Received: 11 May 2021 | Revised: 15 October 2021 | Accepted: 14 December 2021
DOI: 10.1002/eap.2560

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

ARTICLE

Landscape heterogeneity filters functional traits of rice arthropods in tropical agroecosystems

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Funding information
Federal Ministry of Education and Research (BMBF), Grant/Award Number: 01LL0917A; IGA, Grant/Award Number: PrF 2020 020; SustES - Adaptation strategies for sustainable ecosystem services and food security under adverse environmental conditions, Grant/Award Number: CZ.02.1.01/0.0/0.0/16_019/0000797

Handling Editor: Juan C. Corley

Abstract

Biological control services of agroecosystems depend on the functional diversity of species traits. However, the relationship between arthropod traits and landscape heterogeneity is still poorly understood, especially in tropical rice agroecosystems, which harbor a high diversity of often specialized species. We investigated how landscape heterogeneity, measured by three metrics of landscape composition and configuration, influenced body size, functional group composition, dispersal ability, and vertical distribution of rice arthropods in the Philippines. We found that landscape composition and configuration acted to filter arthropod traits in tropical rice agroecosystems. Landscape diversity and rice habitat fragmentation were the two main gradients influencing rice-arthropod traits, indicating that different rice arthropods have distinct habitat requirements. Whereas small parasitoids and species mostly present in the rice canopy were favored in landscapes with high compositional heterogeneity, predators and medium-sized species occupying the base of the rice plant, including planthoppers, mostly occurred in highly fragmented rice habitats. We demonstrate the importance of landscape heterogeneity as an ecological filter for rice arthropods, identifying how the different components of landscape heterogeneity selected for or against specific functional traits. However, the contrasting effects of landscape parameters on different groups of natural enemies indicate that not all beneficial rice arthropods can be promoted at the same time when using a single land management strategy. Increasing compositional heterogeneity in rice landscapes can promote parasitoids but may also negatively affect predators. Future research should focus on identifying trade-offs between fragmented rice habitats and structurally diverse landscapes to maximize the presence of multiple groups of beneficial arthropods.

KEYWORDS

arthropods, biological control, fourth-corner analyses, functional traits, landscape heterogeneity, rice, RLQ analyses

INTRODUCTION

Asian tropical rice agroecosystems are represented by a mosaic of complex spatial patterns created by the rice crop, seminatural habitats, and other land uses (Settele et al., 2015). This is one reason why biodiversity within tropical rice landscapes, including many plant (Fried et al., 2017) and arthropod taxa (Dominik et al., 2017; Schoenly et al., 2010), is often higher than in many natural temperate systems (Pimentel et al., 1992). The heterogeneity of these landscapes is represented by the combination of landscape composition (diversity of landscape features and habitat types) and landscape configuration (size, shape and connectivity of habitat patches) (Seppelt et al., 2016), and is known to influence important ecological processes by determining species distribution, dispersal, and interactions across trophic levels (Fahrig, 2003; Fahrig et al., 2011; Gallé et al., 2019).

The composition of the landscape influences biodiversity as more diverse landscapes (containing a variety of different land-cover types) provide more habitats for species (Benton et al., 2003; Tscharntke et al., 2005). For example, increasing non-crop habitat in rice via habitat manipulation has proven beneficial for some natural enemies of rice pests (Gurr et al., 2016). Moreover, a recent review by Dainese et al. (2019) using a global database has shown that decreasing non-crop habitat in agroecosystems negatively affects the richness of service-providing organisms, such as predators and parasitoids. In a similar manner, the configuration of the landscape may positively affect biodiversity by increasing landscape complementation (Fahrig et al., 2011) and by influencing species movement and spill-overs (Blitzer et al., 2012; Tscharntke et al., 2005). For instance, some natural enemies of rice pests respond positively to increased configurational heterogeneity, measured as the number of rice patches (NP) and connectivity of the rice bunds separating rice patches (Dominik et al., 2018). Although new research has shown that landscape configuration can strongly affect natural enemies and pest populations (Haan et al., 2020), the effects of landscape heterogeneity on pest–enemy dynamics are difficult to predict, as these effects vary across different agroecosystems and for different functional groups (Karp et al., 2018; Martin et al., 2019; Tamburini et al., 2020). For example, little is known about which functional traits shared among species are behind the specific responses of organisms to landscape heterogeneity.

The impacts of landscape heterogeneity and environmental change on arthropod biodiversity in rice agroecosystems have traditionally been investigated using a taxonomic approach by focusing on the distribution of species within a community or by sorting species into functional groups (Dominik et al., 2017; Sattler et al., 2020; Schoenly et al., 2010). However, these approaches have failed to take into consideration the variability of species traits within these functional groups, especially when comparing different regions with different species communities (Mcgill et al., 2006). In recent years, the responses of species functional traits to environmental change have received increased research attention (Duflot et al., 2014; Gámez-Virués et al., 2015; Kleyer et al., 2012). The functional characteristics of a species (i.e., species traits) influence its dispersal, resource acquisition, reproduction, and resilience in the environment (Violle et al., 2007). Within predator assemblages, species that have similar effects on prey populations will often exhibit a diversity of secondary functional traits (Petchey & Gaston, 2002). For example, orb-weaver spiders (e.g., family Tetragnathidae) are more effective in capturing prey with high dispersal ability, whereas hunter spiders (e.g., lycosids) mostly prey on sedentary or less mobile organisms (Michalko et al., 2019). In their review, Gagic et al. (2015) showed that functional trait indices are superior to taxonomic indices in linking diversity to ecosystem functions, including biological control.

The environment can act as an ecological “filter” that selects or excludes species, according to particular functional traits, from the available regional pool (Southwood, 1988). For example, landscape heterogeneity can be considered as an ecological filter that affects the functional composition of carabid and plant communities in temperate areas (Duflot et al., 2014). In a study from Germany, Gámez-Virués et al. (2015) showed that landscape-level effects are critical for maintaining functionally diverse communities, by promoting resilience and stability of functional traits that buffer the negative effects of land-use intensity.

Most previous studies have demonstrated how landscape heterogeneity can shape arthropod communities in rice agroecosystems (Dominik et al., 2018; Sattler et al., 2020; Wilby et al., 2006), yet none of them used a multiple-traits approach, which may help differentiate the effects of environmental pressures on species that differ in their functional traits. While trait–environment approaches have been widely used in temperate ecosystems (Duflot et al., 2014; Gámez-Virués et al., 2015; Kuzmanovic et al., 2017), we are unaware of any studies examining these relationships in tropical rice agroecosystems, which make up one of the largest biomes in tropical Asia. Here, we investigated the distribution of arthropod traits along a gradient of landscape heterogeneity in rice agroecosystems across multiple regions of the Philippines. We focused on body size, dispersal ability, functional groups, and vertical distribution, which are recognized as important ecological traits (Gossner et al., 2013; Schweiger et al., 2005). We sought to answer the following research questions: (1) Does compositional and configurational landscape heterogeneity act as an environmental filter affecting the functional community composition of rice-arthropods? (2) Which functional traits shared among rice-arthropods are behind their specific responses to the different components of landscape heterogeneity?

