

RECOVERY OF LITTER AND SOIL INVERTEBRATE COMMUNITIES FOLLOWING SWIDDEN CULTIVATION IN SARAWAK, MALAYSIA

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ABSTRACT. — Invertebrates in litter and soil play key roles in nutrient cycling and decomposition processes, yet factors affecting their recovery after disturbance remain poorly understood. We compared communities of invertebrates and microhabitat environments in litter and soil among young fallow, old fallow, and primary forest in Sarawak, Malaysia. In this region, fallows, which are secondary forests regenerated after the traditional agricultural practice of swidden cultivation, are a major component of the landscape. Although whole invertebrate communities of both litter and soil in primary forest exhibited relatively distinct taxonomic group composition, the number of taxonomic groups, total number of individuals, and diversity indices did not significantly differ among forest types. Among microhabitat environments, the number of tree species and basal area were the most frequently identified factors affecting the community structures of litter and soil invertebrates. These results suggest that although whole invertebrate communities in litter and soil recovered relatively quickly after swidden cultivation, the alternation of forest structure in fallows may affect taxonomic group composition through changes in diet abundance. Tree species richness and basal area may serve as useful indicators for field verification of the recovery rate of invertebrate taxonomic composition in litter and soil. For termites, only the community structure of soil termites differed significantly among forest types, indicating that soil-feeding termites appear to be more sensitive to disturbances than other types of termites such as wood feeders. Separate comparative studies of litter and soil are needed to reveal the vertical recovery response of invertebrates to disturbance.

KEY WORDS. — biodiversity, conservation, fallow, Lambir, soil macrofauna, soil invertebrates, termite

INTRODUCTION

In large areas of Southeast Asia, tropical rain forests have been replaced with fallows (Schmidt-Vogt et al., 2009), which are secondary forests regenerated after the traditional agricultural practice of swidden cultivation. In this region, many studies of the effects of swidden cultivation on biodiversity have been conducted for various aboveground organisms including invertebrates, vertebrates, and plants (e.g., Nakagawa et al., 2006; Marsden & Symes, 2008; Matsumoto et al., 2009; Sovu et al., 2009). Soil invertebrates play a key role in nutrient cycling, decomposition processes, and modification of the

physical properties of soil (Lavelle et al., 1997, 2006; Yang & Chen, 2009). Agricultural land uses have been reported to exert strong effects on the abundance, biomass, diversity, and community composition of soil invertebrates in Amazonia and African tropical regions (Barros et al., 2002; Sileshi & Mafongoya, 2006; Ackerman et al., 2009; Pauli et al., 2011). However, little is known about the effect of swidden cultivation on the soil invertebrate community in Southeast Asia, despite of information on changes in soil characteristics after swidden cultivation (Hattori et al., 2005; Brearley, 2011). Moreover, recent studies have suggested a potential role of tropical secondary forests in biodiversity preservation

(Barlow et al., 2007; Chazdon et al., 2009; Padoch & Pinedo-Vasquez, 2010; Ziegler et al., 2011; Laurance et al., 2012). Understanding the recovery potential of the community structure of soil invertebrates after swidden cultivation is essential to the restoration and conservation of Southeast Asian tropical rain forests.

In swidden cultivation, farmers abandon the land after a period of crop cultivation and shift to new land, and fallows of different duration since abandonment are distributed throughout the landscape. Forest structure and tree species composition vary along these successional stages of fallows (Fukushima et al., 2008; Ding et al., 2012), likely leading to changes in microhabitat environments such as light conditions, amount of litter and roots, and quality of litter and soil (Lawrence & Foster, 2002; Brearley, 2011). Various biotic and abiotic factors can influence the community structure of soil invertebrates (Negrete-Yankelevich et al., 2008; Ayuke et al., 2011). Identifying the principal factors affecting the recovery of the community structure of soil invertebrates can enhance our insight into the proper management of fallows to improve soil properties.

Here, we studied the effects of swidden cultivation on overall soil invertebrate community structure in Sarawak, Malaysia. Our objectives were to compare and analyse changes in diversity, abundance, and composition of taxonomic and functional groups among young and old fallows and primary forest. Because recent studies have reported that the taxonomic composition of invertebrates differs between litter and soil layers (Doblas-Miranda et al., 2009; Pauli et al., 2011), and because the recovery rate of litter and soil invertebrates may differ after swidden cultivation, litter and soil invertebrates were analysed separately. Among litter and soil invertebrates, termites, which are often dominant invertebrates in tropical soils (Jones & Eggleton, 2000; Tsukamoto & Sabang, 2005), decompose substantial amounts of organic matter at all stages of decomposition from leaf litter to soil humus (Breznek & Brune, 1994; Bignell & Eggleton, 2000). Thus, these comparisons and analyses were also conducted at the species level for termites. We further examined which microhabitat environmental variables were the main factors determining the community structure of whole invertebrates and termites in litter and soil.

