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Research article

How feedback loops between meso- and macrofauna and organic residues contrasting in chemical quality determine decomposition dynamics in soils

Ratikorn Sanghaw [a,c], Patma Vityakon [a,b,*], Frank Rasche [d]

[a] Soil Organic Matter Management Research Group, Khon Kaen University, Khon Kaen 40002, Thailand
[b] Department of Soil Science and Environment, Faculty of Agriculture, Khon Kaen University, Khon Kaen 40002, Thailand
[c] Environmental Science Program, Faculty of Science and Technology, Rajabhat Maha Sarakham University, Maha Sarakham 44000, Thailand
[d] Institute of Agricultural Sciences in the Tropics (Hans-Ruthenberg-Institute), University of Hohenheim, 70593 Stuttgart, Germany

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ABSTRACT

The concept of feedback loops between changes in chemical quality of decomposing organic residues and changes in faunal communities was employed in studying how such feedback loops, representing distinct ecological successional stages, determine decomposition dynamics in soils. A 52-week litterbag decomposition study was superimposed onto an 18-year long term field experiment. Four types of organic residues contrasting in chemical quality (i.e., nitrogen (N), lignin, polyphenols, cellulose) were incorporated into soil annually to assess decomposition and associated meso- and macrofauna communities. In the first 4 weeks after residue incorporation (loop #1), the abundances (densities) of both mesofauna and macrofauna were positively influenced by labile cellulose and N. The mesofauna Collembola and Acari contributed 70–100% and 0–30% to the decomposition, respectively, while the macrofauna beetles and flies contributed 20–90% and 10–66%, respectively. The abundances were highest under groundnut (high N, low lignin) ([1.35 and 0.85 individual number (g dry litter)$^{-1}$] for mesofauna and macrofauna, respectively). The presence of macrofauna at week 2 led to a mass loss ($R^2 = 0.67^{**}$), indicating that macrofauna preceded mesofauna in degrading residue. In week 8 (transition of loop #2 to #3), only macrofauna (beetles dominated contributing 65%) played an important role in lignin decomposition ($R^2 = 0.56^{**}$), resulting in a mass loss ($R^2 = 0.52^{**}$). In week 52 (loop #4) macrofauna, ants (Formicidae) replaced beetles as the dominant decomposers showing a feedback reaction to availability of protected cellulose. The Formicidans contributed 94% to the decomposition and influenced losses of mass ($R^2 = 0.36^{*}$) and N ($R^2 = 0.78^{***}$). The feedback loop concept provides a more comprehensive "two-sided" view into decomposition, as regulated simultaneously by two factors, than earlier "one-sided" approaches to soil fauna-mediated decomposition.

1. Introduction

The chemical quality of organic residues and the composition of the soil fauna are two factors, which both control decomposition

* Corresponding author. Department of Soil Science and Environment, Faculty of Agriculture, Khon Kaen University, Khon Kaen 40002, Thailand.
E-mail address: patma@kku.ac.th (P. Vityakon).

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processes in the soil ecosystem [1,2]. During the decomposition process, changes in each of these factors causes changes in the other in a continuous series of feedback loops between them. This interactive relationship is reflected in the successional stages through which the soil faunal community passes in the course of the decomposition process. However, most published work [3–6] has concentrated on only one or the other of the two factors, while neglecting potential feedback between them during the course of decomposition. Thus, although the feedback concept has been part of ecological theory for more than four decades [7,8], most studies have focused only on changes in the soil faunal community during succession. However, they have not considered the role of feedback between the faunal community composition and the chemical quality of the residues, e.g., Anderson (1975) [9] studied the successional development of the community of soil faunal decomposers in forest leaf litter.

In the course of their development, ecosystems pass through a sequence of successional stages [10]. Each successional stage involves changes in both the species composition of the biotic community and the physicochemical environment. These interactive changes of the two constituents can be conceptualized as feedback loops. In order to take into account such feedback loops, we have developed a conceptual framework, which is based on the model of the decomposition of organic matter in terrestrial ecosystems [11] (Fig. 1). In this model, the course of decomposition is depicted as the decomposition cascade in which each level represents a distinct

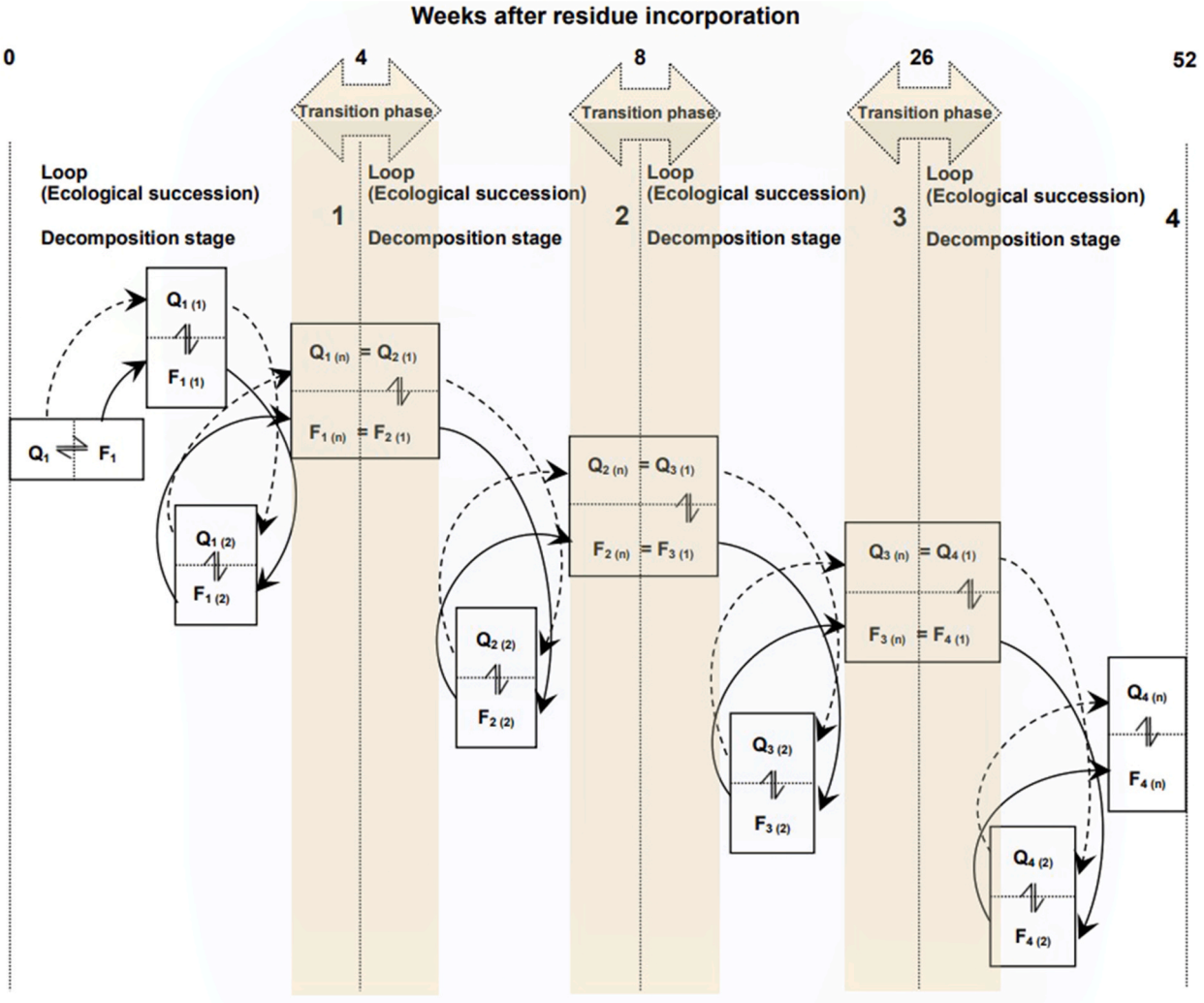


Fig. 1. Conceptual framework of the study showing a decomposition cascade consisting of 4 ecological successional stages or feedback loops which are interactions (⇌) between organic residue with its unique quality or chemical composition (Q) and soil fauna decomposers (F). During the first stage of decomposition (stage 1), new input of organic materials of a certain quality (Q_1) just enters the soil which determines an initial type of fauna (F_1). Following this initial sub-stage of stage 1, there can be many subsequent sub-stages as Q and F interacts with each other to sequentially form Q and F of following sub-stages, i.e., 1(1) … 1(2) …..1(n). A dash-line arrow (⇢) depict changes of chemical composition while a solid line arrow (→) depict changes in fauna communities. Vertical lines specify borders between preceding and succeeding stages where Q and F of the preceding stages become those of the succeeding ones. For example, at the end of stage 1, $Q_{1(n)}$ and $F_{1(n)}$ become $Q_{2(1)}$ and $F_{2(1)}$ respectively of stage 2 of decomposition. Shaded columns signify transition phases between preceding and succeeding decomposition stages. For example, the transition phase at week 4 encompasses the end of stage (or loop#) 1 and the beginning of stage (or loop#) 2.

ecological successional stage. Each successional stage is characterized by a distinctive feedback loop, in which the "chemical quality of organic residues" (Q) at the end of a preceding successional stage determines the "composition of the soil fauna community" (F). The community change determines the chemical quality of remaining organic residues in the next successional stage down the cascade. It is hypothesized that the initial chemical constituents of organic residues selectively favor certain members of the soil faunal decomposer community and thus set the initial course of the cascade. As the cascade proceeds, the residue quality and the soil fauna continue to interact, thus altering continuously over time.

The influence of organic residue quality on the composition and decomposition activities of soil fauna communities has been revealed by several studies. It has been reported that labile nitrogenous compounds in the range of 0.9 to 3.6% led to high abundance of detritivorous macrofauna (millipedes, earthworms), while such concentrations of labile compounds along with soluble polyphenols decreased the abundance of predatory ants and microbivorous mesofauna (springtails, mites) [3,4]. Other studies have shown the influence of soil fauna on decomposition of contrasting quality organic residues. In a study in three close-proximity tropical forest sites in southwestern China, soil fauna exhibited a higher effect on decomposition of low quality (high C/N ratio of 54.8) mixed leaf litter in a rainforest than high quality litter (low C/N ratio 28.9 and 31.8) in a secondary forest and an evergreen broad-leaved forest, respectively [5]. Conversely, a decomposition study in two forest sites, a mixed and a beech forest, in northern Germany showed a higher faunal effect on litter mass loss of high quality (low C/N ratio of 20.5) litter under a mixed forest than litter of low quality (high C/N ratio of 31.2) of a beech forest [6].