MATERIALS AND METHODS

Study regions

The study was conducted within the project LEGATO (Settele et al., 2015) across three 15 × 15 km regions on the island of Luzon in the Philippines (Figure 1). The three regions were (1) a rice landscape in the hilly lowlands of Laguna Province in southern Luzon (PH_1) defined by agro-forestry, with narrow plains and lightly undulating hills characterizing the terrain; (2) an intensively cultivated rice landscape characterized by flat relief with large rice monocultures and few seminatural habitats in Nueva Ecija Province (PH_2) in central Luzon; and (3) a traditional terraced rice system in the mountainous Ifugao Province located in the north of Luzon, where small rivers are commonly used as a natural irrigation system, and where large patches of primary and secondary forest dominate the landscape (for details, see Dominik, 2019). Within each region, 10 core sites were selected along a gradient of landscape intensity for a total of 28 core sites (sampling could not be performed at two core sites in PH_2 due to the presence of planted vegetables instead of rice at the time of sampling). All information regarding site coordinates and locations, in accordance to Gerstner et al. (2017), can be found can be found in the Dryad repository (https://doi.org/10.5061/dryad.pg4f4qrqn) (Dominik et al., 2021).

Arthropod sampling

The rice arthropods were collected during the dry season of 2013 in PH_1 and PH_2 (lowlands) and during the single cropping season of 2014 in PH_3 (highlands). Farmers in the Philippines usually produce two rice crops per year in the lowlands, one during the dry season (January–June) and one during the wet season (June–December), but only one in the highlands (January–June). In addition, the composition of arthropod communities can change between the two cropping seasons (wet and dry seasons; Heong et al., 1991), therefore our analyses focused only on the dry season of 2013 in PH_1 and PH_2 and during the one cropping season for 2014 in PH_3. All samples were collected once at the maximum tillering stage of the rice plant (50 days after transplanting) to ensure consistency of sampling; this stage being generally associated with a maximum abundance of arthropods and a higher functional group diversity (Heong et al., 1991; Sattler et al., 2020; Wilby et al., 2006).

A modified leaf blower-vacuum, similar to the suction sampling method described by Arida and Heong (1992), was used to collect the arthropods. Such suction sampling methods can provide absolute estimates of the densities of plant-dwelling rice arthropods, including arthropods found on the water surface (e.g., *Microvelia douglasi atrolineata* and *Micronecta quadristrigata*) (Zou et al., 2016; but see Dominik et al., 2017). A plastic sampling enclosure of about 1 m^3 with a nylon mesh sleeve on top was placed over four submerged rice hills before suction sampling was performed to prevent the escape of mobile arthropods during sampling. To maximize sampling efficiency, each rice hill was individually vacuumed and suction time was prolonged until all organisms present inside the enclosure were collected (Dominik, 2019; Zou et al., 2016). Starting within the center of each field, five subsamples were randomly taken at approximately 2–3 m intervals along a transect between 7:00 AM and 11:00 AM, under similar weather conditions.

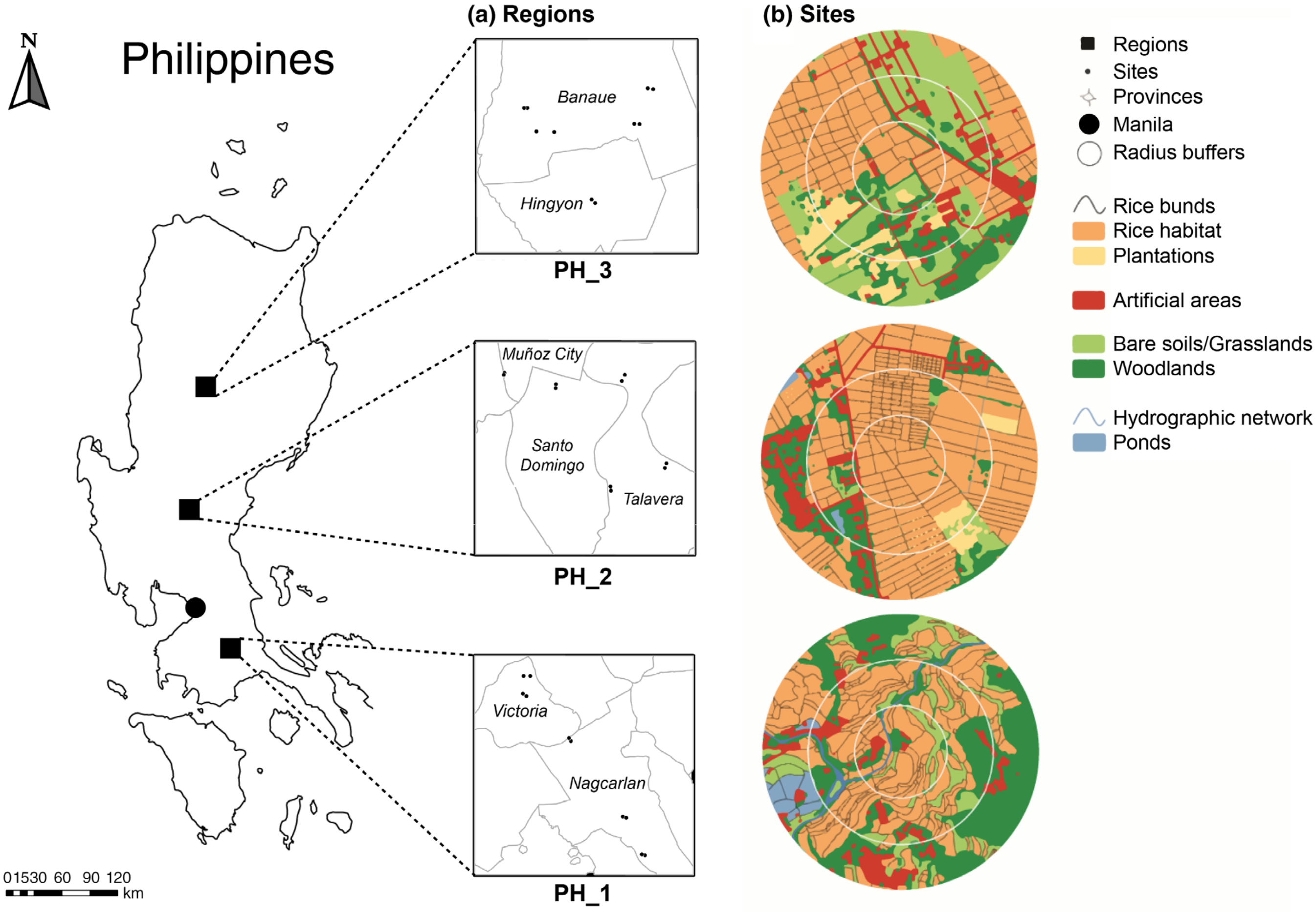

FIGURE 1 Study area on the island of Luzon in the Philippines. (a) Locations of the 15 × 15 km regions in Laguna (PH_1), Nueva Ecija (PH_2), and Ifugao (PH_3). (b) Examples of mapping land cover features within 300-m radius buffers around sites for each region

Collected arthropods were preserved in 70% ethanol, sorted, and identified to species level (or morphospecies level when species could not be determined) using a binocular microscope and based on the taxonomic keys of Barrion and Litsinger (1994). Morphological similarity and poor quality of sampled specimens limited the identification of arachnids to family level.

