



## Small-scale variability in the contribution of invertebrates to litter decomposition in tropical rice fields

Anja Schmidt<sup>a,\*</sup>, Harald Auge<sup>a,b</sup>, Roland Brandl<sup>c</sup>, Kong Luen Heong<sup>d,e</sup>,  
Stefan Hotes<sup>c</sup>, Josef Settele<sup>a,b</sup>, Sylvia Villareal<sup>d</sup>, Martin Schädler<sup>a,b</sup>

<sup>a</sup>Helmholtz-Centre for Environmental Research – UFZ, Department of Community Ecology, Theodor-Lieser-Strasse 4, 06110 Halle, Germany

<sup>b</sup>Div, German Centre for Integrative Biodiversity Research, Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

<sup>c</sup>Department of Ecology, Faculty of Biology, Philipps-University Marburg, Karl-von-Frisch Strasse 8, 35032 Marburg, Germany

<sup>d</sup>International Rice Research Institute, DAPO 7777, Metro Manila, Philippines

<sup>e</sup>Centre for Agricultural Bioscience International (CABI), SE Asia Regional Centre, Serdang, Malaysia

Received 26 February 2014; accepted 20 January 2015  
Available online 28 January 2015

### Abstract

Sustainable management of agricultural systems includes promoting nutrient cycles, which can reduce the need for application of fertilizer. As rice is one of the most important food resources in the world, sustainable management of rice paddies is increasingly in demand. However, little is known about the influence of invertebrates on decomposition processes in these ecosystems. We hypothesized that invertebrates contribute significantly to the decomposition of rice straw in paddies and that their relative contribution is affected by the distance to other landscape structures within fields. We placed rice straw in litterbags of two different mesh sizes which prevent (20  $\mu\text{m} \times 20 \mu\text{m}$ ) or allow (5 mm  $\times$  5 mm) access of invertebrates in six irrigated rice fields for 84 days. In each field, bags were set on three transects running from the bund to the center of the field. Invertebrates significantly increased total rice straw litter mass loss by up to 45% (total decomposition: fine-meshed bags 64%; coarse-meshed bags 83%). Litter mass loss in bags accessed by invertebrates decreased with increasing distance from the bund. Such a spatial trend in litter mass loss was not observed in bags accessed only by microbes. Our results indicated that invertebrates can contribute to soil fertility in irrigated rice fields by decomposing rice straw, and that the efficiency of decomposition may be promoted by landscape structures around rice fields.

### Zusammenfassung

Nachhaltigkeit im bewässerten Tiefland-Reisanbau ist ein wesentlicher Bestandteil zur Sicherung der Nahrungsgrundversorgung eines großen Teils der Weltbevölkerung. Das Verständnis der komplexen Prozesse im Nährstoffkreislauf in Agrarökosystemen kann zu einer Erhöhung der Bodenfruchtbarkeit führen und den Bedarf an Düngemitteln drastisch reduzieren. Die Grundlage für eine natürliche Stickstoffzufuhr, zur Förderung des Pflanzenwachstums, ist die Zersetzung von totem organischem Material, was eine stabile Gemeinschaft von Bodenorganismen voraussetzt. Nichtsdestotrotz ist das Wissen über den Einfluss der Makrofauna auf Zersetzungsprozesse im Boden von Reisökosystemen rar.

\*Corresponding author. Tel.: +49 345 5585405; fax: +49 345 5585329.  
E-mail address: a.schmidt@ufz.de (A. Schmidt).

Ziel dieser Studie war es, den Einfluss von Invertebraten auf die Zersetzungsrates von Reisstroh zu untersuchen und deren Effektivität in Abhängigkeit landschaftlicher Strukturvielfalt in direkter räumlicher Nähe zu den Untersuchungsflächen einzuschätzen. Um zu differenzieren, wie stark der jeweilige Anteil von Invertebraten und Mikroorganismen am Streuabbau ist, wurden Streubeutel mit zwei verschiedenen Maschenweiten (20  $\mu\text{m}$  und 5 mm) verwendet und für 84 Tage auf die Bodenoberfläche bewässerter Reisfelder gelegt. Der Einfluss der Entfernung vom Reisfeldufer auf die Zersetzungsrates sollte mit Hilfe von Transekten, die vom Rand bis zur Mitte von sechs Versuchsfeldern gezogen wurden, ermittelt werden.

Invertebraten erhöhten nicht nur die Menge an insgesamt abgebautem Stroh bis zu 45%, verglichen mit der reinen mikrobiellen Zersetzung, ihr Einfluss nahm auch vom Rand zur Mitte des Feldes hin ab. Die Abbaurates der Mikroorganismen blieb innerhalb des Feldes dagegen relativ konstant.