MATERIAL AND METHODS

Study site. — The study site was located in and around Lambir Hills National Park (LHNP, 4°08'–12°N, 114°00'–07'E, 20–140 m a.s.l.) in Sarawak, Malaysia. The average annual rainfall and mean air temperature at LHNP during 2000–2009 were 2600 mm and 25.8°C, respectively (Kume et al., 2011). The region experiences irregular and short-term droughts, but no seasonally regular dry season occurs (Kume et al., 2011). The forest in LHNP (about 7000 ha) is covered mainly by primary forest dominated by dipterocarp species. The local Iban people around LHNP have performed traditional swidden cultivation to produce rice and vegetables for the past 100 years (Ichikawa, 2003).

In Oct. 2008, 15 plots of 10 × 100 m were established in three forest types along a gradient of vegetative succession following swidden cultivation: five plots each of young fallow, old fallow, and primary forest (controls with no anthropogenic disturbance). Young and old fallows were secondary forests growing on swidden areas abandoned for 5–10 years and for more than 20 years, respectively. Two and three primary forest plots were located in the Canopy Biology Plot and the Crane Plot, respectively (Nakagawa et al., 2000, 2012). In each plot, all trees ≥10 cm in diameter at breast height (DBH; 1.3 m above the ground) were numbered, identified to species (or morphospecies) based on vegetative samples, and measured DBH to the nearest millimeter using a steel tape.

Litter and soil invertebrates sampling. — In Oct. and Nov. 2008, we sampled litter and topsoil invertebrates. In each plot, two 90-m transects were established about 5 m apart, and 10 points were distributed at regular 10-m intervals along each transect (i.e., 20 points per plot, 300 points in total). At each point, a surface soil block (25 × 25 × 5 cm deep) including litter and soil was sampled, and invertebrates of litter and soil were sorted separately. Because a large portion of soil invertebrates is often concentrated at the surface (Anichkin et al., 2007; Doblas-Miranda et al., 2009), only topsoil was sampled. Invertebrates in litter and soil were hand sorted, and individuals were later counted and identified into taxonomic groups in the laboratory (total of 40 taxonomic groups; Appendices 1, 2). These invertebrate taxonomic groups were also classified into four functional groups: ecosystem engineers, litter transformers, predators, and others (Lavelle et al., 1997). Termites were identified to the species level, and all termite genera were then classified into three feeding guilds: fungus, soil, and wood feeders.

Measurement of microhabitat environment. — We quantified 10 variables related to vegetation structure, microhabitat structure, and characteristics of litter and soil. These variables included the observed number of species and basal area (BA) of trees ≥10 cm DBH, distance to primary forest, canopy openness, dry weight of litter and fine roots, concentrations of total phenolics and condensed tannin in litter, soil water content, and soil temperature.

We determined the species richness (number of observed tree species per plot) and BA (m² ha⁻¹) using the tree census data for each plot. The shortest straight distance from each plot to the primary forest of LHNP was calculated to the nearest 1 m using GPS data (Garmin GPSmap 60CSx). For light conditions at the forest floor, percent canopy openness was measured using a digital camera equipped with a fisheye lens (Coolpix 910, Nikon). Ten images were taken at 10-m intervals at 1.2-m height and analysed using CanopOn 2 (CanopOn, 2003). After the invertebrates were hand-sorted, litter and fine roots in the soil were oven-dried for 72 h at 50°C and then weighed to the nearest 0.1 g. Litter samples for chemical analyses were additionally hand collected from four points at 20-m intervals within each plot. At each point, two 25 × 25 cm litter samples (about 5 m apart) were collected and pooled. Litter samples were then dried using silica gel

for 96 h and ground to a fine powder after removing sand and fungi from litter. The concentrations of total phenolics and condensed tannin in the litter were quantified by extraction with 50% methanol and determined using the Folin-Ciocalteu and proanthocyanidin methods, respectively (Julkunen-Tiitto, 1985; Waterman & Mole, 1994). Standards for the assays were gallic acid for total phenolics and cyanidin chloride for condensed tannin.

The soil water content of all plots was measured at four points spaced 20 m apart in each plot on the morning on 28 Oct. 2008 using a Hydro Sense TM (Capbell Scientific Australia Pty. Ltd.) and a Moisture Meter Type HH2 (Delta-T Devices Ltd). At the same points in each plot, measurements of soil temperature were conducted three times (0800, 0900, and 1000 hours) using a digital thermometer (TT508, Tanita). For both soil water content and soil temperature measurements, sensors were placed into the soil at 5-cm depth.

Data analysis. — Four standard indices were used to describe whole invertebrate and termite community structures of litter and soil: the number of taxonomic groups (number of species for termites) per plot, total number of individuals per plot, Shannon diversity index (H'), and Simpson dominance index ($1/D$). For termites, frequency of occurrence, which was the total number of points containing termites per plot, was also used. We compared these community characters and microhabitat environmental variables among forest types using ANOVA. All data were log-transformed (or logit-transformed for percent data; Warton & Hui, 2011) before analyses to improve normality and equality of variances. A χ^2 test was used to determine whether the abundance of each invertebrate functional group and termite feeding guild significantly differed among forest types.

