

# Arthropod Diversity and Community Structure in Relation to Land Use in the Mekong Delta, Vietnam

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## ABSTRACT

Declining biodiversity in agro-ecosystems, caused by intensification of production or expansion of monocultures, is associated with the emergence of agricultural pests. Understanding how land-use and management control crop-associated biodiversity is, therefore, one of the key steps towards the prediction and maintenance of natural pest-control. Here we report on relationships between land-use variables and arthropod community attributes (for example, species diversity, abundance and guild structure) across a diversification gradient in a rice-dominated landscape in the Mekong delta, Vietnam. We show that rice habitats contained the most diverse arthropod communities, compared with other uncultivated and cultivated land-use types. In addition, arthropod species density and Simpson's diversity in flower, vegetable and fruit habitats was positively related to rice cover in the local landscape. However, across the landscape as a whole, reduction in heterogeneity and the amount of uncultivated cover was associ-

ated, generally, with a loss of diversity. Furthermore, arthropod species density in tillering and flowering stages of rice was positively related to crop and vegetation richness, respectively, in the local landscape. Differential effects on feeding guilds were also observed in rice-associated communities with the proportional abundance of predators increasing and the proportional abundance of detritivores decreasing with increased landscape rice cover. Thus, we identify a range of rather complex, sometimes contradictory patterns concerning the impact of rice cover and landscape heterogeneity on arthropod community attributes. Importantly, we conclude that that land-use change associated with expansion of monoculture rice need not automatically impact diversity and functioning of the arthropod community.

**Key words:** community assembly; agroecology; rice; landscape heterogeneity; biodiversity; pest control.

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## INTRODUCTION

In recent years there has been considerable debate concerning the functional significance of biodiversity in ecosystems. In particular, a number of 'ecosystem services' have been identified that are derived from the species co-occurring in our

ecosystems (Daily 1997). Natural pest control delivered by crop-associated biodiversity is one such service (Mooney and others 1995; Schläpfer and others 1999) and recent theoretical and empirical studies have tested the relationship between species diversity and functioning of natural enemy assemblages (Cardinale and others 2003; Finke and Denno 2004; Wilby and Thomas 2002a, b). There is also evidence that changes in the abundance of particular trophic guilds are key to the stability of pest control in rice ecosystems (Schoenly and others 1996; Settle and others 1996). Hence, one challenge in predicting and improving natural pest control in agro-ecosystems is to understand how the diversity and guild structure of arthropod communities is affected by agricultural practice and land use.

Ideas concerning the role of landscape heterogeneity in promoting local species diversity in agro-ecosystems, and particularly the diversity of crop-associated arthropods, are commonly raised in the applied and fundamental literature. Southwood and Way (1970) suggested that the degree of biodiversity in agro-ecosystems depends, in part, on the diversity of vegetation, the intensity of management and the extent of isolation of the crop. From a functional perspective, the importance of habitat heterogeneity in increasing crop-associated diversity has often been discussed (for example, Altieri 1999; Waage 1991; Way and Heong 1994) and the worsening of insect pest problems has been attributed to the expansion of crop monocultures at the expense of natural vegetation (Altieri 1991).

In addition to the impact on aggregate community attributes such as species diversity, landscape structure can also have functionally-relevant impacts on the composition and guild structure of arthropod communities. The spatial arrangement of habitat fragments is known to influence different trophic guilds in different ways. For example, secondary consumers, in particular parasitoids, are known to be relatively sensitive to habitat fragmentation (Kruess and Tscharntke 1994, 2000; Thies and Tscharntke 1999; Tscharntke and Kruess 1999). Although differential impacts on secondary consumer species are of obvious proximate significance for the maintenance of natural pest control services, indirect effects are also likely. Detritivores, for example, although not directly pestiferous, or direct competitors of pest species, support secondary consumers in irrigated rice systems at times when the abundance of herbivores is low (Settle and others 1996). They are, therefore, of crucial importance for the effective natural control of pest species.

In this study, we highlight the changes in arthropod community structure across a gradient of land-use heterogeneity in the Mekong delta, Vietnam. We show that spatial landscape structure and local land management affect species diversity and guild composition of the arthropod community and we discuss the implications of these compositional changes for natural pest control in this rice-based ecosystem.

## METHODS AND MATERIALS

### Study Site Description

The study was undertaken in a rice-dominated agricultural landscape in Tien Giang province, Vietnam. Tien Giang occupies 380,000 ha in the northern Mekong Delta, and approximately 90% of its land is managed for agriculture. Rice is the principal crop and the province produces 130 million tons annually. The study area was located in a representative rice-dominated landscape towards the center of the province surrounded by similar agricultural land for many kilometres in each direction. Across the study area, three rice crops are grown per year (November/December to March/April; April/May to August; August/September to November) resulting in almost continuous cropping, although during the study excessive flooding occurred in September–November at the two northern-most sampling positions, restricting the flooded regions to two crops per year. Water is plentiful in this region and farmers have control over planting time and water management. Within the constraints of the general cropping seasons, planting tends to be synchronous at the scale of individual farms (mean c. 1 ha, range 0.6–2.0 ha), and planting time may vary by up to one month among farms. Post-harvest, crop residues are generally left during the fallow and incorporated into the soil before the following season. The fallow is usually flooded or moist and vegetative and break crops tend not to be grown. On average, farmers in the study area use 3.2 insecticide applications per season (individual fields range between 0 and 7 sprays; transect position averages range between 2.9 and 3.6 sprays) in rice and 1.9 (range 1–4) fungicide applications (unpublished data arising from surveys of > 100 farmers managing the sampled fields, though not relating directly to the sample locations). Pesticide use in rice is similar across the transect, both in terms of the products used and the frequency of application, although insecticide use may be higher in vegetable and fruit production (Van Mele and others 2002). Bunds

