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Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities



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ABSTRACT

Irrigated rice croplands are among the most biologically diverse agroecosystems globally; however, intensification and simplification of farmed areas into homogeneous monocultures can lead to biodiversity loss and a reduction of associated ecosystem services such as natural pest regulation. Understanding how landscape heterogeneity affects the diversity of arthropod communities is therefore crucial for the sustainable management of rice agroecosystems. Here, we examine the influence of fine-scale landscape heterogeneity and regional-scale effects on the arthropod communities of three rice-production regions in the Philippines. Our analysis of 213 arthropod morphospecies (37,339 individuals) collected using two sampling methods at 28 field sites indicated that the rice agroecosystems in each study region had unique arthropod assemblages, likely reflecting region-specific environmental and land-use conditions. For all sites together, we found no effect of fine-scale landscape context (classified as rather high or low heterogeneity sites) on assemblage structure (arthropod abundance, species richness or diversity). When assemblages were analyzed separately, significant effects of fine-scale landscape context were only detected in one region and for two functional groups (predators and detritivores). Elevation gradient, used as a proxy for regional-scale effects in the study regions, explained more than 60% of variance in assemblage structure. Total arthropod abundance and rarefied species richness were negatively related to elevation, suggesting that regional-scale effects rather than fine-scale landscape heterogeneity explained the composition of rice-arthropod communities in landscapes. To further disentangle the complex effects of broad-scale environmental drivers versus fine-scale landscape complexity on arthropod communities and biocontrol services, future research in rice agroecosystems should focus on a more detailed quantification of landscape heterogeneity and examine its effect at multiple spatial scales.

1. Introduction

Rice (*Oryza sativa* L.) is the main staple food for nearly half of the world's population (Zeigler and Barclay, 2008) and is among the most important cereal crops in the developing world (Seck et al., 2012). With the World's human population expected to reach 9.2 billion by 2050 (United Nations, 2013), the demand for rice continues to grow, exerting increasing pressure on rice production systems (Ericksen et al., 2009). Rice agroecosystems have been classified as human-made wetlands

(Ramsar, 2010). Because of their alternate dry and wet conditions and their largely tropical distribution, rice fields have been associated with high biodiversity (Cohen et al., 1994; Settele et al., 1996). Rice production promotes complex landscape mosaics because contiguous dry land is often interspersed with the flooded rice fields. These landscapes can attract a wide range of aquatic animals and plants. For example, Schoenly et al. (1996) recorded more than 600 macroinvertebrate species in conventional-cropped fields in the Philippines, which surpasses that of most natural temperate systems (Pimentel et al., 1992).

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Such high levels of biodiversity support complex interactions among multiple organisms, which help suppress rice pests and diseases and thus enhance rice production via biological control (Altieri, 1999; Bottrell and Schoenly, 2012; Macfadyen et al., 2015). Although agroecosystems are designed and managed by man to provide provisioning ecosystem services such as food, forage and bioenergy (Kremen, 2005), they strongly depend on regulating ecosystem services such as pollination and biocontrol (Power, 2010). The latter is of particular importance in rice agroecosystems as pest damage is considered a major limiting factor (Pathak and Khan, 1994).

Agronomic intensification tends to reduce diversity in agroecosystems through the expansion of farmed land, the loss of field margin vegetation, and high intensity management on existing cropland (Gerstner et al., 2014; Robinson and Sutherland, 2002; Swift et al., 1996). This further leads to the simplification and homogenization of farmed areas, resulting in considerably fragmented semi-natural habitats (Robinson and Sutherland, 2002; Meehan et al., 2011) and a degradation of biodiversity and ecosystem services (Tscharntke et al., 2005). In most agroecosystems, monocultures are characterized by higher levels of pest damage and smaller populations of natural enemies (Power, 2010; Gardiner et al., 2009), whose abundance and diversity are negatively affected by the lack of potential food resources and habitats (Landis et al., 2000). Therefore, understanding the effects of landscape heterogeneity and other environmental drivers on the diversity of arthropod communities is crucial to sustainably manage rice production systems and the surrounding landscapes with a minimum harm to agro-biodiversity (Ericksen et al., 2009).

High landscape heterogeneity, i.e. the fine-scale composition and configuration of crop and non-crop areas, is generally associated with increases in natural enemy abundance and diversity (Thies and Tscharntke, 1999; Gardiner et al., 2009; Woltz et al., 2012). While the role of arthropod diversity in maintaining natural pest regulation is not yet universally accepted as a basic principle by farmers (Bianchi et al., 2006), the evidence that landscape heterogeneity improves biological control is mounting (Bianchi et al., 2006; Letourneau et al., 2009; Chaplin-Kramer et al., 2011; Settle et al., 1996). Complex landscapes with large amounts of semi-natural habitat may benefit arthropod communities by providing (i) refuge from agricultural disturbances (Coll 2009; Kleijn and Sutherland, 2003; Meek et al., 2002), (ii) alternative hosts and prey or nectar resources, which are essential for many insects (Bugg et al., 1998), and (iii) a moderate microclimate, which can promote the survival of, for example, parasitoids that experience shorter lifespans at temperature extremes (Dyer and Landis, 1996, 1997). Although the positive aspects of landscape heterogeneity have been explored across a range of cropping systems and study regions (O'Rourke, 2010; Chaplin-Kramer et al., 2011), little is known about their effects on arthropod communities in complex rice production systems. For example, Wilby et al. (2006) documented landscape impacts on the processes of community assembly in rice, largely through effects on abundance, but they found only weak and sometimes contradictory patterns concerning the impact of rice cover and landscape heterogeneity on arthropod diversity.

In addition to fine-scale landscape heterogeneity, rice arthropod communities are affected by climate, environmental conditions and other landscape and land use factors operating at a regional scale. Regional-scale drivers, such as elevation gradients, provide “natural experiments” for testing the distribution of insect biodiversity (Körner, 2007; Samways, 2007). Elevation is often used as a surrogate variable for investigating the influence of regional climate conditions (Sanders et al., 2003), because both temperature and precipitation are highly correlated with elevation gradients. Temperature, in particular, plays a major role in the life history processes of arthropods (Sinclair et al., 2003), as it affects, among others, body growth and morphology, the number of instars and generations produced per year and the length of the life cycle (Hodkinson, 2005). In rice agroecosystems, the abundance of arthropods have been shown to decrease with increasing elevation

but no significant trends were observed for species richness or diversity (Schoenly et al., 1996, 1998).

