Compensatory mechanisms of litter decomposition under alternating moisture regimes in tropical rice fields

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ABSTRACT

A conversion from permanently flooded rice cropping systems to crop rotations that include non-flooded upland crops is heavily promoted in tropical regions to meet the challenges of sustainable food production while reducing water consumption and trace gas emissions. Shorter periods of flooding and manipulation of fertilizer inputs affect belowground community composition, biomass and functioning. However, there have been no previous studies of how such shifts in rice field management might affect soil biota and decomposition. Our objective was to examine how crop diversification, which demands different moisture regimes and nitrogen inputs, influences belowground invertebrate assemblages and their contribution to the decomposition of crop residues.

We conducted a litterbag experiment in lowland paddy fields at the experimental field sites of the DFG-ICON project (Laguna, the Philippines) that were either continuously flooded, had seasonally alternating wet and dry periods, or were continuously dry. Additionally, subplot treatments within these crop rotations included different N fertilizer management practices. At a total of 36 plots we used litterbags with two different mesh sizes to assess decomposition with and without fauna over a period of 72 days. Furthermore, we sampled soil microfauna and mesofauna in both the wet (rainy) and dry seasons.

Although we found no correlation between faunal abundance and the contribution by invertebrates to rice straw decomposition, we found that soil water content was the decisive factor determining the activity of decomposer invertebrates as well as the composition and abundance of the soil fauna in fields with alternating cropping regimes. The impact of invertebrates on rice straw decomposition was higher under anaerobic than aerobic soil conditions which compensated for reduced microbial decay rates during periods of flooding. In contrast, microbial decomposition rates were higher under aerobic conditions, whereas invertebrates had no apparent effects on the mass loss of rice straw despite their higher abundance in dry fields. Our results demonstrate that invertebrates are essential for the effective decay of rice straw residues under flooded soil conditions, and therefore play an important role in supplying nutrients to flooded rice.

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1. Introduction

Flooded rice cultivation with two to three crops per year is the most predominant agricultural land use system in the lowland tropics and subtropics of Asia (Cassman and Pingali, 1995) and provides about 90 % of the global rice supply (FAOSTAT, 2008; USDA, 2007). Currently, the sustainability of producing rice in flooded fields has been questioned in regard to water use efficiency and greenhouse gas emissions (Bouman et al., 2007; Mueller et al., 2012). A range of management strategies have been developed to reduce water consumption and methane emissions from rice-based cropping systems while ensuring sufficient productivity (e.g. Wassmann and Vlek, 2004). One of the most promising approaches

is the inclusion of non-flooded crops into rice-dominated systems (Bouman et al., 2005; Timsina et al., 2010, 2011). However, crop diversification in rice-based systems also bears the risk of depleting soil nutrients and reducing soil organic matter (Haefele et al., 2013; Witt et al., 2000).

A rich assemblage of organisms inhabits paddy rice soils (Bambaradeniya and Amarasinghe, 2003). These organisms significantly contribute to the decomposition of crop residues and element cycling (Lekha et al., 1989; Schmidt et al., 2015b; Widyastuti, 2002). The belowground community of conventionally managed paddy soils is dominated by aquatic and semi-aquatic oligochaetes and nematodes, whereas microarthropods are generally rare (Watanabe and Roger, 1985). Changes in water management by introducing upland crops together with consequent adjustments in fertilizer use are likely to adversely impact native assemblages of soil animals in rice fields. A reduced contribution by the soil fauna to decomposition processes could also diminish microbial activity and thus the mineralization of both carbon (Setälä et al., 1988) and nitrogen (Huhta et al., 1988). On the other hand, increased niche diversity over time due to crop diversification might stimulate the increase of abundance, richness and functional diversity of belowground fauna (Cancela da Fonseca and Sarkar, 1998) with positive implications for litter decomposition. For example, in continuously flooded fields soil mites and springtails have been shown to play a minor role in the decomposition of organic matter (Widyastuti, 2002), but under aerobic conditions their abundance rapidly increases (Widyastuti, 2002) which might enhance their contribution to the regulation of microflora-mediated decomposition.

Decomposition of soil organic matter is one of the most important ecological processes regulating nutrient cycling and energy flow in the soil (Lekha et al., 1989; Manzoni et al., 2008; Talbot and Treseder, 2011). It is highly interactive and involves a broad spectrum of micro-, meso- and macrofaunal groups (Anderson, 1995; Coleman and Crossley, 1996; Wolters, 1991) that generally have indirect effects on the decay of organic matter, e.g. by increasing the surface area and improving the quality of litter as a substrate for microbial colonization (Heath et al., 1964). Hence, microbial activity and biomass are strongly defined by higher trophic level interactions in soil food webs (Lekha et al., 1989; Singh et al., 2005). In addition, the rate of litter decomposition is triggered by several biotic and abiotic factors such as soil properties (e.g. soil moisture and soil texture; Amato and Ladd, 1992; Clark and Gilmour, 1983; Merckx et al., 1985; Steinberger and Whitford, 1988) and the biochemical composition of the plant residues (e.g. N availability and lignin concentration; Bollen, 1953; García-Palacios et al., 2013; Singh et al., 2005; Tian et al., 1993). Decomposer invertebrates are likely to increase the effectiveness of litter decomposition in flooded rice fields (Schmidt et al., 2015a) where microbial activity is hampered by the high C/N ratios and lignin contents of rice straw as well as the anaerobic conditions of flooded fields (Acharya, 1935; Koegel-Knabner et al., 2010; Schmidt et al., 2015b; Vigil and Kissel, 1991).

Different management practices can have a large impact on the organic C and N balance in the soils of continuous rice cropping and rice-maize rotation systems (Witt et al., 2000). Furthermore, the abundance and composition of soil fauna assemblages are influenced by crop type (Wardle et al., 1999). However, previous studies have not considered how shifts in soil conditions during crop rotations and consequent effects on the composition of soil animal assemblages might affect decomposition and soil nutrient dynamics. Recently, Handa et al. (2014) reported that a reduction in the functional diversity of decomposer organisms slows down the cycling of litter derived C and N across a range of terrestrial and aquatic ecosystems. Furthermore, an increase in plant species richness after the introduction of crop rotations affects the biomass

of microbes and soil animals (Wardle et al., 1999) which in turn might alter the rate of nutrient cycling in the soil. A better understanding of soil-dwelling animals and their impact on the dynamics of decomposition processes in rice-based agroecosystems will be essential for evaluating the benefits and risks associated with the introduction of non-flooded crops into these systems, and hence, for developing effective management strategies for the soils of rice producing regions.

The present study was conducted at the experimental field sites of the ICON ("Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles") research group located in Los Baños (the Philippines). We examined how introducing non-flooded upland crops with different fertilization regimes into the cropping cycles of continuously flooded rice fields alters the assemblages of soil animals and the invertebrate-driven decomposition of rice straw. We addressed the following hypotheses:

Compared to non-flooded fields, microbial litter decomposition in flooded rice fields will decrease due to anaerobic soil conditions, which increases the relative importance of decomposer invertebrates.

The conversion from wet to dry conditions during crop rotation alters the structure of soil invertebrate assemblages. We expect macro- and microarthropod groups to be more abundant under aerobic field conditions.

The lack of aquatic invertebrates and their contribution to decomposition processes in soils of non-flooded fields is compensated by a more abundant and active terrestrial mesofauna.

2. Materials and methods

2.1. Study site

Experiments were conducted at the International Rice Research Institute (IRRI) about 66 km south of Manila (Laguna, the Philippines; elevation: approx. 20 m above sea level; coordinates: lat 14.2, lon 121.4 WGS84 decimal degrees). In this region lowland flooded rice is primarily cultivated in two crop cycles per year, one in the dry season (December–May) and one in the wet season (June–November). Our study was carried out during both seasons in 2013. The site had been used for paddy rice cultivation for several decades prior to the establishment of the field experiment by the ICON group.