Studies on the faunal effect on decomposition are largely confined to either meso- or macrofaunal community members. Some studies focused only on the mesofaunal effect on decay rates of residues in tropical and subalpine forests, while neglecting that of macrofaunal groups (12). Other studies assessed the effect of macrofauna on litter mass loss in either forest or agroecosystems. For example, those studies in a temperate semi-natural broad-leaved woodland associated with recalcitrant oak and beech litter [12], and those of mixed leaf litter in a Hawaiian rainforest [13]. Meanwhile some studies were confined to macrofauna in agroecosystems involving olive orchards in southern Italy [14], and rainfed wheat-paddy cropping systems in the central Himalayan mountains of India [15]. Other studies did not distinguish various groups of soil fauna with respect to their explicit effects on decomposition [6,16,17].

None of the above cited studies employed the feedback loop concept and none of them showed simultaneous effects of organic residue quality and decomposition activities of soil fauna on each other. Particularly important are meso- and macrofauna, which have been shown to enhance decomposition rates. Thus, mesofauna (springtails, mites) increased the decomposition rate of easily decomposable residues (*Laciococca comberi*) from a tropical rainforest in southwest China from 0.3 to 0.4 d^{-1} [18]. Similar increased decomposition rates were also found in litter from a wet subtropical forest in Puerto Rico, i.e., from 0.6 to 2 y^{-1} in high quality litter, *Quercus gambelii*, and from 0.3 to 1.5 y^{-1} in low quality litter of *Cecropia scheberiana* [19]. Macrofauna can enhance the decomposition of recalcitrant residues as shown by higher mass loss of low quality residues (tree prunings, maize, rice straw) in macrofaunal (earthworms, millipedes) included than excluded treatments [20]. Slade and Riutta (2012) [12] also found higher mass losses of recalcitrant oak and beech litter in fauna included mesh bags (5 mm) than fauna excluded bags (1 mm).

It should be pointed out that most decomposition studies have been based on the initial chemical quality of organic residues, including the total content of C, N (including the C/N ratio), lignin, polyphenols [21], and cellulose [16,22,23]. They have been used as indicators of decomposition as influenced by not only microorganisms, but also soil meso- and macrofauna [3,24]. Since various chemical constituents of organic residues have different decomposition rates, they become determinants of soil fauna communities at different successional stages along the decomposition cascade. Therefore, the use of the chemical quality of organic residues during the different stages of decomposition should be used in place of the initial chemical quality to explain community structure and activity shifts of decomposer soil fauna during the course of a decomposition cycle.

In the face of this knowledge gap about the role of feedback between changes in decomposing residues and successional changes in the composition of soil faunal communities in the decomposition cascade (Fig. 1), we undertook this study with the objective of unravelling how feedback loops between meso- and macrofauna and organic residues contrasting in chemical quality determine decomposition dynamics in soils. We hypothesized that during the early stage of decomposition the availability of labile constituents of applied organic residues brought about the feedback response from both meso- and macrofauna which capitalized on these available labile substances. We further hypothesized that, as decomposition continued into the later stages, labile constituents were exhausted, while recalcitrant ones remained, generating conditions that favored macrofauna over mesofauna with consequent changes in the composition of the soil fauna community.

2. Materials and methods

2.1. Study site, design and maintenance of the long-term field experiment

This study was conducted in plots of a long-term field experiment (LTE) which was established in 1995 [25]. Fifty years prior to the establishment of the LTE, the field was converted from forest to experimental plots of field crops (kenaf, cassava, sugarcane) at the research station of the Office of Agriculture and Co-operatives of the Northeast, Khon Kaen province, Thailand (16°20.685′N; 102°49.499′E). The area has an equatorial, winter dry (Aw) climate (KÖppen-Geiger classification) with distinct rainy warm (April–October) and dry cool seasons (November–March). During the litterbag experiment (described in the next section), the temperature ranged between 22.6 and 33.8 °C and the total rainfall amount was 897.5 mm [26]. The site has a coarse-textured soil of Khorat sandy loam (Typic Kandiustult), which is a representative soil that covers approximately 21% of Northeast Thailand. The proportions of sand, silt and clay in the topsoil (0 to 15 cm depth) were 934, 45 and 21 g kg^{-1}, respectively, which contribute to the

sandy texture of the soil. The initial topsoil chemical characteristics were pH (H_2O) 5.5, cation exchange capacity (CEC) 3.5 cmol kg^{-1}, organic C 2.1 g kg^{-1} and bulk density 1.45 g cm^{-3} [25].

A randomized complete block design (RCBD) with three field replications (4 × 4 m plots) was employed. A one-year litterbag experiment was installed in the LTE during its 18th year encompassing May 2012 to April 2013. The residue materials were retrieved from local farming systems surrounding the LTE. They were contrasting in chemical quality expressed in their contents of nitrogen (N), cellulose, lignin, and polyphenols (in g kg^{-1}), including rice (*Oryza sativa* L.) straw (RS: 4.5 N, 449 cellulose, 22.2 lignin, 3.9 polyphenols) groundnut (*Arachis hypogaea* L.) stover (aboveground parts and depodded pulled roots) (GN: 21.2 N, 361 cellulose, 71.4 lignin, 8.1 polyphenols) dipterocarp (*Dipterocarpus tuberculatus* Roxb.) leaf litter (DP: 5.1 N, 271 cellulose, 303 lignin, 68.9 polyphenols) and tamarind (*Tamarindus indica* L.) leaf and petiole litter (dry weight ratio of leaves to petioles = 8/1) (TM: 11.6 N, 212 cellulose, 190 lignin, 27.7 polyphenols). RS and GN residues were cut into pieces of 5–10 cm in length, and DP leaf litter was cut into a rectangular shape of an approximate size of 5 × 10 cm. TM residues were not modified. Preparation of organic residue materials followed the procedures described by Puttaso et al. (2011). Once a year in early May, at the onset of the rainy season, the residues were applied uniformly on the soil surface and manually incorporated with hoes into the soil at 15 cm depth at the rate of 10 t dry matter ha^{-1}. Experimental plot maintenance included frequent light manual weeding employing hand hoes down to about 5 cm from soil surface to minimize soil disturbance. To keep the plots "weed free", weeding was done at least once a month in the rainy seasons and once every two months in the dry seasons.

2.2. Litterbag experiment

For the litterbag experiment, litterbags with a size of 20 × 20 cm were used. There were two mesh sizes: coarse mesh (20 mm) and fine mesh (0.135 mm). The coarse mesh allowed soil fauna of all sizes (size <0.001–20 mm, micro-, meso-, and macrofauna) (Swift et al., 1979) to gain access to the residues inside the bag from the upper side, while microorganisms could access through both sides. The coarse mesh sized bags were of 20 mm mesh only on the upper side, while a smaller mesh size of 2 mm was used on the lower side to prevent the organic material contents from falling out. The 2 mm mesh size used on the lower side of the coarse mesh bag was similar to that used in an earlier litterbag decomposition study of year 13 (2007–2008) of the LTE (Puttaso et al., 2011). The fine mesh excluded soil meso- and macrofauna. Forty grams (oven dry weight equivalent) of each residue (equivalent to 10 Mg DW ha^{-1}) were put into each bag of both mesh sizes. Residue materials were of the same lots of those used in the LTE of the studied year (year 18). They were prepared exactly in the same way as those applied to the LTE as described in earlier section. All residues were in dry condition with average moisture contents of 7–9% dry weight. The residues placed in the litterbags had similar sizes to those incorporated into the plots. The litterbags of each residue type were placed in the field plots corresponding to their residue treatments. A total of 384 litterbags (4 residues × 3 replications × 2 mesh sizes × 2 bags per mesh size × 8 sampling dates during the coarse of 1-year decomposition) were deployed. Pegs were placed in the ground to show the location of the litterbags. The litterbag deployment was timed to coincide (the same day) with the time of the general annual litter incorporation into all plots of the LTE. This litterbag deployment time was designated as the "initial time (time 0)" prior to their retrieval. Litterbags were buried in a single file in all four sides of a plot approximately 40 cm from the edge of the plot, at 15 cm depth which was the level of the general annual litter incorporation of the LTE. Two bags of each mesh size from each field plot were retrieved at 1, 2, 4, 8, 16, 26, 39, and 52 weeks after residue incorporation (WAI). Care was taken that the litterbags remaining in the plots were not disturbed during the removal process.

The retrieval of the bags was carefully conducted to keep the entire content of decomposing residues as well as the fauna decomposers inside the bags. In the field, each retrieved litterbag was initially placed in a tray after which visible macrofauna from each litterbag was manually collected. In the laboratory, remaining litter in litterbags was manually cleaned by removing adhering soils, while the soil fauna remaining and extraneous materials including plant roots and gravels were picked out by hand. The cleaned litter was oven-dried at 60 °C until constant weight to determine the remaining dry mass. Each litter sample was ground (1 mm). A subsample (0.5 to 1.0 g) was ashed at 550 °C for 6 h [27] to adjust the dry weight to an ash-free basis signifying contamination free conditions. The remainder of each ground litter sample was then analyzed to determine its chemical parameters.

2.3. Chemical analysis of remaining residues in litterbags

Chemical analysis of remaining residues were performed in those in the coarse-mesh litterbags only. Total nitrogen (N) was analyzed by the micro-Kjeldahl method. The contents of lignin and cellulose were analyzed by sequential digestion of fiber [28]. Lignocellulose content was obtained after extraction with an acid detergent (acid detergent fiber; ADF) using a fiber analyzer (ANKOM 200/220, Macedon, New York, USA). Lignin content was obtained after hydrolysis with 72% H_2SO_4 (acid detergent lignin; ADL). The content of cellulose was determined from the difference of ADF and ADL. The content of total extractable polyphenols was determined after ground plant residue materials were extracted with 50% methanol, and then measured colorimetrically using the Folin-Denis method [29]. The concentration of each chemical constituent was expressed based on its quantity in the remaining mass (g g^{-1} remaining mass).