We used permutational multivariate analysis of variance (PERMANOVA) to examine whether taxonomic group or species composition of invertebrates and termites in each forest type differed between litter and soil. Nonmetric multidimensional scaling (NMDS) analysis based on the Bray–Curtis similarity index was performed to visualize differences between plots. The position of plots along the NMDS axes was correlated to the following log- or logit-transformed response variables related to microhabitat environment: tree species richness, BA, distance to LHNP, canopy openness, dry weight of litter, and concentrations of total phenolics and condensed tannin for invertebrate and termite communities of litter; tree species richness, BA, distance to LHNP, dry weight of fine roots, soil water content, and soil temperature for invertebrate and termite communities of soil. For the analyses, the matrix of the frequencies of each taxonomic group or species in each plot (points per plot) was used to reduce the bias introduced by the presence of social insects. Mantel tests based on 10,000 permutations were performed to test for correlations between species composition dissimilarity and geographic distance matrices for plots of each forest type, and to check for underlying geographic gradients in species distribution. For these analyses, we used the free software package R version 2.11.1 (R development Core Team, 2010).

RESULTS

Invertebrate communities in litter and soil. — From litter and soil, 10,930 and 16,080 individuals belonging to 40 and 37 taxonomic groups were sampled, respectively (Appendices 1, 2). For the termites, 15 and 17 species were found from litter and soil, respectively (Appendices 3, 4). Although several microhabitat environmental variables significantly differed among forest types, whole invertebrate communities within both litter and soil did not vary among forest types (Table 1). Similarly, the density of each functional group in litter and soil did not significantly differ among forest types, with the exception of the others ($P < 0.01$ in litter and $P < 0.05$ in soil; Fig. 1).

In contrast, characteristics of the soil termite community differed significantly among forest types (Table 1). The number of species, frequency of occurrence, and values of the Shannon and Simpson indices in primary forest were significantly higher than values in young fallow. Significant differences were also detected in the distribution of feeding guilds, and the frequency of soil feeders in young fallow was lower than values in old fallow and primary forest (Fig. 2). However, the litter termite community exhibited no differences among forest types in terms of community structure and feeding guilds (Table 1, Fig. 2).

Taxonomic group and species composition. — We found significant differences in taxonomic group composition of invertebrates and species composition of termites between litter and soil, as well as among forest types (PERMANOVA, $P < 0.05$ in all cases). Within each forest type, geographic distance and dissimilarity in taxonomic group/species composition were not significantly related. The NMDS ordinations for the invertebrate community demonstrated similar taxonomic group composition in young and old fallows, but primary forest exhibited a relatively distinct composition of taxonomic groups in both litter and soil (Fig. 3). In young fallow, bugs (Hemiptera) and earthworms (Haplotaxida) were more abundant than in old fallow and primary forest in litter and soil, respectively (Appendices 1, 2). More adult beetles and mites (Prostigmata) were also found in young and old fallows than in primary forest. The observed number of tree species, BA, and distance to LHNP were significant factors affecting taxonomic group composition in litter and soil ($P < 0.05$). In litter, canopy openness was also related to taxonomic group composition.

For termite species composition, plots were scattered in the NMDS ordination diagram, and no distinct segregation was found among forest types in litter and soil (Fig. 4). No factors were significantly related to the species composition of litter termites, whereas the observed number of tree species and BA affected the species composition of soil termites.

DISCUSSION

Invertebrate communities in litter and soil. — Overall invertebrate communities in litter and soil recovered relatively

quickly after swidden cultivation. Even invertebrates in young fallow (5–10 years after abandonment) exhibited similar values for the abundance, richness, and density distribution of functional groups to those in old fallow and primary forest. Mathieu et al. (2005) also reported that the species richness and occurrence frequency of many soil invertebrates recovered in a 7-year-old fallow in Brazil. Therefore, fallows may play a certain role in the conservation of overall invertebrate communities of litter and soil in the region. For example, highly mobile invertebrate could escape and return after swidden cultivation. A mosaic distribution of small fallow patches of various successional stages within

the landscape may also contribute to the rapid colonisation of invertebrates from the surrounding litter and soil into newly abandoned fields. Rossi et al. (2010) suggested the importance of the spatial arrangement of fallows spanning a large age range after abandonment for the diversity conservation of soil invertebrates.

On the other hand, swidden cultivation did affect the taxonomic group composition of litter and soil invertebrates. Within functional group, the differences in mean density of some taxonomic groups were also found, suggesting that litter and soil invertebrates respond to disturbance differently