Unsere Ergebnisse zeigen deutlich, dass Invertebraten einen großen Einfluss auf die Zersetzung von Reisstroh haben und damit die Bodenfruchtbarkeit positiv beeinflussen können. Zusätzlich konnte eine positive Korrelation zwischen Ufernähe und Abbaugeschwindigkeit von Invertebraten in Reisfeldern nachgewiesen werden, was auf eine höhere Nährstofffreisetzung in den Randbereichen der Felder hindeutet.

© 2015 Gesellschaft für Ökologie. Published by Elsevier GmbH. All rights reserved.

**Keywords:** Litter mass loss; Detritivores; Nutrient supply; *Oryza sativa*; Litterbags; Philippines

## Introduction

The breakdown of organic matter is a crucial mechanism for nutrient cycling and productivity in terrestrial and aquatic ecosystems (Cebrian & Lartigue, 2004). Invertebrates play a key role in the decomposition process in both terrestrial (Swift, Heal, & Anderson, 1979) and aquatic systems (Webster & Benfield, 1986). Among other things, invertebrates break down bigger particles and make them available for microorganisms that decompose the material further and are responsible for nutrient release. These microorganisms are in turn one of the most important sources of energy for many soil (Swift et al., 1979) and aquatic animals (Perry & Sheldon, 1986; Hamilton, Lewis, & Sippel, 1992). Invertebrate decomposers are also known to act as scavengers (Parmenter & MacMahon, 2009). Besides their importance in the decomposition process, invertebrate decomposers were found to be an important food resource for predators (Ishijima et al., 2006; Oelbermann, Langel, & Scheu, 2008). In rice fields, for example, the use of decomposers, like chironomid larvae, as secondary food source allows generalist predators, as e.g. some groups of aquatic Heteroptera, to maintain high abundances throughout the whole rice cycle (Settle et al., 1996). Therefore, the role of invertebrate decomposers in food webs is crucial for the maintenance of ecosystem functions related to nutrient cycling, habitat structure, and community dynamics.

Rice cultivation is one of the most important, stable, and successful agricultural branches in tropical regions, especially in Southeast Asia (Kurihara, 1989). Toward the end of the Green Revolution, after the mid-1960s, rice production was intensified all over the world, especially in Asia (Bambaradeniya & Amarasinghe, 2003). The negative impacts of these agricultural practices for invertebrate food webs in rice fields have been shown mainly for predators and parasitoids, which are the most important natural pest

control agents (Schoenly et al., 1996; Ives & Settle, 1997; Drechsler & Settele, 2001), or on the pest species themselves (Kiritani, 1992; Settele, 1992; Cohen et al., 1994). In contrast, studies on the detritivorous invertebrate fauna in rice ecosystems focused solely on the diversity or the abundance of invertebrate decomposers (Simpson et al., 1993a, 1993b; Simpson, Roger, Oficial, & Grant, 1994) with only speculations about their functional role for decomposition and therefore nutrient dynamics. The lack of such studies in rice fields is surprising since the soil fauna is known to contribute substantially to nutrient dynamics and productivity in agro-ecosystems (Benckiser, 1997). Generally, there is no conceptual consensus about the role of invertebrate decomposers in freshwater ecosystems. Moreover, studies in tropical freshwater ecosystems have been done mainly in streams (Hagen et al., 2012), and to our knowledge, virtually no information on the contribution of invertebrates to litter decay in other tropical freshwater ecosystems, such as rice fields, is available. In general, the contribution of fauna to the decomposition process in the tropics is suggested to be high both in terrestrial and aquatic habitats (Wall et al., 2008). However, compared to terrestrial habitats invertebrate activity and litter characteristics might be of lower importance during the initial phase of litter decay in aquatic ecosystems as due to higher leaching of organic and mineral compounds mass loss tends to be high (Treplin & Zimmer, 2012).

The decomposition process in irrigated rice fields may differ from “real” aquatic systems in many aspects. For example, tillage and application of fertilizer and pesticides can change soil and water properties. Various studies have demonstrated an influence of nutrient concentrations in water on microbial-driven decomposition dynamics, with prevalent positive effects of nutrient addition on the decay rate (Webster & Benfield, 1986). Thus, the intensive application of fertilizers may lessen the relative importance of invertebrates in the decomposition process. Furthermore, fields are often

irrigated only during certain periods of the year and regularly fall dry. Thus, macro-decomposers strictly bound to a water habitat may not establish stable populations or may not reach high abundances.