Average minimum, mean and maximum temperatures during the time of our experiment (2012/12–2013/11) were 24.0, 27.7 and 31.5 °C. The climate is characterized by a high intra-annual variation of precipitation. The average rainfall per month during the dry season (2012/12–2013/05) was 87.4 mm and average monthly rainfall during the wet season (2013/06–2013/11) was 343.0 mm.

The soil is of volcanic origin and clay-dominated. It is classified as Andaqueptic Haplaquoll (USDA classification) with 54.2 % clay, 32.8 % silt and 13 % sand. The bulk density of the topsoil (0–0.1 m) is 1.0 kg dm^{-3}, the average pH is 6.1 and the organic C content is about 1.8 %.

2.2. Study design

Fieldwork was conducted at the experimental site (36 plots; 4 crop rotations × 3 fertilizer treatments × 3 replicates) of the ICON project ("Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles"). The 12 core fields (530–549 m^2 each, total area of about 150 × 100 m) are arranged in two rows with six fields in each row (see Fig. 1 for the core field design). The fields were separated by field bunds and encompassed by grass verges (5 m in diameter). Since the dry
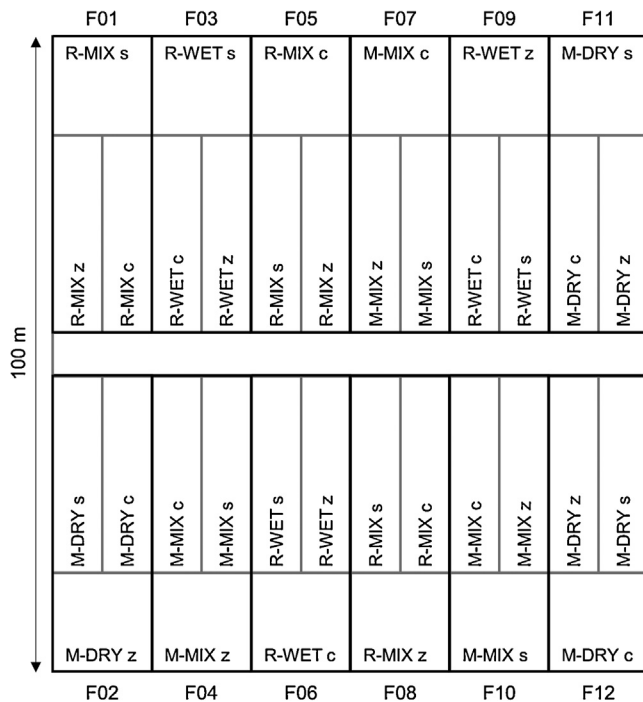
Fig 1. Setup of the ICON field experiment ("Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles"; Los Baños, the Philippines; scheme of the core field design). The 12 fields (530–549 m^2 each) are arranged in two rows. The fields are managed with four different crop rotations (R-WET: flooded rice in dry and wet season; R-MIX: aerobic rice in dry season − flooded rice in wet season; M-MIX: maize in dry season − flooded rice in wet season; M-DRY: maize in dry season − aerobic rice in wet season). Each field is split into two plots (159–197 m^2 each) with three different N fertilizer management regimes (z: no N fertilization; c: conventional N fertilizer application (130 kg N ha^{-1}); s: site-specific N fertilizer application (180 kg N ha^{-1})).

season 2012, the fields had been managed with four different cropping systems. One was continuously flooded to represent the traditional double-rice cropping system with two seasons of lowland flooded rice per year (*Oryza sativa* L., NSIC Rc222, Tubigan 18; henceforth abbreviated by 'R-WET', see Table 1). In two intermittently submerged rotations, flooded rice during the wet season was followed by an upland crop during the dry season which consisted of either aerobic rice (NSIC Rc192, Sahod Ulan 1; 'R-MIX') or maize (*Zea mays* L., Pioneer hybrid P3482YR; 'M-MIX'). The fourth treatment was a continuously aerobic crop rotation where maize was grown in the dry season and aerobic rice in the wet season ('M-DRY').

Each field was split into three plots; each with a similar surface area (159–197 m^2) separated by field bunds, and managed with three different N fertilizer treatments which were randomized over two parallel rectangles of about 24 × 6 m and one square plot of approximately 12 × 12 m. One plot per field received no N fertilization ('zero N'), the second one was conventionally fertilized

Table 1
Crop rotations of the ICON field experiment ("Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles"; Los Baños, the Philippines) and the respective crops cultivated in the dry and the wet seasons.

	Crop rotation	
Acronym	Dry season	Wet season
R-WET	Flooded rice	Flooded rice
R-MIX	Aerobic rice	Flooded rice
M-MIX	Maize	Flooded rice
M-DRY	Maize	Aerobic rice

('conv N', 130 kg N ha^{-1}) based on local farmers' practices, and the third treatment was fertilized following the site-specific N fertilization method ('site-spec N') which represents a dynamically adjusted nutrient management strategy where fertilizer inputs are calculated with the IRRI 'Rice Crop Manager' (http://webapps.irri.org/ph/rcm/) for site-specific conditions (estimated as 180 kg N ha^{-1}). Critical time points for fertilizer application were determined with the IRRI leaf color chart according to the chlorophyll content (LCC, Witt et al., 2005). N fertilizer was applied as urea three times a season. Additionally, muriate of potash and Solophos were applied at seasonal rates of 30 kg ha^{-1} K$_2$O and 30 kg ha^{-1} P$_2$O$_5$ for rice, and 30 kg ha^{-1} K$_2$O and 50 kg ha^{-1} P$_2$O$_5$ for maize, respectively.

Rice seedlings (flooded and aerobic rice) were sown to seed beds in a greenhouse and transplanted to the fields 21 days after seeding (2–3 seedlings per hill with 0.2 × 0.2 m spacing). Flooded rice fields were kept submerged (approx. 0.05 m water body) after crop establishment (31 days after seeding) until two weeks before harvest. Land preparation consisted of soaking, plowing and puddling as well as harrowing and leveling. Maize and aerobic rice were grown in non-puddled soil. Fields were irrigated when rainfall was insufficient. Drainage ditches prevented fields with upland crops from flooding during heavy rains. Maize was planted with 0.25 × 0.75 m seed spacing.

After harvest maize plants were cut to ground level and removed from the fields with root residues remaining in the field (110 days after sowing). Rice plants were cut to approx. 5 cm above the soil level (aerobic rice: 89 days after transplanting; flooded rice: 100 days after transplanting). All residues were incorporated into the soil during land preparation for the next plant growth season. Manual weeding and rodent control were performed once per season as well as molluscicide (organic "Kuhol buster" – saponin) and fungicide ("Score") application.