2.4. Soil fauna community analysis

Prior to the lay out of the litterbags, the extraction of soil meso- and macrofauna was manually collected in two selected locations in the opposite sides of each field plot in designated areas where litterbags were to be placed as described in the litterbag experiment section above. The collection was done in prepared quadrats (each 20 × 20 cm) at the soil depth of 0–15 cm. The volume of soils from

each quadrat were brought to the laboratory to collect remaining fauna, which could not be directly collected in the field. This sampling of soil fauna was just before the litterbag experiment was started (time 0). During the course of the litterbag experiment, visible macrofauna from each litterbag were manually collected at each of the eight sampling intervals in the field and some in the laboratory as described in the section on litter bag experiment above. Those macrofauna remaining in the litterbag, which could not be manually collected in the field and laboratory due to their smaller sizes and rapid movement, were extracted by heat using a Berlese funnels apparatus with 25 Watt bulbs [30]. The heat source was placed 10 cm above the top of the sample for three days. Soil fauna were forced to move downwards, collected in a container, and preserved in 75% ethanol.

Soil mesofauna were classified taxonomically into orders accompanied by their trophic groups while soil macrofauna were

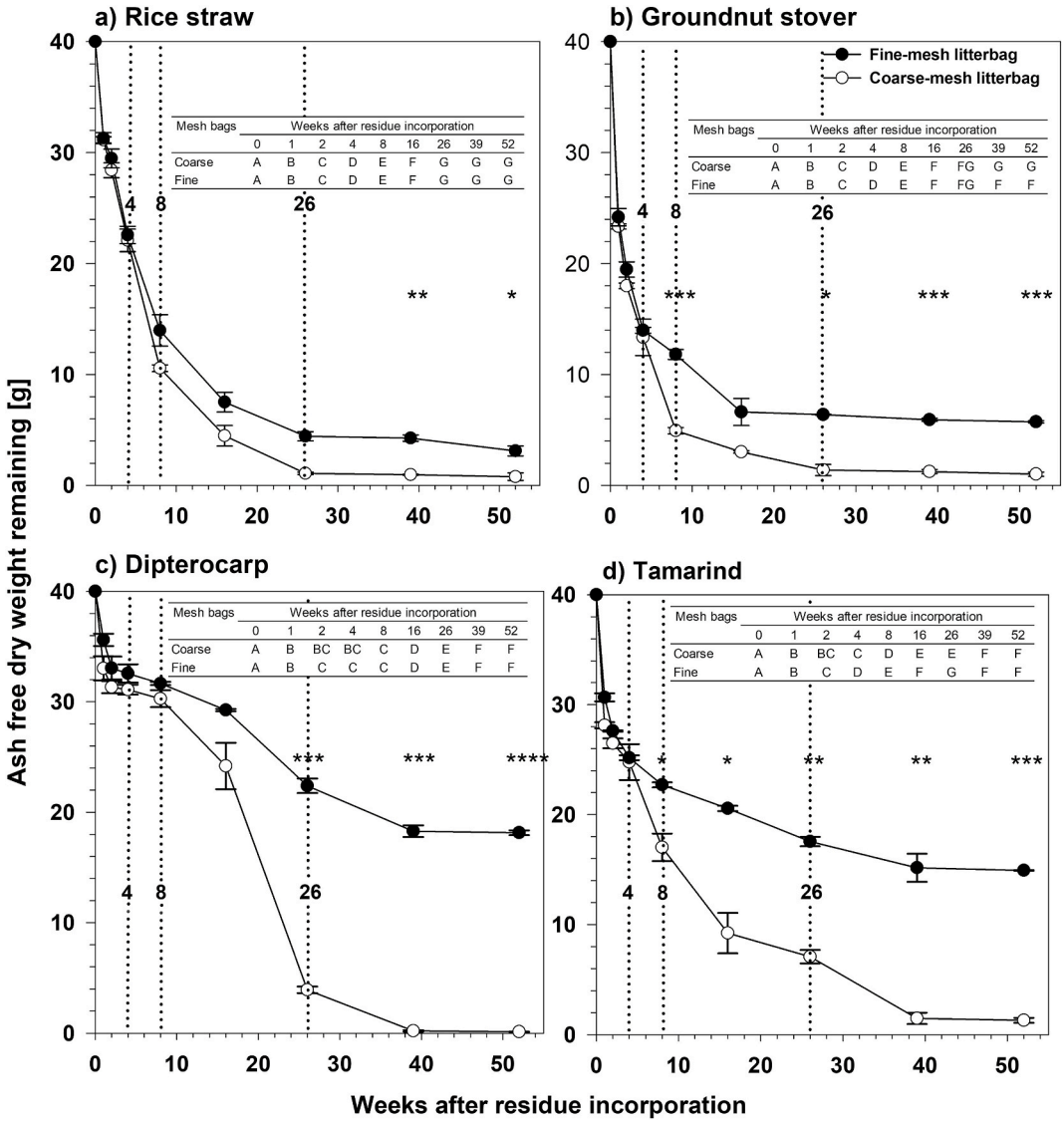
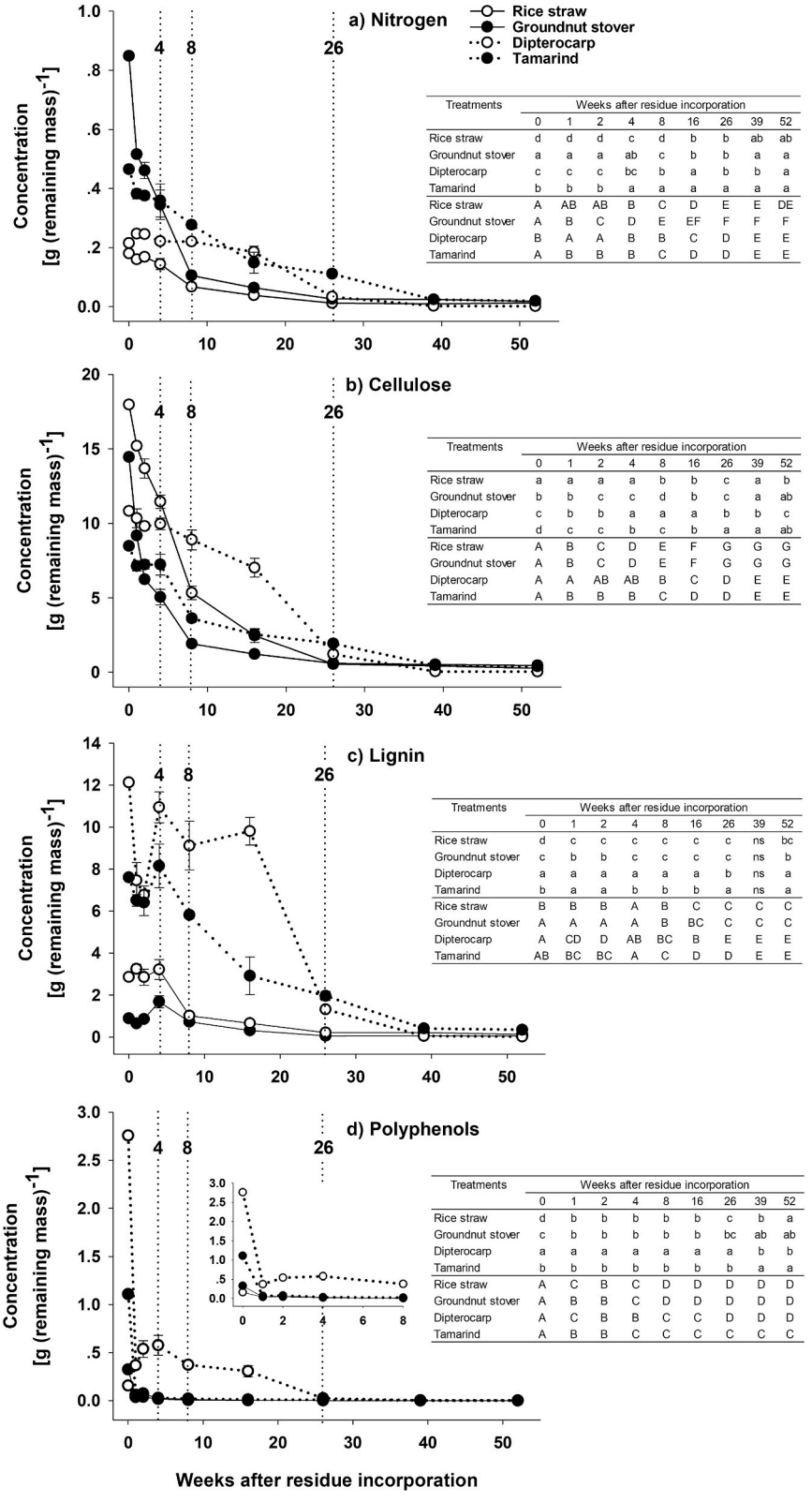


Fig. 2. Ash free dry weight remaining (g) of: a) rice straw; b) groundnut stover; c) dipterocarp leaf litter; and d) tamarind leaf and petiole litter in coarse-and fine-mesh sized litter bags at various weeks after residue incorporation

Asterisks represent significant differences: $*P < 0.05$; $**P < 0.01$; $***P < 0.001$) of mean comparisons between mesh sized litter bags (paired *t*-test) at each sampling date. Vertical bars represent standard error of the mean (SEM). Vertical dash lines accompanied by the values 4, 8, and 26 weeks specify borders between preceding and succeeding feedback loops or decomposition stages, i.e., the value '4 weeks' is the border between the feedback loops 1–2, '8 weeks' is between 2 and 3, and 26 weeks' is between 3 and 4. Means in the same row followed by different uppercase letters are significantly different at $p < 0.05$ (LSD) error of the mean (SEM). Vertical dash lines accompanied by the values 4, 8, and 26 weeks specify borders between preceding and succeeding feedback loops or decomposition stages, i.e., the value '4 weeks' is the border between the feedback loops 1–2, '8 weeks' is between 2 and 3, and 26 weeks' is between 3 and 4. The inset table accompanying each figure shows comparisons among residue treatments and sampling time. Means in the same column followed by different lowercase letters and means in the same row followed by different uppercase letters are significantly different at $p < 0.05$ (LSD).



