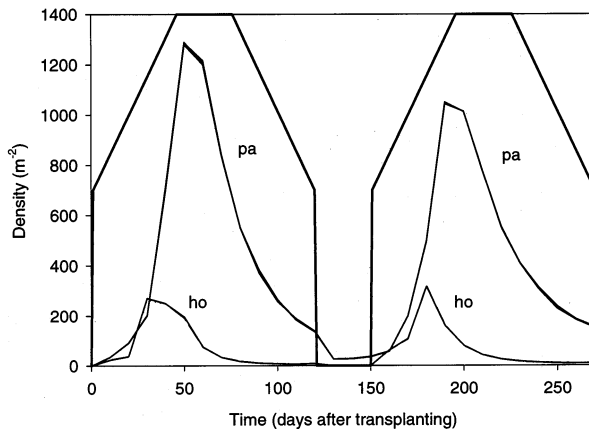


Fig. 4. Temporal development of hopper (ho) and parasitoid (pa) densities in modern rice fields (two cropping seasons in each of the three rice compartments; ecological scenario C, i.e. pessimal conditions for the mirid; mirid density is very low (see Table 5)). The bold line indicates the changing habitat quality as the crop develops (range from 0 to 1). All three rice compartments are transplanted at the same time (synchronous cropping).

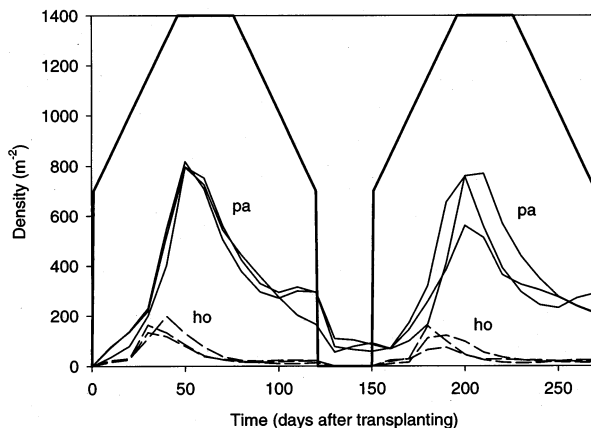


Fig. 5. Same as Fig. 4, but the staggering time is 60, i.e. the early rice compartment is transplanted 60 days before the median compartment which in turn is 60 days ahead of the late compartment (continuous cropping). In the figure, the hopper and parasitoid dynamics in the three rice compartments are superimposed such that the transplanting times of all three compartments appear on the same point of the time axis.

ecological scenario we are interested in how the choice of the land use scenario affects hopper abundance in the rice fields. From Table 5 and Table 6 we find the following results:

3.3.1. Effect of synchronous and asynchronous cropping:

In the standard scenario (A) and in the two scenarios where non-rice habitat suitability is optimal or pessimal (F and G), a staggering time of zero (synchronous cropping regime) leads to the lowest hopper abundance. In these scenarios both mirids and parasitoids can persist in the rice fields (Table 5 and Table 6). As the parasitoids can persist in non-rice habitats, too (e.g. Yu et al., 1996), they are always present in the system. As soon as a rice field is transplanted, they can immigrate at high rates. In contrast, the mirid can persist only in rice fields. If cropping is synchronised, after the harvest, there are no mirids in the system and at the next transplanting they have to immigrate from outside the system. Therefore the mirid's presence is reduced in a synchronous cropping regime (see below). As shown in Fig. 2, if mirids eat parasitised eggs their reduction reduces hopper abundance, and as synchronous cropping reduces mirid abundance, it reduces hopper abundance, as well.

The situation is reversed in scenarios B to E and A' where the living conditions for mirids and parasitoids are altered. Table 5 and Table 6 show that if the conditions for mirids are optimal (Scenario B) or if the conditions for parasitoids are pessimal (E) there are almost no parasitoids in the system and (apart from the spiders) the only enemy is the mirid. Here the inhibitory effect of the mirid (result 1) is negligible and hopper abundance is minimised by maximising the abundance of the mirid. This is done by asynchronous cropping (see above).

(4) In scenarios A', C and D, the conditions for mirids are unfavourable or those for the parasitoids are very favourable. Here the parasitoids are the dominating control agents (Table 5 and Table 6). In Fig. 4 one can see that synchronous cropping leads to strong fluctuations in hoppers and parasitoids while in Fig. 5 (continuous crop-

ping) the numbers of parasitoids and hoppers fluctuate less strongly and are lower.