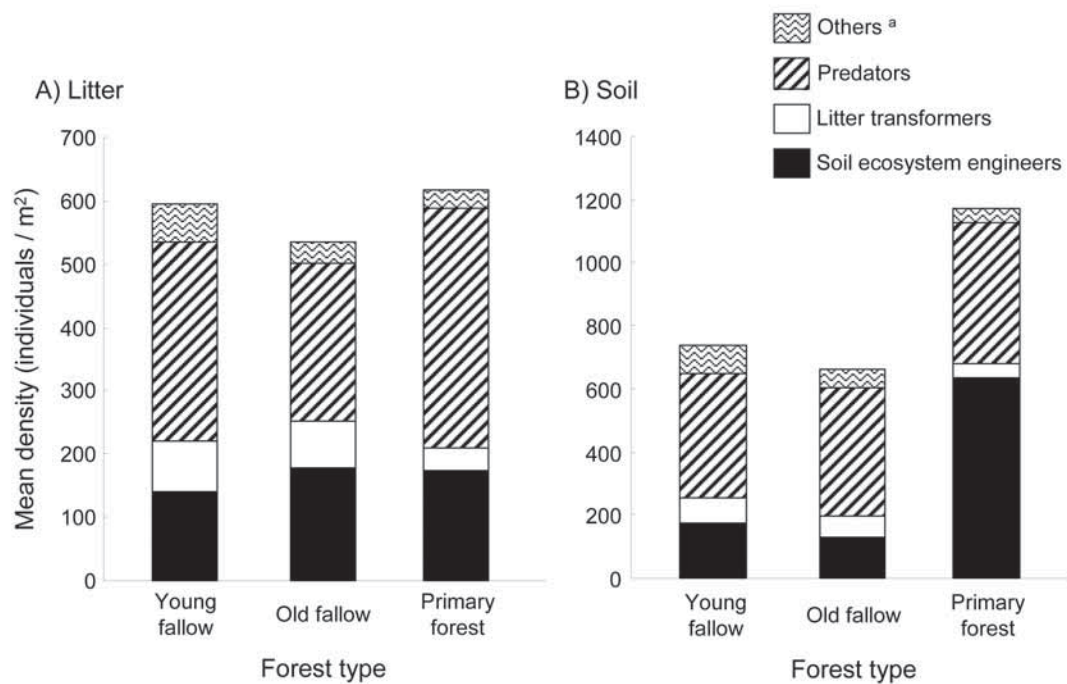


Fig. 1. Individual density distributions of different functional groups in litter (A) and soil (B) within the three forest types. ^a Significant difference was detected among forest types in litter ($P < 0.01$) and soil ($P < 0.05$).

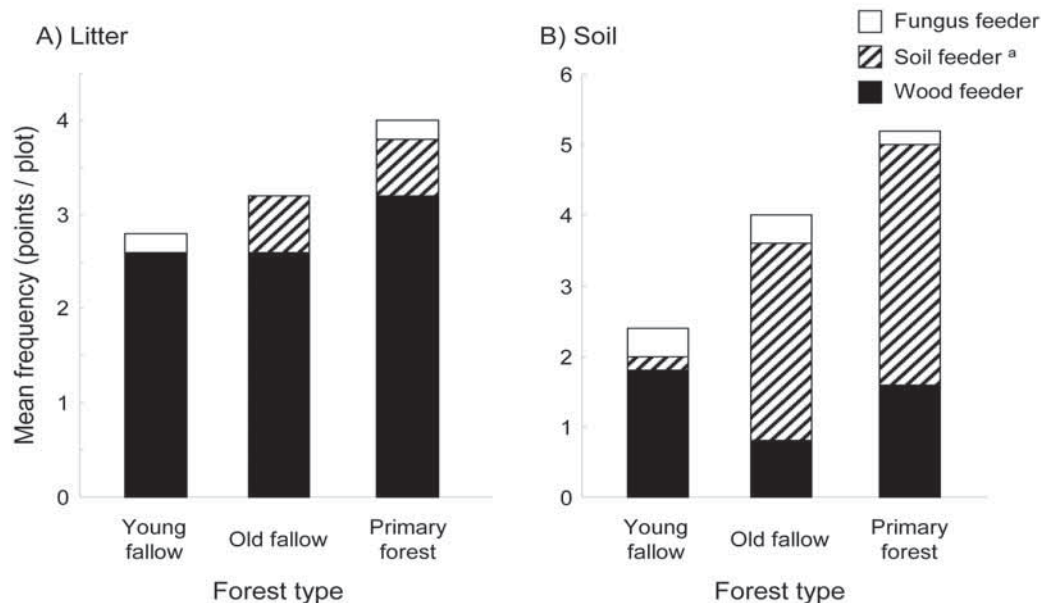


Fig. 2. Termite frequency distribution of different feeding guilds in litter (A) and soil (B) within the three forest types. ^a Significant difference was detected among forest types in soil ($P < 0.05$).

Table 1. Description of microhabitat environment and invertebrate and termite communities of litter and soil (mean \pm SE) in young fallow, old fallow, and primary forest in Sarawak, Malaysia.