Whilst much emphasis has been placed in the past on describing the rice arthropod community itself (Heong et al., 1991, 1992; Schoenly et al., 1996, 1998; Settle et al., 1996), few studies so far have investigated the potential effect of fine-scale landscape heterogeneity or regional-scale effects on these communities. In this study we examine whether fine-scale landscape heterogeneity is positively related to arthropod diversity, particularly the diversity of natural enemies, in tropical rice fields. To do this we examined arthropod community structure at sites with either fine-scale high or low landscape heterogeneity within a 100 m radius and along an elevation gradient in the Philippines. By including sites at different elevations, we could examine the relative contribution of regional-scale effects and fine-scale habitat heterogeneity in structuring the communities. Furthermore, we assessed the utility of two sampling methods for examining aspects of rice arthropod community ecology.

2. Material and methods

2.1. Study sites

The study was conducted in three areas of 15×15 km (henceforth ‘region’) located on the island of Luzon in the Philippines (Fig. 1). These were the focal sites of a larger research project on sustainable rice production (LEGATO: Settele et al., 2015). The first region (PH_1) was situated in Laguna Province, southern Luzon, with study sites ranging in elevation from 25 m to 290 m asl. In these hilly lowlands, irrigated rice is double cropped, such that a standing rice crop including a ratoon crop is present during most of the year. Narrow plains and lightly undulating hills characterize the terrain. There are no remaining natural forests in the region, but agro-forestry is dominated by coconut plantations and other fruit trees. The second region (PH_2) was located in the Nueva Ecija Province of Central Luzon, at an altitude ranging from 45 to 60 m asl. This typical lowland region is characterized by flat relief with large expanses of irrigated rice and only few semi-natural non-crop habitats. Rice is double cropped using comparably high levels of mechanization and agricultural inputs. The third region (PH_3) was located in the mountainous Ifugao Province, at an elevation ranging from 780 to 1300 m asl. The terrain is diverse and characterized by rice terraces that are believed to have existed for up to 2000 years. The region also includes large patches of primary and secondary forest habitats. Traditional rice varieties are cultivated with relatively low mechanization and few agricultural inputs, typically with one crop per year, see Klötzbucher et al. (2015) and Burkhard et al. (2015) for additional details of the study regions and sites.

To examine the influence of fine-scale landscape heterogeneity on arthropod community composition, five pairs of fields (i.e. 10 core sites) were selected within each region (Fig. 1b) according to the composition of the surrounding landscape, resulting in a total of 28 core sites (sampling could not be performed at two of the core sites in PH_2, because vegetables and not rice were grown at the time of sampling). The mean distance between two core sites within each pair was ~ 369 m and ranged from ~ 177 m to ~ 1192 m. The core sites being relatively close to each other, they primarily differed in fine-scale landscape heterogeneity within each region while other potential regional-scale effects were similar for each pair. For each site, landscape surface coverage and the proportion of rice fields within a 100 m radius were visually estimated by the same observer. Each pair of sites consisted of: (a) a rice field surrounded by high heterogeneity (i.e., the proportion of rice surrounding the core site was substantially lower than 50% with dominance of non-rice habitats including other crops, forests or settlements); (b) a rice field surrounded by low heterogeneity (i.e., more than 50% of the surface coverage consisted of rice fields and with little non-rice habitat). Selected within consistent frame conditions, we assume that the low and high fine-scale heterogeneity sites

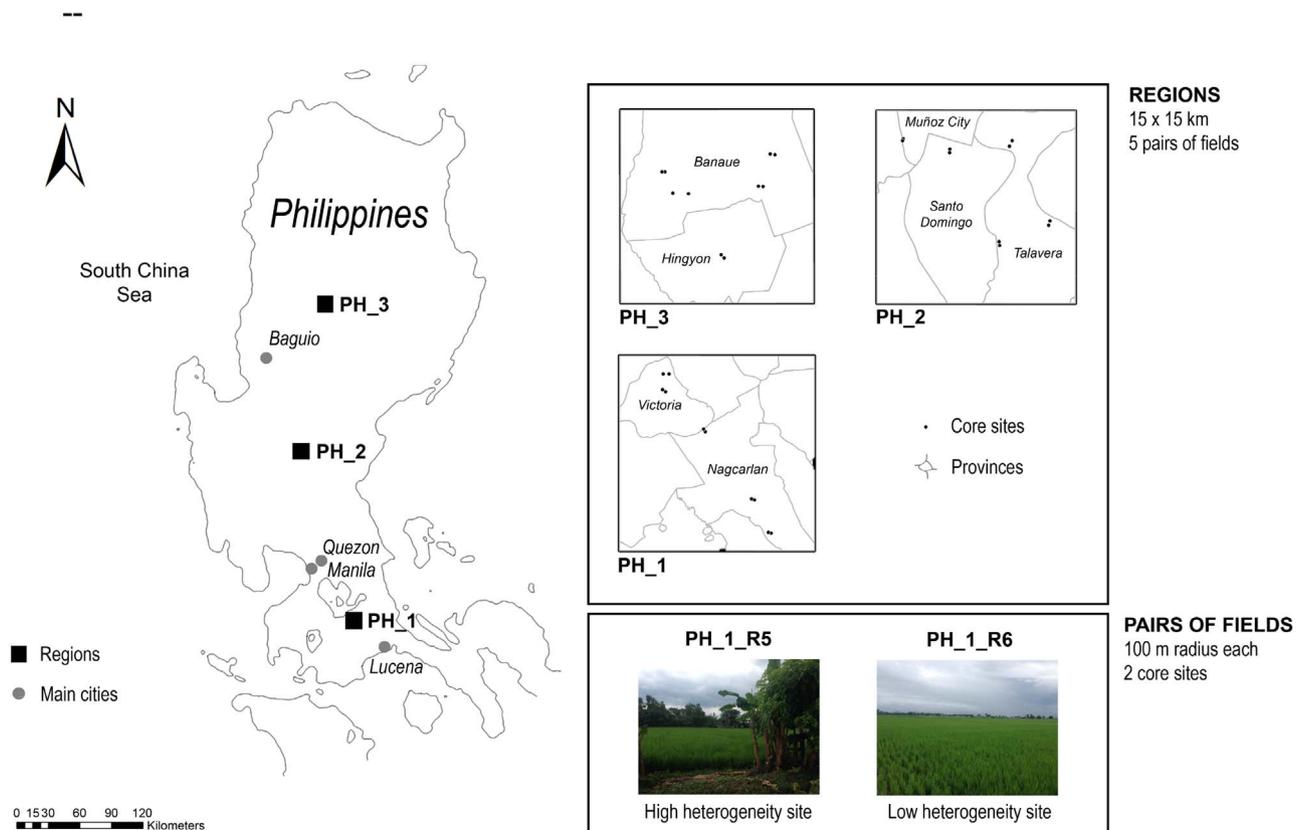


Fig. 1. Study area on the island of Luzon in the Philippines and locations of the 15 × 15 km regions in Laguna (PH_1), Nueva Ecija (PH_2) and Ifugao (PH_3). Locations of the core sites within each region and an example of high and low heterogeneity sites are presented.

allow a meaningful comparison of landscape heterogeneity and are also representative of the region in which they were sampled.