Arthropod traits

Trait information for all insects was extracted at the genus or species level from the literature and based on expert opinion (Barrion & Litsinger, 1994; Heong & Hardy, 2009; Pathak & Khan, 1994). Due to a general lack of information concerning rice arachnids, trait information was extracted at the family level only. However, the trait structure is generally conserved across higher taxonomic levels (Dolédec et al., 2000). Following Gossner et al. (2015), Birkhofer et al. (2015, 2017), and Seibold et al. (2019), we chose important functional traits that can be shared across different arthropod taxonomic groups. Four functional traits related to body size, dispersal ability, functional group, and vertical stratum were selected comprising 13 trait categories (Table 1). A fuzzy-coding approach was used to quantify the affinity of each morphospecies for a given trait category (Chevenet et al., 1994). A score of 0 was assigned to each morphospecies if there was no affinity for a trait category, 1 if there was low affinity, 2 if there was medium affinity, and 3 if the affinity was strong. Subsequently, these scores were converted as frequency distributions of trait categories within each functional trait (i.e., for each given morphospecies, the sum of all trait categories for each functional trait equals 1).

1. Body size was categorized into four trait categories, based on the mean body length in millimeters for both sexes. Body size is typically related to many life-history traits such as fecundity, life span, and growth rate (Peters, 1983)
2. Dispersal ability was distributed into three trait categories (low dispersal, medium dispersal, and high dispersal

TABLE 1 List of functional traits and categorical traits selected for the arthropod morphospecies

Functional traits	Categorical traits	Description
Body size	$x < 2$; $2 < x < 3$; $3 < x < 5$; $x > 5$	Mean body length in mm for both sexes
Dispersal ability	Low	Flightless insect species
	Medium	Insect species displaying wing dimorphism
	High	Fully winged insect species
Functional group	Herbivores, predators, parasitoids	Main species diet
Vertical distribution	Water, base, canopy	Main vertical habitat layer in which the species was usually observed as an adult

ability) according to wing morphology and behavioral traits (e.g., ballooning) due to the lack of information in regards to typical dispersal distances for rice arthropods. All flightless insect species (apterous) were classified into the low dispersal category. Insect species displaying wing dimorphism were assigned to the medium dispersal category. For example, the brown planthopper *Nilaparvata lugens* can exhibit both the fully winged macropterous and truncate-winged brachypterous forms at the adult stage. Their wing dimorphism is mostly determined by food availability in the nymphal stage of the corresponding generation. The brachypterous forms are most prevalent at the maximum tillering stage (i.e., 50 days after transplanting) and before the rice begins to senesce, and they generally infest the rice fields. The macropterous forms on the other hand are responsible for colonizing new fields when food becomes scarce. Fully winged insect species (macropterous) were classified to the high dispersal category. Although arachnids were mainly grouped into the low dispersal category, an additional score was assigned to the high dispersal category based on the spider's ability to ballooning (Bell et al., 2005).

3. Functional group was classified into three trait categories based on the diet breath of each morphospecies during the adult stage. The different trait categories were as follows: (1) herbivores, (2) predators, and (3) parasitoids (following Moran & Southwood, 1982).
4. Vertical distribution was defined as the main vertical habitat layer in which the species was usually observed as an adult. Because rice arthropod species occupy various crop strata (e.g., aquatic predators present on the water surface, hunting spiders at the base of the plant, and parasitoids at the canopy of the plant), vertical distribution was used as a trait for resource use. Three trait categories were distinguished between water bodies, base of the rice plant, and rice canopy.

Landscape heterogeneity

Landscape heterogeneity was quantified by calculating three independent metrics of landscape composition and configuration. All landscape features were identified and mapped at the scale of effect previously identified for rice arthropods (Dominik et al., 2018), that is, within a 300-m radius around each core site using GIS-Software (ArcGIS 10.3, ESRI) and high-resolution SPOT-5 DIMAP images (2.5 m). Additionally, our photo-interpretation was verified by collecting ground-truth data in June 2014 and misclassifications were corrected when necessary. Land cover features were classified into eight final categories: rice fields, woodlands, grasslands, artificial areas, plantations, rice bunds, hydrographic network, and ponds.

As a measure of compositional landscape heterogeneity, we used Shannon's Diversity Index (SHDI), calculated based on all eight land cover categories. Landscape diversity (SHDI) and the proportion of rice habitat (PLAND_Rice) were highly correlated with each other ($r = 0.70$, $p < 0.000$; Appendix S1: Figure S1), thus the proportion of rice habitat was not included in the analyses. Landscape diversity is generally perceived as a critical aspect of landscape heterogeneity, as many arthropods may be associated with a single land use category (i.e., rice herbivores are mostly found in the rice habitat). However, increasing landscape diversity does not necessarily enhance the diversity of natural enemies (Dominik et al., 2018), nor does natural pest control automatically decline in simplified landscapes dominated by continuous rice fields (Wilby et al., 2006; Zou et al., 2020). Fields at different stages of the rice plant harbor different communities of arthropods (Wilby et al., 2006), suggesting that the configuration of the rice habitat in asynchronous rice landscapes may play an important role in shaping rice-arthropod communities. Therefore, as a measure of configurational landscape heterogeneity, we calculated two metrics focusing simply on the configuration of the rice field class: number of patches and core area index (CAI). The rice habitat being usually composed of several rice fields (typically 1–3 ha) interconnected by a network of rice bunds, we first calculated the NP as a measure of fragmentation of the rice habitat, which represents the magnitude of rice patch subdivisions into numerous smaller rice patches. Rice terraces found in the mountainous regions consist of a mosaic of rice patches that greatly differ in size and shape. In contrast, rice fields in the lowlands are often large and of rectangular shape to facilitate agriculture intensification. Thus, we calculated the CAI to quantify the percentage of available rice area composed of core, based on a 1-m edge effect (bund; McGarigal & Marks, 1995). For example, a large rice patch of rectangular shape typically found in the lowlands will have a higher CAI than a small rice patch of irregular shape commonly found in rice terraces. The CAI does not confound area and configuration and therefore better embodies the configuration effect as it is more an edge-to-interior ratio. None of the selected landscape metrics (SHDI, NP, and CAI) were correlated with each other (Appendix S1: Figure S1) and all landscape metrics were calculated using Fragstats 3.3 (McGarigal & Marks, 1995).