	Young fallow			Old fallow			Primary forest			<i>F</i> ¹
Litter invertebrate community										
No of group (per plot)	26.8	±	0.8	27.2	±	3.1	27.6	±	0.9	0.2
Total individuals (per plot)	596.0	±	186.0	535.0	±	232.0	618	±	307.0	0.2
Shannon index (H')	1.9	±	0.4	2.0	±	0.5	1.8	±	0.3	0.3
Simpson index (1/D)	3.8	±	1.1	4.5	±	2.0	3.5	±	1.0	0.4
Soil invertebrate community										
No of group (per plot)	27.4	±	3.8	26.0	±	2.4	27.2	±	1.6	0.3
Total individuals (per plot)	736.6	±	21.5	662.7	±	251.4	1173.0	±	1033.0	1.0
Shannon index (H')	2.1	±	0.3	2.0	±	0.1	1.8	±	0.2	2.4
Simpson index (1/D)	5.0	±	2.1	3.8	±	0.5	3.3	±	0.7	2.5
Litter termite community										
No of species (per plot)	2.4	±	1.8	2.4	±	1.3	3.2	±	1.8	0.4
Total individuals (per plot)	204.1	±	139.0	247.4	±	176.0	165.3	±	169.0	0.8
Frequency (points per plot)	2.8	±	2.2	3.2	±	1.9	4.0	±	2.4	0.5
Shannon index (H')	0.9	±	0.6	1.0	±	0.1	1.0	±	0.6	0.2
Simpson index (1/D)	2.8	±	1.3	2.7	±	0.3	3.0	±	1.6	0.4
Soil termite community										
No of species (per plot)	2.0	±	0.7	3.2	±	1.1	4.0	±	0.7	7.4 **
Total individuals (per plot)	77.0	±	81.6	59.0	±	69.1	596.8	±	1038.0	2.4
Frequency (points per plot)	2.4	±	1.5	3.8	±	0.8	5.2	±	2.4	4.6 **
Shannon index (H')	0.6	±	0.4	1.1	±	0.4	1.3	±	0.2	5.5 **
Simpson index (1/D)	2.0	±	0.6	3.2	±	1.2	3.7	±	0.6	5.8 **
Microhabitat environment										
Recovery time (years)	5–10			20–40			–			–
Tree species (/0.1ha)	11.4	±	0.5	30.2	±	17.8	37.0	±	9.1	14.3 **
Tree basal area (m²/ha)	12.9	±	10.3	26.7	±	7.5	40.8	±	14.0	6.6 **
Distance to LHNP (m)	1044.9	±	511.8	976.6	±	483.0	0.0			470.8 ***
Canopy openness (%)	11.3	±	1.9	10.5	±	1.3	7.5	±	0.6	13.2 ***
Litter dry weight (g/sample)	53.1	±	11.5	59.6	±	14.5	73.9	±	18.9	2.2
Litter total phenolics (mg/g)	8.2	±	1.3	9.5	±	1.6	10.1	±	2.8	0.9
Litter condensed tannin (mg/g)	1.1	±	0.3	1.3	±	0.3	0.9	±	0.2	3.7 *
Fine root dry weight (g/sample)	33.7	±	6.3	34.5	±	13.3	35.1	±	1.0	0.1
Soil water content (%)	35.9	±	5.9	35.2	±	4.5	35.6	±	5.8	0.1
Soil temperature (°C)	26.0	±	0.3	25.5	±	0.3	25.2	±	0.3	7.5 **

¹The significance of *F* values from the ANOVA is indicated by: **P*<0.1, ***P*<0.05, ****P*<0.01.

and further accumulation of species-level data is necessary to understand the mechanism causing the difference in response. Fallows contained more disturbance-tolerant taxonomic groups such as mites. The observed higher density of earthworms in young fallow was consistent with previous studies (Mathieu et al., 2005; Pauli et al., 2011). The alteration of forest structure in fallows may result in high abundances of bugs and beetles through changes in diet abundance. Species-specific characteristics of litter determine the decomposer community below the canopy (Negrete-Yankelevich et al., 2008). Indeed, the observed number of tree species and BA were always selected as factors determining the taxonomic group composition of litter and soil invertebrates and the species composition of soil termites. These two variables, especially BA, are easier to measure in the field relative to

a full-scale litter and soil invertebrate survey (sampling, hand sorting, and identification). Although further studies are necessary to identify the primary mechanisms determining the local taxonomic composition of litter and soil invertebrates, tree species richness and BA may be useful indicators for field verification of the recovery rate of invertebrate taxonomic composition, which serves an important role in the regulation of soil conditions and plant growth through decomposition processes (Berg et al., 2001; Setälä, 2002; Yang & Chen, 2009).

Termite communities in litter and soil. — The recovery response of the termite community to swidden cultivation differed between litter and soil. The species richness and abundance of litter termites did not differ among forest types,

whereas soil termites in primary forest exhibited higher richness and abundance than did communities in young fallow, suggesting a slower recovery of soil termites compared with litter termites. Food resources on which termites depend may affect the recovery process, which should be reflected by the composition of feeding guilds. Soil-feeding termites appear to be more sensitive to disturbances than other types of termites such as wood feeders (Eggerton et al., 1996; Bandeira et al., 2003), and the same pattern was observed in

the present study (Fig. 2). Soil feeders can create and maintain soil conditions that are favourable to plant growth (Dibog et al., 1999), and this function is especially crucial in tropical rain forests, which are often associated with low-fertility soils (Baillie, 1996; Baillie et al., 2006). The soil termite community and the frequency of soil feeders in old fallow had recovered, as these variables did not significantly differ between old fallow and primary forest. Thus, longer fallow periods, such as more than 20 years, are needed to restore