2.2. Arthropod sampling

Arthropods were sampled using a sweep net method and a vacuum (blow-vac) method similar to the one described by Arida and Heong (1992). For sweep netting, we used a standard canvas sweep net and performed thirty sweeps per sample at each core site while walking twice at a constant pace along a randomly established transect. For vacuum sampling, we used a custom built sampling enclosure of about 1 m side length that was placed over four rice hills to prevent any escape of mobile invertebrates. The suction time was prolonged until all organisms present inside the enclosure were collected by vacuum pressure into collection vials. Within each core site, five vacuum samples were taken at random locations.

Sampling for both methods was conducted in the center of each core rice field between 0700 and 1100 h, after morning dew had evaporated. In irrigated rice fields, the composition of the terrestrial arthropod communities changes with development of the rice crop and between cropping seasons (wet and dry seasons: Heong et al., 1991). Farmers in the Philippines usually produce two rice crops per year in the lowlands – one during the dry season (January to June) and one during the wet season (June to December) – but only one in the highlands (January–June). Therefore, to ensure consistency of sampling, the data collection was conducted during the dry season of 2013 in PH_1 and PH_2 and during the one-cropping season for 2014 in PH_3. In PH_2, vegetables were grown in the two core sites in 2013, thus limiting the pair of sites to four in this region. Sampling was performed at the maximum tillering stage of the rice plant (50 days after transplanting) because this stage is generally associated with a maximum abundance of arthropods (Wilby et al., 2006; Heong et al., 1991).

Sampled invertebrates were preserved in 70% ethanol. Most insects

were identified using a binocular microscope to species level (or morphospecies level when species level was not possible) based on Barrion and Litsinger (1994); however, dipterans and collembolans, as well as arachnids were only identified to family level due to the morphological similarity at the pre-adult stages and the quality of the samples. In addition, the arthropods were grouped into functional guilds as follows: detritivores/tourists, invertebrate predators, parasitoids and herbivores. The “detritivores/tourists” guild is composed of detritivores and non-predatory species which have no direct association with the rice plant but which may be attracted to surrounding habitats (Moran and Southwood, 1982).

2.3. Statistical analyses

2.3.1. Characterization of the arthropod community

We characterized arthropod community structure as determined for each sampling method in each core site by calculating the abundance of all species, species richness (S) and the Shannon-Wiener index of species diversity (H'). To measure the differences in species structure among study sites, we performed non-metric multidimensional scaling (NMDS) ordinations after computation of a Bray-Curtis dissimilarity matrix based on arthropod abundances. The arthropod mean abundance data were square-root transformed prior to analyses, in order to reduce the influence of the most abundant species. As an additional test, we performed Ward's hierarchical cluster analysis of the Bray-Curtis dissimilarity matrix. Ward's algorithm is based on minimizing variances in hierarchically identified assemblages and performs well with aggregated data, for which the Bray-Curtis measure is generally recommended (Singh et al., 2010). The significance of the differences between arthropod assemblages derived from the Bray-Curtis matrix was assessed with a perMANOVA test. We also used a Mantel's test of spatial autocorrelation (based on a geographical distance matrix) to examine spatial dependence between study sites. Finally, we calculated

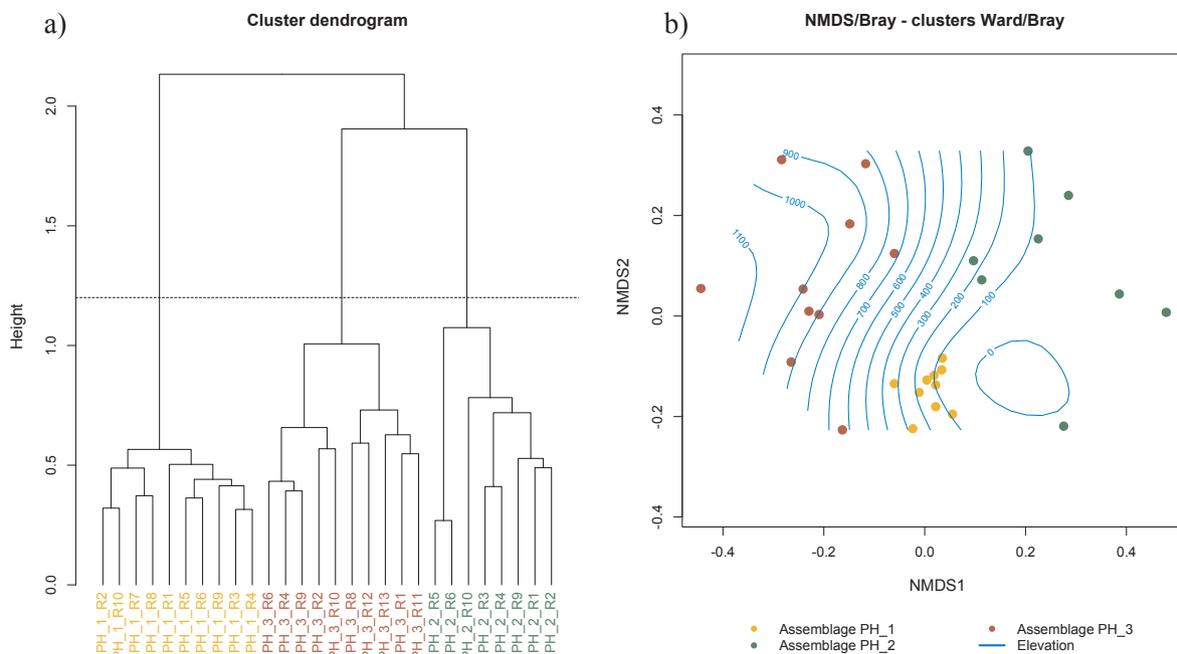


Fig. 2. (a) Ward's hierarchical cluster analysis based on Bray-Curtis dissimilarity matrix using square-root transformed arthropod mean abundance data of 28 core sites (data shown for the blow-vac samples). The cluster analysis identified three distinct assemblages (distinguished by color), each associated with one region. Core sites are abbreviated using the following nomenclature: PH represents the region; R represents the core site (i.e. PH_1_R2: Core site number 2 located in the region PH_1). (b) Non-metric multidimensional scaling (NMDS) analysis of the Bray-Curtis dissimilarity matrix (data shown for the blow-vac samples). The distance between sites indicates similarity of the arthropod community—the closer, the more similar. The variable that best explained the assemblage structure (i.e. elevation) is shown as surface fitting.

the relative contributions of each species to the similarities within each assemblage using a SIMPER analysis, which examines the percentage contribution each species makes to the similarity within and dissimilarity between assemblages (Clarke et al., 1993).