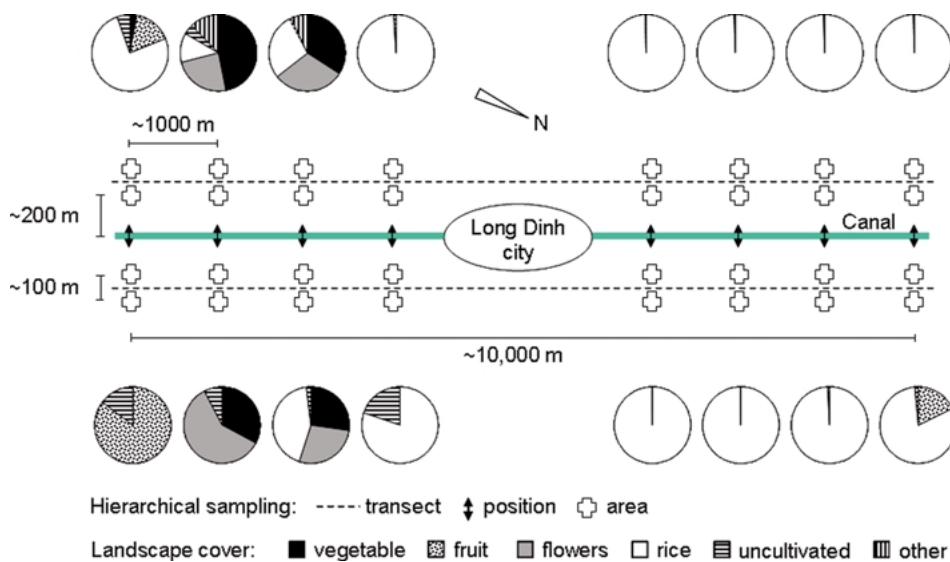


Figure 1. Schematic representation (not to scale) of the sampling regime imposed around the town of Long Dinh in Tien Giang province in southern Vietnam. Pie charts indicate the cover of habitat types as assessed from range finder data recorded in July 1998.

between fields are not generally managed systematically, but may be sown with grass (*Bracharia* spp.).

## Sampling

Between September 1997 and December 1998, suction samples of the arthropod community were taken at approximately 1-month intervals from a series of sampling points across a gradient of land use ranging from almost pure rice landscapes, to mixed cropping landscapes of vegetables and fruit. Sampling points were arranged hierarchically around two parallel transects centered on the town of Long Dinh ( $10^{\circ}25' N$ ,  $106^{\circ}15' E$ ). Sampling was done using a modified blow-vac sampler (Arida and Heong 1992; International Rice Research Institute (IRRI), Los Baños, Philippines). The transects were approximately 10 km long, one lying to the north side of a large canal (c. 50 m wide), and the other to the south side (Figure 1). The primary sampling locations (transect positions) were at approximately 1-km intervals parallel with the canal (the two central locations were not sampled as they are inside the limits of Long Dinh town). At each of these primary locations, two sampling areas were identified on each side of the canal (that is, two for each transect). The first was at a distance of approximately 200 m perpendicular to the canal and the second approximately 100 m further away from the canal. Within each sampling area, five suction samples were taken from the vicinity of permanently marked sampling points, at least two from rice habitat, and at least two from non-rice habitat. Thus, on each sampling date, 160 samples

were taken (2 transects  $\times$  8 positions  $\times$  2 areas  $\times$  5 samples). The sampling method allowed collection of all arthropods from the vegetation and surface of soil or water (in flooded habitats to a depth of c. 2 cm) in the volume enclosed by a cylinder of 40-cm diameter and 1-m depth. Sampling was done exhaustively, until no live arthropods were visible in the sampling cylinder. All collected arthropods were immediately stored in 60% alcohol, before being identified in the laboratory. For each sample, the habitat type from which the sample was taken was recorded. Additionally, in July 1998, local land use in the vicinity of each sampling area was assessed using a rangefinder. From a point at the center of each pair of sampling areas, landscape use was estimated along four 200-m transects in the principal compass directions.