Statistical analyses

The relationships between rice-arthropod traits and landscape heterogeneity were investigated by the combination of RLQ (R-mode linked to Q-mode) (Dolédec et al., 1996) and fourth-corner analyses (Legendre et al., 1997). The RLQ and fourth-corner analysis have been widely and successfully used in ecological studies (Kleyer et al., 2012) focusing on benthic macroinvertebrates (Kuzmanovic et al., 2017), bats (Núñez et al., 2019), carabids and plants (Duflot et al., 2014), and ladybird beetles (Liere et al., 2019).

We used RLQ analysis to answer the first research question about whether landscape heterogeneity acts as an environmental filter of functional community composition of rice arthropods. RLQ is a special form of correspondence analysis used to investigate the main co-structures between traits and environmental variations mediated by species abundance (Dolédec et al., 2006). It allows for the simultaneous analysis of three tables: an environmental table (named R: 3 landscape metrics × 28 sites), a species traits table (named Q: 58 species × 13 trait categories), and a species abundance table (named L: 58 species × 28 sites) that is used as the link between Q and R. Prior to the analyses and after selecting the species occurring in at least 10% of the sites (i.e., 58 species, Appendix S1: Table S1), the species abundance table was subject to a correspondence analysis (CA) as recommended by Dolédec et al. (1996). We first standardized the abundance of arthropods across all taxa using Hellinger transformations. By giving low weights to values with low counts and zeros, Hellinger transformations can account for the regional differences in environmental gradients identified across the three studied regions of the Philippines (Dominik et al., 2017). Then, we performed a principal component analysis (PCA) and a fuzzy principal component analysis (FPCA) on the environmental table and the trait table, respectively, by considering species and site weights derived from the correspondence analysis species scores. The prevailing co-correlation between arthropod traits and landscape metrics is defined by the first axis, and each successive axis summarizes the remaining co-correlation. We further assessed the overall significance of the relationship between species traits and landscape heterogeneity via a Monte-Carlo test using 49,999 random permutations of the table rows of R (model 2) and of the table rows of Q (model 4) (see Dray et al., 2014 for more details). To determine the optimal number of clusters based on Euclidian distances between species along the first two RLQ axes and clustered via Ward's hierarchical clustering, we used Calinski-Harabasz stopping criterion (Kleyer et al., 2012).

In addition to the classic RLQ analysis, we performed a partial-RLQ analysis to test the potential effect of the "region" covariates, where the covariable represents a partition of samples into groups (in this case, the groups are the three regions PH_1, PH_2, and PH_3). Based on Wesuls et al. (2012), we compared the percentage of co-inertia explained by the most representative axis of partial-RLQ with the axis of the basic-RLQ to test the relevance of the "region" covariates.

To answer our second research question and further explore the relationships between species traits and landscape heterogeneity, we performed a fourth-corner analysis, using a combination of model 2 and model 4 (Dray et al., 2014). The fourth-corner analysis method was used for statistical power by testing the correlation between each arthropod trait and each landscape metric, using Pearson *r* correlation coefficients (Dray et al., 2014). In addition, we investigated the significance of associations between individual landscape metrics and the combination of traits, and individual trait categories and the combination of landscape metrics using a combination of RLQ and fourth-corner analysis (as suggested by Dray et al., [2014] and Kuzmanovic et al., [2017]). A total of 13 trait categories and 3 landscape metrics could lead to 39 significant trait–landscape relationships. Therefore, due to multiple-test comparisons, we used 49,999 permutations, and applied the false-discovery-rate adjustment method (FDR) to correct *p* values (Benjamini & Hochberg, 1995). To account for the presence of spatial autocorrelation in our data (see Dominik et al., 2017), we integrated a new randomization approach based on Moran's spectral randomization (MSR) in the fourth-corner analysis (Braga et al., 2018). While adding the MSR method provides total control over Type I error rates, it can also lead to a decrease of power in the statistical analyses (Braga et al., 2018). Moreover, ter Braak et al. (2012) have shown that the fourth-corner analysis has good power with more than 100 species, reasonable power for 50 species, and some power for 30 species ($n = 58$ species in the present study). Consequently, the fourth-corner analysis conducted in our study can be considered highly conservative with respect to Type I errors.

We performed all statistical analyses using the open source R software version 4.0 (R Core Team, 2020). We used the library vegan (Oksanen et al., 2007) for the cluster analysis and Hellinger transformations, and the library ade4 (Dray & Dufour, 2007) for the RLQ and fourth-corner analyses.

RESULTS

Separate analysis of the three tables R, L and Q

The first and second axes of the correspondence analysis (CA) performed on the rice-arthropod abundance data (L table) accounted for 16.94% and 12.34% of the total variance, respectively (Appendix S1: Table S2). By isolating the sites from each region, the two first CA axes clearly suggested that each region had relatively distinct arthropod assemblages (see Dominik et al., 2017) (Appendix S1: Figure S2a).

The PCA performed on the landscape metrics table (R table) yielded a first and second axis that, respectively, explained 45.21% and 40.57% of the total variance (Appendix S1: Table S2). The first PCA axis discriminated the sites with high landscape diversity (SHDI) and small irregular patches of rice (CAI), for example, sites mostly found in the PH_3 region, from the sites with low landscape diversity (SHDI) and with large regular patches of rice (CAI), for example, mainly the sites located in the PH_2 region (Appendix S1: Figure S2b). The second PCA axis showed an ecological gradient mostly dominated by the NP, separating highly fragmented rice habitats from landscapes with fewer NP.

Finally, the first two axes of the FPCA performed on the rice-arthropod traits (Q table) accounted for 36.72% and 26.80% of the total variance, respectively (Appendix S1: Table S2). Herbivores, medium-sized, and low dispersal arthropods were associated with the negative end of the first PCA axis. The second axis separated small and high dispersal arthropods living at the rice canopy (e.g., parasitoids) from low dispersal arthropods occupying the lower levels of the vertical distribution, such as hunting spiders and aquatic predators (Appendix S1: Figure S2c).