In order to determine if the sampling method had an effect on the identified arthropod composition, we used a Mantel's test to examine the concordance between dissimilarity matrices constructed using data collected by each sampling method. In addition, we compared the total mean abundance (square-root transformed) of the 20 most common species (representative of each order) sampled by each sampling method using a one-way analysis of variance (ANOVA). We also used an unpaired *t*-test to compare rarefied species richness across all regions between the two sampling methods. The rarefaction method was used here as it standardizes the measure of species richness, accounting for potential bias from different sampling efforts or other factors that may lead to large differences in the number of collected individuals among samples (Gotelli and Colwell, 2010).

2.3.2. Regional-scale effects and fine-scale landscape heterogeneity

In addition to distinguishing the two levels of landscape heterogeneity at sampling sites, we examined the effects of three basic environmental variables that are typical drivers of species distributions and community composition: elevation, mean annual temperature and mean annual rainfall (Atauri and de Lucio, 2001; Moreno-Rueda and Pizarro, 2007). The mean annual temperature and rainfall were both accessed from the CliMond archive at a resolution of 90 m (Kriticos et al., 2012). Elevation was obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) v2 at a 30 m resolution (<https://pdaac.usgs.gov/>). As elevation and climate conditions are often closely related, we used Pearson's correlation coefficients to test for multicollinearity among environmental variables (Appendix A in the Supplementary material). As their variability was high among regions but low within regions, these predictors can be potentially confounded with other factors specific to regions PH_1, PH_2 and PH_3 such as environmental variables or larger-scale landscape structure.

To examine the influence of regional effects on the arthropod assemblages derived from the Bray-Curtis dissimilarity matrix, we used the *envfit* function from the *vegan* package (R Core Team, 2016). This function calculates the goodness of fit statistics provided by the squared correlation coefficient as a measure of separation among the different levels of the variables. The significant factor with the highest fit was then plotted on the MDS (Oksanen et al., 2016).

We also examined the impact of regional-scale effects and fine-scale landscape heterogeneity on species abundance, richness and diversity. First, we assessed the variable effects on the total mean abundance (square-root transformed), total rarefied species richness and total species diversity for all samples across all study regions using a one-way ANOVA. As an alternative, we tested the same variables with a linear mixed effect model using 'region' as a random effect. Second, we repeated the same analysis for the mean abundance (log transformed) of the morphospecies, which contributed the most to the similarities within each assemblage. Third, separately for each identified assemblage (PH_1–PH_3), we compared the abundance, richness and diversity measures between core sites with high and low levels of fine-scale landscape heterogeneity using a Student's *t*-test. We performed this additional analysis separately for each assemblage, in order to avoid the potential effect of region and account for the lack of spatial independence.

Then we provided the same comparison between sites with high and low levels of fine-scale landscape heterogeneity for both the functional groups in each assemblage and for the morphospecies which contributed the most to the similarities within each arthropod assemblage using a Student's *t*-test. Prior to statistical tests, we tested the normality of our data using the Shapiro-Wilk normality test. In the case of non-normal distributions, we used the Mann-Whitney tests instead of the *t*-tests. All statistical analyses were conducted in R version 3.1.1 (R Core Team, 2016).

3. Results

3.1. Characterization of the arthropod community

We recorded a total of 37,339 individuals representing 213 different arthropod morphospecies across the three different regions (Appendix B Supplementary material). The overall mean abundance was $69.8 (\pm 8.6)$, mean species richness was $14 (\pm 1.6)$ and mean species diversity was $3 (\pm 0.1)$ per core site for the sweep-net samples. Estimates of species diversity were similar between sampling methods; however, the estimated mean abundance (38.6 ± 3.7) and species richness (8.7) per core site was lower from the blow-vac samples.

Using the NMDS and Ward's cluster analysis for the arthropod community collected with the blow-vac sampling method, we identified three significantly different assemblages (perMANOVA, $R = 0.35$, $P = 0.001$), representing the three study regions PH_1, PH_2 and PH_3 (Fig. 2). An additional significant assemblage (PH_3b) was identified in the highland region when the analyses were applied to the sweep-net samples (Appendix C Supplementary material). In addition, significant spatial autocorrelation was observed among the core sites, as showed by a strong correlation between the dissimilarity matrix and a matrix of geographic distances between individual sampling plots (Mantel's $R = 0.41$, $P = 0.001$).

Located in the hilly Laguna Province, the assemblage PH_1 was the most homogeneous (average intra-group similarity: 58%) and its mean abundance (59.3 ± 2.8), species richness (17.3 ± 0.8) and species diversity (3.59 ± 0.05) were higher than the overall mean values across all regions. The arthropod communities located in PH_1 were characterized by a high abundance of detritivores/tourists such as chironomids, collembolans and other dipterans (~28% of the overall contribution; Fig. 3). The two main planthopper species, the brown planthopper, *Nilaparvata lugens*, and the whitebacked planthopper, *Sogatella furcifera*, were equally abundant. The predators were mostly represented by dwarf spiders (Linyphiidae) and wolf spiders (Lycosidae) (11% of the contribution). Based on their low intra-group similarity, both assemblages PH_2 and PH_3 (39% and 38%, respectively) were more heterogeneous than the assemblage PH_1. High abundances of lady beetles of the genus *Micraspis* and dwarf spiders were recorded in PH_2 (~22% contribution). While *N. lugens* contributed ~29% to the whole PH_2 assemblage, *S. furcifera* contributed less than 1% of the assemblage. On the other hand, in the PH_3 region, *S. furcifera* contributed ~19% to the assemblage, as opposed to *N. lugens* with less than 1%. The predatory mirid bug *Cyrtorhinus lividipennis* was collected in relatively high numbers at all sites in PH_3 (Fig. 3).