(5) Altogether, one can conclude that if both mirids and parasitoids are present, synchronous cropping seems to lead to the lowest hopper numbers, because synchronous cropping reduces the abundance of the mirids which is beneficial to the parasitoids (assuming that the mirid eats parasitised eggs). If in contrast the mirids are the dominating enemies, continuous cropping allows them to persist in the system and reduces hopper numbers. If the parasitoids dominate, continuous cropping seems to reduce fluctuations and abundance of hoppers and parasitoids altogether.

3.3.2. *Effect of proportions of habitat compartments:*

(6) A high proportion of vegetable fields within the non-rice habitat reduces hopper numbers. This may be explained by the fact that the habitat quality for hoppers and their oviposition rate is greater in vegetable fields than in forest habitat. Therefore there are more hopper eggs in vegetable fields, leading to better conditions for the parasitoids to reproduce than in forest and thus to higher parasitoid abundance. Therefore vegetable fields are important parasitoid sources, and as the parasitoids are very efficient enemies, a large proportion of vegetable fields within the non-rice habitat leads to the lowest hopper numbers. There is no clear result whether a high proportion of modern or traditional rice fields leads to lower hopper abundance.

3.3.3. *Effect of proportion of non-rice habitat in the landscape*

(7) In scenarios B and E where either mirid conditions are optimal or parasitoid conditions are pessimal, hopper abundance is minimised when the proportion of non-rice habitat is maximised (land use scenario 10). In these two scenarios either the conditions for mirids are optimal or those for the parasitoids are pessimal. As the mirid is an important enemy of the parasitoids (assuming it eats parasitised eggs), in both scenarios parasitoids have difficulty to establish themselves where the mirid is present, i.e. in the rice fields (Table 5 and Table 6). The parasitoids

persist in rice fields only through immigration from non-rice habitats which act as a parasitoid source. The higher the proportion of non-rice habitats, the larger the parasitoid source, the higher the immigration of parasitoids into rice fields and the higher their ability to keep hopper numbers low.

(8) In the other ecological scenarios the parasitoids can establish themselves against the mirid and here parasitoid numbers are related to the density of host eggs which is higher in rice fields than in non-rice habitat. Therefore parasitoid density in rice fields is higher than in non-rice habitat, i.e. here the non-rice habitats act as a sink. The larger the area of the sink the more parasitoids are lost from the rice fields. This parasitoid loss increases hopper abundance in the rice fields and therefore the proportion of non-rice habitat should be small to minimise parasitoid loss and to minimise hopper abundance in rice fields (but see effect of proportions of habitat compartments).

4. Discussion

Throughout the last decades, generalisations about the effects of synchronisation and landscape structure have been sought. Reviews of Elton (1958) and Pimentel (1961) already have stated, that pest outbreaks are more likely in monocultures than in polycultures. Thus, in monocultures, the aim of pest control would rather be to reduce the pest populations than to stabilise the populations fluctuations, as often is the case in polycultural systems (compare Root, 1973; Brandenburg and Kennedy, 1982; Russell, 1989; Andow, 1991).

Empirical studies, however, show that there is no clear trend that pest abundance is lower in polycultures than in monocultures. Andow (1986, 1991) has summarised, that in polycultures in 60% of the studies analysed monophagous herbivores have been reduced compared to monocultures, while in 8% they have been increased. Polyphagous herbivores have increased in 40% of the species analysed, while in 28% their density was reduced. Whether in Ifugao we have mono-

or polycultures, depends on the definition, which is again scale dependant. If we look at single land use units (like fields, which are all comparatively small in the area), we can regard large portions of our system as monoculture, while the whole landscape might include many different land use units and thus can be defined as polyculture (compare Conklin, 1980; Herzmann et al., 1998).

Although the model we used in this study is quite complex, it ignores a lot of the system's spatial structure, such as limited dispersal distance of the organisms and small scale heterogeneities within individual fields (scale of meters; Kuno, 1978). These heterogeneities may have an effect on the species interactions, because the probability of an encounter may depend on the spatial distribution of the species in its habitat (compare approach of Ives and Settle, 1997). Secondly, we could not explicitly consider all species that are relevant in the system. Instead we formed groups that contain various species with similar ecological functions (guilds). These simplifications kept the model tractable but made it unsuitable for quantitative predictions, so we focused on qualitative results which proved to be biologically plausible.