However, most aquatic invertebrate decomposers are not restricted to aquatic habitats throughout their life cycles. Some insects, which can be also found in irrigated rice fields, are involved in the decomposition process during their aquatic larval stages, e.g., chironomid larvae, and populate the surrounding terrestrial habitats as adults. The impact of surrounding landscape structures on ecosystem functions has repeatedly been shown for different arable fields (e.g., Perfecto and Vandermeer, 2002; Diekötter, Wamser, Wolters, & Birkhofer, 2010; Woodcock et al., 2010). The spatial variability is often reflected by a decrease in diversity and corresponding ecosystem functions (e.g., pollination) in agro-ecosystems with increasing distance from surrounding landscape structures (e.g., Klein, Steffan-Dewenter, & Tscharntke, 2003; Klein, 2009). However, invertebrate decomposers are often ignored in such studies despite their known importance for ecosystem functioning.

Here, we investigated whether invertebrate decomposers play an important role in the decomposition process and if this function is mediated by the distance from surrounding terrestrial habitats. As a proxy for decomposition we measured litter mass loss of rice straw in litterbags with and without access for invertebrates in paddy fields surrounded by six different landscape structures reflecting a broad spectrum of prevalent structures in the region of Laguna, Philippines. We tested the following hypotheses: (1) the invertebrate fauna contributes considerably to the litter mass loss of rice straw in paddy fields, and (2) the contribution of invertebrates to the decomposition process in rice fields decreases with increasing distance to the surrounding landscape structures. We assumed invertebrates to have a lower influence on litter mass loss in the middle of the fields, e.g., as many of them depend on surrounding structures in their adult stage (e.g. chironomids).

## Materials and methods

### Study site

The study was conducted in the Laguna province on the island of Luzon, Philippines, in one of the lowland, rice-dominated regions (Legato-site-label: PH.1; Klotzbücher et al., 2015) as part of the LEGATO project (Settele et al., 2015). Laguna lies southeast of the capital Manila (WGS84: 14.2 N; 121.4 E) and is characterized by a diverse landscape structure consisting of intensively used agricultural areas and near-natural forests, gardens, and various types of plantations. Field sites were located within an area of around 100 km<sup>2</sup>. The soil in this area is of volcanic origin, and a high proportion consists of clay and loam. The aquatic decomposer mesofauna is dominated by annelids, nematodes and

**Table 1.** Description of the six study sites and their different surrounding structures.

Site label	Area (m <sup>2</sup> )	Description of adjacent surroundings
“Forest”	1200	3 sides – forest; 1 side – rice
“Bushes”	2000	2 sides – approx. 20 m wide strip of shrub land (bordering a forest); 2 sides – rice
“Rice”	800	4 sides – rice
“Wild meadow”	1600	1 side – wild unmanaged area; 3 sides – rice
“Farm”	600	1 side – area with a house incl. a small yard with free-range chickens; 3 sides – rice
“Vine”	500	1 side – vines; 3 sides – rice

chironomid larvae with other invertebrate groups in smaller abundances (unpubl.).

Wet rice in the lowlands of Luzon Island (Philippines) is mostly cultivated in two crop cycles per year, one in the dry season (December–May) and one in the wet season (June–November). A crop cycle (without the fallow period) lasts around 100 days. Our study was carried out during the wet season from June to September in 2012. During this time, the monthly rainfall varied between 75 and 465 mm, and the average temperature varied between 25 and 25.9 °C. Weather data were provided by the Climate Unit of the International Rice Research Institute, Los Baños, Laguna, Philippines.

Around 20 days after seed sowing, rice seedlings were transplanted separately in the field. Paddies were drained 2–3 weeks before harvesting, i.e., 80–90 days after transplanting.

### Study design

Six rice fields surrounded by different landscape elements, representative for the region, were chosen (Table 1). Field management was carried out according to the usual management scheme including fertilizers, pesticides etc. It is important to note that this study was not designed to compare different landscape structures, but to get an idea about how structures around rice fields in general can affect invertebrate contribution to litter mass loss.