Sogatella furcifera and chironomids were the most abundant arthropods collected in the sweep nets (~50% of the total abundance), while *N. lugens*, *S. furcifera* and chironomids were most abundant in the blow-vac samples (more than 30% of the total abundance). In addition, *N. lugens*, *S. furcifera*, chironomids, *Tetragnatha* spp. (Tetragnathidae), *Microvelia atrolineata*, dwarf spiders, wolf spiders, and collembolans (Isotomidae) were the most widely distributed arthropods according to blow-vac samples (present at more than 80% of core sites). *Nilaparvata lugens*, *Tetragnatha* spp., *Aranaea* spp. (Araneidae), chironomids, dipterans (other than chironomids) and *Micraspis* spp. were the most widely distributed species according to the sweep net samples (present in more than 80% of core sites). Sampling method had a significant effect on the relative abundances of most morphospecies (Fig. 4). When comparing rarefied species richness for the populations sampled by blow-vac and sweep net, we found a statistical difference for the region PH_1 ($t = -3.635$, $P = 0.003$) and PH_3 ($t = -8.644$, $P < 0.001$) but no difference for PH_2 ($t = -1.745$, $P > 0.05$). Despite these differences in detected abundance and rarefied species richness, the results of the Mantel test showed a significant concordance between the blow-vac and sweep net sampling methods (Mantel's $R = 0.56$; $P = 0.001$), indicating a similarity of the overall species composition for both sampling methods.

3.2. Regional-scale effects and fine-scale landscape heterogeneity

The pairwise Pearson's correlation tests between temperature, precipitation and elevation revealed that all variables were highly collinear ($|r| > 0.7$, $P < 0.05$). We therefore used only elevation in further analyses as a proxy for overall regional-scale effects in the study regions (i.e. other climatic, environmental and broad-scale landscape conditions).

For both dissimilarity matrices based on the two sampling methods, we found no effect of fine-scale landscape heterogeneity on the assemblage structure ($P > 0.05$). In contrast, elevation explained 65% of variance in the blow-vac samples and 68% of variance in the sweep net samples ($P < 0.001$). An elevation gradient fitted on the NMDS plot is shown in Fig. 2b for the blow-vac community and in Appendix C.2 Supplementary material for the sweep net community.

We also found no effect of fine-scale landscape heterogeneity on the total mean abundance, total species richness or total species diversity of the arthropod communities across all study sites. However, both the total mean abundance and total species richness of the communities were significantly negatively correlated with elevation ($F = 6.206$, $P < 0.05$ and $F = 9.175$, $P < 0.01$, respectively). When 'region' was included as a random effect, it substituted the influence of elevation (the range of elevation differed greatly among regions, while being lower within each region) but provided the same results regarding the effects of fine-scale landscape heterogeneity. We found no effect of landscape heterogeneity at this scale on those morphospecies that contributed the most to each assemblage across all study sites. However, we found multiple effects of elevation on the majority of morphospecies examined based on both the blow-vac and sweep net samples. Whereas most of the responses were negatively correlated with elevation, we found a positive correlation with elevation for the abundances of *S. furcifera* and *C. lividipennis* ($F = 5.789$, $P < 0.03$ and $F = 4.988$, $P < 0.02$ respectively) (Appendix D Supplementary material).

Comparing sites with high and low heterogeneity separately for each identified assemblage, we found significant differences only for abundance ($t = 2.814$, $P < 0.05$) and species richness ($t = -3.225$, $P < 0.02$) in PH_1 for samples collected with the blow-vac method (Fig. 5). In all other cases no significant differences were observed. Similarly, our results showed a significant effect of fine-scale landscape heterogeneity on only a few functional groups. For the blow-vac method, we found significant differences between high and low heterogeneity sites only for the abundance of detritivores and predators in PH_1 ($t = 3.149$, $P < 0.05$ and $t = 2.503$, $P < 0.05$, respectively) (Fig. 6), and the diversity of herbivores in PH_3 ($t = 2.449$, $P < 0.05$) (Appendix E Supplementary material). For the sweep net method, only the diversity of predators was affected by fine-scale landscape heterogeneity in PH_1 ($t = -2.571$, $P < 0.05$) (Appendix F Supplementary material). Furthermore, we found a significant effect of landscape heterogeneity at this scale only on two morphospecies (out of a total of 16) for the blow-vac community. In PH_1, the parasitoid *Oligosita* spp. was positively correlated with fine-scale landscape heterogeneity ($t = 0.345$, $P < 0.03$), while the aquatic predator *M. atrolineata* was negatively correlated with fine-scale landscape heterogeneity ($W = 16$, $P < 0.02$).

4. Discussion

We recorded a total of 213 morphospecies across the three regions, which correspond well with the number of species documented by Barrion et al. (1994) (240 species) and by Heong et al. (1991) (212 species). In Barrion et al. (1994), Los Baños (Laguna Province) showed the highest diversity of arthropods ($H' = 12.75$), while Banaue (Ifugao Prov.) had a lower diversity ($H' = 5.70$) and Cabanatuan (a city located in Nueva Ecija Prov.) exhibited the lowest diversity ($H' = 4.70$). Our results corroborate these findings, with PH_1 accounting for the highest