2.2.1. Litterbags

In order to quantify the contribution by decomposer invertebrates to total rates of decomposition, nylon litterbags (15 × 20 cm) with two different mesh sizes (Bokhorst and Wardle, 2013) were filled with 10 g of litter (air-dried, chopped rice straw; *Oryza sativa* L., variety NSIC Rc222) and subsamples were retained for initial moisture and chemical analyses. The fine-meshed litterbags had a mesh size of 20 × 20 μm and allowed access of microbes and some microfauna (protozoans, micro-nematodes) while the coarse-meshed bags had a mesh size of 5 × 5 mm. Tian et al. (1992) found no difference in rates of rice straw decomposition between mesh sizes of 2 × 2 mm and 7 × 7 mm. Henceforth, we will refer to the litter mass loss in fine-meshed bags as 'microbial decomposition'. Litter mass loss from coarse-meshed litterbags will be ascribed to the combined effects of microbial decomposition and faunal contribution to straw breakdown. Following Bradford et al. (2002) we consider the physical breakdown of plant material by the decomposer fauna and the consequent loss of small straw fragments from coarse-meshed bags as a functional role of decomposer invertebrates in the decomposition process and as part of the catabolic degradation process (Schädler and Brandl, 2005; but also see Frouz et al., 2015). Two weeks after transplanting or seeding (dry season: 2013/01/23; wet season: 2013/07/09) one fine- and one coarse-meshed litterbag were embedded in the upper soil layer in the middle of each field (5–10 cm below the soil surface) with a minimum spacing of 20 cm between bags (total number of bags: 72 per season). Litterbags were retrieved after 72 days of exposure in the field (approx. two weeks before harvest; DS: 2013/04/05; WS: 2013/09/19). After retrieval of the bags, soil particles, roots, and other alien plant material adhering to the straw were removed. The cleaned straw was dried at 60 °C for at least three days and weighed to the nearest centigram to calculate

litter mass losses. The C and N contents of the original straw as well as retrieved straw from each litterbag were determined using an 'Elementar Vario EL element analyzer' (Elementar Analysengeräte GmbH, Hanau, Germany).

2.2.2. Soil sampling

Soil biota was sampled from all 36 plots. The field sampling was carried out twice each season (DS: 2013/01; WS: 2013/07; in total 144 sample sets). On each date, five soil core subsamples (approx. Ø 2 cm, 10 cm depth) were taken per plot for the extraction of nematodes following a modified Cobb's decanting and sieving method (Cobb, 1918). The nematodes were identified to genus level and assigned to feeding groups (Yeates et al., 1993). For the mesofauna, two soil cores (approx. Ø 5 cm, 10 cm depth) were taken. Following the extraction by means of the MacFadyen high-gradient method (MacFadyen, 1961) microarthropods were sorted, counted and identified to suborder or family level. The second soil core sample was manually sieved and decanted for the extraction of *Enchytraeidae* (potworms) which were then suspended in 70 % ethanol and counted. Additional cores (Ø 5 cm, 10 cm depth) were used for the analyses of soil water content and total organic C content by the dry combustion method. As a proxy for fungal infestation, ergosterol, a fungal cell-membrane component, was measured according to Djajakirana et al. (1996). It was extracted from field-moist soil of 1 g dry weight with 100 ml distilled ethanol. The solution was shaken at 250 rev min^{-1} for 30 min. Ergosterol was quantified by reversed-phase HPLC with 100 % methanol as mobile phase and detected at a wavelength of 282 nm (Heinze et al., 2010).

2.3. Data analysis

We carried out split–split plot ANOVAs using general linear mixed models (GLMM) Type III sum of squares (procedure MIXED, SAS 9.2) to analyze litter-, C- and N mass loss as well as the relative contents of C and N in dependence on *crop* (crop rotation; 4 levels within main plot), *fert* (fertilizer treatment; 3 levels within sub plot) and *mesh* (mesh size of litterbags; 2 levels within sub–sub plot) as well as their interactions. The factors *field(crop)* (main plot error) and *fert* × *field(crop)* (sub plot error) were introduced as random factors. Dry and wet season were analyzed separately to account for the fundamentally different climatic conditions and to allow independent tests of the effect of the current status of flooding in the different crop rotations on the observed variables. C and N mass loss were calculated by including the straw dry weight and its relative C and N contents, respectively, before setting and after retrieving of litterbags. To describe the sole influence of decomposer invertebrates on litter mass loss (by excluding the proportion of microbial decomposition on litter mass loss in coarse-meshed bags) the log response ratio was calculated (LRR; ln of litter mass loss in coarse-meshed bags divided by litter mass loss in fine-meshed bags).

Using the same statistical procedure, soil fauna data and ergosterol content were analyzed (split–split plot ANOVA) according to *crop* (crop rotation; 4 levels within main plot), *fert* (fertilizer treatment; 3 levels within sub plot) and *time* (soil core sampling date; 4 levels within sub–sub plot for soil fauna/2 levels within sub–sub plot for ergosterol) as well as their interactions. Again the terms *field(crop)* (main plot error) and *fert* × *field(crop)* (sub plot error) were introduced as random factors. Contrasts and post-hoc Tukey's HSD tests were carried out to reveal significant differences between the respective factor levels within factors.

To analyze community structures soil mesofauna and nematode abundances were calculated as individuals per m^2 and standardized using z-transformation. To reveal relations between assemblages of soil fauna abundance and the crop rotations (*crop*;

categorical, 4 levels) within the two seasons (*time;* categorical, 4 levels) a redundancy analysis – RDA (Rao, 1964; van den Wollenberg, 1977) was carried out using R 2.1.4.2., package *vegan* (Oksanen et al., 2007). The variable *fert* (categorical, 3 levels) did not significantly influence the community structure and was therefore removed from the model. We used this specific multivariate method, which requires linear relationships between faunal groups as well as between assemblages and environmental variables (Euclidean metric), because of the homogeneity in our dataset and the short environmental gradient (Dormann and Kühn, 2008; Leyer and Wesche, 2007). According to Lepš and Šmilauer (2003) the use of linear methods is appropriate, if the longest gradient calculated using DCA/DCCA is smaller than 3. In our dataset the longest gradient was 1.9.

Analyses of co-variance (ANCOVA) were used to analyze the relationship between litter mass losses and selected soil-dwelling fauna groups including the same fixed and random factors as in the above described ANOVAs on litter mass losses. Faunal groups were included successively as covariates to reveal linear relationships of variances.

Structural equation models (SEM) are generally used to test for direct and indirect interaction effects between independent and measured variables in a single model (Grace, 2006). Seven observed endogenous variables were included in the model (SPSS Amos 22.0.0): soil water content, ergosterol content, log response ratio (LRR) of litter mass loss (as a proxy for invertebrate driven decomposition rates) and the abundance of Oribatida, Collembola, bacterial feeding Nematoda and fungal feeding Nematoda, respectively. Two categorical exogenous predictor variables (crop rotation and fertilizer treatment) with four and three factor levels, respectively, were transformed into dummy variables to include them in the model. To achieve this, a categorical variable with k distinct values has to be converted into $(k–1)$ dummy variables with binary coding [0,1]. Therefore, *crop* was transformed into three variables (M-DRY, M-MIX, R-MIX) and *fert* into two variables ('conv' – conventional fertilization, 'site' – site specific fertilization). Dummy coding of categorical variables with more than two levels compares the respective variables with the remaining "uncoded" control variable. Thus, the effect of one dummy variable on an endogenous response variable has to be interpreted in relation to the one variable not included in the model (R-WET for *crop* and 'zero' N for *fert*). For example, if a dummy variable has a negative regression weight of −0.4 on a response variable, the effect of the dummy variable is 40 % more negative than the effect of the control variable. As dummy variables are not independent of each other they need to be co-varied in the model. Model fitting was performed by the stepwise removal of insignificant and weak relationships with confirmation of adequate model fits by a decrease of CAIC (Bozdogan, 1987) of more than 2 (Grace, 2006) and non-significant χ^2-tests ($P > 0.05$). However, in the wet season we observed only low abundances of the decomposer taxa and therefore excluded the SEM for this season.