To investigate the contribution of invertebrates to litter mass loss, we placed 10 g of litter (air-dried rice straw; *Oryza sativa*, variety NSIC Rc 222) in 15 cm × 20 cm nylon bags of two mesh sizes: fine, 20 μm × 20 μm mesh size, which gives access to microbes (bacteria, fungi, etc.) only; and coarse, 5 mm × 5 mm mesh size, which gives access also to invertebrates (Tian, Kang, & Brussaard, 1992). The filled litterbags were set in the fields in June/July 2012 after rice

seedlings had been transplanted. Pairs of bags, one fine and one coarse meshed, were placed along three transect lines on the soil surface in every field and fixed to the ground by coarse nylon nets and bamboo sticks. Transect lines in each field were 4 m apart and reached from the bund to the middle of the field ( $7.5 \pm 1.9$  m, mean  $\pm$  SD). Due to the different dimensions of the fields transect lines varied in length. Depending on the size of the particular field, 5–10 pairs of bags were placed on each transect line, with 1 m between each pair; the first pair was placed directly next to the bund, but still within the field. The two bags of one pair were placed directly next to each other with no space in between. Litterbag gradients were always established from one particular border of the field and if a site neighbored the respective structure on one side only, this side was chosen.

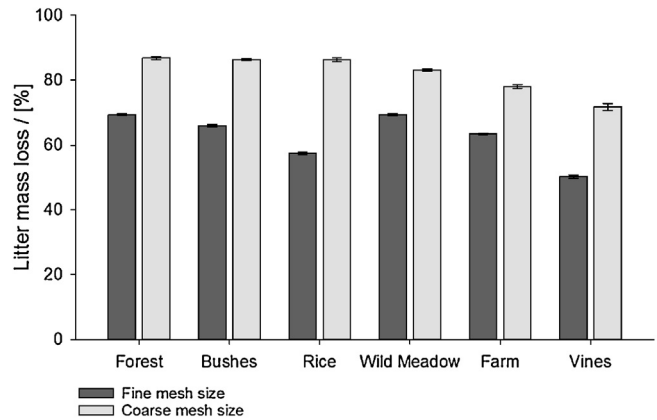
Litterbags were retrieved 84 days after setting and before rice harvesting in August/September 2012. Soil particles, roots, and other alien plant material adhering to the litter were removed, and the remaining straw was dried at  $60^\circ\text{C}$  for 3 days and weighed to the nearest centigram.

## Data analysis

To account for the difference in weight between air-dried and oven-dried straw several samples of air-dried straw were weighed before and after drying in the oven for 3 days at  $60^\circ\text{C}$ . The average weight loss of all samples due to moisture loss was then subtracted from the original 10 g before calculating litter mass losses. The percent loss in litter mass was logit transformed prior to all statistical analyses for approximation of normal distribution and reduction of variance heterogeneity. Using a nested general linear mixed model (GLMM) type III sum of squares (procedure MIXED, SAS 9.2.), litter mass loss was analyzed in dependence on *mesh size*, *site*, and the co-variable *distance from bund*. Transects were considered random and nested in *site*. The least-square means were calculated for the six levels of the factor *site*. To illustrate the contribution of invertebrate decomposers to litter mass loss depending on the distance to the bund within a paddy, the percentage litter mass loss was normalized to the specific effects of the factor *site*. This was done by subtracting the particular estimated mean value for each site from the corresponding logit-transformed litter mass loss.

## Results

At all six sites, the mean litter mass loss of the coarse-meshed bags ( $83 \pm 8\%$ , mean  $\pm$  SD) was higher than in fine-meshed bags ( $64 \pm 7.5\%$ , mean  $\pm$  SD) (Fig. 1). Thus, invertebrates had a significant influence on litter mass loss (highly significant factor *mesh size*; Table 2). However, litter mass loss due to invertebrates varied across sites (significant *mesh size*  $\times$  *site* interaction; Table 2).



**Fig. 1.** Percent litter mass loss in fine-meshed and coarse-meshed litterbags at the six sites with different surrounding landscape structures (means  $\pm$  SE).

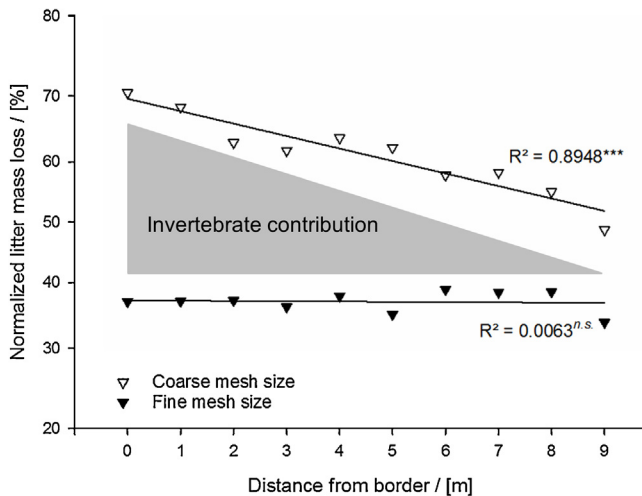
Across all sites, the overall litter mass loss in coarse-meshed bags decreased with increasing distance from the bund of the paddy (Fig. 2). The overall litter mass loss in fine-meshed bags, however, stayed relatively constant at the different locations within the field. These results indicated that the invertebrate contribution to litter mass loss decreased with increasing distance from the bund.