An important result of our study is that the conditions one may find in the field are very much dependent on specific ecological conditions and not only on the landscape structure and the farming practices. This is illustrated in result (3) where the landscape structure is kept constant, but the quality of one landscape compartment has a strong effect on pest abundance. If one looks at results (7) and (8), one can see that the proportion of non-rice habitat has a strong impact on hopper abundance, which is mainly due to the fact, that non-rice habitats may act as sources or sinks of natural enemies, depending on biological characteristics and effects like the availability of alternative prey for predators (compare Way and Heong, 1994; Settle et al., 1996). Thus, the dynamics of the arthropods and particularly the pests may differ considerably, even if the cropping regime in the rice fields is not changed.

Furthermore, not only can different pest abundances be obtained with the same cropping regime, but the question which cropping regime

leads to the lowest pest abundance, depends on ecological details, as well. Whether synchronous (as recommended by Oka (1979, 1983), Loevinsohn et al. (1988), Oka (1988)) or asynchronous cropping (regarded as potentially better by Ives and Settle, 1997) leads to lower pest abundance very much depends on the interaction of the enemies (compare Heong et al., 1992; Hare, 1994; Litsinger, 1994), particularly the role of the mirid *Cyrtorhinus lividipennis*. The question whether the mirid *Cyrtorhinus lividipennis* eats parasitised eggs or not, is crucial for the identification of the cropping regime with the lowest hopper numbers. If the mirid has an adverse effect on the parasitoids, cropping regimes that keep its numbers low (synchronous transplanting) seem to be optimal, while in the other cases the mirid should be preserved by asynchronous cropping.

Consequently, we have to reject the view of Ives and Settle (1997), that predator migration among asynchronously planted fields will generally decrease pest densities. As could be shown in our example, simply treating predators as one and pests as another 'guild' is not adequate for the complexity of interactions.

The possibility of finding a 'unique optimal' cropping regime is further reduced if one considers not only the temporal averages of arthropod densities but also their seasonal maxima. We looked at these maxima, too, and could not find clear patterns in the results at all. Sometimes the maxima behaved similar to the temporal averages, sometimes they behaved opposite. The variability in the results may be further increased if one considers each individual species explicitly rather than summarising them into a small number of groups as we did in this study.

Altogether our model results suggest that general rules for 'optimal' cropping regimes with respect to predator-prey interactions are difficult to derive as these are very much influenced by the type of integration of different strategies and tactics (compare Smith, 1994) and the ecology of the species involved. In particular, the effects of traditional and modern rice growing practices in Luzon depend on the characteristics of the natural enemies in the landscape and our hypothesis that traditional farming practices are always superior

to modern ones has to be rejected. In particular, the strategy of synchronising pest control measures across wide geographical regions without knowing the role of predators in controlling pest densities needs serious reconsideration, as was already stated by Ives and Settle (1997).

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Appendix A. Detailed description of model parameterisation

A.1. Reproduction of hoppers and effect of habitat quality

The oviposition rate of hoppers decreases with increasing hopper density N via N^{-a} where a is some positive constant and ranges from 0.33 to 0.66 (Fig. 6; Denno et al., 1994; Hirano and Fujii, 1995; Matsumura, 1996). The number of eggs laid by a female during its lifetime lies between 200 and 350 (e.g. Pathak, 1968; Denno and Perfect,

1994) but can be five times higher than this (Mochida and Okada, 1979). Although the oviposition rate depends on the species, according to the references, it does not seem to differ systematically between the two groups of monophagous and polyphagous hoppers. Therefore, the same oviposition rate is assumed for both groups (see above), and the values of 200 and 350 are used as bounds on its range.