Treatments	Weeks after residue incorporation								
	0	1	2	4	8	16	26	39	52
Rice straw	d	d	d	c	d	b	b	ab	ab
Groundnut stover	a	a	a	ab	c	b	b	a	a
Dipterocarp	c	c	c	bc	b	a	b	b	a
Tamarind	b	b	b	a	a	a	a	a	a
Rice straw	A	AB	AB	B	C	D	E	E	DE
Groundnut stover	A	B	C	D	E	EF	F	F	F
Dipterocarp	B	A	A	B	B	C	D	E	E
Tamarind	A	B	B	B	C	D	D	E	E

Treatments	Weeks after residue incorporation								
	0	1	2	4	8	16	26	39	52
Rice straw	a	a	a	a	b	b	c	a	b
Groundnut stover	b	b	c	c	d	b	c	a	ab
Dipterocarp	c	b	b	a	a	a	b	b	c
Tamarind	d	c	c	b	c	b	a	a	ab
Rice straw	A	B	C	D	E	F	G	G	G
Groundnut stover	A	B	C	D	E	F	G	G	G
Dipterocarp	A	A	AB	AB	B	C	D	E	E
Tamarind	A	B	B	B	C	D	D	E	E

Treatments	Weeks after residue incorporation								
	0	1	2	4	8	16	26	39	52
Rice straw	d	c	c	c	c	c	c	ns	bc
Groundnut stover	c	b	b	c	c	c	c	ns	b
Dipterocarp	a	a	a	a	a	a	b	ns	a
Tamarind	b	a	a	b	b	b	a	ns	a
Rice straw	B	B	B	A	B	C	C	C	C
Groundnut stover	A	A	A	A	B	BC	C	C	C
Dipterocarp	A	CD	D	AB	BC	B	E	E	E
Tamarind	AB	BC	BC	A	C	D	D	E	E

Treatments	Weeks after residue incorporation								
	0	1	2	4	8	16	26	39	52
Rice straw	d	b	b	b	b	b	c	b	a
Groundnut stover	c	b	b	b	b	b	bc	ab	ab
Dipterocarp	a	a	a	a	a	a	a	b	b
Tamarind	b	b	b	b	b	b	b	a	a
Rice straw	A	C	B	C	D	D	D	D	D
Groundnut stover	A	B	B	C	D	D	D	D	D
Dipterocarp	A	C	B	B	C	C	D	D	D
Tamarind	A	B	B	C	C	C	C	C	C

(caption on next page)

Fig. 3. Changes in concentrations [g (g remaining mass)$^{-1}$] of a) nitrogen, b) cellulose, c) lignin, and d) polyphenols under coarse mesh litter bags at various weeks after residue incorporation. Vertical bars represent standard
error of the mean (SEM). Vertical dash lines accompanied by the values 4, 8, and 26 weeks specify borders between preceding and succeeding feedback loops or decomposition stages, i.e., the value '4 weeks' is the border between the feedback loops 1-2, '8 weeks' is between 2-3, and 26 weeks' is between 3-4.. The inset table accompanying each figure shows comparisons among residue treatments and sampling time. Means in the same column followed by different lowercase letters and means in the same row followed by different uppercase letters are significantly different at $p < 0.05$ (LSD).

taxonomically classified in more detail into orders and families [31–33]. In some cases when the specimens were intact, they were classified down to the genus level. Similar to the mesofauna, trophic groups were identified for each taxonomic category of macrofauna. The individual meso- and macrofauna in each order were counted using a microscope. The density of soil meso- and macrofauna [individual number (g dry litter)$^{-1}$] was calculated to relate this to the remaining mass (g dry weight) in the litterbags and to remaining contents of the other chemical quality parameters. This analysis revealed that macrofauna appeared to be more dominant in their influence on decomposition than mesofauna. This prompted further detailed taxonomic classification of macrofauna as described above.

2.5. Statistical analysis

Repeated measurement analysis of variance (ANOVA) based on a randomized complete block design (RCBD) was applied to evaluate the effects of treatment, time, and treatment × time interaction on densities of mesofauna and macrofauna. Mean comparisons among residue treatments and time period were assessed by the least significant difference (LSD), and standard error of the means (SEM). Soil fauna densities were log (x+1) transformed prior to ANOVA. Multiple regression analyses were performed to determine the relative contribution (% of R^2) of concentrations of single chemical constituents of the organic residues to density of soil meso- and macrofauna. Linear and non-linear regressions were employed to determine the effect of soil meso- and macrofauna densities on decomposition as indicated by changes in mass and chemical composition of the decomposing organic residues. Linear regression analysis was employed to determine the effect of chemical composition on soil fauna communities. In effect, the feedback loops between the two factors "chemical quality of organic residues" (Q) and "composition of the soil fauna community" (F) (Fig. 1) could be determined by these statistical procedures. These statistical analyses were performed with the statistical package Statistics 10 (Analytical Software, Tallahassee, FL, USA). Multivariate analysis of meso- and macrofaunal community data were performed with the PRIMER software version 6 (Primer-E Ltd., Plymouth, UK) [34]. First, a two-way crossed analysis of similarity (ANOSIM) based on Bray-Curtis similarity coefficients was applied [35]. A similarity matrix was generated for all possible pairs of sample [36,37]. The similarity matrix was then used for ANOSIM to test the hypothesis that the composition of studied faunal communities (F) was altered by chemical quality of organic residues (Q) over the course of the decomposition (T). ANOSIM is based on rank similarities between the sample matrix and produces a test statistic called '*R*' [36,37]. A 'global *R*' was first calculated in ANOSIM, which evaluated the overall effect of a factor in the data set. This step was followed by a pairwise comparison, whereby the magnitude of '*R*' indicated the degree of separation between two tested communities. An '*R*' score of 1 indicated a complete separation, while 0 indicated no separation, between groups [34,36]. Similarity percentage analysis (SIMPER) was used to identify the proportional contribution of dominant faunal groups to the community similarities among organic residue treatments and decomposition time. The differences in all statistical analyses were considered significant at $P < 0.05$.

3. Results

3.1. Dynamics of residue decomposition

The pattern of litter weight change (ash free dry weight remaining) (Fig. 2) of each contrasting quality residue was used to divide decomposition into four stages. Decomposition during the period from the initial time to the end of stage 1 during which mass sharply decreased in easily decomposable residues, RS and GN, in both coarse and fine mesh sized bags (Fig. 2a and b). However, in resistant residues, DP and TM, significant mass decrease only took place during the first week of decomposition. During stage 2 of decomposition (Fig. 2), mass remaining in coarse-mesh was distinctly lower than that in fine-mesh litterbags. The lower mass remaining in coarse mesh than fine mesh litterbags became even more distinctive during stage 3 of decomposition, in all residues except RS (Fig. 2b–d). The mass remaining became stable in stage 4 as compared to the earlier stages, particularly in the more easily decomposable residues RS and GN. However, the resistant residues, DP and TM, still showed significant mass losses during weeks 26–39 ($P < 0.05$).

Precipitous decrease of N concentration of decomposing residues during stage 1 and 2 was shown by GN ($P < 0.000$). After stage 2, all residues showed continuous gradual decrease of N to the end of stage 3 (week 26) ($P < 0.05$) (Fig. 3a). Cellulose concentrations of all residues continuously decreased to the end of stage 3 (week 26) ($P < 0.05$), at which time the decrease was more than 96% in the more easily decomposable residues, RS and GN (Fig. 3b). However, regarding the recalcitrant residues, DP only showed a sharpe decrease ($P < 0.05$) later in week 39 or 99.5% decrease, while TM showed an early sharp decrease (16% decrease) ($P < 0.05$) from week 0 to week 1 followed by a sharper decrease in week 39 ($P < 0.05$) (93% decrease relative to week 4). Lignin concentrations decreased during the first half of stage 1 of decomposition (week 0–2) of only resistant residues, DP and TM ($P < 0.05$). After week 2, lignin concentration increased to peak at week 4 in all residues except GN ($P < 0.05$). After stage 1 (week 4), lignin concentrations

dropped again to week 26 (end of stage 3) in all residues ($P < 0.05$). In stage 4, only lignin in the resistant residues continued to drop to week 39. The concentration of polyphenols of all residue types decreased sharply during the initial period of stage 1 of decomposition (week 1) ($P < 0.05$), i.e., ≥80% decrease from the initial concentrations (Fig. 3d). In stage 3 of decomposition (week 8–26), only DP displayed a decrease in polyphenol concentrations ($P < 0.05$).

3.2. Dynamics of soil meso- and macrofauna communities

Macrofauna density (F) was affected by organic residue types (Q) ($P < 0.05$) as different from mesofauna density ($P = 0.068$) over the course of the decomposition period (T) ($P < 0.01$ and $P < 0.001$, respectively). An interaction between Q and T was found for the communities of mesofauna ($P < 0.001$) and macrofauna ($P < 0.01$) (Table 1).

In addition, the "chemical quality of organic residues" (Q) factor had a strong influence on the densities of decomposer meso- and macrofauna communities (F) over time (T) ($P < 0.001$) (Table 2). For both density of mesofauna and density of macrofauna, '*R*' values calculated from factor "T" were generally higher than those calculated from factor "Q".

The density of mesofauna during stage 1 of decomposition, in the RS and GN treatments increased throughout and peaked at the end of this stage (week 4) (Fig. 4a). At week 4, GN had highest density of mesofauna followed by RS and TM, while that of DP was the lowest ($P < 0.05$). Collembolans (order Collembola) had a distinctively higher proportional contribution to the community similarity of mesofauna than Acari (order Acarina) in all residues (Table 3a, Supplementary Table 3a) and all stages of decomposition up to week 16 (Table 4a, Supplementary Table 4a). During stage 2 of decomposition (week 4–8), the density of mesofauna sharply decreased in both RS and GN. After the end of stage 2 (week 8) through to stage 4 (week 26–52), the density of mesofauna in both RS and GN remained stable at low levels. In the low quality residues, DP, and TM, the densities of mesofauna were low throughout the decomposition period (Fig. 4a).