## Data Collation and Analysis

Data from the samples were collated into a relational database, along with supplementary data concerning the arthropods (feeding guild, development mode, feeding location and taxonomic information) and the samples (date, habitat type, transect, position and sampling area). Where possible, identification was done to the species level with reference to extensive collections and experience held at IRRI, though in some cases only the family or genus was identifiable and in these cases, morphospecies were identified. Each individual was listed as adult or immature accounting for differences in habitat use or feeding guild. In cases of uncertainty, feeding guild was ascribed based on general knowledge of the higher taxon, if unambiguous, otherwise the record was omitted from the

analyses involving feeding guilds. Habitat type was usually the crop or vegetation type at the point of sampling, but for sampling points in rice fields, the crop stage was recorded as the habitat type (seedling, tillering, booting/flowering, milk/ripening, stubble, ratoon or harrowed). For each sample we calculated species density (number of species recorded per sample, uncorrected for the number of individuals), diversity (Simpson's Index:  $1/\sum p_i^2$ ; Simpson 1949) and arthropod abundance (number of individuals sampled irrespective of species richness), enabling us to explore effects of the various habitat/land characteristics in terms of three complementary response variables. Simpson's index was chosen as it is relatively insensitive to abundance changes, is weighted towards the most abundant species (in contrast to species density), and is considered superior to rarefaction for ranking communities (Lande and others 2000; Magurran 2004).

Data were analysed using linear mixed effects models (S-plus 6.0, Insightful Corp., 2001) following procedures described in Crawley (2002). This technique allows the hierarchical spatial structure in the data to be accounted for, thus avoiding problems of spatial pseudo-replication, while retaining the variance structure of the raw data. The spatial sampling levels in the data were specified in the statistical models as nested random factors; date, transect within date, position within transect and sampling area within position. To derive the fixed-factor explanatory variables, the four rangefinder transects taken at each sampling area were combined and the following variables were calculated: (1) *vegetation richness*—the number of vegetation types occurring in the area (total number of crop types plus uncultivated land-use types in the area), (2) *crop richness*—the number of crop types encountered, (3) *rice cover*—the proportion of the landscape under rice cultivation and (4) *uncultivated cover*—the proportion of the landscape not cultivated. These four variables and habitat type at the sample location were included in models as fixed effects, and model simplification was performed in an analogous way to stepwise multiple regression. Factors were deleted from the full model in reverse order of their explanatory power using maximum likelihood (ML) parameter estimation. Only those factors whose deletion caused a significant reduction in the explained deviance of the model were retained in the minimum adequate model. Quoted parameter estimates are derived from the minimum adequate model with restricted maximum likelihood estimation (REML) in all cases. All models were checked for

mis-specification using standard plots of residuals (Crawley 2002). Similar models excluding habitat type were used to analyze samples originating from single habitat types. Transformation of the response variable was undertaken where necessary.

## RESULTS

### Patterns Across All Habitat Types

The experimental design ensured that herbaceous layer invertebrates were sampled from a variety of landscapes ranging from mixed-cropped areas comprising fruits, vegetables, flowers and rice, to landscapes completely dominated by rice production (Figure 1). At the extremes, one sampling area had no rice occurring within the range-finder sample compared with several areas that were more than 99% rice. The invertebrate samples were taken from 18 different habitat types, though inferences of habitat differences in the arthropod community metrics must be treated with caution since the more structurally complex habitats (such as the fruit orchards) were not adequately sampled using the suction method. Nevertheless, the samples are representative of the herbaceous layer in these habitats. Across all samples, those from mature rice and uncultivated areas had the highest species density, Simpson's diversity and abundance (Figure 2). Within the rice habitats, Simpson's diversity and species density increased from the seedling stage through to a maximum at the milk/ripening stage, whereas abundance was maximal at the tillering and booting/flowering stage, falling off slightly at the milk/ripening stage. Relatively high Simpson's diversity and abundance were maintained after harvesting in rice stubble or in ratoon growth, but after harrowing, abundance, Simpson's diversity and species density fell to very low levels. The mixed model analysis of all habitats together indicated that there were significant differences among habitats in species density, Simpson's diversity and total abundance (Table 1). In addition to habitat, vegetation richness, rice cover and, marginally, uncultivated cover had statistically significant effects on arthropod species density and Simpson's diversity. All coefficients were positive, but interpretation of the analysis is complicated by strong correlations among the continuous explanatory variables. The coefficients reported reflect the independent correlations between each significant explanatory variable and community attribute, that is, the predicted relationship with all other explanatory variables kept constant. Actual (non-independent) coefficients, reflecting the observed