Eggs are deposited evenly during the entire oviposition period (which for simplicity we equate with the females life time), and the total number of eggs laid by a female is correlated to life time and oviposition period (Mochida and Okada, 1979). If we assume life times between 18 and 28 days (see below), the egg numbers above (200...350) translate to daily oviposition rates of between 12 and 20 eggs. We assume that this 'normal' range refers to medium to low densities of 100 hoppers per m^2 of optimal rice habitat. At higher/lower densities the oviposition rate is reduced/increased (see above). Because of the hyperbolic dependence shown in Fig. 6, the oviposition rate would increase indefinitely as hopper density gets very low. Above we mentioned that the oviposition rate can be 5 times higher than the normal range, which means daily oviposition rates between $5 \cdot 12 = 60$ and $5 \cdot 20 = 100$. We regard this as an upper limit.

These oviposition rates refer to 'optimal' rice habitat. As 'optimal' we define rice in the ripening stage. In suboptimal habitat the oviposition rate is reduced by a habitat quality factor < 1 . We combine ideas of Cheng and Holt (1990) and own observations to obtain a simple model for the time dependence of the habitat quality factor in traditional and modern rice fields (Fig. 3). This model implicitly includes some dependence of the hopper population on the proportion of brachypterous adults (Cheng and Holt, 1990). In non-rice habitats (forest and vegetable fields) the habitat quality factor is assumed to be zero for monophagous hoppers and constant at a low level for polyphagous hoppers (0.1–0.5 in vegetable fields and 0.05–0.15 in forest habitat). As in our simple spatial model we take an average over all vegetable fields. The quality value used is an average over new and abandoned vegetable fields of various successional stages.

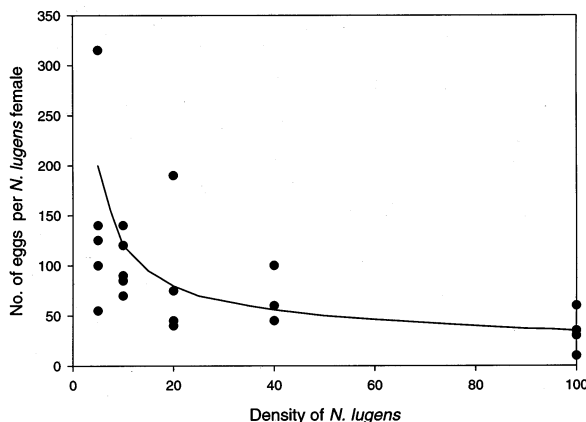


Fig. 6. Influence of hopper density on female fecundity in greenhouse populations of *Nilaparvata lugens* (after Heong, 1988).

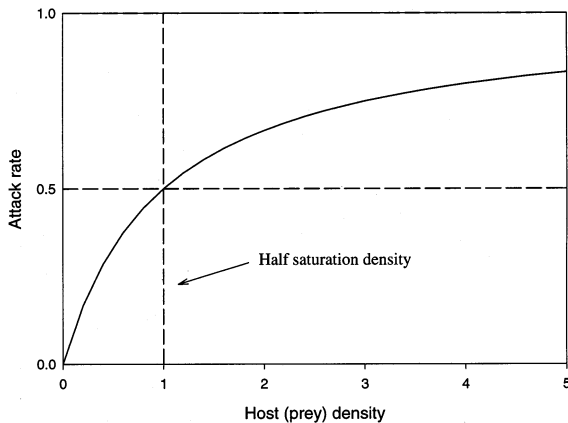


Fig. 7. Holling-Type-II functional response relationship. The attack rate is scaled in units of the saturation level as a function of host (or prey) density. Both axes have a linear scale.

A.2. Parasitization, predation, and reproduction of mirids

In the modelling of parasitization and predation it is important to consider that these processes act on faster time scales than the dynamics of the population themselves (Arditi and Ginzburg, 1989). The critical point here is that the attack rate of predators and parasitoids depends on prey density. While the predators are hunting and killing their prey, they reduce their resource which in turn reduces hunting success and attack rate. This circular dependence in the attack rate causes errors in the model, but we found that hours are a sufficient temporal resolution to reduce this error to an acceptable minimum.

A.2.1. Parasitization of hopper eggs by parasitoids

The only quantitative study on the functional response of parasitoids relevant to rice ecosystems we found was an experiment of Vien and Heong (1993) who studied the daily attack rate of *Anagrus flaveolus* WATERHOUSE in response to the densities of BPH and GLH eggs. The environment selected for the study was a 3 cm diameter, 30 cm high mylar cage with 60 day old rice trimmed to four tillers. From their results we derived the saturation level of the daily attack

rate and the half saturation density where the attack rate is half its saturation level (cf. Fig. 7). The results varied considerably between eggs of different hopper species, leading to saturation levels between 7 and 67 attacks per day and half saturation densities between 43 and 160 eggs on four tillers. High attack rates refer to BPH, low rates to GLH eggs.