Furthermore, the effect of distance from the bund varied across sites (significant *site*  $\times$  *distance from bund* interaction; Table 2). At four sites (landscape structures: vines, rice, bushes, and forest), litter mass loss decreased with increasing distance to the bund. At the other two sites (with structures farm and wild meadow) litter mass loss increased with increasing distance to the bund, but  $R^2$  values indicated stronger negative correlations than positive ones (Fig. 3).

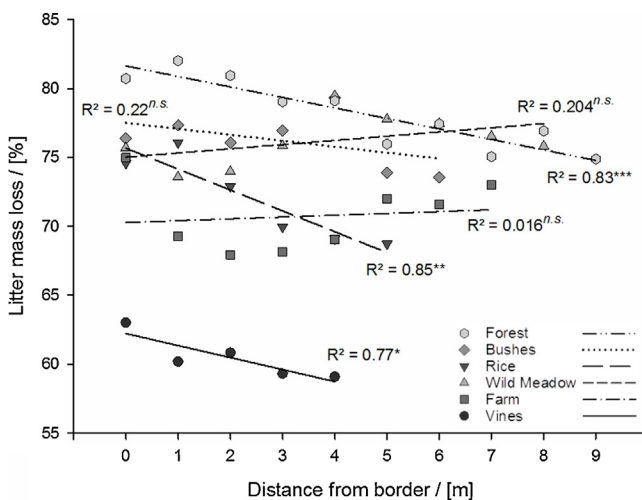
**Table 2.** Effects of *mesh size*, *site*, and *distance from bund* as well as their interactions on mass loss of rice straw litter (logit-transformed) using a GLMM type III sum of squares.

Factors	Decomposition rate		
	df	F	p
Mesh size	1	180.92	<0.001
Site	5	7.83	0.002
Distance from bund	1	13.75	0.003
Mesh size $\times$ site	5	5.13	0.009
Mesh size $\times$ distance from bund	1	11.7	0.005
Distance from bund $\times$ site	5	4.61	0.014
Distance from bund $\times$ mesh size $\times$ site	5	2.88	0.062

Factor *mesh size* represents the bags of two mesh sizes ( $5\text{ mm} \times 5\text{ mm}$  and  $20\ \mu\text{m} \times 20\ \mu\text{m}$ ) used in every plot, factor *site* represents the six fields with different surrounding landscape structures, and the co-variable *distance from bund* represents the continuous effect of the location of litterbags within the fields (linearly from the bund to the middle of the field). The model also includes the random effect *transect* nested in *site* (three transect lines per site); the factor itself and its interactions are not shown.



**Fig. 2.** Correlation of percent litter mass loss from fine- and coarse-meshed bags with *distance from border*.  $R^2$  values indicate the strength of the correlations ( $p > 0.05^{n.s.}$ ,  $p \leq 0.001^{***}$ ). Percentage litter mass loss was controlled for site effects.



**Fig. 3.** Correlation of mean percent litter mass loss at the six sites with *distance from border*.  $R^2$  values indicate the strength of the correlations ( $p > 0.05^{n.s.}$ ,  $p \leq 0.05^*$ ,  $p \leq 0.01^{**}$ ,  $p \leq 0.001^{***}$ ).

## Discussion

Although the potential of decomposition of straw from cereals for soil fertility and site productivity has been highlighted in several studies (Mary, Recous, Darwis, & Robin, 1996; Bhogal, Young, & Sylvester-Bradley, 1997; Yadvinder-Singh et al., 2004), the importance of invertebrate decomposers in rice paddies has been underestimated and rarely studied in the past (Settle et al., 1996). The results reported here support our hypothesis that invertebrates significantly contribute to litter mass loss of rice straw in tropical paddy fields. Hence, invertebrates might be crucial for the establishment of sustainable agriculture in rice-dominated areas by increasing the soil fertility in irrigated rice fields. As

the field management was done as ‘business as usual’, pesticides might have had negative effects on the invertebrate abundance during our study. The effect of the invertebrate fauna on decomposition could therefore have been underestimated, making our results a conservative measure of their contribution and our conclusions on their potential role in ecosystem functioning even more robust. As our study was carried out in conventionally managed rice fields, our results reflect the processes invertebrates have on decomposition in a much more realistic way than a study on pesticide free paddies could have achieved.