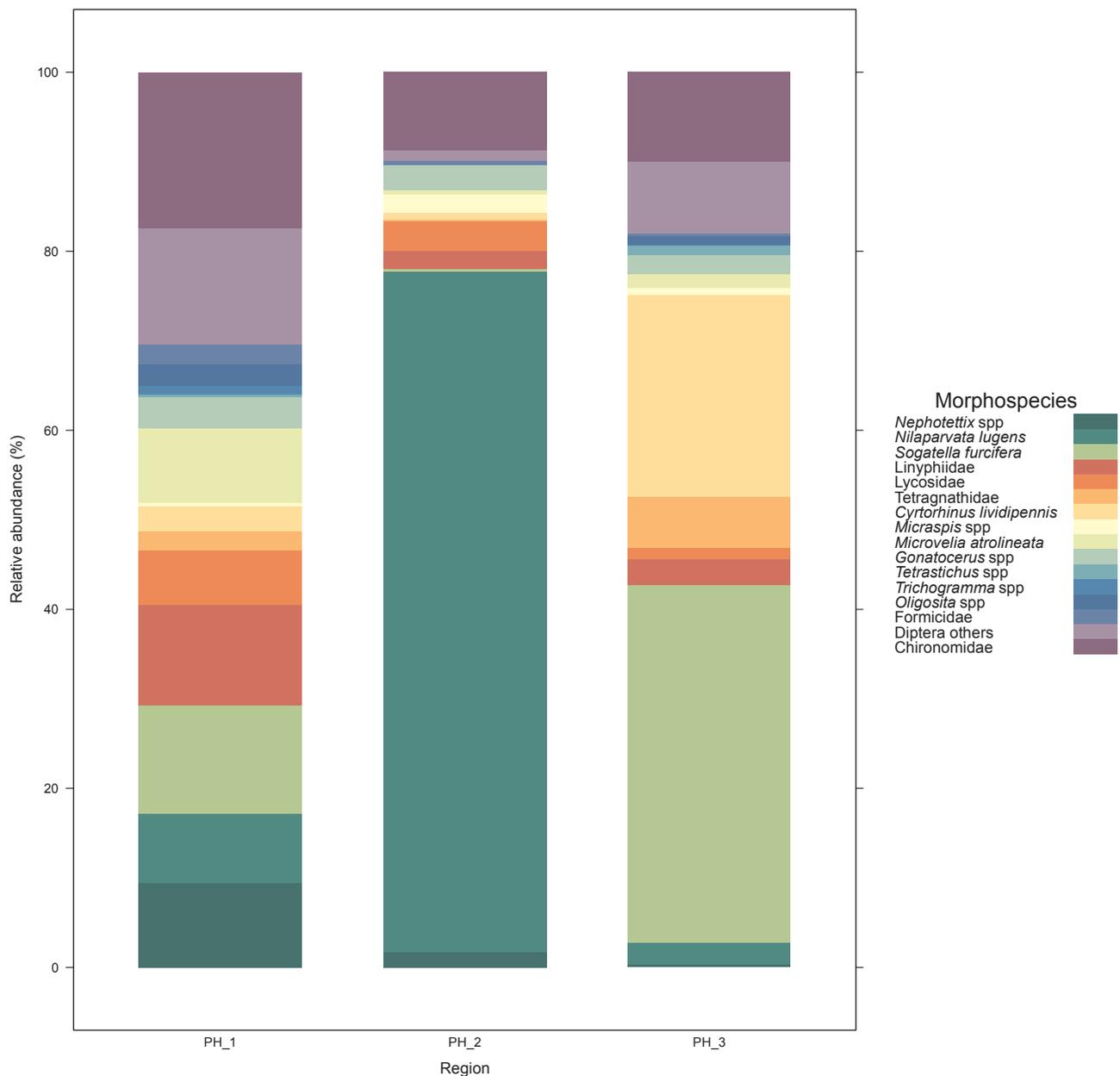


Fig. 3. Relative abundances of 16 morphospecies (calculated by SIMPER analysis) that contributed the most to the similarities within each arthropod assemblage identified based on Bray-Curtis dissimilarity matrix (data shown for the blow-vac samples).

species diversity, followed by PH_3 and PH_2. Our results showing that assemblages PH_3 and PH_2 are the most dissimilar (75.9% based on NMDS) also corroborate with Schoenly et al. (1996) who indicated that rice communities in Banaue and Cabanatuan were the least taxonomically similar (25%).

Although most of the common arthropod species were present in all three regions, the community structure differed from one region to another, resulting in three distinct assemblages. The positive spatial autocorrelation identified among core sites further supports this observation, showing that samples collected from nearby locations were also compositionally more similar than samples from locations further apart. The assemblage located in PH_1 included a higher number of species, a higher relative abundance and higher species diversity of the rice arthropods than the assemblages in regions PH_2 and PH_3, in addition to being more homogeneous than the other two sites. The PH_1 assemblage had also a relatively high number of detritivores that can potentially boost the abundance of generalist predators, which use detritivores as an alternative prey and may contribute to the relatively

high resilience of irrigated rice systems (Settle et al., 1996). The high number of detritivores likely supported high numbers of two generalist spider families, Linyphiidae and Lycosidae, as found in the Laguna region. The most common species of these two families are the lycosid *Pardosa pseudoannulata* and the linyphiid *Atypena formosana* (Barrion and Litsinger 1984; Kenmore et al., 1984; Sigsgaard 2000), which are important regulators of rice herbivores (Reddy and Heong, 1991). This was also reflected in our results, as *N. lugens*, *S. furcifera* and the green leafhopper *Nephotettix* spp. were the three main rice herbivores found in similar numbers across the PH_1 assemblage.

The assemblage PH_2 of Nueva Ecija had the lowest abundance, species richness and diversity of arthropods and had higher evenness than the other two assemblages, as is expected in intensive monoculture systems. *Nilaparvata lugens* was the dominant herbivore in PH_2, contributing to nearly one third of the total assemblage, while *S. furcifera* and *Nephotettix* spp. were largely absent. However, low numbers of predators and parasitoids were observed, likely due to the low quality of potential habitats caused by the high proportion of rice monocultures

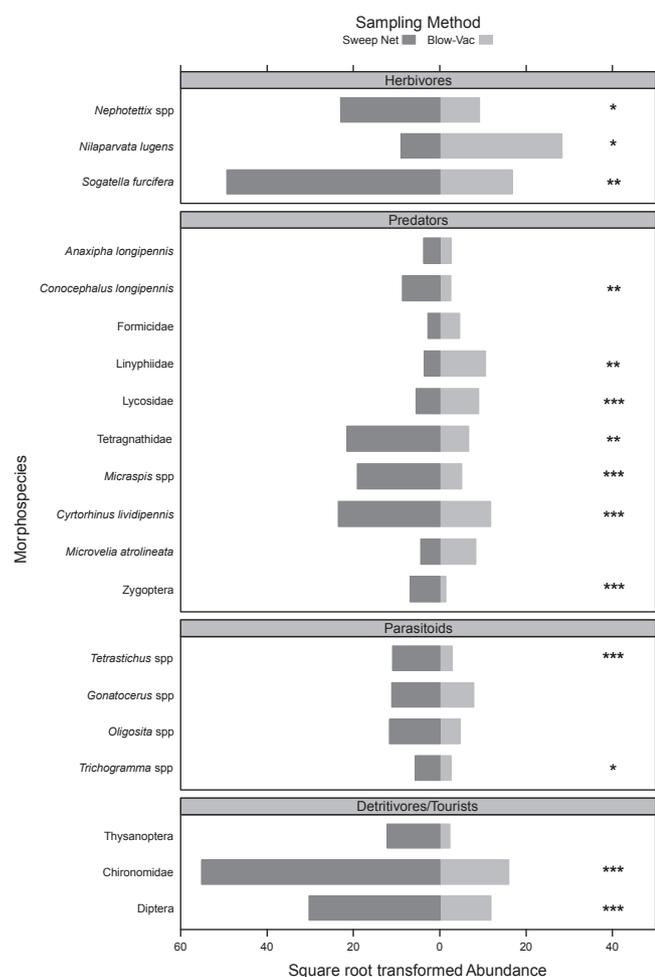


Fig. 4. Comparison of the mean abundance of the 20 most common morphospecies collected with blow-vac and sweep net. The list of morphospecies is grouped into four functional groups (from top to bottom: Herbivores, Predators, Parasitoids, and Detritivores/Tourists). Significant differences between sampling methods are indicated by asterisks located next to the bar plots (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$).

in the region. In addition, *N. lugens* populations are known to increase drastically when main predators are removed (Kenmore et al., 1984). Modern rice varieties that are often accompanied by high levels of mechanization and chemical inputs (Burkhard et al., 2015) may also explain the disrupted assemblage structure in this region.