In the field we find a mix of various species of host eggs. The average attack rate on this mix of host eggs is the average of the attack rates on the individual host species weighted by their relative abundance in the egg mix. The average saturation levels obtained in this procedure certainly do not encompass the full range from 7 to 67 per day given above, because these extreme values are assumed only when all host eggs are GLH or BPH eggs, respectively. An equivalent result is obtained for the half saturation densities. We assume saturation level and half saturation density of the parasitoid group in the rice field to range between 14 and 40 attacks per day and between 70–130 eggs per four tillers, respectively. Chandra (1980) studied the attack rate of other parasitoid species under experimental conditions and found values for the saturation level close to or within this range.

In traditional rice fields the number of tillers per m^2 is in the order of 120, in modern rice fields we observe values in the order of 200 (Settele, 1992). This leads to half saturation densities between $70 \cdot 30 = 2100$ and $130 \cdot 50 = 6500$ eggs per m^2 . For simplicity, we use the same half saturation densities in all rice fields and use the given values as bounds on their plausible range. Various studies (e.g. Miura (1990) for a species of *Gonatocerus*) show that parasitoid females lay the majority of their eggs on the first 2 days after reaching maturity. We assume that the total number of eggs a parasitoid can lay during its life time is up to twice as high as the saturation level of the daily attack rate. We assume that the attack rate is independent of the type and spatial distribution of the plants the host eggs are deposited on. Therefore, the same functional response is used for all habitat components of the landscape, including non-rice habitats. Of course, if hopper egg density is lower in non-rice habitats, so will be the parasitoids' attack rate.

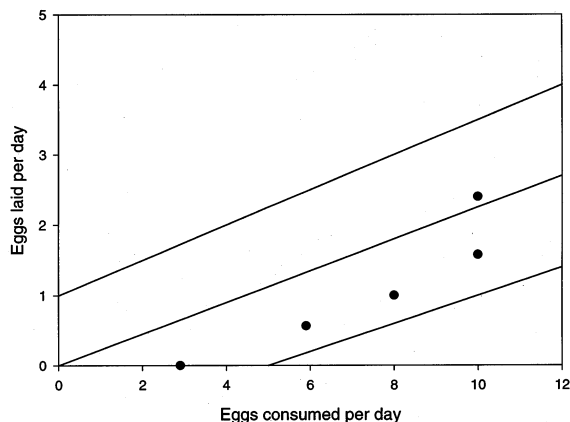


Fig. 8. Daily oviposition rate of *Cyrtorhinus lividipennis* as a function of the daily consumption of hopper eggs. The dots are data from Chua and Mikil (1989). The lines mark bounds and median of the plausible range.

While *A. flaveolus* has a wide range of host species, the other parasitoids of the genera *Gonatocerus* and *Oligosita*, have restricted — partly overlapping, partly complementary — ranges of host species (van Vreden and Abdul Latif, 1986; Litsinger et al., 1987; Yu et al., 1996). In our model, the groups of monophagous and polyphagous hoppers and the parasitoids consist of a mix of various species. The most plausible assumption therefore is that the group of parasitoids as a whole is fully polyphagous on each of the two groups of hopper species.

Switching between different host species occurs at a certain rate. The net rate of parasitoids that switch from one host to another is assumed to be the product of the probability of a parasitoid encountering an ‘alien’ egg and, in the case of an encounter, the probability to actually switch. The former is given by the relative abundance of ‘alien’ eggs, the latter may range from 50% (Yu et al., 1996) per generation (which is about 20% per day assuming a life time of 4 days) to 100% (Vien and Heong, 1993).