The first two axes of the basic-RLQ explained 97.52% of the total variation, whereas those of the partial-RLQ explained 99.25% (Appendix S1: Table S2). The percentage explained by the first axis of the partial-RLQ was similar to the percentage explained by the first axis of the basic-RLQ (75.83% and 71.21%, respectively), meaning that the scores of landscape metrics and arthropod traits on the first axis of the basic-RLQ were not notably influenced by the effect of "region." The sites along the RLQ axes and the separate PCA axes (R table) were similarly ordinated (Appendix S1: Figure S2d). Although the first CA axes (L table) clearly separated the sites from each region, the RLQ axes took into account the variability of sites expressed along both the L and R tables, thus reducing the potential variability of the "region" covariate. Therefore, only the results of the basic-RLQ are described and reported in the manuscript.

RLQ analysis

The first RLQ axis, explaining 71% of the total variation, mainly separated the sites with low landscape diversity (SHDI) and with a high NP from the sites with high landscape diversity (SHDI) and with a low NP (Figure 2). Thus, the first RLQ axis represented a gradient of landscape diversity (SHDI) from left to right and a gradient of fragmentation of the rice habitat (NP) from right to left. The second axis, explaining 26% of variation, showed an ecological gradient dominated by the core area of rice (CAI), clearly separating the small irregular patches of rice from the large and regular patches of rice. The relationship between rice-arthropod traits and landscape heterogeneity was globally significant (model 2 simulated $p < 0.002$; model 4 simulated $p < 0.013$).

Six clusters of common traits were identified based on the mean position of each species on both RLQ axes (Figure 3; but see Appendix S1: Figure S3 for more details) by examining the categorical traits that were shared among species filtered by different types of landscape heterogeneity. The first cluster mostly grouped herbivores with high dispersal ability that occurred exclusively in the rice canopy. This cluster mainly favored highly heterogeneous sites (SHDI). Cluster 2 was solely composed of small macropterous parasitoids living at the rice-canopy, and were most likely to be found at sites with high landscape diversity (SHDI). Arthropods from cluster 3 were medium to large predators, displaying variable dispersal abilities and found in all vertical distributions. This assemblage of aquatic predators, rove beetles, and spiders mostly occurred in highly fragmented rice habitats (NP) with small rice patches of irregular shape (CAI). Cluster 4 was composed of herbivores with a low dispersal ability that occurred in the rice canopy. These medium-size Hemiptera favored habitats with large patches of rice of regular shape (CAI). Cluster 5 included

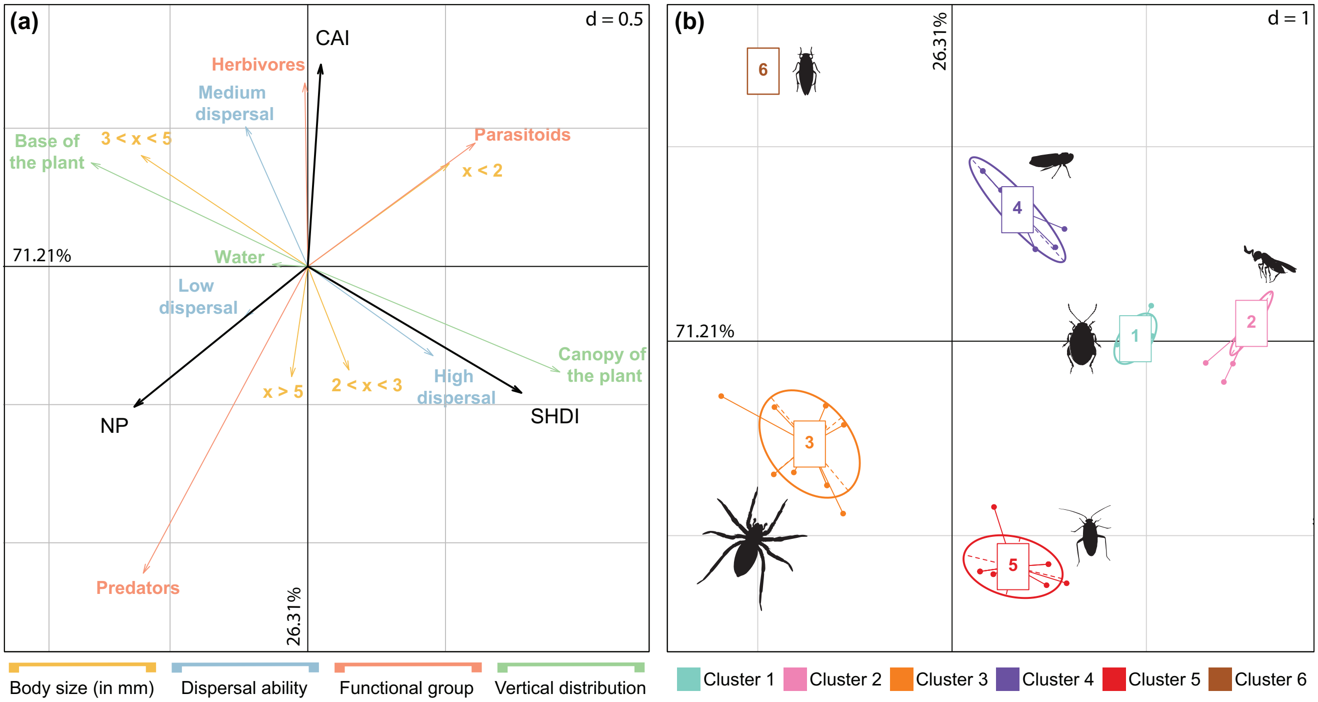

FIGURE 2 RLQ biplot showing the decomposition of co-correlations between landscape metrics and categorical traits, constrained by the abundance of arthropods. (a) Coefficients for categorical traits and landscape metrics (SHDI, NP, CAI) for the RLQ analysis. The size and direction of landscape metrics and categorical traits are represented by arrows. (b) Scores for arthropod species in the RLQ analysis. A total of six cluster groups were identified from cluster analysis along the first two RLQ axes, as indicated by different colors. CAI, core area index; NP, number of rice patches; RLQ, R-mode linked to Q-mode; SHDI, landscape diversity

predators of various sizes that live in the rice canopy. These mostly comprised high dispersal predators such as *Cyrtorhinus lividipennis* and spiders with low dispersal ability, such as orb weavers of the family Tetragnathidae. These predators favored highly fragmented rice habitats (NP) with small and irregular patches of rice (CAI), and highly heterogeneous sites (SHDI). Finally, cluster 6 exclusively grouped two species of planthoppers: the brown planthopper *N. lugens* and the white-backed planthopper *Sogatella furcifera*. Both are rice pests of medium size with intermediate dispersal ability (brachypterous) that occupy the base of the rice plant. They were mostly found in low heterogeneous landscapes (SHDI) with numerous (NP) large rice patches of regular shape (CAI). Eigenvalues of arthropod traits and landscape metrics that best explained the variability of rice arthropods and clusters among sites are shown in Appendix S1: Figure S4.