Density of macrofauna under GN peaked with highest density among all residues at the end of stage one (week 4) (Fig. 4b). Moreover, the density of macrofauna under GN was higher than that of all other treatments in week 2 ($P < 0.05$). Coleopterans were the dominant group contributing to the community similarity at 69% in week 2 and increasing to reach the first peak at 90% in week 4 (end of stage 1 of decomposition) (Table 4b). The contributions of Coleopterans to decomposition were higher in GN (81%) and TM (71%) than RS (42%) and DP (24%) during the whole period of decomposition (Table 3b, Supplementary Table 3b). The density of macrofauna in stage 2 declined in the GN treatment to week 8, but it remained higher than in the other treatments. After week 8, density of macrofauna under all treatments remained stable at low levels until the end of the decomposition period (Fig. 4b). The contributions of Coleopterans to decomposition declined to 65% in week 8 (stage 2) and 55% in week 16 (stage 3), prior to dramatically increasing to 100% during the early part of stage 4, week 26 and 39, while in week 52 at the end of stage 4, the contribution of Coleopterans dramatically declined to 6% (Table 4b). Out of the eight families of Coleopterans found, two were detritivores, i.e., Scarabaeidae (dung beetles) in both their adult and larval stages [38] and Staphylinidae (rove beetles) in their adult stage [39] (Table 4b, Supplementary Table 4b).

Hymenopterans (Hymenoptera, Formicidae, ants) were present and had low to moderate contributions to decomposition (6–24%) during stages 1 through 3 (Table 4b). During the early part of stage 1, their contributions were low (6–14%) but they were present in more diverse species of Formicidae in week 1 than week 2 where only two species persisted, i.e. *Monomorium* sp., and *Solenopsis* sp. In stage 2 (week 8) and stage 3 (week 16), the contributions of Formicidae increased to 20% and 24%, respectively. After week 16, Formicidae made no further contribution until at the end of the final stage in week 52 where Hymenopterans became dominant contributing 94% to decomposition from a single species of *Solenopsis* (Table 4b). Hymenopterans (Hymenoptera, Formicidae, ants) were present and had low to moderate contributions to decomposition (6–24%) during stages 1 through 3 (Table 4b). During the early part of stage 1, their contributions were low (6–14%) but they were present in more diverse species of Formicidae in week 1 than week 2 where only two species persisted, i.e. *Monomorium* sp., and *Solenopsis* sp. In stage 2 (week 8) and stage 3 (week 16), the contributions of Formicidae increased to 20% and 24%, respectively. After week 16, Formicidae made no further contribution until at the end of the final stage in week 52 where Hymenopterans became dominant contributing 94% to decomposition from a single species of *Solenopsis* (Table 4b).

It is notable that in stage 3 (week 8–26), several additional groups of macrofauna had moderate contribution to decomposition including Isoptera (Termitidae, termites) (15%), Opisthopora (earthworm) (12%) and Homoptera (Aphidoidea, aphids) (10%) (Table 4b). During the initial stage (week 1), the contribution of Diptera (Cecidomyiidae, hessian flies) in their adult and larvae stages

Table 1
Repeated measurement analysis of variance (ANOVA) showing the effect of residue types, time (week) or decomposition stage, and their interaction on density of soil meso- and macrofauna.

Source of variance	*df*	Density of mesofauna		Density of macrofauna	
		F	*P*	*F*	*P*
Block	2				
Residues (Q)[a]	3	3.53	0.0682	6.16	0.0178
Time (T)[b]	7	9.60	0.0000	3.03	0.0090
Q × T	21	3.67	0.0001	2.64	0.0020

[a] Residues refer to the 4 treatments (rice straw (RS), groundnut stover (GN), dipterocarp leaf litter (DP), tamarind leaf and petiole litter (TM)).
[b] Time refers to decomposition time at 1, 2, 4, 8, 16, 26, 39, and 52 weeks after residue incorporation.

Table 2
Two-way crossed analysis of similarity (ANOSIM) showing the effect of factors on the soil meso- and macrofauna community as accessed by their densities.

Factors	Mesofauna community (F)		Macrofauna community (F)	
	Global *R*	*P*	Global *R*	*P*
Residues (Q)[a]	0.518	0.001	0.864	0.001
Time (T)[b]	0.728	0.001	0.985	0.001

[a] Residues refer to the 4 treatments (rice straw (RS), groundnut stover (GN), dipterocarp leaf litter (DP), tamarind leaf and petiole litter (TM).
[b] Time refers to the decomposition time at 1, 2, 4, 8, 16, 26, 39, and 52 weeks after residue incorporation.

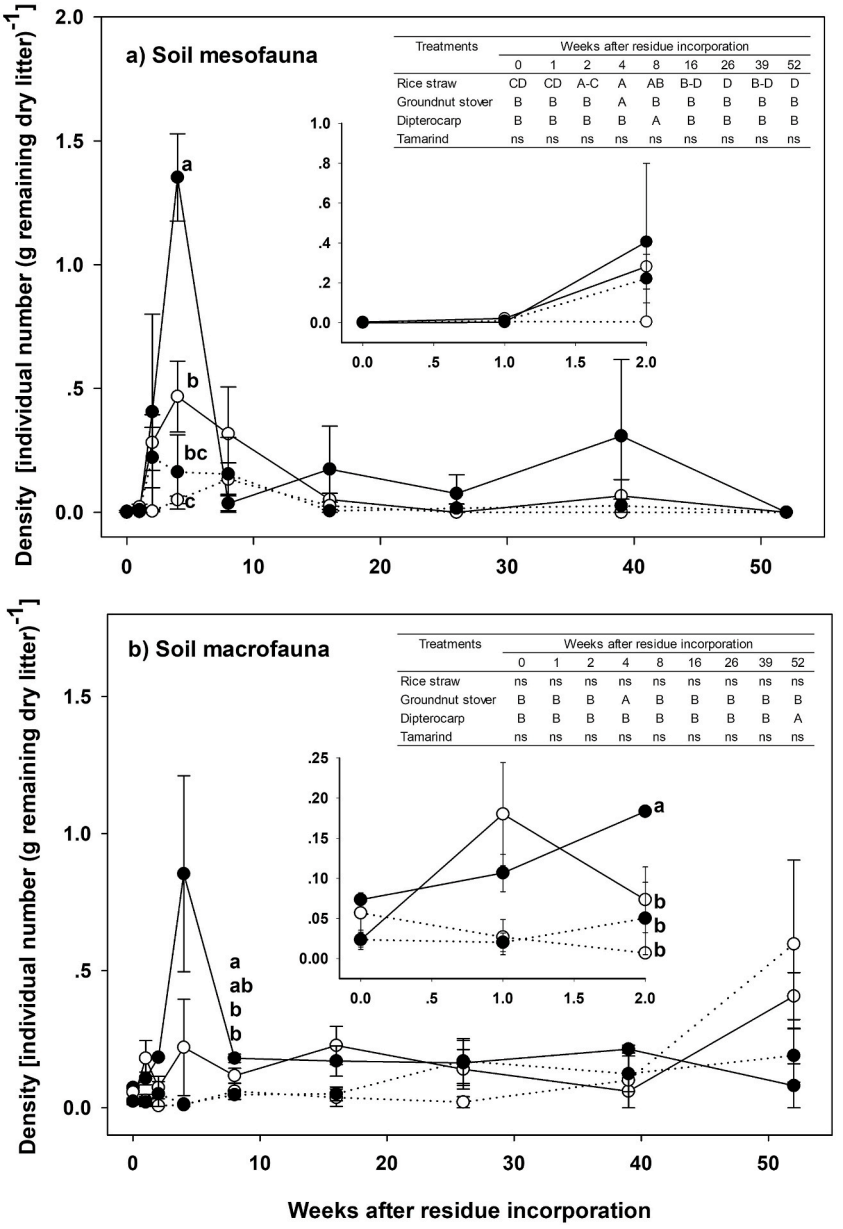


Fig. 4. Temporal pattern of density [individual number (g remaining dry litter) $^{-1}$] of (a) soil mesofauna and b) soil macrofauna. At each sampling date, means accompanied by different letters are significantly different at $P < 0.05$ (LSD). The inset table accompanying each figure shows comparisons of sampling times within each residue treatment. Different letters in the same row show significantly different at $p < 0.05$ (LSD). Data of fauna were transformed by log (x+1) before density calculations. Vertical bars represent standard error of the mean (SEM).

Table 3
Two-way similarity percentage analysis (SIMPER) to explain the effect of organic residue types on dominant groups of a) mesofauna and b) macrofauna to support the community differences as calculated by analysis of similarlity.

a) Mesofauna

Treatments	Contribution of mesofauna	Dominant groups of mesofauna	
	(%)	Order	Common name
Rice straw	73.0	Collembola	Springtails
	27.1	Acari	Mites
Groundnut stover	62.3	Collembola	Springtails
	37.7	Acari	Mites
Dipterocarp	100.0	Collembola	Springtails
Tamarind	53.6	Collembola	Springtails
	46.4	Acari	Mites

b) Macrofauna

Treatments	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
Rice straw	42.2	Coleoptera	Scydmaenidae		Ant-like stone beetles	Adult
			Carabidae		Ground beetles	Adult
			Staphylinidae		Rove beetles	Adult
			Staphylinidae		Rove beetles	Larvae
			Scolytidae		Bark/Ambrosia beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Adult
			Elateridae		Click beetles	Adult
			Unidentifiable		Beetles	Adult
			Unidentifiable		Beetles	Larvae
	41.5	Hymenoptera	Formicidae	*Monomorium* sp.	Black ants	Adult
				Solenopsis sp.	Fire ants	Adult
			Formicidae	Unidentifiable	Ants	Adult

b) Macrofauna

Treatments	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
Rice straw (con'd)	12.5	Diptera	Cecidomyiidae		Hessian fly	Adult
			Unidentifiable		Flies	Adult
			Unidentifiable		Flies	Larvae
			Unidentifiable		Flies	Pupa
	3.8	Opisthopora	Unidentifiable		Earthworms	Adult
Groundnut stover	81.3	Coleoptera	Scydmaenidae		Ant-like stone beetles	Adult
			Carabidae		Ground beetles	Adult
			Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Adult
			Staphylinidae		Rove beetles	Larvae
			Scolytidae		Bark/Ambrosia beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Larvae
			Coccinellidae		Lady beetles	Larvae
			Curculionidae		Bark beetles	Adult
			Unidentifiable		Beetles	Adult
			Unidentifiable		Beetles	Larvae
	15.0	Diptera	Cecidomyiidae		Hessian fly	Adult
			Unidentifiable		Flies	Adult
			Unidentifiable		Flies	Larvae
			Unidentifiable		Flies	Pupa
	3.7	Hymenoptera	Formicidae	*Monomorium* sp.	Black ants	Adult
				Pristomyrmex sp.		Adult
				Solenopsis sp.	Fire ants	Adult
				Crematogaster sp.	Arboreal ants	Adult
				Unidentifiable	Ants	Adult
Dipterocarp	54.6	Hymenoptera	Formicidae	*Pristomyrmex* sp.		Adult
				Solenopsis sp.	Fire ants	Adult
				Unidentifiable	Ants	Adult

b) Macrofauna

Treatments	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
Dipterocarp (Cont.)	24.2	Coleoptera	Carabidae		Ground beetles	Adult