A.2.2. Consumption of hopper and parasitoid eggs by mirids

Laba and Heong (1996) quantitatively investi-

gated the functional response of adult mirids to eggs of BPH and WBPH and identified it as Type-II (cf. Fig. 7). With arguments similar to above (the mirid showed no preference for either type of egg), we obtain a saturation level of the females’ daily feeding rate ranging from 16 to 22. The half saturation density lies between 170 and 230 eggs on four tillers or 5100 and 11 500 eggs per m². Males (i.e. half of the total adult population) eat 30% less than the females (Laba and Heong, 1996) and nymphs eat about 75% less (see below). Egg consumption may vary among individual mirids, some eating more, some less than average. As the oviposition rate depends on egg consumption in a non-linear way (see below), such variation is very important. For each female mirid, we sample the number of eggs eaten from a Poisson distribution with the mean given by the functional response relationship.

A.2.3. Reproduction of mirids

Chua and Mikil (1989) performed an experiment where mirids were fed with BPH eggs. Each day the mirids were provided with a certain number of eggs and eggs not eaten were removed the next day. For various amounts of daily food provision (5, 10, 15, 20, and 30), adult life time, total number of eggs produced per female, and total food consumption per female were determined. Rather than plotting each of these three quantities as a function of food provision, we can use the last two quantities to plot total number of eggs produced versus total number of BPH eggs consumed. Incorporating the information on adult life time, we can plot the number of eggs produced per day versus the number of eggs eaten each day (Fig. 8). One can see that a certain threshold number of eggs has to be consumed before reproduction takes place. In contrast to this result, Sivapragasam and Asma (1985) found that even without eggs, a female mirid lives for about 6 days and produces nine eggs during that time. To account for these observations, we define two plausible bounds on the relationship between hopper eggs consumed and eggs laid per day (Fig. 8).

A.2.4. Consumption of adults and nymphs of hoppers and mirids by spiders

In experiments with a single prey species, *P. pseudoannulata* showed a Type-II functional response (IRRI, 1985; Heong and Rubia, 1989; Heong et al., 1991; Döbel and Denno, 1994) (cf. Fig. 7). The saturation level of the spiders daily attack rate was found to be 6, 12, and 22 for GLH, BPH, and mirids, respectively. There have been no studies comparing attack rates of spiders on adults and on nymphs. We assume the same functional response for both stages of prey. We take 6 and 12 as bounds on the saturation level of the overall attack rate of *P. pseudoannulata* on hopper adults and nymphs. The overall saturation level on mirids is assumed to range from 20 to 24.

The only study that provides quantitative results on the half saturation density was by Heong and Rubia (1989). Here half the saturation level was reached at 8–12 hoppers in a 19 cm diameter cage which translates to a half saturation density of about 250–400 hoppers per m². According to Heong et al. (1991), the spider's half saturation density on mirids is higher than that on hoppers by about 50%.

These functional response relationships were obtained from experiments with a single prey species which receives 100% of the spider's hunting time. In the field however, the generalist wolf spider feeds on hoppers, mirids, and many other species. Therefore, the share of total hunting time the spider spends on an individual prey species will be lower by some 'hunting factor' < 1, and so will be the number of individuals killed from that prey species. A simple but plausible estimate of the hunting factor for a prey species *P* is the relative abundance of *P*. If *P* has a very low density, it receives only a small share of the spider's hunting time and its hunting factor is small. With increasing density, the hunting factor increases and saturates at a value of 1 when 100% of the spider's hunting time is spent on *P* (as in a single-species experiment). In all, the hunting factor for a particular prey species can be described by a saturating function such as the one shown in Fig. 7. We set a range for the saturation density (i.e. the prey density where the hunting factor is 0.5) between 1500 and 2500 individuals per m². At

plausible hopper densities around 500 per m², this leads to hunting factors for hoppers around 0.2. In an experiment, hopper densities of 500 per m² would lead to attack rates in the order of 5–10 hoppers by each spider (see above). Multiplication with the hunting factor leads to one or two hoppers killed by each spider in the field. This is very close to an observation by Kiritani and Kakiya (1975).

Conceptually, in the web building Tetragnathidae the situation is much simpler. It shows no functional response and mortality due to these spiders is independent of prey density. For simplicity we assume that all species, including hoppers and mirids are caught in the web with the same probability. According to Shepard et al. (1987), *Tetragnatha* spp. kill about 2–3 prey each day. If we assume that the total number of prey items suitable to *Tetragnatha* is in the order of a few 1000 individuals per m² individual daily mortality due to *Tetragnatha* is around 0.001 and 0.003. We admit that this feeding model is very crude and heuristic, but at this stage, it is the only quantitative estimate we have.