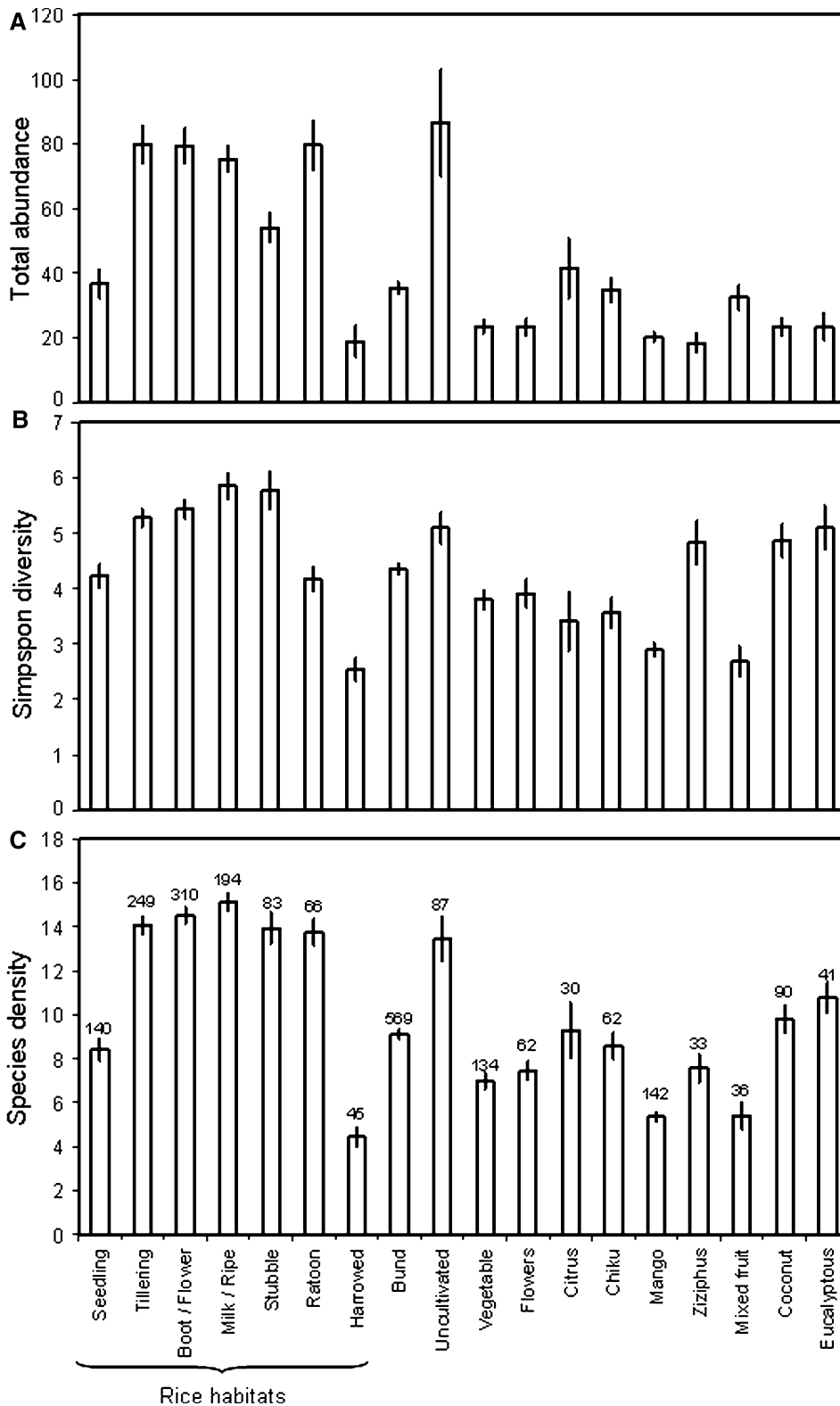


Figure 2. **A** Mean abundance (number of organisms per sample), **B** species diversity (reciprocal Simpson's index) and **C** species density in suction samples from habitat types in Mekong Delta. Bars denote standard errors and the numbers above columns represent the number of samples on which the mean is based.

patterns with co-variation among explanatory variables, were also derived by addition of the term to a model containing only habitat type and the random effects. For species density, for example,

non-independent coefficients revealed a negative effect of increasing rice cover (coefficient = -0.071), but positive effects of uncultivated cover (coefficient = 0.476) and vegetation richness

**Table 1.** Results of Linear Mixed Model Analysis of Arthropod Abundance, Species Density and Simpson's Diversity

Fixed effects	df	Coefficient	L. ratio	P	Random effects	Variance component
Species density ( $\log_e$ )						
Habitat type	17	–	536.0	< 0.001		
Rice cover	1	0.346	6.53	0.011	Date	0.011
Non-crop cover	1	0.985	3.87	0.049	Transect	< 0.001
Crop number	1	–	0.26	N.S.	Position	0.054
Vegetation number	1	0.081	12.57	< 0.001	Area	0.215
Abundance ( $\log_e$ )						
Habitat type	17	–	478.9	< 0.001		
Rice cover	1	–	0.48	N.S.	Date	0.047
Non-crop cover	1	–	0.24	N.S.	Transect	< 0.001
Crop number	1	0.022	4.22	0.04	Position	0.074
Vegetation number	1	–	0.03	N.S.	Area	0.715
Simpson index ( $\log_e$ )						
Habitat type	17	–	160.7	< 0.001		
Rice cover	1	0.229	9.762	0.002	Date	< 0.001
Non-crop cover	1	–	3.295	0.070	Transect	< 0.001
Crop number	1	–	0.156	N.S.	Position	0.032
Vegetation number	1	0.069	14.89	< 0.001	Area	0.014

Data from all habitat types were included in the analysis.

(coefficient = 0.043). By contrast, for arthropod abundance only crop number and habitat were significant explanatory variables of abundance, crop number having a small but positive coefficient. For the analysis of all habitats combined, the variance components of all random factors were generally small compared with the residual variance, but sampling area formed the highest component for abundance and species density suggesting that the most unexplained variance occurred at this spatial scale.