3. Results

3.1. Litter decomposition

The mass loss of rice straw from coarse- and fine-meshed litterbags was affected by the four crop rotations (significant *crop* × *mesh* interactions, Table 2). In both seasons, flooded rice fields had higher litter mass loss and higher N content in the straw retrieved from coarse-meshed bags compared to the fine-meshed ones (Fig. 2 A–D). Independent of the respective crop rotation, no significant impact of mesh size on these two parameters could be established during the aerobic stage (Fig. 2A–D). However, compared to the initial conditions, the relative N content generally

Table 2
The effects of *crop, fert, mesh* and their interactions on litter mass loss of rice straw and the N and C contents of the retrieved straw using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	Litter mass loss (%)			N content (%)			C content (%)		
	Df	F	P	Df	F	P	Df	F	P
Dry Season									
crop	3,8	1.89	0.21	3,8	8.31	0.01	3,8	12.7	**0.002**
fert	2,16	0.25	0.78	2,16	4.67	**0.03**	2,16	0.16	0.86
mesh	1,24	9.54	**0.005**	1,24	5.60	**0.03**	1,24	38.8	**<0.0001**
crop × fert	6,16	0.67	0.68	6,16	1.49	0.24	6,16	0.29	0.93
crop × mesh	3,24			3,24	23.1	**<0.0001**	3,24	10.3	**0.0001**
fert × mesh	2,24	0.46	0.64	2,24	0.36	0.7	2,24	2.45	0.11
crop × fert × mesh	6,24	0.14	0.99	6,24	1.80	0.14	6,24	0.90	0.51
Wet Season									
crop	3,8	2.96	0.1	3,8	4.64	**0.04**	3,8	0.80	0.53
fert	2,16	1.16	0.34	2,16	0.17	0.84	2,16	0.91	0.42
mesh	1,22	390	**<0.0001**	1,22	213	**<0.0001**	1,22	5.58	**0.03**
crop × fert	6,16	0.25	0.95	6,16	0.61	0.72	6,16	0.63	0.7
crop × mesh	3,22	28.1	**<0.0001**	3,22	10.9	**0.0001**	3,22	7.20	**0.001**
fert × mesh	2,22	0.20	0.82	2,22	0.58	0.57	2,22	0.92	0.41
crop × fert × mesh	6,22	0.48	0.82	6,22	0.76	0.61	6,22	0.43	0.85

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), the factor *fert* is the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *mesh* the two mesh sizes (5 mm and 20 μm) used in every plot. The model also includes the random effects of *field(crop)* (crop nested in field) and *fert × field(crop)*; their effects and interactions are not shown.

increased during the decomposition process (Fig. 2 C + D; initial N content of the straw = 0.6 %). Contrast tests of the *crop × mesh* interaction comparing the state of flooding in the particular season (flooded vs. non-flooded; $P < 0.05$) revealed that the flooding regime had a much stronger impact on litter mass loss and N content (for both mesh sizes) than the mode of crop rotation. In contrast, C content was significantly different in non-flooded fields and identical under flooded conditions (Fig. 2 E + F). However, the decomposition process did not consistently alter the C content (Fig. 2 E + F; initial C content of the straw = 36.8 %). Total losses of C and N were smallest from fine-meshed bags placed in rice fields that were flooded in that particular season (Table A.1; Fig. A.1 A–D in Supplementary materials). The highest amounts of C and N were lost from coarse-meshed litterbags of flooded fields as well as from litterbags of both mesh sizes of non-flooded fields. No significant difference in the range of depletion of these elements was evident (Fig. A.1 A–D in Supplementary materials). C/N ratios in litterbags with different mesh size and placed in different crop rotations mirror this pattern with lowest values in straw residues of coarse-meshed bags in all fields as well as of fine-meshed bags during dry cropping. Highest values were found in fine-meshed bags during flooded conditions (Table A.1; Fig. A.1 E + F in Supplementary materials). With the single exception of the N content in the dry season, no significant effects of the factor *fert* or its interaction with the factors *crop* and *mesh* on mass losses of rice straw, C and N as well as on C and N content were detected (Table 2 and Table A.1 in Supplementary materials).

Ergosterol content in the soil indicates a negative correlation between fungal infestation and litter mass loss in fine-meshed bags ($r^2 = 0.25$; $P \leq 0.001$; Fig. 3A). Moreover, fungal infestation was positively correlated to the log response ratio of litter mass loss ($r^2 = 0.29$; $P \leq 0.001$; Fig. 3B; ANOVA table see Table A.2 in Supplementary materials).

3.2. Invertebrate fauna

Mites and collembolans were the most abundant groups, with the highest abundance recorded in the dry season (Fig. 4A + B). The factors *crop* and *time* as well as their interaction significantly affected the abundance of all selected soil mesofaunal groups (except for *crop* on springtails; Table 3). The mode of crop rotation significantly altered the abundance of Acari in the way that the highest values were recorded in M-DRY and the lowest in R-WET at

the end of the dry season (Fig. 4A). Crop rotations also affected the abundance of springtails (Fig. 4B). However, this effect was confined to the beginning of the dry season, with the highest values occurring in M-MIX and the lowest in R-WET. In general, the abundance of the soil mesofauna was very low in R-WET and at all fields during the wet season (Fig. 4C). Fertilization significantly affected soil mesofauna abundance only in interaction with time (Table 3).

According to the redundancy analysis, the first RDA axis explained 8 % (Table A.3 in Supplementary materials; $P = 0.005$) of the total variance and mostly represented the 'DS-end' (end of dry season) level of the variable *time* (Fig. 5; see also Table A.4 in Supplementary materials – highest absolute value at RDA 1). The second axis accounted for 4 % (Table A.3 in Supplementary materials; $P = 0.005$) of variance and was related to the level 'DS-start' (start of dry season) of the variable *time* (Fig. 5; see also Table A.4 in Supplementary materials – highest absolute value at RDA 2). In total, 14 % of the variance in the dataset was explained by the six constrained RDA axes. Of this variance, 57 % was explained by RDA 1 and 26 % by RDA 2 (Table A.3 in Supplementary materials). The two environmental factors *crop* and *time* significantly influenced the abundance of different soil invertebrate groups (both $P = 0.005$; all results of ANOVA permutation tests are given in Table A.5 in Supplementary materials). Analyses of covariance revealed no significant relationship between litter mass loss from litterbags and the abundance of different soil invertebrate groups.