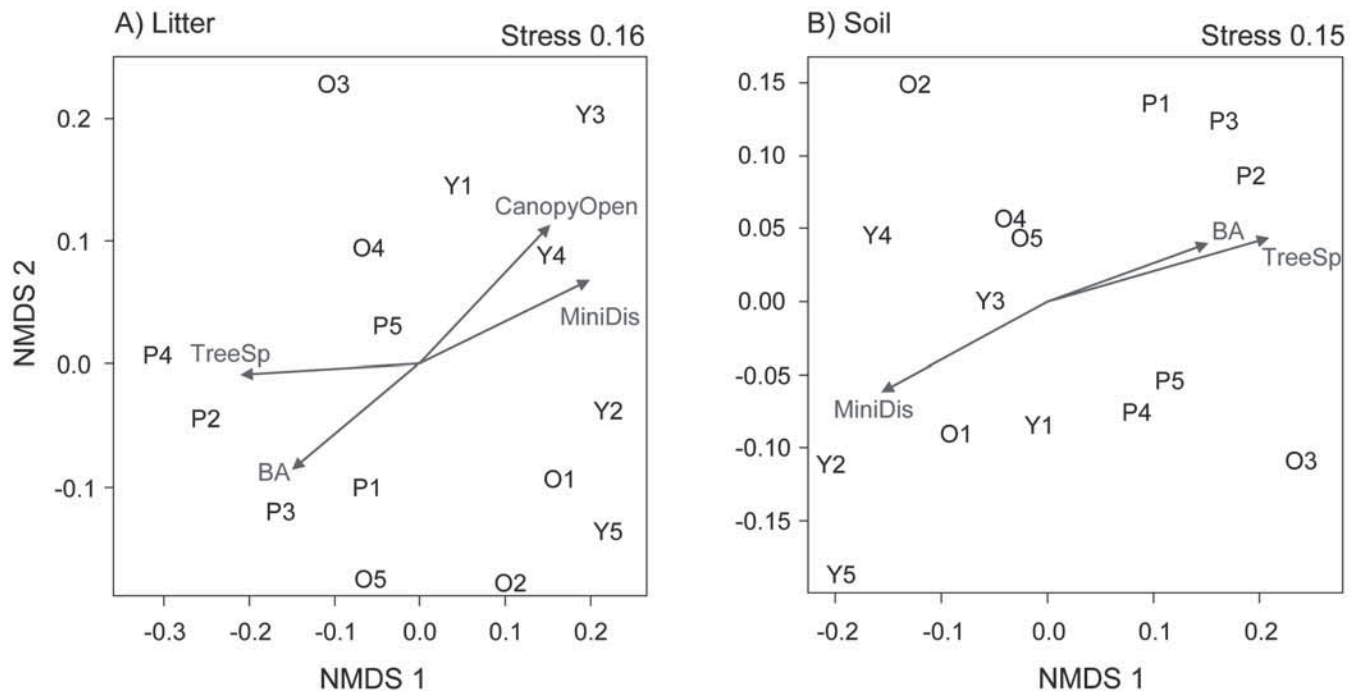


Fig. 3. Nonmetric multidimensional scaling (NMDS) analysis of litter (A) and soil (B) invertebrates and relationship ($P < 0.05$) with microhabitat environmental factors in young (Y) and old (O) fallows and primary forest (P). BA: tree basal area; CanopyOpen: canopy openness; MiniDis: the shortest straight distance from each plot to the primary forest of LHP; TreeSp: observed number of tree species.