### Patterns Across Individual or Grouped Habitat Types

There were variable relationships between the landscape variables and community attributes at different stages of the rice crop, though the coefficients were generally weak. There was no significant effect on Simpson's diversity at any stage. However, at the seedling stage, crop richness had a marginally significant effect on abundance ([ $\log_e$  transformed] coefficient = 0.06, L. ratio = 3.90,  $P = 0.048$ ). In addition, there was a significant effect of crop richness on species density (coefficient = 0.47, L. ratio = 6.08,  $P = 0.014$ ) at the tillering stage and of vegetation richness at the flowering stage (coefficient = 1.162, L. ratio = 8.68,  $P = 0.003$ ).

For the non-rice habitats, the number of samples was too low for individual analysis, with the exception of bunds (the water control barriers between flooded paddy fields). Therefore, habitats were grouped into two aggregates representing fruit (Chiku, ziziphus, mixed orchards, citrus and mango) and flowers/vegetables. Analysis of the samples from bunds showed no significant effect of the landscape variables on abundance, but a significant effect of vegetation richness on species density (coefficient = 0.06, L. ratio = 7.33,  $P = 0.007$ ). For Simpson's diversity, there was a significant and relatively strong effect of rice cover (coefficient = 0.59, L. ratio = 12.58,  $P < 0.001$ ), and weak effects of vegetation richness (coefficient = 0.09, L. ratio = 9.98,  $P = 0.002$ ), and uncultivated cover (coefficient = 0.02, L. ratio = 5.58,  $P = 0.018$ ).

For the samples from fruit orchards, rice cover was again a strong and significant correlate of species density (coefficient = 2.94, L. ratio = 5.52,  $P = 0.019$ ), Simpson's diversity ([ $\log_e$  transformed] coefficient = 0.79, L. ratio = 12.8,  $P < 0.001$ ) and abundance ([ $\log_e$  transformed] coefficient = 0.82, L. ratio = 10.9,  $P = 0.001$ ).

For the flower and vegetable habitats, rice cover (coefficient = 0.70, L. ratio = 20.0,  $P < 0.001$ ) and uncultivated cover ([ $\log_e$  transformed] coefficient = 1.84, L. ratio = 11.2,  $P < 0.001$ ) were

significant correlates of species density and Simpson's diversity (rice cover, coefficient = 1.86, L. ratio = 9.76,  $P = 0.002$ ; uncultivated cover, coefficient = 0.05, L. ratio = 6.34,  $P = 0.012$ ). Crop richness was a significant, but weak, negative correlate of abundance ( $[\log_e]$  transformed] coefficient =  $-0.06$ , L. ratio = 7.21,  $P = 0.007$ ).

### Guild Composition in Samples From Rice Habitats

The proportional abundance (arc-sine transformed) of parasitoids (L. ratio = 17.23,  $P < 0.001$ ), predators (L. ratio = 30.71,  $P < 0.001$ ) and detritivores (L. ratio = 19.05,  $P < 0.001$ ) varied significantly among the rice growth stages, as did absolute abundance (Figure 3). Numbers of parasitoids and predators peaked early in the crop cycle at the tillering stage, whereas herbivore numbers peaked later at the booting/flowering stage. Although detritivore numbers peaked at the milk/ripening stage, their numbers were relatively stable through the cropping season.

Analysis of landscape impact on the absolute abundance of feeding guilds revealed few significant relationships, though there was a significant positive effect of vegetation richness on the absolute abundance of detritivores, which was consistent across the growing season from seedling to ripening ( $[\log_e]$  transformed] coefficient = 0.16, L. ratio = 12.36,  $P < 0.001$ ). Changes in guild structure are, perhaps, better indicated by changes in proportional abundance of the guilds. For proportional abundance (arc-sine transformed), there was no significant relationship for parasitoids or herbivores, but for predators there was a strong and significant positive effect of rice cover (coefficient = 0.26, L. ratio = 11.51,  $P < 0.001$ ) and a weak effect of crop richness (coefficient = 0.02, L. ratio = 6.90,  $P = 0.009$ ). For detritivores, there was a significant negative effect of rice cover (coefficient =  $-0.15$ , L. ratio = 11.79,  $P < 0.001$ ), on their proportional abundance and a significant interaction between rice cover and the rice stage from which the samples were taken (L. ratio = 15.25,  $P = 0.004$ ). This interaction seems largely to be due to a difference between seedling rice and the later growth stages; the proportion of detritivores was higher at the seedling stage than the other growth stages in rice-dominated landscapes, but this effect was not seen in landscapes of lower rice cover (Figure 4).

We also tested the composition of life-history types within the herbivore guild to test whether these data corroborate the theoretical prediction

that the endopterygote herbivores should increase in incidence relative to exopterygote herbivores in communities of lower natural enemy diversity (Wilby and Thomas 2002b). There was no significant relationship between natural enemy (predators plus parasitoids) species richness or parasitoid species richness and the proportion of endopterygote herbivores. However, consistent with theoretical predictions, there was a significant negative relationship between the proportion of endopterygote herbivores (arc-sine transformed) and predator species richness (coefficient =  $-0.012$ , L. ratio = 5.17,  $P = 0.023$ ).