Fitting of the structural equation model (SEM) required the stepwise removal of unimportant relationships (regression lines) until the best fitted model was achieved (model fit indices of fitted model: $\chi^2 = 11.0$, Df = 28, $P = 0.998$, CAIC = 134.75; for initial model see Fig. A.2 in Supplementary materials). The fitted SEM (Fig. 6; for regression weights see Table A.6 in Supplementary materials) revealed that 70 % of the variation in litter mass loss caused by invertebrates can be explained by the net effects of its predictors. The strongest impact on litter mass loss was mediated through soil water content (Table A.6 in Supplementary materials – highly significant positive regression weight of 0.72) which in turn was solely determined by the three dummy variables describing the crop rotations (M-DRY, M-MIX, R-MIX; all three rotations with dry cropping during the dry season). All three path coefficients had negative correlation values, hence R-WET most positively affected soil water content (see Fig. A.3 in Supplementary materials for
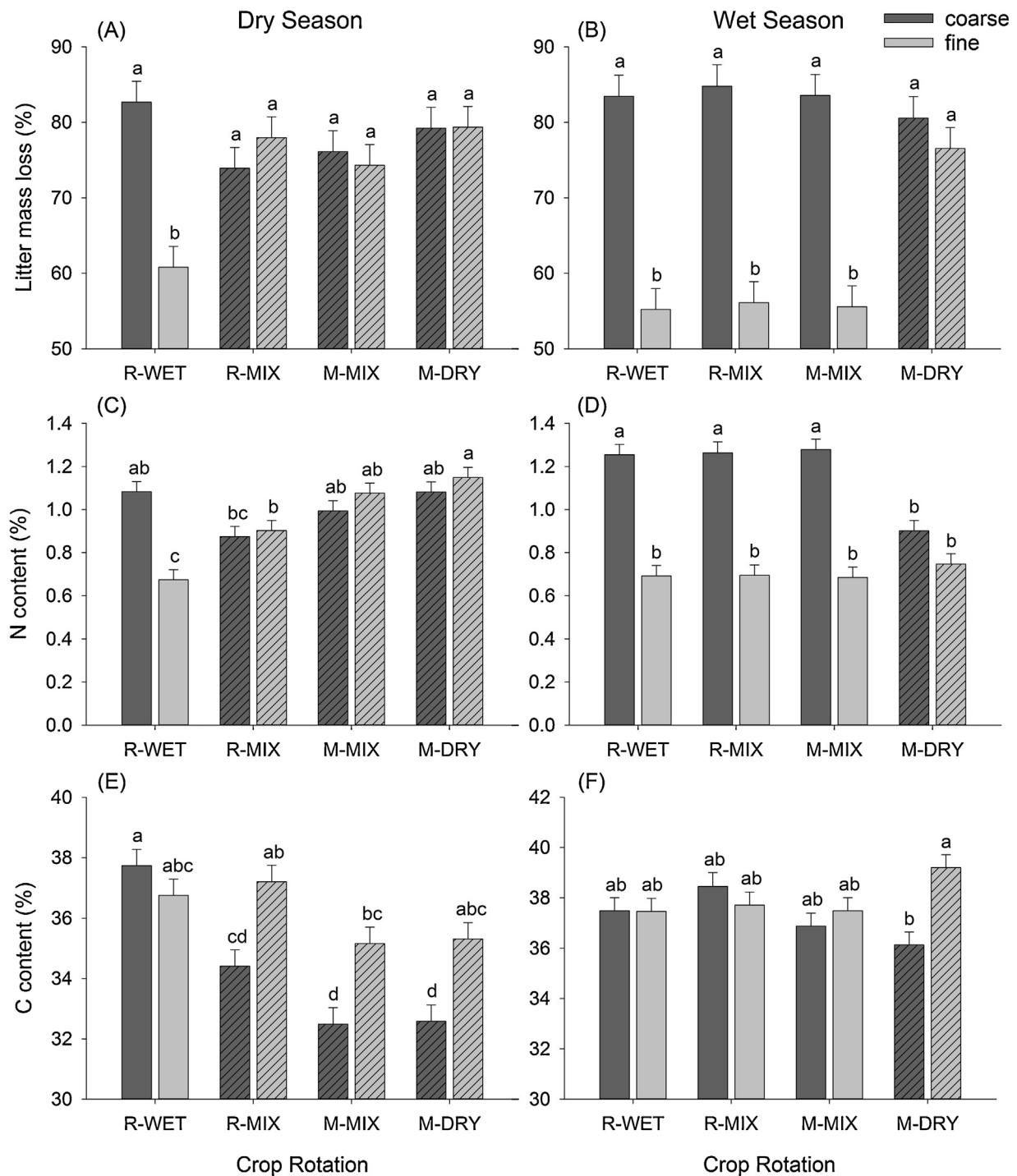
Fig. 2. Percent litter mass loss (A/B), N content (C/D) and C content (E/F) (means + standard error SE) of rice straw retrieved from fields with different crop rotations (*crop*, for abbreviations see Table 1) in coarse-meshed (decomposition by invertebrates and microorganisms) and fine-meshed (decomposition by microorganisms) litterbags. A, C, E: dry season; B, D, F: wet season. Hatched bars represent the aerobic variants in the particular season. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Values of the original straw: N = 0.6 %, C = 36.8 %.

details; ANOVA results are summarized in Table A.7 in Supplementary materials). No direct or indirect effect of fauna abundance on invertebrate-driven litter decomposition in the dry season could be detected. The abundance of bacterial feeding nematodes was reduced by the M-DRY treatment with a path coefficient of −0.45, while the abundance of Oribatida was supported by M-DRY (regression weight: 0.51). This corresponds to the ANOVA results (Fig. 4). Compared to the zero N management, conventional and site specific fertilization treatments significantly increased the

abundance of bacterial feeding nematodes with path coefficients of 0.35 and 0.41, respectively. With a regression weight of −0.44, soil water content had a direct negative effect on the total abundance of collembolans, while conventional fertilization of fields (compared to zero N) significantly increased the abundance of this taxon (regression weight: 0.32).

Analyses of co-variance with LRR of litter mass loss as independent variable and different fauna groups as co-variables (abundance of nematodes – bacterial feeding, fungal feeding,
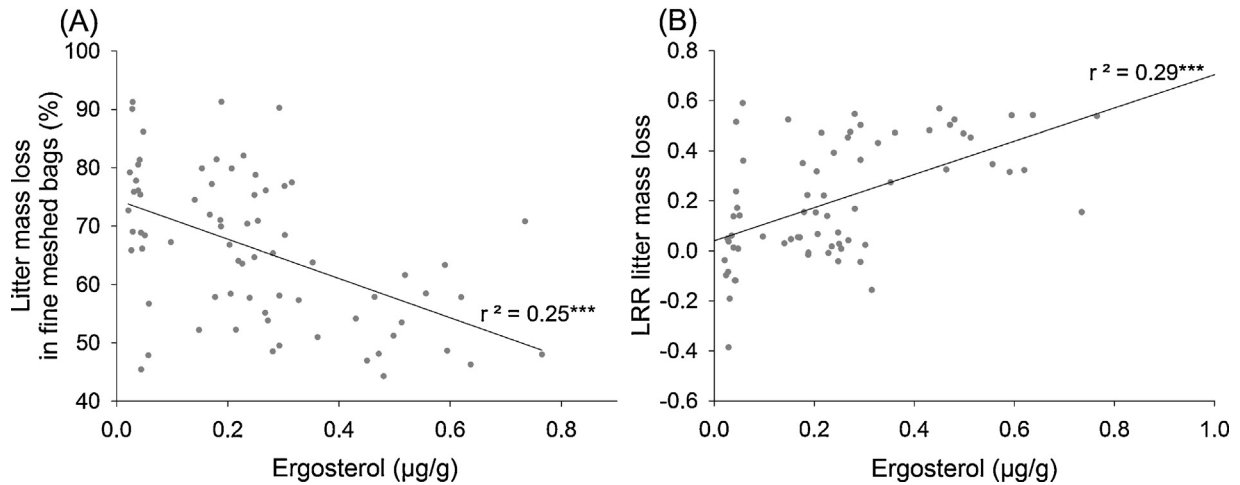
Fig. 3. Linear regressions between (A) microbial contribution to litter mass loss (fine-meshed bags) with the ergosterol content in the soil (μg per g soil dry mass); and (B) the log response ratio of litter mass loss and ergosterol content in the soil . Both graphs present data collected in the dry and the wet season 2014 from the ICON ("Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles") experimental plots representing different crop rotations with cultivation of either flooded rice, aerobic rice or maize (for details on crop rotations and the experimental setup see Table 1 and Fig. 1); $P \leq 0.001$***.