In the mountainous region of PH₃ Ifugao, *S. furcifera* was by far the most dominant herbivore species, representing nearly 20% of the total assemblage, whereas *N. lugens* contributed only 1%. The population of both herbivores in PH₃ was likely regulated by a combination of various predators such as *P. pseudoannulata*, *A. formosana*, *Tetragnatha* spp. and *C. lividipennis* (Barrion and Litsinger, 1984). The predatory bug *C. lividipennis* is a major predator of delphacids that consumes planthopper eggs and nymphs (Sigsgaard, 2007) and can consume over seven *N. lugens* nymphs daily (Reyes and Gabriel, 1975). The high numbers of *C. lividipennis* in PH₃ can be explained by the overwhelming presence of *S. furcifera* nymphs collected in the samples (~70% of nymphs collected).

Our results did not confirm the hypothesis that landscape heterogeneity within 100 m of sampling locations has a positive effect on the arthropod community. We found no effect of fine-scale landscape heterogeneity on assemblage structure and no differences in arthropod relative abundances, species richness or diversity between sites with a high and low level of landscape heterogeneity. Even when examining each identified assemblage separately, we found significant effects only in PH₁. Similarly, only one parasitoid and one predator out of the 16

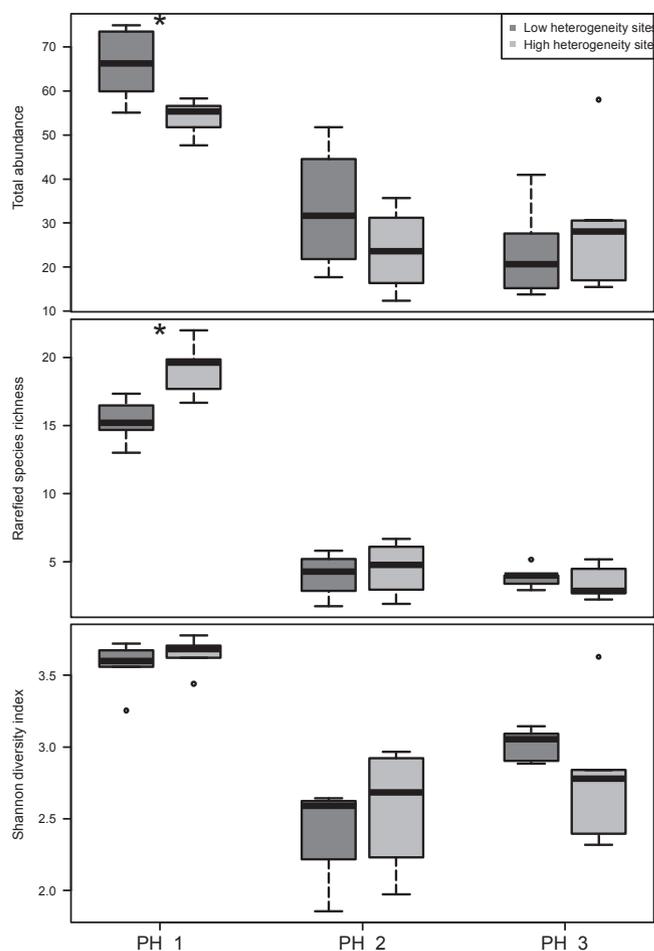


Fig. 5. Box-plots of the total mean abundance, rarefied species richness and species diversity (Shannon diversity index) of arthropods in sites with high (dark grey) and low (light grey) levels of fine-scale landscape heterogeneity (data shown for the blow-vac samples). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) are indicated by asterisks.

morphospecies involved in the analyses, responded to landscape heterogeneity at this scale. In agreement with other studies of arthropods in agroecosystems (Altieri and Letourneau 1982; Weibull et al., 2003; Wilby et al., 2006), the locations with higher landscape heterogeneity in PH₁ had higher species richness. However, the lower total abundance and lower abundance of both predators and detritivores in PH₁ suggest that the increased species richness observed in more heterogeneous sites may be compensated by lower abundances, especially in these two guilds. For herbivores, we observed greater species diversity in the more heterogeneous sites of PH₃, but the predator group was neither more abundant nor diverse and therefore we cannot make any conclusion about the effect of landscape heterogeneity at this scale on natural pest control in our study regions.

These complex but largely inconclusive results regarding landscape heterogeneity may have several explanations. First, regional-scale effects, including effects of elevation, climatic conditions but potentially also landscape structure at a broader spatial scale than measured in our study, were more important than fine-scale landscape heterogeneity in explaining the composition of rice arthropod communities. Indeed, when we used elevation as a proxy for all regional-scale effects in the study regions, it explained the majority of variance (> 60%) in the assemblage structure based on the dissimilarity matrices (Fig. 2b, Appendix C.2 Supplementary material). The differences in the variability of arthropod composition among study regions can be further illustrated by the differences in variability of elevation and climate conditions in those regions (Appendix A Supplementary material).