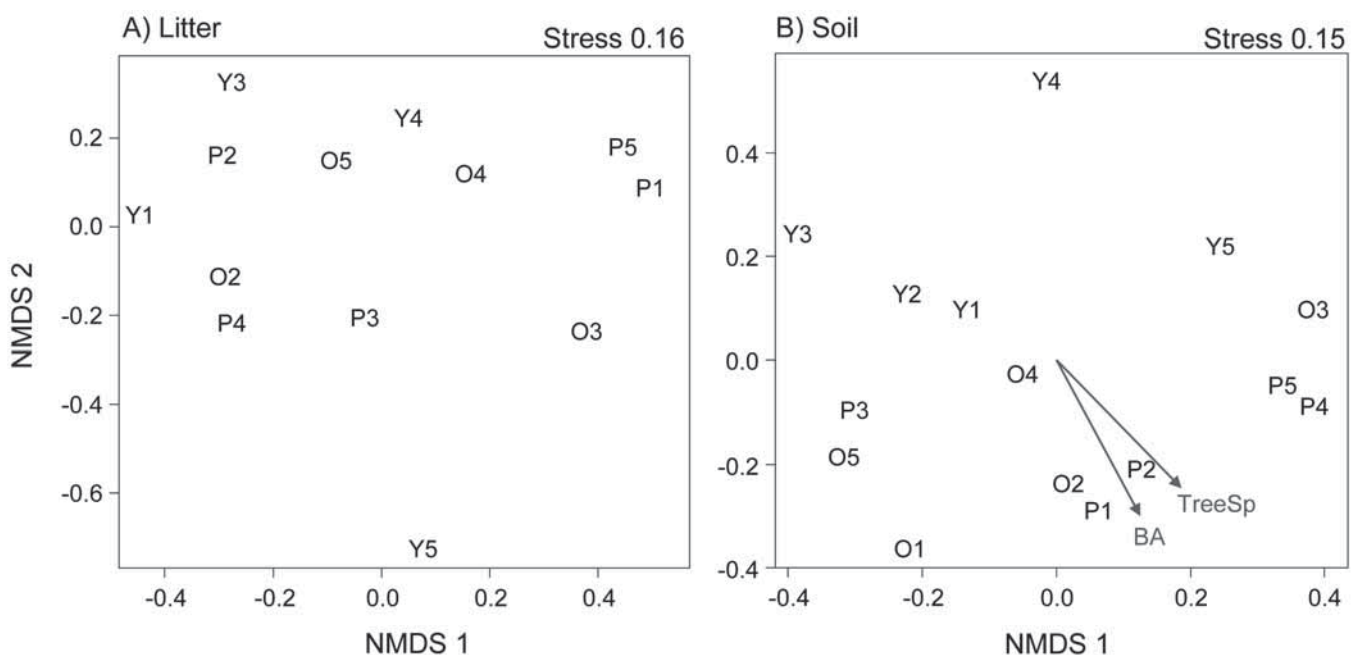


Fig. 4. Nonmetric multidimensional scaling (NMDS) analysis of litter (A) and soil (B) termites and relationship ($P < 0.05$) with microhabitat environmental factors in young (Y) and old (O) fallows and primary forest (P). BA: tree basal area; TreeSp: observed number of tree species.

Appendix 1. Mean \pm SE density (individuals / m²) and total individuals of litter invertebrates at each forest type.

	Young fallow			Old fallow			Primary forest			Total N
Gastropoda	0.6	\pm	0.3	0.5	\pm	0.2	0.8	\pm	0.3	12
Oligochaeta										
Haplotaxida	0.3	\pm	0.2	0.3	\pm	0.2	1.9	\pm	0.7	16
Tubificida	1.8	\pm	1.4	2.9	\pm	1.4	2.7	\pm	1.1	46
Arachnida										
Scorpionida	0.0	\pm	0.0	0.0			0.5	\pm	0.3	3
Pseudoscorpiones	1.8	\pm	1.0	4.3	\pm	2.2	10.2	\pm	3.7	102
Opiliones	8.5	\pm	2.0	6.1	\pm	1.1	3.7	\pm	0.3	114
Araneae	19.2	\pm	2.9	19.4	\pm	2.3	21.4	\pm	2.7	375
Thelyphonida	0.0			0.2	\pm	0.2	0.0			1
Schizomida	0.0			0.2	\pm	0.2	0.0			1
Acari										
Gamasida	8.8	\pm	4.1	9.8	\pm	2.5	9.3	\pm	3.8	174
Prostigmata	12.5	\pm	2.2 ^a	12.3	\pm	1.1 ^a	3.8	\pm	1.1 ^b	179
Astigmata	0.0			0.3	\pm	0.3	0.0			2
Oribatida	2.6	\pm	1.0	3.8	\pm	1.3	1.3	\pm	0.6	48
Crustacea										
Isopoda	30.2	\pm	11.3	43.5	\pm	16.9	16.5	\pm	2.1	564
Amphipoda	0.0			0.2	\pm	0.2	0.0			1
Diplopoda										
Polydesmida	8.2	\pm	3.4	6.2	\pm	2.0	5.9	\pm	1.6	127
Chordeumatida	1.4	\pm	0.5	0.5	\pm	0.2	0.5	\pm	0.2	15
Polyxenida	0.3	\pm	0.2	0.2	\pm	0.2	0.5	\pm	0.3	6
Chilopoda										
Lithobiomorpha	4.5	\pm	1.8	2.6	\pm	1.4	0.6	\pm	0.3	48
Scolopendromorpha	1.9	\pm	0.9	2.7	\pm	0.5	4.0	\pm	1.3	54
Geophilomorpha	5.0	\pm	1.8	3.5	\pm	0.9	3.5	\pm	1.1	75
Symphyla	1.1	\pm	0.4	1.9	\pm	0.5	0.3	\pm	0.2	21
Insecta										
Collembola	6.1	\pm	1.7	8.5	\pm	3.8	4.0	\pm	1.0	116
Diplura	1.3	\pm	0.4	1.0	\pm	0.5	1.0	\pm	0.5	20
Thysanura	0.2	\pm	0.2	0.3	\pm	0.3	0.3	\pm	0.2	5
Orthoptera	3.4	\pm	0.9	2.2	\pm	0.7	3.0	\pm	1.1	54
Grylloblattodea	0.2	\pm	0.2	0.2	\pm	0.2	0.8	\pm	0.6	7
Dermaptera	1.4	\pm	0.6	0.0	\pm	0.0	0.2	\pm	0.2	10
Isoptera	139.0	\pm	91.3	175.7	\pm	110.6	169.1	\pm	73.9	3024
Blattodea	5.8	\pm	1.6	4.6	\pm	0.8	4.2	\pm	0.8	91
Psocodea	0.3	\pm	0.3	0.0			0.0			2
Thysanoptera	1.0	\pm	0.6	0.6	\pm	0.3	0.0			10
Hemiptera	13.9	\pm	2.3 ^a	5.6	\pm	1.0 ^b	5.1	\pm	1.2 ^b	154
Lepidoptera (larvae)	0.2	\pm	0.2	1.1	\pm	0.3	1.6	\pm	0.6	18
Diptera (larvae)	23.8	\pm	19.0	3.5	\pm	1.4	2.4	\pm	1.2	186
Coleoptera										
Pselaphinae	4.8	\pm	0.8 ^a	2.6	\pm	0.9 ^{ab}	1.4	\pm	0.3 ^b	55
Staphylininae	9.4	\pm	3.1 ^a	3.8	\pm	1.5 ^{ab}	1.9	\pm	0.6 ^b	95
Other Coleoptera (larvae)	7.8	\pm	4.4	5.1	\pm	0.5	4.0	\pm	1.5	106
Other Coleoptera (adult)	14.1	\pm	1.7 ^a	5.0	\pm	1.8 ^b	6.1	\pm	0.9 ^{ab}	157
Hymenoptera										
Formicidae (larvae)	17.0	\pm	9.3	17.3	\pm	10.0	42.4	\pm	7.5	479
Formicidae (adult)	234.7	\pm	43.2	171.8	\pm	27.3	280.3	\pm	82.3	4293
Others	2.9	\pm	0.6	5.0	\pm	2.2	2.4	\pm	0.8	64
Total N	3724			3345			3861			10930