Fourth-corner analysis

The fourth-corner analysis detected few significant associations between arthropod traits and landscape heterogeneity metrics (Figure 4a). Highly fragmented rice habitats (NP) positively influenced predators. In contrast, landscape diversity (SHDI) was positively associated with species present in the rice canopy.

By combining RLQ and fourth-corner analyses, additional relationships (1) between individual traits and RLQ axes and (2) between individual landscape metrics and RLQ axes were detected. In contrast to the classic fourth-corner analysis that detected few significant associations between individual traits and individual metrics, these results suggest that a combination of landscape metrics (SHDI and NP), rather than individual metrics, influences a combination of arthropod traits. Although landscape diversity (SHDI) was positively correlated with the first RLQ trait axis, the NP was negatively associated with the first RLQ trait axis (Figure 4c). Moreover, arthropods of medium-size (3–4 mm), arthropods mostly found at the base of the plant, and predators were negatively related to the first RLQ landscape axis (Figure 4b). Meanwhile, very small arthropods (<2 mm), arthropods occupying the rice-canopy, and parasitoids were positively correlated with the first RLQ landscape axis. None of the landscape metrics and arthropod traits were correlated with the second RLQ axis.

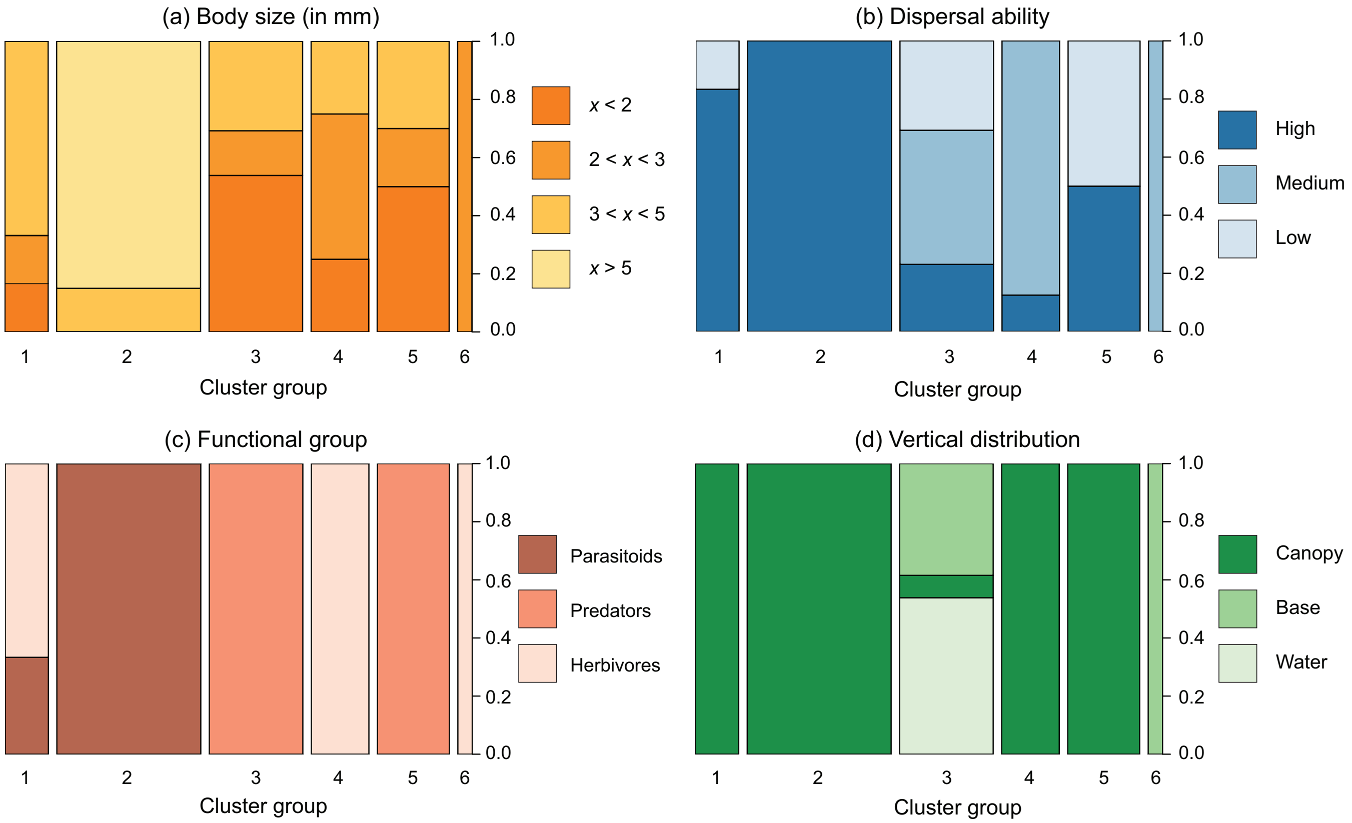

FIGURE 3 Categorical traits shared by the six identified clustered groups associated with landscape heterogeneity based on the mean position of each species on both RLQ (R-mode linked to Q-mode) axes. The width of the bars represents the relative abundance of each cluster group and its relative proportions of each cluster assigned to each different categorical traits are represented by the height of the bar for each functional trait: (a) body size (in mm), (b) dispersal ability, (c) functional group, and (d) vertical distribution

DISCUSSION

Our findings elucidate for the first time the importance of both landscape composition and configuration, represented by the combination of three gradients (NP, SHDI, and CAI), as filters of the functional trait composition of rice arthropods. The fragmentation of the rice habitat (NP) into numerous smaller rice patches had a positive effect on predator species. When the amount of rice habitat is held constant, increasing fragmentation (fragmentation per se, sensu Fahrig [2017]) implies smaller distances between patches, which reduces habitat isolation and facilitates immigration of low mobility species (Fahrig, 2003), such as spiders. Additionally, more fragmented habitats generally contain more edge, which can have a positive effect on the distribution of certain species (Fahrig, 2003), and a higher level of interdigitation of different habitat types, which can increase both habitat complementation and supplementation for these species (Dunning et al., 1992). Increasing the NP, irrespective of habitat amount, may also increase the occurrence of different crop types or rice crops at various temporal stages, altering the community of rice arthropods (Wilby et al., 2006). Indeed, two key spiders in rice, *Atypena formosana* and *Pardosa pseudoannulata*, are known to use different rice habitats (fallow fields, rice bunds, different crop stages, etc.) to find alternative food resources (Barrion & Litsinger, 1994) and are among the first generalist predators to colonize newly planted rice fields (Sigsgaard, 2010). For aquatic species that depend on the availability of water in each rice patch, the proximity to other irrigated rice patches will determine how easily these species can move between rice habitats.