plant-feeding and omnivorous nematodes; mesofauna – Collembola, Acari) showed no direct relation between the measured litter mass loss assigned to decomposer invertebrates and their abundance in either season. Even though the abundance of the analyzed soil fauna taxa was lowest in irrigated rice fields and

abundance data does not promote direct evidence for invertebrate activity increase, the relative change of C and N content in the straw of litterbags incubated in the soil indicate the contribution of invertebrates to rice straw decomposition during irrigated rice cultivation.
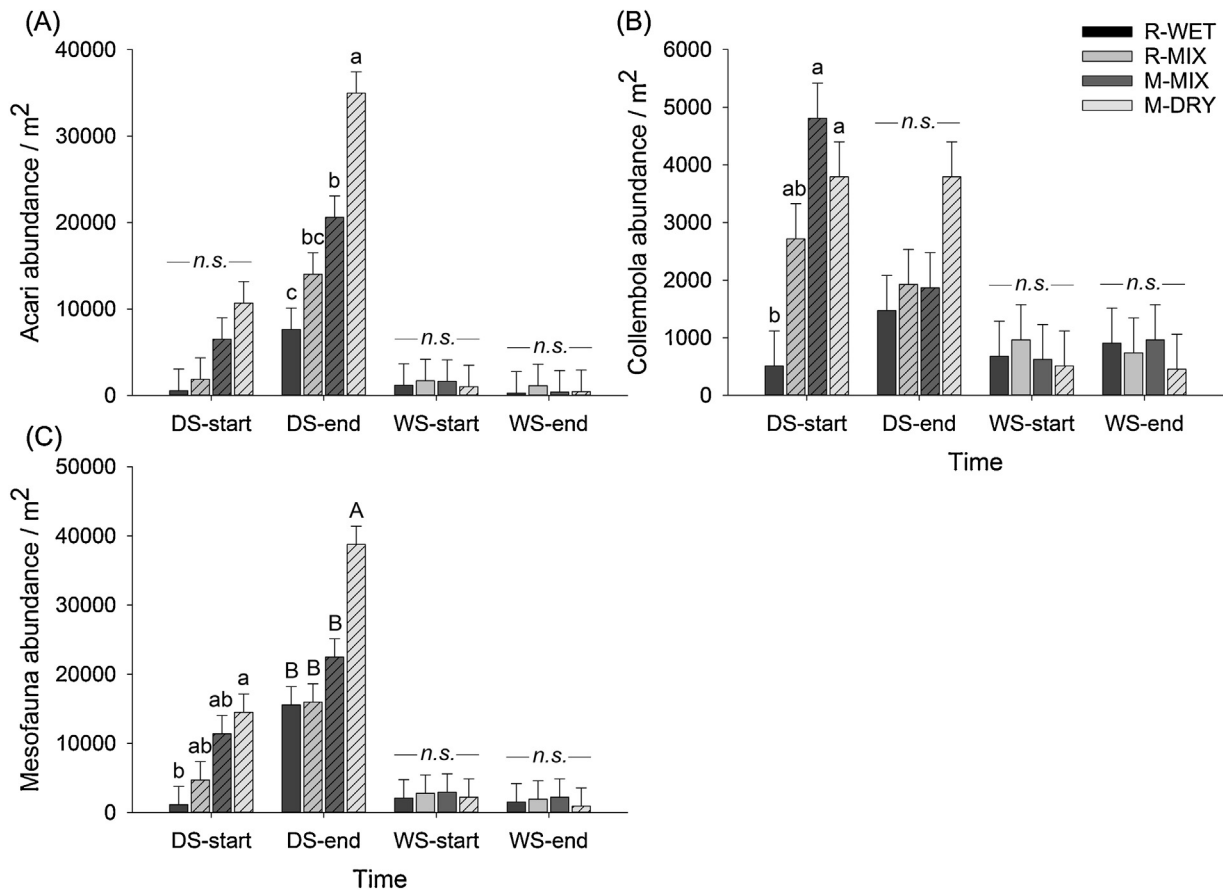

Fig. 4. Abundance of soil mites (A) and springtails (B) per crop rotation (*crop*, for abbreviations see Table 1) at the four sampling times; panel (C) shows the total number of all mesofaunal groups (number of individuals, means + SE). Hatched bars represent the aerobic variants in the particular season. Different letters above the bars indicate significant differences between means (Tukey's HSD, $P \leq 0.05$). Post-hoc comparisons were only made within one point in time, not between sampling times.

Table 3
The effects of *crop, fert, time* and their interactions on selected mesofaunal groups using a GLMM type III sum of squares. Significant effects are indicated in bold font.

Factors	Acari/m^2			Collembola/m^2			Abundance of all mesofaunal groups/m^2		
	Df	F	P	Df	F	P	Df	F	P
crop	3,8	8.44	0.01	3,8	2.43	0.14	3,8	9.26	0.01
fert	2,16	2.63	0.1	2,16	0.95	0.41	2,16	3.21	0.07
time	3,72	53.9	**<0.0001**	3,72	16.1	**<0.0001**	3,72	56.7	**<0.0001**
crop × fert	6,16	0.97	0.48	6,16	2.71	**0.05**	6,16	1.48	0.25
crop × time	9,72	5.56	**<0.0001**	9,72	3.45	**0.001**	9,72	4.29	**0.0002**
fert × time	6,72	2.25	**0.04**	6,72	2.40	**0.04**	6,72	2.84	**0.02**
crop × fert × time	18,72	0.58	0.9	18,72	1.52	0.11	18,72	0.65	0.85

Factor *crop* represents the 4 different crop rotations (R-WET, R-MIX, M-MIX, M-DRY), the factor *fert* is the effect of the three different fertilizer treatments (zero, site specific, conventional), and factor *time* the effect of the four different points in time the mesofauna was collected (DS-start, DS-end, WS-start, WS-end). The model also includes the random effects of *field(crop)* (crop nested in field) and *fert × field(crop)*; their effects and interactions are not shown.

4. Discussion

Our findings close a gap in scientific knowledge on the role of invertebrates in the decay of crop residues and on the processes of fauna-mediated carbon and nitrogen turnover in tropical paddy fields (but see e.g. John et al., 2015; Schmidt et al., 2015a; Settle et al., 1996). The results of the present study confirm that decomposer invertebrates are key organisms for promoting the effective decay of organic matter in rice-based agroecosystems. This was mainly indicated by the much higher mass loss of rice straw in coarse-meshed litterbags compared to fine-meshed bags, which corroborates the results of earlier field studies conducted under similar conditions (e.g. Schmidt et al., 2015a,b; Widyastuti, 2002) and supports our first hypothesis that invertebrates
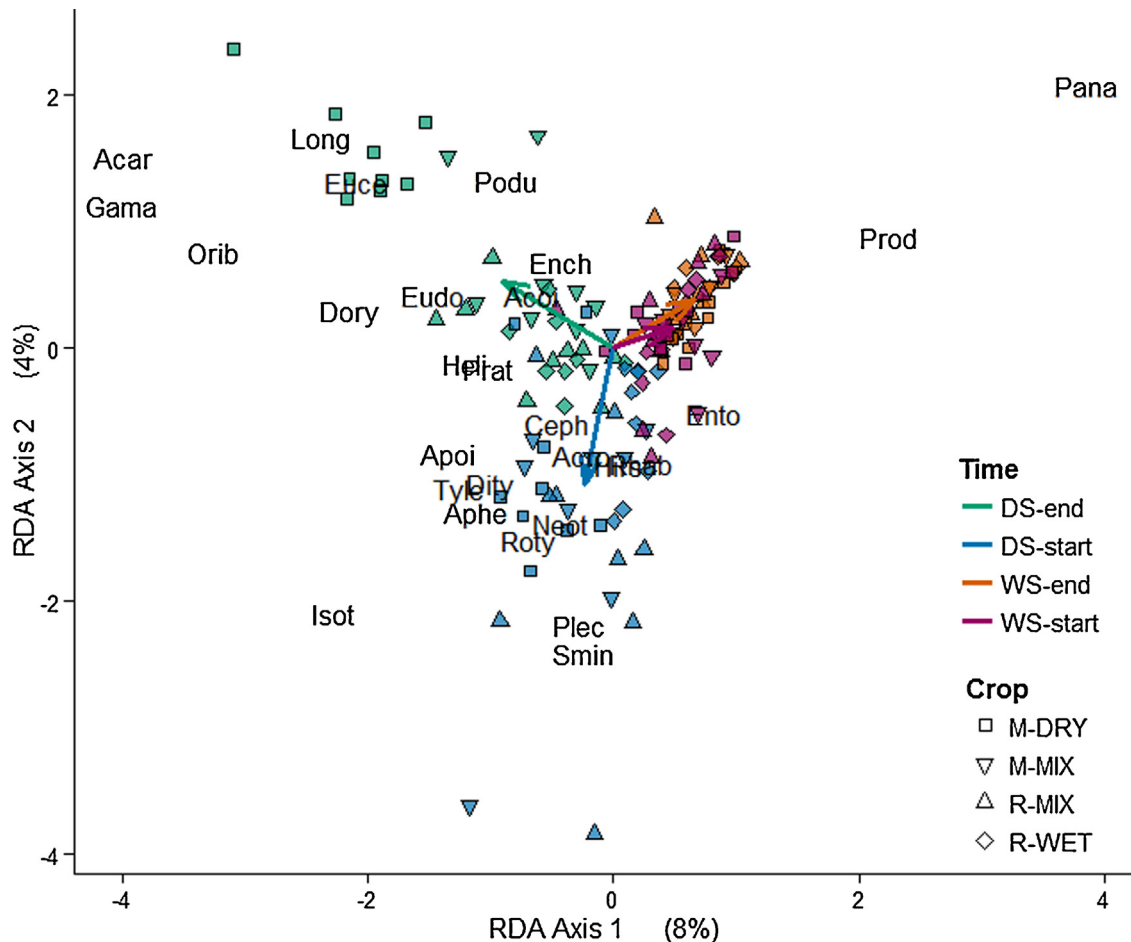