(*continued on next page*)

Table 3 (*continued*)

b) Macrofauna						
Treatments	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
			Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Larvae
			Unidentifiable		Beetles	Larvae
	21.2	Isoptera	Termitidae	*Odontotermes* sp.		Adult
				Unidentifiable	Termites	Adult
Tamarind	70.6	Coleoptera	Scydmaenidae		Ant-like stone beetles	Adult
			Carabidae		Ground beetles	Adult
			Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Adult
			Staphylinidae		Rove beetles	Larvae
			Scarabaeidae		Scarab/Dung beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Larvae
			Unidentifiable		Beetles	Adult
			Unidentifiable		Beetles	Larvae
	24.6	Hymenoptera	Formicidae	*Pristomyrmex* sp.		Adult
				Solenopsis sp.	Fire ants	Adult
				Crematogaster sp.	Arboreal ants	Adult
				Unidentifiable	Ants	Adult
	4.8	Homoptera	Aphidoidea		Aphids	Adult

was predominant (66%) to the community similarity (Table 4b) after which their contribution gradually decreased. In week 2, flies (adult, pupa, and larvae) constituted a moderate share of 14%. In week 4, the contribution of Diptera, at the larvae stage, decreased further to 10%.

3.3. Feedback loops in the decomposition cascade

At the onset of the first feedback loop (week 1), only the density of macrofauna was strongly influenced by residue quality (Fig. 5a and b), which was lignin (94% of R^2) (Fig. 5b). As decomposition continued into week 2, the density of mesofauna was strongly influenced by cellulose (81%) and N (19%) concentrations of decomposing residues ($P < 0.05$) (Fig. 5a). Nevertheless, no feedback reaction of mesofauna was found on cellulose and N concentrations resulting in none of its influence on mass loss ($P > 0.05$) (Fig. 6a). The density of macrofauna in week 1, unlike that of mesofauna, was highly influenced by lignin concentration. However, the influence of lignin decreased sharply from week 1 (94%) to week 2 (38%) (Fig. 5b). At the same time, the influence of cellulose concentration in decomposing residues as a determinant of density of macrofauna dramatically increased from week 1 (4%) to week 2 (62%) (Fig. 5b). These results point to a close interaction between lignin and cellulose in determining the density of macrofauna. A feedback reaction was noted for density of macrofauna during loop #1 (week 2), which had an effect on mass loss ($R^2 = 0.67$; $P < 0.01$) (Fig. 6a) and showed a tendency to alter the concentrations of lignin ($R^2 = 0.40$; $P \leq 0.1$) and polyphenols ($R^2 = 0.30$; $P \leq 0.1$) of decomposing residues (Fig. 6a).

In the next stage (loop #2) during weeks 4 to 8, which constitute the early decomposition stage of the decomposition cascade, starting from week 4, lignin replaced cellulose as the predominant carbonaceous quality parameter influencing density of mesofauna (43%) (Fig. 5a). Moreover, N became more influential (57%) than it had been in the preceding initial period (week 1). In the transition into loop #2 of decomposition (week 4), density of mesofauna replaced that of macrofauna in having dominant feedback reactions (Fig. 6b). The feedback reaction of mesofauna was shown by strong effects on remaining mass ($R^2 = 0.69$; $P < 0.001$), cellulose ($R^2 = 0.63$; $P < 0.05$), and lignin ($R^2 = 0.35$; $P < 0.05$) (Fig. 6b). Nitrogen replaced cellulose to become a major determinant of density of macrofauna (60%) (Fig. 5b). In addition, there were negative relationships between the lignin-to-N ratio of decomposing residues and the densities of both mesofauna ($R^2 = 0.56$; $P < 0.05$) and macrofauna ($R^2 = 0.52$; $P < 0.05$) (Fig. 7). Similar to mesofauna, macrofauna density had a strong influence ($R^2 = 0.35$; $P < 0.05$) on mass loss of decomposing residues in week 4 (Fig. 6b).

In the intermediate decomposition stage (weeks 8 to 26, stage 3 or loop #3), however, no influence of any chemical constituent on density of mesofauna was observed ($P > 0.05$) (Fig. 5a). For density of macrofauna, the influence of lignin disappeared, while polyphenols became influential (24%) in week 8 (Fig. 5b), while the influence of N became less prominent (56%) than it was in stage 1 (week 4). However, in the middle part of this stage (week 16), residue N contents became the totally dominant quality parameter influencing density of macrofauna ($P < 0.05$). During this stage, the feedback reaction of decomposer fauna switched again from mesofauna to solely macrofauna (Fig. 6c and d) as follows: In week 8, there were decreasing concentrations of N ($R^2 = 0.52$; $P < 0.01$), cellulose ($R^2 = 0.36$; $P < 0.05$), lignin ($R^2 = 0.56$; $P < 0.01$) and the consequent mass loss ($R^2 = 0.52$; $P < 0.01$) (Fig. 6c), while in week 16, there were decreasing concentrations of N ($R^2 = 0.34$; $P < 0.05$) (Fig. 6d).

During the final stage of decomposition (stage 4 or loop #4), which is weeks 26 to 52, lignin (59%) and N (35%) became the most prominent parameters influencing density of macrofauna, while polyphenols decreased to 7% below week 8 (Fig. 5b). Finally, at the end of loop #4 (week 52), cellulose became the only parameter having a total influence on density of macrofauna. Correspondingly, the feedback reaction during loop #4, particularly week 52, revealed a strong influence of density of macrofauna on remaining mass

Table 4
Two-way similarity percentage analysis (SIMPER) to reveal the most dominant groups of soil mesofauna (a) and macrofauna (b) communities that contributed prominently to the decomposition at different stages as calculated by analysis of similarlity.

a) Mesofauna

Week	Contribution of mesofauna	Dominant groups of mesofauna	
	(%)	Order	Common name
1	100	Collembola	springtails
	69.15	Collembola	Springtails
	30.85	Acari	Mites
4	67.25	Collembola	Springtails
	32.75	Acari	Mites
8	100	Collembola	Springtails
16	100	Collembola	Springtails
26 All similarities are zero			
39 All similarities are zero			
52 All similarities are zero			

b) Macrofauna

Week	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
1	65.8	Diptera	Cecidomyiidae		Hessian fly	Adult
			Cecidomyiidae		Hessian fly	Larvae
	20.1	Coleoptera	Scydmaenidae		Ant-like stone beetles	Adult
			Carabidae		Ground beetles	Adult
			Staphylinidae		Rove beetles	Adult
			Staphylinidae		Rove beetles	Larvae
			Scolytidae		Bark/Ambrosia beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Adult
	14.14	Hymenoptera	Formicidae	*Monomorium* sp.	Black ants	Adult
				Pristomyrmex sp.		Adult
				Solenopsis sp.	Fire ants	Adult
				Crematogaster sp.	Arboreal ants	Adult

b) Macrofauna

Week	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
2	69.03	Coleoptera	Scydmaenidae		Ant-like stone beetles	Adult
			Carabidae		Ground beetles	Adult
			Staphylinidae		Rove beetles	Adult
			Scolytidae		Bark/Ambrosia beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Adult
			Scarabaeidae		Dung beetles	Larvae
	14.14	Diptera	Cecidomyiidae		Hessian fly	Adult
			Unidentifiable		flies	Pupa
			Unidentifiable		flies	Larvae
	5.71	Hymenoptera	Formicidae	*Monomorium* sp.	Black ants	Adult
				Solenopsis sp.	Fire ants	Adult
4	90.06	Coleoptera	Carabidae		Ground beetles	Adult
			Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Larvae
			Elateridae		Click beetles	Adult
			Curculionidae		Bark beetles	Adult
	9.94	Diptera	Unidentifiable		flies	Larvae

b) Macrofauna

Week	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
8	65.35	Coleoptera	Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Adult
			Staphylinidae		Rove beetles	Larvae
			Scarabaeidae		Scarab/Dung beetles	Larvae
	19.69	Hymenoptera	Formicidae		Ants	Adult
	14.96	Isoptera	Termitidae	*Odontotermes* sp.	Termites	Adult
16	54.98	Coleoptera	Carabidae		Ground beetles	Adult
			Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Larvae

(*continued on next page*)

Table 4 (*continued*)

b) Macrofauna						
Week	Contribution of macrofauna	Dominant groups of macrofauna				Growth stages
	(%)	Order	Families	Genus	Common name	
			Scarabaeidae		Scarab/Dung beetles	Adult
	23.74	Hymenoptera	Formicidae	Unidentifiable	Ants	Adult
	11.68	Opisthopora	Unidentifiable		Earthworms	Adult
	9.60	Homoptera	Aphidoidea		Aphids	Adult
26	100	Coleoptera	Carabidae		Ground beetles	Adult
			Carabidae		Ground beetles	Larvae
			Staphylinidae		Rove beetles	Adult
			Scarabaeidae		Scarab/Dung beetles	Adult
39	100	Coleoptera	Carabidae		Ground beetles	Adult
			Carabidae		Ground beetles	Larvae
			Scarabaeidae		Scarab/Dung beetles	Larvae
			Coccinellidae		Lady beetles	Larvae
52	93.90	Hymenoptera	Formicidae	*Solenopsis* sp.	Fire ants	Adult
	6.10	Coleoptera	Carabidae		Ground beetles	Larvae
			Unidentifiable		Beetles	Adult