A.3. Development of all species

Beside species variability, we have to consider the effect of temperature on development of the hoppers. Egg development times for (monophagous and polyphagous) hoppers under various temperatures range from 6 to 12 days (Pathak, 1968; Mochida and Okada, 1979; Mochida, 1982; IRRI, 1983; van Vreden and Abdul Latif, 1986). According to Mochida (1982), development time at a mean daily temperature $T = 21^{\circ}\text{C}$ ('cold' season) is 12 days for BPH and 10 days for WBPH. The values for $T = 23^{\circ}\text{C}$ ('warm' season) are 10 and 8, respectively. We set $d_{\text{av}}(21^{\circ}\text{C}) = 11\text{d}$; $d_{\text{av}}(23^{\circ}\text{C}) = 9\text{d}$; $d_{\text{min}}(21^{\circ}\text{C}) = 8\text{d}$; $d_{\text{min}}(23^{\circ}\text{C}) = 6\text{d}$. Using the same references, we obtain for hopper nymphs $d_{\text{av}}(21^{\circ}\text{C}) = 17\text{d}$; $d_{\text{av}}(23^{\circ}\text{C}) = 13\text{d}$; $d_{\text{min}}(21^{\circ}\text{C}) = 11\text{d}$; $d_{\text{min}}(23^{\circ}\text{C}) = 10\text{d}$.

The development of mirid eggs takes about 1 week (van Vreden and Abdul Latif, 1986; Shepard et al., 1987). Because of individual variability, some eggs will develop faster than others. We set

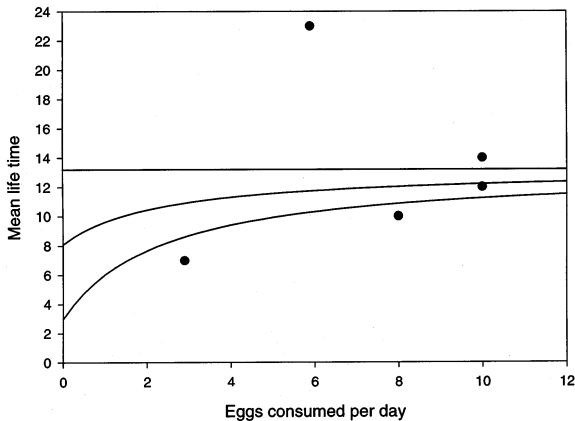


Fig. 9. Mean life time of adult *Cyrtorhinus lividipennis* as a function of the daily consumption of hopper eggs. The dots are data from Chua and Mikil (1989). The lines mark bounds and median of the plausible range.

$d_{av} = 7$ days and $d_{min} = 6$ days. Nymphs take on average 10–13 days to develop into adults (Sivapragasam and Asma, 1985; Chua and Mikil, 1989). We set $d_{av} = 12$ days and $d_{min} = 10$ days.

Parasitoid eggs take on average 11–13 days for development, depending on the species (Chandra, 1980). We set $d_{av} = 12$ days and $d_{min} = 8$ days.

A.4. Survival

A.4.1. Survival of hoppers

At a temperature of $T = 21^\circ\text{C}$, hatchability (hatching rate) of hopper eggs is about 80% for WBPH and 60% for BPH; at $T = 23^\circ\text{C}$ the values are 85 and 81%, respectively (Mochida and Okada, 1979; Mochida, 1982).

At the relevant temperatures the survival of nymphs (from hatching to maturity) is nearly constant at 95% and is identical for WBPH and BPH (Mochida, 1982). However, nymphal survival is reduced by intraspecific competition (Denno et al., 1994). We assume that nymphal survival of 95% is obtained only at low densities below $N < 50$ nymphs per m^2 . At higher densities we assume that nymphal survival is reduced by a factor of $(50/N)^{-a}$ where the value of a chosen is identical to the value used in the section on hopper reproduction (see Appendix A1).

We assume that the life time of adults is density-independent (cf. Denno et al., 1994), but depends on species and temperature. With arguments similar to above, it ranges from 20 to 28 days ($T = 21^\circ\text{C}$) and 18 to 20 days ($T = 23^\circ\text{C}$) (Pathak, 1968; Mochida, 1982).