The two main gradients representing landscape diversity (composition of the landscape) and fragmentation of the rice habitat (configuration of the rice fields' class) pointed in opposite directions; hence compositionally heterogeneous landscapes in our study sites tend to have less fragmented rice habitats and vice versa. Additionally, a third gradient separated the large and regular rice patches found in the lowlands (PH_1 and PH_2) from the irregular and smaller rice patches of the mountainous region (PH_3). This third gradient that was mainly influenced by the size and shape of the rice patches

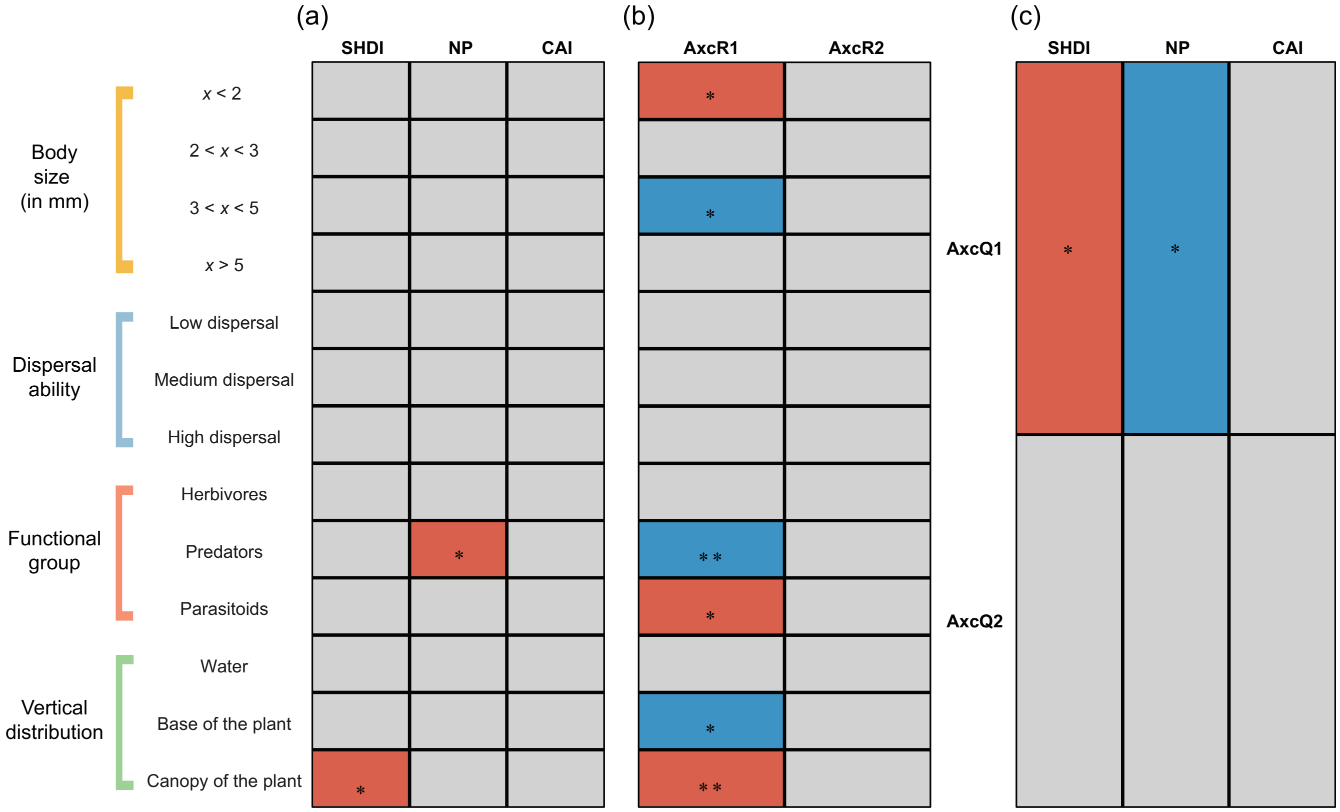

FIGURE 4 Results of the fourth-corner analysis and the combined approach between fourth-corner and RLQ analysis. (a) Relationships between individual categorical traits and individual landscape metrics resulting from the fourth-corner analysis, (b) correlations between individual categorical traits (FPCA loadings) and the RLQ landscape metrics axes (AxcR), and (c) correlations between individual landscape metrics (PCA loadings) and the RLQ trait axes (AxcQ). Significant positive associations are represented by red cells, whereas significant negative associations are represented by blue cells (p-adjusted < 0.05). The significance level is given by asterisks (*$p < 0.05$, **$p < 0.01$). Nonsignificant relationships are represented by gray cells. CAI, core area index; NP, number of rice patches; RLQ, R-mode linked to Q-mode; SHDI, landscape diversity

(CAI), pointed in the opposite direction to the gradients influenced by the fragmentation of the rice habitat (NP) and landscape diversity (SHDI). Thus, the mountainous region of PH_3 was characterized by highly heterogeneous sites subdivided in multiple smaller rice patches of irregular shape. On the other hand, the lowland region of PH_2 was characterized by compositionally homogeneous landscapes comprising larger but fewer rice patches of regular shape. Finally, the lowland hilly region of PH_1 shared similar landscape structures with both the PH_2 and PH_3 regions. Although sampling time differed between PH_3 (2014) and the lowland regions PH_1 and PH_2 (2013), this temporal mismatch would have had minimal effects on our results, considering that land-management practices, rice varieties, and climatic conditions were relatively constant across the years (Horgan, Dominik, Srinivasan, Mundaca et al., unpublished data; Appendix S1: Figure S5).

Highly fragmented rice habitats (NP) and less diverse landscapes (SHDI) favored relatively large predatory species such as generalist spiders and rove beetles that mostly inhabit the base of the rice plant. These results corroborate the findings of Gámez-Virués et al. (2015) that generalist species with relatively large body sizes were favored in simplified landscapes. In addition, Dominik et al. (2017) showed that predator numbers were higher at sites in the Philippines with lower compositional heterogeneity. In contrast, Duflot et al. (2014) found that large and low mobility carabids in temperate agricultural landscapes were associated with highly diversified landscapes. The availability of resources in the landscape for each taxon strongly determines the response of body size to habitat fragmentation (Hillaert et al., 2018). These contrasting results may be explained by the fact that, in diverse temperate landscapes, species use a combination of annual crops and woody habitats, and benefit from edges between habitats (Tscharntke et al., 2005), whereas, in tropical rice agroecosystems, predator abundance is affected more by trophic interactions than by landscape structures (Dominik et al., 2018).