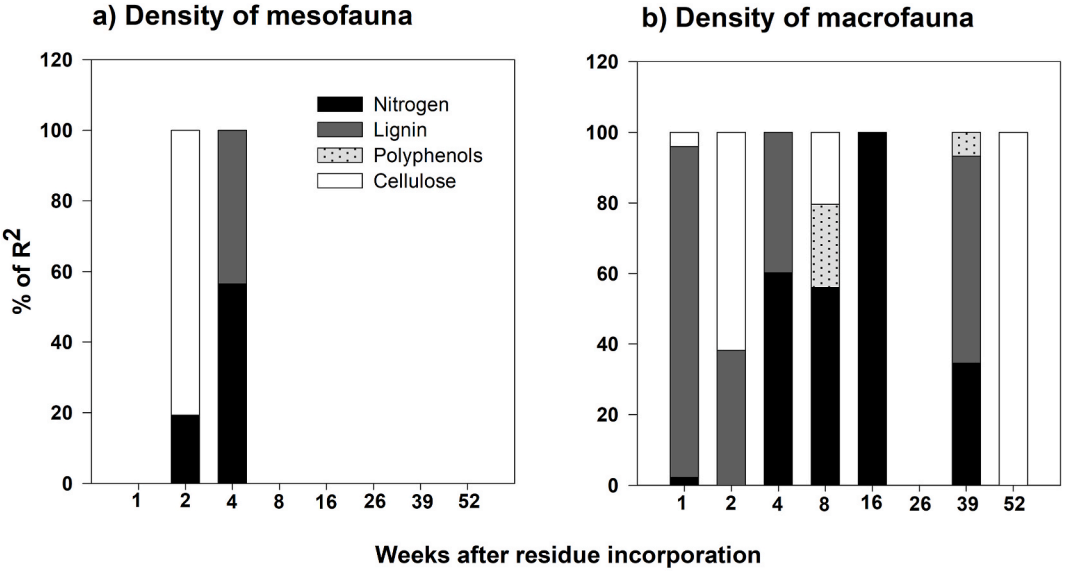


Fig. 5. Relative contribution of single chemical parameters to density [individual number g remaining dry litter) $^{-1}$] of: a) mesofauna and b) macrofauna at various weeks after residue incorporation.

($R^2 = 0.36$; $P < 0.05$) and N concentration ($R^2 = 0.78$; $P < 0.001$) of decomposing residues (Fig. 6e).

4. Discussion

In this paper, we have introduced the ecological concept of feedback loops representing individual ecological successional stages along a decomposition cascade. This is a novel approach of revealing the extent to which interacting effects or feedback reactions of decomposing residues of contrasting chemical quality and community shifts of fauna decomposers, influence decomposition dynamics in soils. Accordingly, we will examine the feedback reactions that occur in each successional stage in turn:

Loop # 1: Feedback reactions between soil fauna communities and chemical quality of residues during the early stage of decomposition.

In the initial phase (week 1) of the early stage of decomposition (i.e., loop #1), only density of macrofauna was strongly affected by lignin (Fig. 5b). At this stage the lignin concentrations under recalcitrant residues, DP and TM, decreased (Fig. 3c). The lignin constituent of these residues may have attracted macrofauna with their ability to degrade lignin including cecidomyiids (Cecidomyiidae, Diptera, hessian flies) [40–43] and diverse families of Coleopterans (beetles) [44] and formicidans (Formicidae, Hymenoptera, ants) (Table 4b). This finding suggests the need to modify the first part of our hypothesis to consider that during the early stage of decomposition not only labile but also recalcitrant constituents of organic residues brought about the feedback response from the

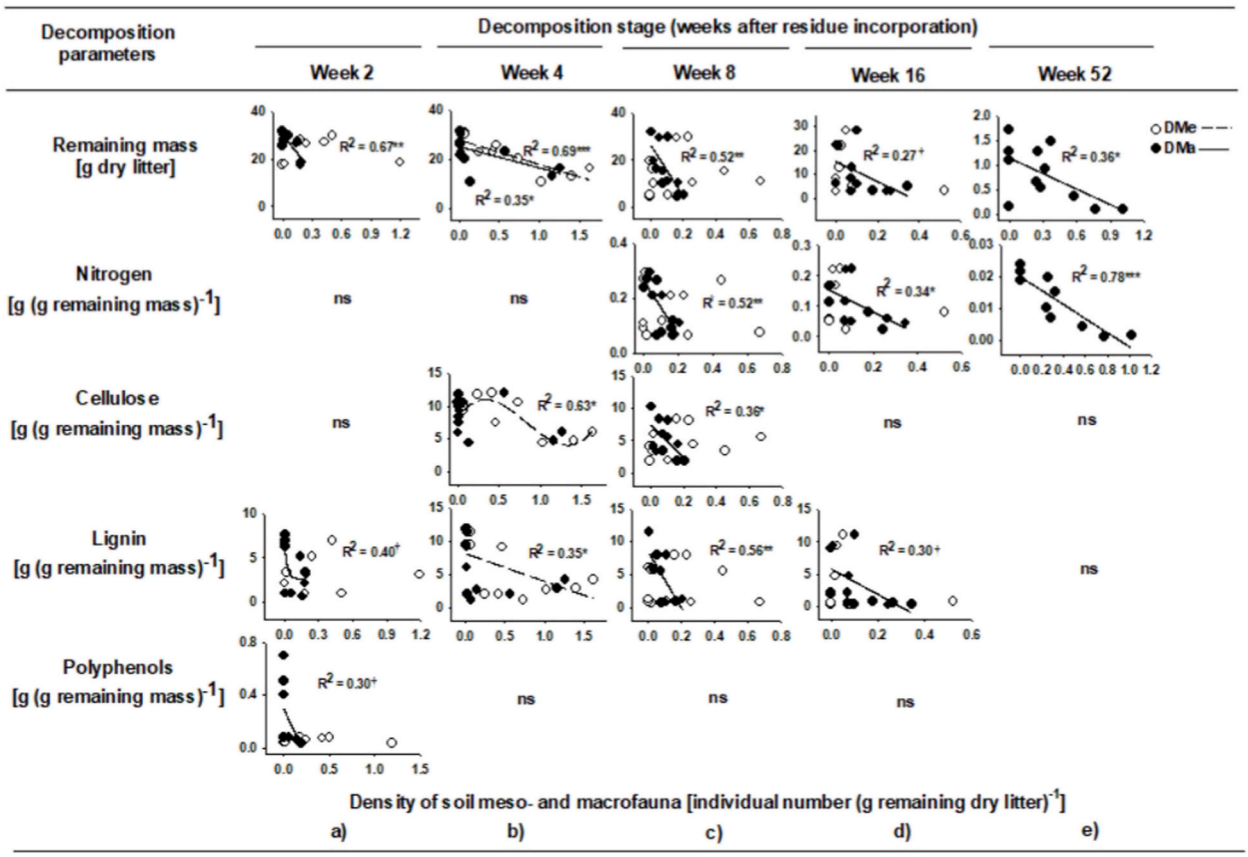


Fig. 6. Relationship between density of soil meso- and macrofauna [individual number (g remaining dry litter) $^{-1}$], and mass remaining (g dry litter) and litter concentrations of chemical parameters [g (g remaining mass) $^{-1}$] in the coarse mesh litterbags during a) week 2, b) week 4, c) week 8, d) week 16, and e) week 52 of decomposition period.
$^{\dagger}P < 0.1$: $^{*}P < 0.05$: $^{**}P < 0.01$; $^{***}P < 0.001$; ns (non-significant: $P > 0.05$).

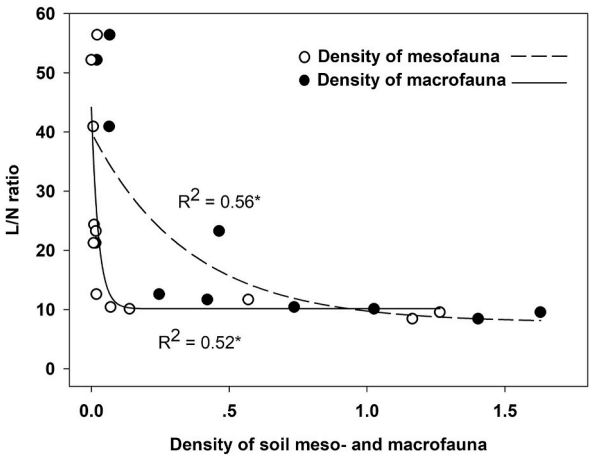


Fig. 7. Relationship between density of soil meso- and macrofauna [individual number (g remaining dry litter) $^{-1}$] and the ratios between lignin/N of the remaining residues at week 4 after residue incorporation. $^{*}P \leq 0.05$.

meso- and in particular macrofauna.

During the entire first stage (weeks 1–4), there were contrasting trends of chemical quality changes between easily decomposable (i.e., RS and GN) and more recalcitrant (i.e., TM and DP) residues (Fig. 3). The decreases in cellulose concentrations in all residues

indicating its bioavailability prompted increasing densities of both soil mesofauna (e.g., Collembolans) and macrofauna dominated by Dipterans (Cecidomyiidae) followed by diverse families of Coleopterans and to a smaller extent several genus of Formicidans (Hymenoptera) (Table 3a, b) with known ability to degrade cellulose [45–47]. Cedidomyiid larvae were able to hydrolyze cellulose through enzyme secretion as demonstrated in a study on colonization of cecidomyiids on beech leaf litter in a beech forest [42]. Cecidomyiids play an important role in decomposition of leaf litter in both temperate [41,42] and tropical ecosystems [43]. Not only the larvae but also Cecidomyiid adults feed on litter as its colonization was found in leaf litter in the tropical rain forest of Mt. Makiling in the Philippines during the first 10 weeks of decomposition [43].