Fig. 5. Euclidean distance biplot based on a redundancy analysis (RDA); faunal groups of soil samples are represented by their 4- letter abbreviations (see below). Site scores are shown with different shapes depending on their affiliation to the particular crop rotation (*crop*, for abbreviations see Table 1), and different colors illustrate the corresponding point in time of each season (*time*). Treatment arrows represent the factor *time*. Axis 1 explains proportionally 8 % ($P \le 0.01$) of the variation in the dataset; Axis 2 accounts for 4 % ($P \le 0.01$) of the variation. **Abbreviations of faunal groups:** Ench – Enchytraeidae; *Acari:* Orib – Oribatida, Gama – Gamasina, Acar – remaining Acari from soil samples (others than Orib and Gama); *Collembola:* Smin – Sminthuridae, Isot – Isotomidae, Podu – Poduromorpha, Ento – Entomobryomorpha; *Bacterial feeding nematodes:* Acro – *Acrobeles* spp., Acoi – *Acrobeloides* spp., Ceph – *Cephalobus* spp., Euce – *Eucephalobus* spp., Pana – *Panagrolaimus* spp., Plec – *Plectus* spp., Rhab – *Rhabditis* spp.; *Fungal feeding nematodes:* Apoi — *Aphelenchoides* spp., Aphe — *Aphelenchus* spp., Neot — *Neotylenchus* spp.; *Omnivorous nematodes:* Dory – *Dorylaimus* spp., Eudo – *Eudorylaimus* spp., Prod – *Prodorylaimus* spp.; *Plant feeding nematodes:* Dity – *Ditylenchus* spp., Heli – *Helicotylenchus* spp., Hirs – *Hirshmanniella* spp., Long – *Longidorus* spp., Prat – *Pratylenchus* spp., Roty – *Rotylenchus* spp., Tyle – *Tylenchus* spp. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
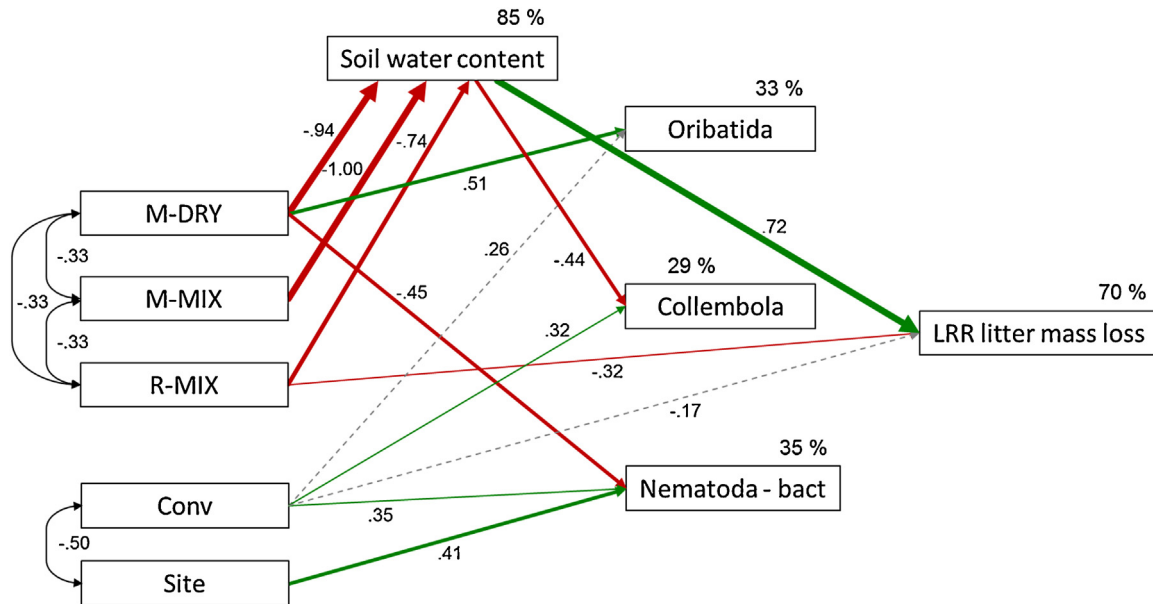
Fig. 6. SEM (Structural Equation Model; see Materials and methods 2.3). The fitted model presents data collected in the dry season from the ICON ("Introducing Non-Flooded Crops in Rice-Dominated Landscapes: Impact on Carbon, Nitrogen and Water Cycles") experimental plots representing different crop rotations with cultivation of either flooded rice, aerobic rice or maize (for details on crop rotations and the experimental setup see Table 1 and Figure 1); model fit indices: $\chi^2 = 11$, Df = 28, $P = 0.99$, CAIC = 134.75; numbers above factors and regression lines represent standardized estimates of explained variance and regression weights; higher regression weights are indicated by thicker lines, for details on regression weights see Table A.6 in Supplementary materials; red lines represent negative path coefficients, green lines represent positive paths, dashed lines represent non-significant paths; "Nematoda − bact" = bacterial feeding nematodes; "Collembola" = total abundance of all groups of collembolans; M-DRY, M-MIX, R-MIX = crop rotations (see Table 1); "Conv" = conventional fertilization treatment; "Site" = site specific fertilization treatment; "LRR litter mass loss" = log response ratio of litter mass loss. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