Most invertebrate decomposers in freshwater systems are not restricted to aquatic habitats throughout their life cycles. Therefore, the abundance, diversity and species composition of invertebrates in rice fields might be closely linked to the surrounding landscape. Using litter mass loss as proxy we hypothesized that the contribution of invertebrates to the decomposition process in rice fields decreases with increasing distance to the bunds. Overall, we found that invertebrate decomposition indeed declined with increasing bund distance. One reason for this could be the heterogeneous within-field flooding where paddies are often more constantly flooded at the borders than in the middle, which would negatively affect aquatic invertebrates along with their decomposition activity. In contrast, litter mass loss of rice straw assigned to microbial decay activity was not affected by the distance to the bunds and microbial decay processes are also known to be sensitive to changes in water availability. For example, studies in peat soils showed that microorganisms are very sensitive to water and oxygen availability (Jaatinen, Fritze, Laine, & Laiho, 2007; Kwon, Haraguchi, & Kang, 2013). A drop in water along with the consequential increased oxic conditions would result in a shift of the microbial community structure (Kwon et al., 2013) and an increase in microbial biomass (Mäkiranta et al., 2009) and activity (Freeman et al., 1996) and therefore lead to a drastic increase of the microbial decay rate. As this was not the case, the observed decrease of invertebrate decomposition activity with increasing distance to the surroundings can probably be attributed to the spatial effects of the surrounding landscapes themselves and not to a decrease in water availability in the middle of the field. Future studies should investigate if different landscape structures also have different effects on decomposer invertebrates, which would account for the importance of structural diversity also at smaller spatial scales and the necessity to conserve and establish a certain level of landscape heterogeneity for sustainable and ecological rice agriculture.

When we examined the spatial effects within the fields on the total litter mass loss assigned to invertebrate and microbial decomposition, differences between the six fields became apparent. In two of the six fields the litter mass loss increased with increasing distance from the bund. In contrast, the other four fields showed the reverse pattern, i.e., litter mass loss decreased with increasing distance from the bund. As our study was not intended to describe differences between

specific landscape structures, our design only allows us to interpret the general patterns a set of landscape structures has on litter mass loss and how invertebrates are influenced by them. As we only sampled during one season and only during the irrigated phase of the rice paddy cycle, possible reasons for the contrasting patterns between sites could be different water depths, which can range between 5 and 30 cm, or varying durations of flooding (Bambaradeniya & Amarasinghe, 2003). More shallow water depths result in higher and more rapidly changing temperatures and oxygen levels, especially between day and night (Bambaradeniya & Amarasinghe, 2003). As stated above, invertebrates as well as microorganisms are quite sensitive to rapid environmental changes which is why different patterns of litter mass losses assigned to their joint decomposition activities can arise between sites.

Our study aimed at demonstrating the general importance of invertebrate decomposers in rice fields. Future studies should extend the period of investigation up to at least two rice cycles and focus on a systematic comparison of how differently structured surroundings of paddy fields influence the activity of invertebrate decomposers. Especially the question whether intensively used and therefore more homogeneous landscapes support a lower diversity and abundance of decomposer invertebrates should receive attention. The results of such studies would help in establishing and maintaining diverse structures with sustainable ecosystem functions at local and regional scales.

## Conclusion

In our study, we demonstrated that invertebrate decomposers substantially contribute to the decomposition process in irrigated rice fields. Our results indicated that invertebrate decomposers can be expected to be important for soil fertility and site productivity. Crop residue management strategies should consider invertebrates when using straw to improve soil conditions. The contribution of invertebrates to the litter mass loss of rice straw, as a proxy for decomposition, decreased with increasing distance to the bund on most sites tested, which could indicate that the surrounding landscape structure may influence the assemblages of invertebrate decomposers. Future studies should evaluate in more detail how land management and landscape structure surrounding rice fields contribute to the maintenance of ecosystem services, such as nutrient cycling provided by invertebrate decomposers.

## Acknowledgements

The study is part of the international project “LEGATO” (Land-use intensity and Ecological Engineering – Assessment Tools for risks and Opportunities in irrigated

rice based production systems – [www.legato-project.net](http://www.legato-project.net)), funded by the German Federal Ministry of Education and Research (BMBF, 01LL0917A, 01LL0917L), within the BMBF-Funding Measure “Sustainable Land Management” (<http://nachhaltiges-landmanagement.de/en/>).