Less fragmented rice habitats (NP) in diverse landscapes (SHDI) favored the small arthropods such as parasitoids that are mostly found in the rice canopy. Parasitoids are recognized as key regulators of rice herbivore populations (Horgan et al., 2017; Kenmore et al., 1984) and can travel great distances in search for suitable hosts (Antolin & Strong, 1987). By increasing the diversity and density of habitats, for example, flowering plants on rice bunds, the parasitism of planthopper eggs can be enhanced (e.g., Philippines: Horgan et al., 2017, Vu et al., 2018). Positive effects of non-crop habitats on the abundance of the parasitoid *Anagrus* spp. have also been previously confirmed in rice landscapes (Gurr et al., 2011). However, several authors found no effects of flower strips on parasitoid populations at field scales (Horgan et al., 2017; Lin et al., 2011; Yao et al., 2012) or found no evidence that landscape composition positively affects the abundance of egg parasitoids (Sann et al., 2018; Zou et al., 2020). Nevertheless, landscape heterogeneity in these studies was measured at different scales (field or landscape scale) and sometimes with only a simplistic quantification of the landscape structure (rice habitat vs. agroforest).

Although landscape diversity (SHDI) has been shown to reduce the abundance of herbivores in the Philippines, especially planthoppers (Dominik et al., 2018), we did not find any effect of landscape diversity on herbivores as a functional group. However, the RLQ analysis successfully separated brachypterous herbivores from macropterous herbivores on the landscape diversity gradient. Polyphagous fully winged arthropods such as leaf beetles of the genus *Chaetocnema* and the subfamily *Galerucinae* have a wide range of hosts (Heinrichs et al., 1982), and may benefit from non-crop habitats by visiting alternative food sources when rice is absent. On the other hand, hemipteran rice pests such as *N. lugens* and *S. furcifera* feed primarily on rice (Heinrichs & Medrano, 1984). Therefore, hemipteran rice pests depend less on non-crop habitats and are more likely to show a positive density-area relationship in rice habitat (Dominik et al., 2018). These findings showed that landscape diversity can have multiple and contrasting filtering effects on different species from the same functional groups according to their diet breath (i.e., herbivores).

Finally, the third gradient played a lesser role in filtering rice-arthropod traits, but selected mostly against predators in large and regular rice fields (CAI). Small and irregular patches (CAI) favored predators independently of the vertical distribution they occupied or their dispersal ability. Clusters 3 and 5, which comprised predators of rice pests, were represented by species with larger body sizes than the ones grouped in the other clusters. Larger body size is generally associated with smaller patches, since larger species can better disperse between smaller, more isolated patches as opposed to the larger patches commonly observed in intensified monocultures (Gámez-Virués et al., 2015). These results are thus in agreement with Settle et al. (1996), who demonstrated that large monocultures of rice delayed the colonization by predators in Indonesia. In addition, this gradient separated the more intensive rice fields of the lowlands (PH_1 and PH_2) from the traditional rice fields of the uplands (PH_3), indicating that predators are more dominant in less intensive rice fields. In contrast, hemipteran prey species represented by cluster 6 and, to a lesser degree, cluster 4 were observed at the opposite end of the configurational landscape gradient, favored by intensive rice fields found in the lowlands. Indeed, agriculture in the lowlands is generally associated with higher chemical inputs (i.e., pesticides, fertilizers, etc.) and mechanization over large monocultures of rice, whereas the size of the rice patches in the mountainous region are too small and inaccessible for mechanization. Furthermore, most of the farmers in the lowlands use high yield varieties and chemical inputs, while rice-farming systems in the mountainous region rely more on traditional rice varieties and fewer chemicals (Settele et al., 2018). Land management effects may play an important role in shaping rice-arthropod communities, though these effects followed similar trends in response to both fragmentation and diversity of the landscape in our study sites (Dominik et al., 2017). Nevertheless, future studies should aim to tease these effects apart.

Our study is the first to demonstrate the role of landscape heterogeneity as an ecological filter of the functional composition of rice-arthropod communities, selecting for or against specific and multiple functional traits. However, the contrasting effects of landscape parameters on parasitoids and predators, that is, species important for biological pest control, indicate that not all beneficial rice arthropods can be promoted at the same time with a single land management strategy. Highly fragmented rice habitats provided a more suitable habitat for predators (e.g., spiders) and medium-sized arthropods living at the base of the rice plant (e.g., planthoppers). Meanwhile, sites with high compositional heterogeneity promoted small species (e.g., parasitoids) living in the rice plant canopy. These findings imply that the rice habitat itself may provide more important resources for predators than non-crop habitats. We therefore suggest that a higher NP, especially at different crop stages (asynchronous planting), offers the advantage of creating refuges for migrating arthropods (Bottrell & Schoenly, 2012). Although we measured landscape diversity as the diversity of non-crop habitats surrounding the rice fields (woodlands, artificial areas, etc.), the diversity of the rice habitat itself (rice at a different growth stage, fallowed fields, ratoons, different varieties, etc.) was not considered.

However, temporal and spatial manipulation of the rice habitat via asynchronous planting or intercropping in many small rather than a few large patches could provide natural enemies with a continuous source of food and refugia. Therefore, future research aiming at improving biological pest control should focus on identifying thresholds of landscape heterogeneity between fragmentation and landscape diversity gradients that offer the most suitable habitat for both the parasitoids and predators, the natural enemies of herbivorous pests in rice agroecosystems.

ACKNOWLEDGMENTS

This study was funded by the German Federal Ministry of Education and Research (BMBF) as part of the LEGATO project (grant number: 01LL0917A) within the BMBF-Funding Measure "Sustainable Land Management." T. Václavik was also supported by the grant IGA PrF 2020 020 (Palacký University Olomouc) and the project "SustES—Adaptation strategies for sustainable ecosystem services and food security under adverse environmental conditions" (CZ.02.1.01/0.0/0.0/16_019/0000797). The authors are grateful to Sylvia "Bong" Villareal and Josie Lynn Catindig for their assistance with the identification of arthropods. Christophe Dominik especially thanks Jesus and Marlynne Bustamante, Liberty Almazan, Alberto Naredo, Vincent Virtudes, Reyuel Quintana, Iza Arida, Chloé, Anna, Jerry, and Raymond for the help provided during fieldwork.

CONFLICT OF INTEREST

All authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

Christophe Dominik, Tomáš Václavík, Ralf Seppelt, and Josef Settele conceived the idea and designed methodology; Christophe Dominik and Finbarr G. Horgan collected the data; Christophe Dominik analyzed the data and led the writing of the manuscript. All authors contributed critically to the drafts, gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data and site coordinates (Dominik et al., 2021) are available in Dryad at https://doi.org/10.5061/dryad.pg4f4qrqn.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher’s website.

How to cite this article: Dominik, Christophe, Ralf Seppelt, Finbarr G. Horgan, Josef Settele, and Tomáš Václavík. 2022. “Landscape Heterogeneity Filters Functional Traits of Rice Arthropods in Tropical Agroecosystems.” *Ecological Applications* 32(3): e2560. https://doi.org/10.1002/eap.2560