A.4.2. Survival of mirids

Hatchability of mirid eggs was 43% in a study by Sivapragasam and Asma (1985). We assume a range between 35 and 50%. For the nymphs of *C. lividipennis*, Chua and Mikil (1989) performed similar experiments as described for the adults above. Similar to above, we can plot nymphal survival versus eggs consumed during nymphal period. Knowing nymphal development time (see below), we can plot nymphal survival versus eggs consumed per day. We found that nymphs never ate more than six eggs per day and nymphal survival was proportional to the number of eggs eaten. To reach 100% survival, a number of five to seven eggs had to be eaten every day.

To obtain the life time of adults, we used the results of Chua and Mikil (1989) (cf. above) and plotted adult life time versus eggs consumed each day (Fig. 9). We fitted two lines through the data points. One of the lines considers all five points, the other line excludes the outlier with 22 days. The two lines provide bounds on the mirid's (expected) adult life time. van Vreden and Abdul Latif (1986) give an estimate of 2 weeks which agrees to our upper bound and Sivapragasam and Asma (1985) found life times of 2–7 days if no hopper eggs were available and 4–12 days with hopper eggs, which roughly agrees to our lower bound.

A.4.3. Survival of parasitoids

We have no information at all on the hatchability of parasitoids. To obtain some estimate we assume that it may be of the same order as the hatchability of mirids (0.4). We assume that parasitoid hatchability ranges from 0.3 to 0.5. For a species of *Gonatocerus*, Sahad (1982) found a sex ratio of 3:1–4:1 females per male in the progeny. As we count parasitoid females only, we are interested in the female offspring which is 75–80% of total offspring in the example. Altogether, be-

tween 20 and 40% of eggs laid become female parasitoids.

The life time of the parasitoids relevant in the system ranges from 2 to 6 days, depending on the species (for instance, Chandra, 1980; Shepard et al., 1987). We assume the same life time for all parasitoids and use 2 and 6 days as bounds on its range. The decay rate of unviable eggs is assumed to range from 0.05 to 1 which corresponds to life times between 0 and 20 days.

A.5. Dispersal of hoppers and mirids

Cheng and Holt (1990) provide an estimate of 0.002 immigrant WBPH per hill ($= 0.04 \text{ m}^{-2}$). In newly transplanted rice fields, Heong et al. (1992) found initial densities of 0.01 BPH per hill ($= 0.2 \text{ m}^{-2}$). We take these two values as bounds on the daily large scale immigration rates of hoppers. In aerial catches, Riley et al. (1987) found between 6 and 15 times more mirids than BPH. Bounds on the daily immigration rate of mirids are then 0.6 and 1.5 per m^2 . In contrast to hoppers, mirids may immigrate into non-rice habitats, as well, but then are assumed to move into rice fields the next model day.

The emigration rate of hoppers from non-rice habitats, e_{nr} , is assumed constant in time and to range from 0.1 to 0.3 per day. In rice fields emigration of hoppers increases during the cropping season, as well as in the ratoon season, from zero to some maximum value e_{max} . Even near the end of the rice or ratoon season, we assume that a rice field is still more attractive to hoppers than non-rice habitats. Therefore e_{max} should be smaller than e_{nr} . We assume $0.25e_{\text{nr}} < e_{\text{max}} < 0.5e_{\text{nr}}$.

Similar to hoppers, the daily emigration rate of mirids increases during the rice season from zero to some maximum value assumed at the end of the season. Other than in hoppers, the emigration rate remains on that level if a ratoon season follows. We assume that this level may range from 0.1 to 0.3.

The daily emigration rate of parasitoids is assumed constant in time and to range from 0.1 to 0.3 in all rice and non-rice habitats.

A.6. Spiders

As described, spider abundance is assumed to be proportional to the habitat quality factor (Fig. 3). As various reports of the International Rice Research Institute (e.g. annual reports of IRRI) indicate (for typical results, see also Heong et al. (1992) and Barrion et al. (1994)), the level of the spider maximum in the middle of the rice season ranges from 70 to 150 per m^2 . The same references show that the abundance ratio of *P. pseudoannulata* to Tetragnathidae ranges from 1:1 to 2:1. Non-rice habitats are less suitable to spiders, especially to *P. pseudoannulata*. Here spider abundance is only 20–50% (*P. pseudoannulata*) and 30–70% (Tetragnathidae) compared to the value found in optimal rice habitat (Settele, 1992).

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