We thank Liberty Vertudez and Rowena Dela Rosa of CESD at International Rice Research Institute (IRRI) for helping to prepare the litterbags and Antonio Salamatin, Deomedez Izon, and Danilo Vasquez for helping with setting and retrieving the bags.

## References

- Bambaradeniya, C. N. B., & Amarasinghe, F. P. (2003). *Biodiversity associated with the rice field agroecosystem in Asian countries: A brief review. Working Paper 63*. Colombo, Sri Lanka: International Water Management Institute.
- Benckiser, G. (1997). *Fauna in soil ecosystems: Recycling processes, nutrient fluxes, and agricultural production*. New York/Basel/Hong Kong: Marcel Dekker Inc.
- Bhagal, A., Young, S. D., & Sylvester-Bradley, R. (1997). Straw incorporation and immobilization of spring-applied nitrogen. *Soil Use and Management*, *13*, 111–116.
- Cebrian, J., & Lartigue, J. (2004). Patterns of herbivory and decomposition in aquatic and terrestrial ecosystems. *Ecological Monographs*, *74*, 237–259.
- Cohen, J. E., Schoenly, K., Heong, K. L., Justo, H., Arida, G., Barrion, A. T., et al. (1994). A food-web approach to evaluating the effect of insecticide spraying on insect pest population-dynamics in a philippine irrigated rice ecosystem. *Journal of Applied Ecology*, *31*, 747–763.
- Diekötter, T., Wamser, S., Wolters, V., & Birkhofer, K. (2010). Landscape and management effects on structure and function of soil arthropod communities in winter wheat. *Agriculture, Ecosystems and Environment*, *137*, 108–112.
- Drechsler, M., & Settele, J. (2001). Predator-prey interactions in rice ecosystems: Effects of guild composition, trophic relationships, and land use changes – A model study exemplified for Philippine rice terraces. *Ecological Modelling*, *137*, 135–159.
- Freeman, C., Liska, G., Ostle, N. J., Lock, M. A., Reynolds, B., & Hudson, J. (1996). Microbial activity and enzymic decomposition processes following peatland water table drawdown. *Plant and Soil*, *180*, 121–127.
- Hagen, E. M., McCluney, K. E., Wyant, K. A., Soykan, C. U., Keller, A. C., Luttermoser, K. C., et al. (2012). A meta-analysis of the effects of detritus on primary producers and consumers in marine, freshwater, and terrestrial ecosystems. *Oikos*, *121*, 1507–1515.
- Hamilton, S. K., Lewis, W. M., & Sippel, S. J. (1992). Energy-sources for aquatic animals in the orinoco river floodplain – Evidence from stable isotopes. *Oecologia*, *89*, 324–330.
- Ishijima, C., Taguchi, A., Takagi, M., Motobayashi, T., Nakai, M., & Kunimi, Y. (2006). Observational evidence that the diet of wolf spiders (Araneae: Lycosidae) in paddies temporarily depends on dipterous insects. *Applied Entomology and Zoology*, *41*, 195–200.
- Ives, A. R., & Settle, W. H. (1997). Metapopulation dynamics and pest control in agricultural systems. *American Naturalist*, *149*, 220–246.