### DISCUSSION

Two principal themes emerge from our data analysis. First, the broad patterns in arthropod community assembly and structure observed are similar to those reported for other areas of south-east Asia, suggesting that our results may be of broad relevance. Second, the study also highlights specific influences of landscape context on arthropod community attributes, with implications for the impact of land-use and management on ecosystem services. It should be noted that these relationships were observed in a real agricultural setting in which cropping synchrony, pesticide inputs and large-scale landscape factors were not controlled. Although these other factors are of undoubted importance in determining arthropod community structure in rice (Way and Heong 1994), they did not vary systematically across our land-use gradient. Such factors together with other local management variations are, however, potential contributors to the high variability in our dataset. Indeed, the variance components of the random explanatory variables show area (different sampling sites within the positions along the transect) to be the most important random factor with respect to abundance and species density (Table 1), probably reflecting differences in local management (for example, pesticide use).

One of the most striking general patterns is that rice fields host a relatively abundant and diverse arthropod fauna; this is clear despite the limitations of our sampling in some of the tall-stature vegetation, and supports previous assertions for tropical irrigated rice with minimal insecticide use (Bambaradeniya and others 2004; Schoenly 1998; Schoenly and others 1994; Settle and others 1996; Way and Heong 1994). Mature rice communities ranked highest in abundance, species density and Simpson's diversity, rivalled only by the samples taken from uncultivated vegetation, a diverse

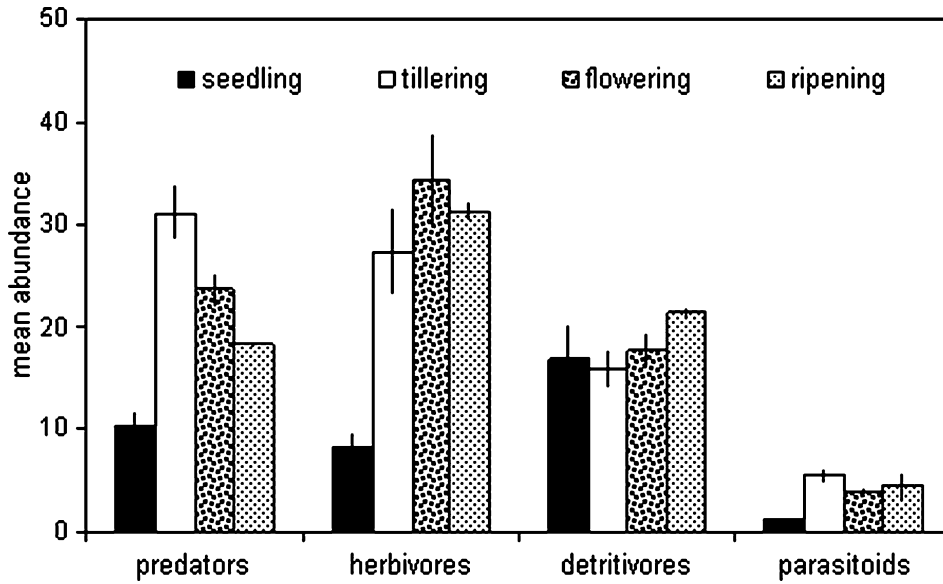


Figure 3. Mean abundance (number of organisms per sample) of arthropods in the four recorded trophic guilds across all samples from the different stages of the rice crop. Bars denote standard errors of the means.