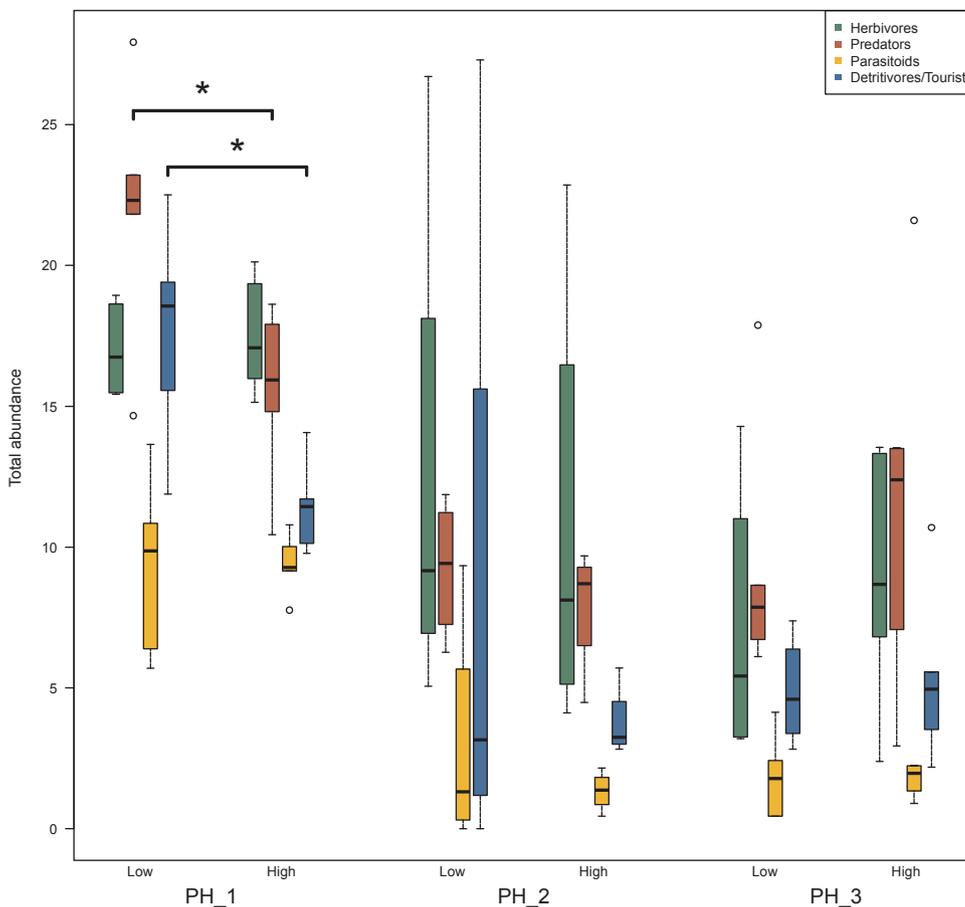


Fig. 6. Box-plots of the total mean abundance of functional groups for low heterogeneity sites (“Low”) and high heterogeneity sites (“High”) across the three regions (data derived from the blow-vac). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) between low and high heterogeneity habitats are indicated by asterisks above and between boxes.

Moreover, not only did we find that total arthropod abundances decreased with increasing elevation, similarly as in Schoenly et al. (1996), but we also found that the total rarefied species richness decreased with increasing elevation. In addition, our results are in agreement with the conclusions of Hodkinson (2005); who showed that responses of species abundance to elevation are known to vary with taxa and location. While the abundance of most of the morphospecies such as *N. lugens*, *Nephotettix* spp., lycosids, linyphiids and chironomids decreased with elevation, two species, *S. furcifera* and *C. lividipennis*, found in high numbers in PH_3 were positively affected by elevation. These findings are also supported by a previous study showing that elevation is a limiting factor for the fitness of *N. lugens* (Settele, 1992).

Second, the investigated arthropod communities were potentially co-affected by other factors that are unique to each study region but were not accounted for in the design of our analysis. Our study was conducted in a real agricultural setting in which land-use intensity, cropping synchrony, pesticide inputs or other land management factors were not controlled. Although we assume that these factors did not vary systematically across the sites with high and low levels of fine-scale landscape heterogeneity, their specific character in each study region may have contributed to the high variability in our dataset and to the clear differences in the assemblage structure among study regions. In addition, the variability of elevation and climate was high among regions but low within regions. This further suggests that the effects of other factors specific to the regions, such as broad-scale landscape structure or the intensity of land use, cannot be fully disentangled from the overall regional effects without specifically controlling for them in the analysis.

Third, the scale and the binary distinction between sites with high and low heterogeneity may be insufficient to detect landscape effect on the rice arthropod fauna. While the differentiation of the two landscape heterogeneity levels around sampled fields was consistent for all

regions, the broad-scale landscape structure among the three regions varies considerably (Burkhard et al., 2015). For example, the overall region PH_1 in Laguna is characterized by rice production landscapes with close proximity to numerous agricultural fields, gardens, ponds and semi-natural habitats. In contrast, rice fields in the region PH_2 of Nueva Ecija occupy over 95% of the land area, with each field being separated only by a network of terrestrial bunds combined with a low diversity of other habitats. Although the scale of a few hundred meters was previously found sufficient to show landscape effects in rice agroecosystems (Wilby et al., 2006), many rice invertebrates are known to migrate over considerably larger distances (e.g. Reynolds et al., 1999). In addition, the potential effects of a broad-scale landscape structure were likely confounded with the influence of environmental conditions that we accounted for in the analysis at the regional scale. Therefore, we suggest that future research should focus on a more detailed quantification of landscape heterogeneity (e.g. using metrics of landscape composition, configuration and intensity of use (Seppelt et al., 2016)) and examine its effect at multiple spatial scales that match the migratory abilities of the investigated rice arthropods.

We used two different sampling methods to assess the arthropod communities in the rice fields. The sweep net method was more efficient to sample leaf canopy arthropods such as chironomids, other dipterans, parasitoids and long-jawed orb weavers (Tetragnathidae). Samples taken with the sweep net were collected typically at the top of the rice canopy, since the lower surface of the plant was unreachable without damaging the plant. Arthropods that dwell low on the plant or on the water surface, i.e. *N. lugens*, dwarf spiders or lycosids, were caught in significantly greater numbers by the blow-vac. The combination of multiple sampling methods in rice fields is thus generally advised to properly assess arthropod biodiversity (Doxon et al., 2011). However, in our study, while differences in abundance of specific taxa were observed between sampling methods, both methods provided

samples with similar species composition. This suggests that, in cases of limited time or resources, the use of only one method may be acceptable when the focus is on community composition rather than on species abundance.

5. Conclusion

We characterized and compared rice arthropod communities from three important rice production regions in the Philippines that differed in environmental conditions as well as in their level of landscape heterogeneity. Two principal insights are provided by our analyses. First, the rice agroecosystems in each study region had relatively distinct arthropod assemblages, likely reflecting specific environmental conditions or land management factors in the regions. Second, the effect of fine-scale landscape heterogeneity was identified only in one region and only for two functional groups and two morphospecies, suggesting that regional-scale effects rather than fine-scale landscape heterogeneity explain the composition of rice arthropod communities in the study area. To further disentangle the complex effects of broad-scale environmental drivers versus fine-scale landscape context on arthropod communities and the biocontrol services, future studies of rice agroecosystems should apply more complex procedures of quantifying the spatial structures of rice fields and the surrounding habitats and examine their effect at multiple spatial scales.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2017.06.011>.

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