contribute to the decomposition of rice straw in paddy fields. Although the abundance of soil fauna was low in flooded rice fields, evidence for invertebrate activity in decomposition processes was provided by the relative change of C and N content in the straw that had been retrieved from the litterbags. Nitrogen concentration in straw retrieved from fine-meshed bags of flooded fields did not differ from the initial reference values. Similarly, there was no reduction in carbon concentration in straw from either type of litterbag. In contrast, the increase of nitrogen concentration in rice straw retrieved from coarse-meshed litterbags accounts for a comparably faster release of other components, such as silicon and potassium (Christensen, 1985; Saha et al., 2009). Nevertheless, increased nitrogen concentration along with constant relative carbon content also points to a faster loss of C compared to N. As this pattern can only be found in straw retrieved from coarse-meshed bags of flooded fields, it can be ascribed to the activity of the decomposer invertebrates. Hence, under flooded conditions the loss of carbon is probably triggered by the soil fauna, whereas the breakdown of nitrogen seems to be primarily microbial-driven. Furthermore, the higher absolute release of nitrogen from straw in coarse-meshed litterbags compared to fine-meshed ones suggests that invertebrates had a stimulatory effect on the activity of micro-decomposers. Microbial decay rates are highly influenced by the availability of C and N in litter and soil (Jansson, 1958; Knapp et al., 1983; Tian et al., 1995). Relatively high C/N ratios in the residues of rice straw (approx. 61:1, see S 2) compared to other herbaceous plants (ranging from 19:1 to 30:1; see e.g. Schädler et al., 2003) may hamper the efficiency of microorganisms during decomposition. However, by breaking down the plant material into smaller pieces and mixing these with soil, decomposer invertebrates increase the residue-soil area of contact, creating a more stable and favorable environment for microbial colonization (Cogle et al., 1987; Singh et al., 2010). In turn, the microbiota colonizing straw increase its nutritional value (Graca, 2001; Martinez et al., 2014; Perez et al., 2014) and thus create a more attractive resource for

detritivores (Bradford et al., 2002). This is supported by our results showing the positive correlation between fungal biomass (measured as ergosterol content) and invertebrate-driven rice straw decomposition (log response ratio of litter mass loss) under flooded conditions. In general, microbial mineralization processes are known to be limited in anaerobic environments like in flooded paddy soils (Acharya, 1935); however, invertebrates completely compensated for reduced microbial activity under these conditions.

Under aerobic conditions, microbial decomposition rates were relatively constant during the whole year as indicated by similar levels of mass loss from litterbags placed in dry fields during both seasons. However, fungal biomass was considerably higher in the wet season. Hence, microbial decomposition during dry cropping might have been primarily driven by bacteria, whereas fungi play an apparently greater role in the decay processes during flooded phases. This is in agreement with previous studies which identified fungi as major drivers of microbial decomposition under anaerobic conditions in soil (Baldy et al., 2007; Bergfur and Friberg, 2012). Reduced microbial decomposition under the unfavorable conditions in flooded paddy fields reaffirms the key role of decomposer invertebrates in crop residue decay through both direct and indirect effects (Reddy et al., 1994; Santos and Whitford, 1981; Widyastuti, 2002).

A number of studies across a range of agroecosystems have demonstrated the impact of soil fauna on litter decomposition (e.g. Gießelmann et al., 2010; Schädler and Brandl, 2005; Wall et al., 2008). However, the results of similar research in other cropping systems cannot be simply extrapolated to rice paddies as regular flooding creates a unique habitat that harbors quite peculiar assemblages of decomposers in both the water and the top soil (Bambaradeniya and Amarasinghe, 2003). Decomposer invertebrates in flooded rice fields are mostly represented by (semi-)aquatic and edaphic taxa including chironomid larvae, enchytraeids, microcrustaceans and nematodes (Bambaradeniya and

Amarasinghe, 2003; Kurihara, 1989; Simpson et al., 1993a, 1993b; Weerakoon and Samarasinghe, 1957). Their abundance is highly dependent on rice cultivation practices and may drop to zero during dry intercrop phases (Al-Shami et al., 2010). However, the classical flooded rice paddy invertebrate community tends to quickly recover after relatively short fallow phases with no standing water. Some species are known to be present only for a short time during the flooded phase of rice cultivation. These are often aquatic taxa like chironomid larvae which also include detritivore species (Settle et al., 1996; Stevens et al., 2006). Often, it is hard to make a clear separation between the soil-dwelling and aquatic decomposer fauna in submerged fields as certain taxa (most of which we did not study, e.g. chironomid larvae, Tubificidae, Gastropoda etc.) may partly inhabit both the top soil and water (Kurihara, 1989). Non-flooded agricultural soils in turn harbor a tremendous diversity of predominantly terrestrial micro- and mesofauna groups (Wardle et al., 2004) including soil nematodes, springtails, mites and enchytraeids (da Silva Moço et al., 2009; Giller, 1996; Sileshi and Mafongoya, 2006). In our study, soil mesofauna abundance was generally higher during dry upland cropping compared to flooded conditions. As a consequence, soil fauna abundance was very low in the fields with continuous flooding (R-WET) throughout the year.

The soil faunal assemblages of flooded rice cultivation systems are adapted to periodic changes in water availability between cropping and fallow phases (Bambaradeniya and Amarasinghe, 2003). The establishment of crop rotations with alternating flooded and non-flooded crops greatly extends dry periods. However, contrary to our expectations the prolonged time of dry phases did not adversely affect the activity of decomposer invertebrates during the succeeding wet phase. This is consistent with the finding that the faunal contribution to litter mass loss was always highest in flooded paddy fields.

We expected a significantly higher abundance of terrestrial invertebrates in the fields with continuous dry cropping (M-DRY); however, we recorded similar shifts in faunal assemblages and abundance between dry and wet seasons in soil of these fields as in those subjected to the rotated moisture regime (M-MIX, R-MIX). This can presumably be attributed to a generally high content of soil moisture during the wet season independent of irrigation or drainage. Hence, soil water content seems to be the major determinant for soil invertebrate abundance and assemblage composition rather than the crop rotations *per se*. This conclusion is supported by the observation that season (wet or dry) explained most of the variability in the taxonomic composition of soil fauna. Furthermore, the abundance of selected decomposer groups (mites and springtails) was directly or indirectly promoted by lower soil water content in the dry season. Similar effects of climatic seasonality on soil mesofauna abundance have been reported for other tropical agricultural (Badejo, 1990; Singh and Ray, 2015) and forest ecosystems (Boinski and Fowler, 1989). We expected terrestrial taxa to functionally compensate for the decrease of rice straw decomposition by (semi-) aquatic invertebrates during dry cropping. Despite a significantly higher abundance of soil mesofauna in drained fields, their contribution to litter mass loss was negligible. This lack of relationship between faunal assemblages and invertebrate-driven decomposition rates in any season refutes our third hypothesis. Obviously, the highly enhanced microbial decomposition activity compensated (or maybe even overcompensated) the reduced contribution of decomposer invertebrates during dry phases and might have supported the increase in soil fauna abundance. The comparable total amount of decomposed straw during both seasons promotes the general concept of alternating phases of dry cropping and irrigated rice cultivation for a significant reduction of water consumption and greenhouse gas emission.

5. Conclusions

Our study demonstrated that the conversion from continuously flooded rice cultivation to an alternating cropping regime which involves dry upland crops significantly alters the composition of the soil-dwelling fauna as well as its contribution to decomposition processes. Under flooded soil conditions, the invertebrate-driven decomposition of rice straw completely compensated for low microbial decay rates. In contrast, during dry cultivation phases, microbial decomposition rates are significantly accelerated while the contribution of invertebrates is of lower magnitude despite an increase in soil invertebrate abundance. This indicates a complementarity of decomposition pathways in different cropping regimes. We conclude that the introduction of non-flooded upland crops into the rice cycle bears only negligible risks for efficient litter decomposition as a fundamental ecosystem service and is therefore a promising approach for increasing sustainability in rice production systems.

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.apsoil.2016.05.014.

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