Diverse Coleopterans belonging to as many as seven families were found during the stage 1 (weeks 1–4) (Table 4b). Out of these families, two were dominant, i.e., scarabaeids (Scarabaeidae, dung beetles) and staphylinids (Staphylinidae, rove beetles). Coleopterans have been found to degrade lignocellulose constituent of the cell wall of plant litter [44]), and those in animal dung (86% cellulose in ruminant) [48]. A dominant cellulose degrading mechanism operating in different families of Coleopterans is the association of Coleopterans, both adults and larvae, with intestinal microorganisms, fungi, actinomycetes, and bacteria. These gut microorganisms provide lignin and cellulose digesting enzymes as demonstrated in the family Passalidae colonizing logs in subtropical forests of Costa Rica [44]. In addition to the Passalids, the families Scarabaeidae, and Staphylinidae found in this current study were also revealed in the referenced study [44] which implied that these Coleopterans may have symbiotic relations with their gut microorganisms, which enable them to digest complex molecules like lignocellulose. Regarding scarabaeids (dung beetles), some species have been found to play indirect roles in microbial litter decomposition. These indirect roles involve changes in soil physical conditions (aeration and water holding capacity) resulting from the beetles' activities, such as burrowing tunnels in the soil beneath the dung piles through which they transport the manure underground [38]. These altered soil conditions are more favorable to microbial activities in litter decomposition. In a study in the French Mediterranean region, scarabaeids were found to contribute to microbial litter decomposition through the indirect mechanisms involving burrowing tunnels in the soil beneath the dung piles to transport the manure underground and had limited direct contribution on litter decomposition [49]. Another lignocellulose degradation mechanism found in some families of Coleopterans (beetles) involve their symbiotic relationships with lignin degrading Basidiomycota. The beetles carry the spores of these fungi in their specialized organ, mycangia, to be deposited on their targeted substrates, e.g., wood. Scolytids or bark/ambrosia beetles (Coleoptera, Scolytidae), which were identified in this study (Table 4b), have been shown to employ such a mechanism [50]. Kamolmanit et al. (2013) [51] identified cellulolytic Basidiomycota (e.g., *Cryptococcus podzolicus*) as a dominant fungal taxon in the TM treatment plots of the long-term experiment where the current study was conducted.

During the first part of this early stage (weeks 1 and 2) the genus *Solenopsis* (Formicidae, ants) appeared to be dominant contributor to decomposition (Table 4b). The larvae of a species of *Solenopsis*, i.e., *S. invicta* Buren (Hymenoptera, red imported fire ants – RIFA) in its fourth-instar stage, have been shown to possess symbiotic bacteria in their guts which are used to perform their special role in the ant colony in digesting solid foods [52]. In addition to gut microbial communities, Formicidans have symbiotic relationship with fungi they cultivated in their nests or ant hills. Some of these fungi are identified as cellulolytic active, e.g., *Trichoderma* spp., and *Penicillium* spp. found in India [53] and Eastern Spain [54]. The altered conditions of ant nests, including high content of organic matter and plant nutrients (N, P, K, Ca, and Mg), have been found to stimulate decomposition activities of mesofauna, e.g., mites, and collembolans, as well as microfauna, i.e., nematodes, and microorganisms within the nests [55].

The decreased lignin concentrations under DP and TM treatments prior to week 2 (Fig. 3c) was reflected in the composition of the macrofauna, where Coleopterans (beetles) increased until week 4 (Table 4b). Coleopterans possess several mechanisms aiding in degrading lignocellulose as described earlier. Recalcitrant substances [5,12] particularly lignin [56] constituents of plant residues have been found to be highly influential on the abundance of macrofauna, such as woodlice, earthworms and millipedes [56].

Loop #2: Prominent feedback reactions of mesofauna in response to interaction between lignin and nitrogen of the residues.

During the next decomposition stage from week 4 to 8 (loop #2), N exerted a greater influence on the densities of both mesofauna and macrofauna than in the initial stage (Fig. 5). During week 4, GN and TM with their high initial N concentrations fueled the decomposition of carbonaceous constituents (e.g., lignin) as found by Kunlanit et al. (2014) [22] working on the same soils originated from year 13 of the LTE as this study. These workers determined molecular structure (functional groups) of bulk soils SOC treated with contrasting quality residues. They found that GN and TM containing higher N and lignin than RS produced a higher quantity of labile (carbohydrates) and aromatic SOC components of bulk soils [22]. Our results showed that mesofauna were largely responsible for the mass loss (Fig. 6b) resulting from the decomposition of lignin and cellulose. This was also related to the changes in the lignin/N ratio (Fig. 7). Likewise, mesofauna, predominantly springtails with their affinity to litter-derived N [18], replaced macrofaunal beetles as the dominant decomposer group.

Loop #3: Feedback reactions of macrofauna in response to changes in N, cellulose and polyphenols constituents of decomposing residues.

In loop #3 (week 8–26), macrofauna again replaced mesofauna as the dominant decomposers. Their contribution to the observed mass loss and the accompanying decrease in N (Fig. 6c) reflected the increasing influence of residue derived polyphenols (Fig. 5b). A close interaction between N as a stimulant and polyphenols as a deterrent in controlling the decomposition habits of a macrofauna group (notably Coleopterans) has been reported by Ikonen et al. (2002) [57]. At this stage, the resistant residues DP and TM showed an increased decomposition of lignin and cellulose and loss of N (Fig. 3a–c), which was attributed to increased activities of macrofauna (i.e., Coleopterans [beetles], Formicids [ants] and to a lesser extent Isopterans [termites], and Opisthoporans [earthworms]) (Table 4b). The increased macrofaunal activities were prompted by the availability of cellulose exposed after degradation of lignin originated from the resistant residues themselves [1]. Lignin degradation capacities of these above macrofauna have been well demonstrated to be due to their symbiotic relationships with their gut microbes dominantly fungi (white rot and brown rot fungi) as found in the wood-feeding insects, e.g., cerambycid beetles (*Anoplophora glabripennis* or Asian long-horn beetles) [58,59] and termites (*Zootermopsis augustifolis*), a

lower termite species [58]. Formicidans also have high capacities to degrade cellulose through their symbiotic relationships with microbes both in their nest and inside their guts as discussed in loop #1 above. The presence of homopterans (aphids) may have been connected to the presence of the Formicidans (ants) as the aphids provide the ants with nutritive honey dew, and in return they are protected and transported by the ants [60]. However, the aphids were unlikely to have contributed to residue decomposition as they feed entirely on phloem sap of living plants [61]. Similar to ants (Hymenoptera), fungus-growing termites rely on both an external symbiotic relationship with fungi cultivated in the mound and a consortium of gut fungi and bacteria to degrade lignin and gain access to cellulose [62,63]. The degradation of lignin by macrofauna was accompanied by significant N losses during the early part of this stage (weeks 8 and 16) (Fig. 6c and d). These results corroborated those of Yang et al. (2012) [18], which showed that mechanical fragmentation of residues by macrofauna brought about N loss.

Loop #4: Feedback reactions solely from macrofauna continued in response to changes in N, lignin and polyphenol constituents of decomposing residues.

In the early part of the final decomposition stage (week 26 to 39), macrofauna (i.e., Coleopterans, beetles) continued as the dominant decomposer group (100%) (Table 4b) driven by lignin, N, and to a considerably lesser extent, polyphenols (Fig. 5b), in resistant residues, especially TM (Fig. 3a, c, d). Decomposition by Coleopterans (*Agelastica alni*, leaf beetles) is reportedly controlled by a close interaction between N and polyphenols [57]. The multiple mechanisms that Coleopterans, notably the Scarabaeidae and Staphylinidae, employed to degrade lignocellulose have been discussed in the section on loop #1 above.

In the final stage (week 52) of loop #4, Formicidans (*Solenopsis* sp., fire ants), a predator (Supplementary Table 4b), replaced the Coleopterans, as the dominant contributor to decomposition (94%) (Table 4b). That the *Solenopsis* sp. may have preyed on the Coleopterans is suggested by Kaplan and Eubanks (2002) [64], who found that a *Solenopsis* sp., notably *S. invicta* (RIFA), was a major predator of the larvae of lady beetles (Coleoptera: Coccinellidae) in cotton fields in the southern United States. During the final stage (week 52), the cellulose constituent of decomposing residues had total influence (100%) on the density of macrofauna (Fig. 5b) dominated by Formicidans (*Solenopsis* sp.) (Table 4b). As was discussed earlier in regard to loop #1 and loop #3, Formicidans have high capacities to degrade cellulose. It is likely that they were attracted by remaining cellulose which was more strongly protected by lignin than those available during the earlier stages of decomposition [65]. The feedback reaction to the availability of cellulose during the final stage (week 52) was seen in the high density of Formicidans which decreased the mass and N of decomposing residues (Fig. 6e). Ants, including the *Solenopsis* sp. identified in this study, have been found to accelerate litter decomposition in a tropical rain forest in Costa Rica [66]. The ants acted as a top predator in a trophic cascade by preying on mesoarthropods, e.g., Collembolans and Acari, which grazed on microbial decomposers. The resulting reduction in grazing pressure on microbial decomposers led to increased litter decomposition. In addition, the results of residue N loss (Fig. 6e) were corroborated by ants (*Formica polyctena*) mediated decomposition of Norway spruce litter [67].

5. Conclusions

The concept of feedback loops was employed in this study to reveal the simultaneous effects of the two regulating factors, i.e., the chemical quality of organic residues (Q) and the composition of the soil fauna community (F) on each other during the decomposition process. We view the chronosequence of feedback loops as a series of ecological successional stages in the decomposition cascade. The mechanisms underlying the observed decomposition phenomena during the successional stages were explained by various ecological principles, including, but not limited to, symbiosis between faunal and microbial communities, and trophic functions and interactions. It was concluded that the concept of feedback loops provides a more comprehensive, "two-sided", view into decomposition, which is an improvement over earlier "one-sided" investigations of soil fauna-mediated decomposition. By employing residues of differing chemical quality in this study, we have also unravelled the ways in which various quality parameters selectively channel faunal successions during decomposition in soil treated with different residues. Our findings provide support for the concept of using mixed residues of different chemical quality to enhance diverse communities of decomposer organisms, both fauna and microorganisms, to interact on the basis of their trophic functions to restore and improve soil fertility.

Author contribution statement

Ratikorn Sanghaw, PhD: Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Patma Vityakon, PhD: Conceived and designed the experiments; Performed the experiments; Analyzed and interpreted the data; Contributed reagents, materials, analysis tools or data; Wrote the paper.

Frank Rasche, Ph.D.: Analyzed and interpreted the data; Wrote the paper.

Data availability statement

Data will be made available on request.

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Declaration of interest's statement

The authors declare no competing interests.

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Appendix A. Supplementary data

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