- Jaatinen, K., Fritze, H., Laine, J., & Laiho, R. (2007). Effects of short- and long-term water-level drawdown on the populations and activity of aerobic decomposers in a boreal peatland. *Global Change Biology*, *13*, 491–510.
- Kiritani, K. (1992). Prospects for integrated pest-management in rice cultivation. *Jarq-Japan Agricultural Research Quarterly*, *26*, 81–87.
- Klein, A. M. (2009). Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *Forest Ecology and Management*, *258*, 1838–1845.
- Klein, A. M., Steffan-Dewenter, I., & Tschamtko, T. (2003). Fruit set of highland coffee increases with the diversity of pollinating bees. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 955–961.
- Klotzbücher, T., Marxen, A., Vetterlein, D., Schneiker, J., Türke, M., van Sinh, N., et al. (2015). Plant-available silicon in paddy soils as a key factor for sustainable rice production in Southeast Asia. *Basic and Applied Ecology*, *16*, 665–673.
- Kurihara, Y. (1989). Ecology of some ricefields in Japan as exemplified by some benthic fauna, with notes on management. *Internationale Revue der Gesamten Hydrobiologie*, *74*, 507–548.
- Kwon, M. J., Haraguchi, A., & Kang, H. (2013). Long-term water regime differentiates changes in decomposition and microbial properties in tropical peat soils exposed to the short-term drought. *Soil Biology and Biochemistry*, *60*, 33–44.
- Mäkiranta, P., Laiho, R., Fritze, H., Hytönen, J., Laine, J., & Minkkinen, K. (2009). Indirect regulation of heterotrophic peat soil respiration by water level via microbial community structure and temperature sensitivity. *Soil Biology and Biochemistry*, *41*, 695–703.
- Mary, B., Recous, S., Darwis, D., & Robin, D. (1996). Interactions between decomposition of plant residues and nitrogen cycling in soil. *Plant and Soil*, *181*, 71–82.
- Oelbermann, K., Langel, R., & Scheu, S. (2008). Utilization of prey from the decomposer system by generalist predators of grassland. *Oecologia*, *155*, 605–617.
- Parmenter, R. R., & MacMahon, J. A. (2009). Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. *Ecological Monographs*, *79*(4), 637–661.
- Perfecto, I., & Vandermeer, J. (2002). Quality of agroecological matrix in a tropical montane landscape: Ants in coffee plantations in Southern Mexico. *Conservation Biology*, *16*, 174–182.
- Perry, S. A., & Sheldon, A. L. (1986). Effects of exported seston on aquatic insect faunal similarity and species richness in lake outlet streams in Montana, USA. *Hydrobiologia*, *137*, 65–77.
- Schoenly, K., Cohen, J. E., Heong, K. L., Litsinger, J. A., Aquino, G. B., Barrion, A. T., et al. (1996). Food web dynamics of irrigated rice fields at five elevations in Luzon, Philippines. *Bulletin of Entomological Research*, *86*, 451–466.
- Settele, J. (1992). Auswirkungen der Intensivierung des Naßreisbaus auf die terrestrischen Arthropodengemeinschaften philippinischer Reisterrassen. *PLITS*, *10*(3). Weikersheim, Germany: Margraf.
- Settele, J., Spangenberg, J. H., Heong, K. L., Burkhard, B., Bustamante, J. V., Cabbigat, J., et al. (2015). Agricultural Landscapes and Ecosystem Services in South-East Asia – The LEGATO-Project. *Basic and Applied Ecology*, *16*, 661–664.
- Settle, W. H., Ariawan, H., Astuti, E. T., Cahyana, W., Hakim, A. L., Hindayana, D., et al. (1996). Managing tropical rice pests through conservation of generalist natural enemies and alternative prey. *Ecology*, *77*, 1975–1988.
- Simpson, I. C., Roger, P. A., Oficial, R., & Grant, I. F. (1993a). Density and composition of aquatic oligochaete populations in different farmers ricefields. *Biology and Fertility of Soils*, *16*(1), 34–40.
- Simpson, I. C., Roger, P. A., Oficial, R., & Grant, I. F. (1993b). Impacts of agricultural practices on aquatic oligochaete populations in ricefields. *Biology and Fertility of Soils*, *16*(1), 27–33.
- Simpson, I. C., Roger, P. A., Oficial, R., & Grant, I. F. (1994). Effects of nitrogen fertilizer and pesticide management on floodwater ecology in a wetland ricefield – II. Dynamics of microcrustaceans and dipteran larvae. *Biology and Fertility of Soils*, *17*(2), 138–146.
- Swift, M. J., Heal, O. W., & Anderson, J. M. (1979). *Decomposition in terrestrial ecosystems* (Vol. 5) Berkeley: University of California Press.
- Tian, G., Kang, B. T., & Brussaard, L. (1992). Biological effects of plant residues with contrasting chemical-compositions under humid tropical conditions – Decomposition and nutrient release. *Soil Biology and Biochemistry*, *24*, 1051–1060.
- Treplin, M., & Zimmer, M. (2012). Drowned or dry: A cross-habitat comparison of detrital breakdown processes. *Ecosystems*, *15*, 477–491.
- Wall, D. H., Bradford, M. A., St. John, M. G., Trofymow, J. A., Behan-Pelletier, V., Bignell, D. D. E., et al. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology*, *14*, 2661–2677.
- Webster, J. R., & Benfield, E. F. (1986). Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, *17*, 567–594.
- Woodcock, B. A., Redhead, J., Vanbergen, A. J., Hulmes, L., Hulmes, S., Peyton, J., et al. (2010). Impact of habitat type and landscape structure on biomass, species richness and functional diversity of ground beetles. *Agriculture, Ecosystems and Environment*, *139*, 181–186.
- Yadvinder-Singh, Bijay-Singh, Ladha, J. K., Khind, C. S., Khera, T. S., & Bueno, C. S. (2004). Effects of residue decomposition on productivity and soil fertility in rice – Wheat rotation. *Soil Science Society of America Journal*, *68*, 854–864.