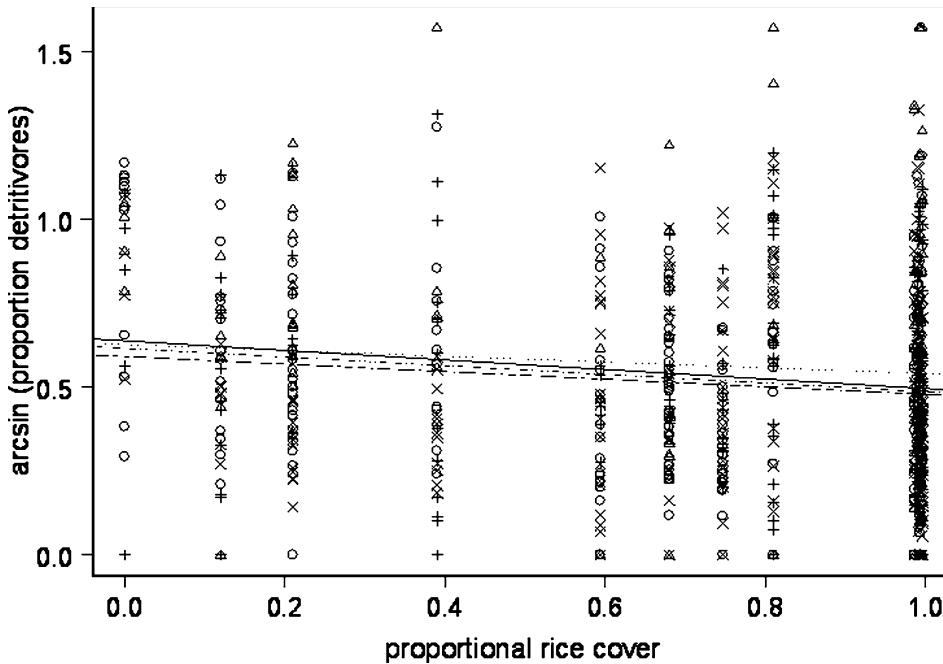


Figure 4. The significant relationship between the proportion of rice cover in the landscape and the proportion of detritivores in samples from rice crops. A statistically significant interaction between rice cover and crop stage is displayed as distinct relationships for each crop stage. (Dotted line and triangle seedling, dashed line and diagonal cross tillering, solid line and circles flowering, dash and dotted line and vertical cross ripening).

group of habitats which includes the bunds between fields which tend to be colonized by natural vegetation (though on occasion they may be seeded with grass species (*Bracharia* spp.) or cleared with herbicides). Our data also highlight the importance of seasonal re-colonization in determining arthropod community structure in rice habitats: Although invertebrate abundance, species density and Simpson's diversity were relatively low at the seedling stage, there was a marked increase in all three variables by the tillering stage when maximum abundance was reached, and species density and Simpson's

diversity continued to rise slightly through to harvest. This is a similar pattern of community assembly reported in other regions of south-east Asia (for example, Heong and others 1991). Notable changes in guild composition through the rice growing season were also observed. There was early season numerical dominance of detritivorous species (at the seedling stage), whereas predator abundance peaked at the tillering stage (presumably supported largely by detritivorous prey) and herbivores at the booting/flowering stage. High abundance of detritivores in the early part of the season has been shown to be key to the stability



of generalist predator abundance and control of major pests such as the brown planthopper (Settle and others 1996).

An important finding of this study is that local landscape structure had a significant impact on guild structure and community attributes. Many significant relationships between landscape variables and community attributes were demonstrated in our study, although on the whole these were weak with small effect sizes despite the extent of the land-use gradient, which varied from highly heterogeneous areas with virtually no rice, through to areas with 99% rice cover. Although our gradient covers a large range of landscape heterogeneity over the scales encompassed by the study area, rice arthropods may be influenced by landscape factors over larger spatial scales, and in some regions extensive rice monoculture may be grown over a larger area than in our study area (for example, Settle and others 1996). The heterogeneity gradient is probably of moderate extent compared with conditions found in other rice growing regions in the tropics. However, part of the apparent insensitivity to landscape structure appears to be due to the potential for conflicting or divergent patterns to overlay one another. For example, the loss of heterogeneity as we move to extensive rice monoculture does appear to lead to a reduction in diversity overall, but an interesting and novel output of our study is that this net effect seems to result from a composite of negative effects due to loss of heterogeneity and compensating positive effects of increasing rice cover. The component correlations suggest that there is likely to be a trend in the species composition as well as species density, with species density of rice-associated arthropods actually increasing, despite reduced species density overall. Our results broadly concur with previous suggestions that the diversity of crop-associated organisms decreases as we move towards extensive monoculture (Altieri 1991). Several studies have shown that increased landscape heterogeneity results in increased local species richness (Altieri and Letourneau 1982; Weibull and others 2003) and abundance of invertebrates (Elliott and others 1999; Sunderland and Samu 2000), although it has been observed that this applies only to trophic generalists (Jonsen and Fahrig 1997). Clearly our data show that local landscape factors, at scales of 100s of meters, influence arthropod community composition, even though we know that many rice invertebrates are able to migrate over much larger distances than those encompassed in our study area (Rutter and others 1998; Reynolds and others 1999).

In addition to these general patterns across all habitats, specific landscape effects were found for individual habitat types. Species density and Simpson's diversity of arthropods in the fruit orchards and flower/vegetable crops were positively related to rice cover. It seems that the relatively low arthropod diversity and abundance in these land-use types, largely as a result of much higher pesticide use (Van Mele and others 2002), may be boosted by the proximity of the more diverse rice fields. Again, this highlights another potential trade-off in landscape management. Although, in general, arthropod diversity decreases as the amount of rice cover in the landscape increases, there may be benefits, in terms of increased diversity in low-diversity habitats, of being situated in a landscape of relatively high-diversity rice fields. This was also true for the bunds in which the proportion of rice cover was the strongest correlate of Simpson's diversity. There has been speculation that bunds may be important refuges for natural enemies in rice ecosystems (Way and Heong 1994), although their functional relevance is doubtful in moderately asynchronous, continuous cropping systems such as those in our study area where there is almost continuous rice in the landscape (W. H. Settle, personal communication).

For rice habitats, significant effects of the landscape variables on Simpson's diversity, species density and abundance were relatively few, although they are potentially indicative of important functional effects. In the early stages of rice growth there was a positive effect of crop richness on species density and abundance at the seedling and tillering stages. On average in the tillering stage, species density increased by 0.47 per sample for an increase of one crop type in the local landscape. On first reflection this appears to be a small effect, although it refers to increases in species density recorded at very small spatial scales ( $0.125 \text{ m}^2$ ), and should be judged against background species densities (Figure 2). The absence of Simpson's diversity effects suggest that the increase in species density here was driven primarily by increased arthropod abundance. Similarly, vegetation richness was positively correlated with arthropod species density in booting/flowering rice (increase of 1.2 species per sample for each additional vegetation type), but there was no effect on Simpson's diversity. Clearly, the structure of the surrounding landscape influences arthropod community assembly through the cropping season confirming previous predictions for rice agro-ecosystems (Drechsler and Settele 2001; Heong and others 1991; Heong and others 1992). Our data suggest that arthropods may col-

onize the early stages of the rice crop in greater numbers in mixed-cropping landscapes resulting in increased local species density, and that a similar effect (based on vegetation number rather than crop number) emerges later in the season at the booting/flowering stage. As early colonization of rice crops by invertebrates, and generalist predators in particular, is key to efficient natural pest control in rice ecosystems (Schoenly and others 1996; Stettle and others 1996; Way and Heong 1994), this would suggest a benefit for natural pest control of mixed cropping landscapes in this region.

Further indication of the potential functional effects of landscape structure was found in the analysis of guild structure in rice habitats. There was a positive relationship between vegetation richness and detritivore abundance, and a negative relationship between rice cover and the proportion of detritivores in the community, although this trend was less evident at the seedling stage than the later stages (Figure 4). Conversely, the strongest effect for predator proportional abundance was rice cover, with a positive coefficient, although the absence of an absolute abundance effect suggests that this may arise from reduced abundance in the other trophic groups. While predators appear to be less sensitive to loss of landscape heterogeneity than other groups, detritivores, which have been shown to be of particular importance in supporting predators in the early stages of the crop (Settle and others 1996), are particularly sensitive. However, detritivore response to landscape rice cover was minimal at the key seedling stage compared with later stages in the crop (Figure 4). We suggest that the resistance of the predator guild and the relatively small impact on detritivores in the early season support the conclusion that natural pest control in rice may not be adversely affected by decreasing landscape heterogeneity in this region. This is consistent with the contention that low pesticide inputs and continuous cropping systems, as employed in this region, are beneficial for natural pest control in irrigated tropical rice (Way and Heong 1994; but see Loevinsohn and others 1993). Previous work has shown that in extensive rice production systems, heterogeneity in the cropping pattern has a major impact on arthropod diversity, because asynchronous production ensures continuous refuge for arthropods in rice fields (Settle and others 1996). At the study site, it appears that the relatively small amount of cropping asynchrony was sufficient to maintain diversity in the rice fields.

Other indications of functional relationships within the arthropod community were also evi-

dent. Specifically, in the samples from rice habitats there was a significant reduction in the proportion of endopterygote relative to exopterygotes herbivores as predator species richness increased. This is consistent with the theoretical prediction arising from food web models, that natural control of endopterygotes is likely to be more sensitive than that of exopterygotes to declining natural enemy diversity. This is because individual natural enemy species tend to interact with single life stages in endopterygotes, in contrast to exopterygotes, resulting in less functional redundancy in natural enemy guilds attacking endopterygotes compared with those attacking exopterygotes (Wilby and Thomas 2002b).

In summary, our study shows that rice fields in this part of the Mekong delta house a relatively diverse and abundant arthropod fauna, even in landscapes approaching 100% rice cover. The high diversity may be relatively unusual compared with other crops but it does point to the potential for maintaining biodiversity under fairly intensive production. The arthropod community associated with rice exhibited characteristic seasonal differences in guild structure due to patterns in community assembly through the cropping season. As, expected, arthropod diversity across all land-use types generally declined as we moved along the land use gradient towards extensive rice monoculture, although this effect was weak due to a compensating positive effect of increased cover of rice, the most diverse vegetation type. Arthropod diversity in other land-use types also benefited from the increased cover of species-diverse rice fields. With particular reference to diversity and community structure in rice (that is, the arthropods that will impact pest control within the crop), we found that landscape diversity influenced the processes of community assembly in rice, largely through effects on abundance rather than diversity, and that the predator guild was least affected. Understanding and managing the potential trade-off between biodiversity (and associated services) and intensification has been highlighted as a major challenge in sustainable agriculture (for example, Thomas 1999). For tropical irrigated rice it appears that natural enemy diversity and pest control function can be maintained under simplified monocultures in which there is no large-scale synchronous fallow, or high external inputs of pesticides and fertilizer (for example, Cohen and others 1994; Way and Heong 1994; Schoenly and others 1996; Settle and others 1996).

In general terms, this study highlights the considerable complexity in trying to understand effects

of changes in landscape structure and land-use patterns on diversity and functioning, with many variables and interactions acting at different hierarchies; and this with a fairly narrow focus on a subset of the local invertebrate community. Although this result is not necessarily surprising, there is now substantial interest from a range of stakeholders (for example, researchers, conservationists, farmers, policy makers, and so on) in understanding how changes in land-use affect biodiversity and ecosystem functioning.

Satisfying the goals and expectations of these different stakeholders will likely require a greater integration of observational and manipulative approaches supported by sound taxonomy.

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