Different letters indicate significant differences in mean density of each taxonomic group among forest types.

Appendix 2. Mean \pm SE density (individuals / m²) and total individuals of soil invertebrates at each forest type.

	Young fallow			Old fallow			Primary forest			Total N
Gastropoda	0.5	\pm	0.3	0.2	\pm	0.2	0.0			4
Oligochaeta										
Haplotaxida	89.0	\pm	17.5 ^a	59.0	\pm	19.6 ^{ab}	20.8	\pm	3.4 ^b	1055
Tubificida	9.0	\pm	3.5	12.2	\pm	2.9	16.0	\pm	6.1	232
Arachnida										
Scorpionida	0.0			0.0			0.3	\pm	0.2	2
Pseudoscorpiones	2.2	\pm	1.2	2.1	\pm	1.0	4.3	\pm	1.4	54
Opiliones	2.1	\pm	0.5	5.8	\pm	1.3	5.3	\pm	1.1	82
Araneae	32.8	\pm	9.6	26.7	\pm	3.7	34.2	\pm	4.3	586
Schizomida	2.2	\pm	1.2	1.3	\pm	0.6	2.1	\pm	0.7	35
Acari										
Gamasida	2.6	\pm	1.4	6.1	\pm	3.6	2.2	\pm	0.5	68
Prostigmata	19.8	\pm	4.8 ^a	10.9	\pm	3.1 ^{ab}	4.2	\pm	0.5 ^b	218
Oribatida	1.6	\pm	0.6	0.3	\pm	0.2	0.3	\pm	0.2	14
Crustacea										
Isopoda	49.4	\pm	24.3	45.0	\pm	20.2	25.9	\pm	3.5	752
Amphipoda	0.2	\pm	0.2	0.0			0.0			1
Diplopoda										
Polydesmida	18.2	\pm	5.0	9.3	\pm	2.0	9.8	\pm	3.0	233
Chordeumatida	1.3	\pm	0.3	1.3	\pm	0.7	1.9	\pm	0.5	28
Chilopoda										
Lithobiomorpha	4.2	\pm	1.6	4.3	\pm	1.0	1.1	\pm	0.2	60
Scolopendromorpha	10.2	\pm	3.2	6.6	\pm	2.4	7.8	\pm	2.6	154
Geophilomorpha	12.3	\pm	4.2	9.9	\pm	2.3	11.8	\pm	1.2	213
Symphyla	1.3	\pm	0.5	1.6	\pm	0.6	2.6	\pm	1.3	34
Insecta										
Collembola	2.1	\pm	1.7	1.8	\pm	0.8	0.6	\pm	0.3	28
Diplura	17.3	\pm	4.1	15.5	\pm	3.8	13.3	\pm	3.7	288
Thysanura	0.0			0.3	\pm	0.2	0.0			2
Orthoptera	1.4	\pm	0.9	0.6	\pm	0.6	1.9	\pm	0.7	25
Grylloblattodea	0.2	\pm	0.2	0.0			0.0			1
Dermaptera	0.6	\pm	0.2	0.0			0.3	\pm	0.2	6
Isoptera	77.0	\pm	36.5	59.0	\pm	30.9	596.8	\pm	464.3	4580
Blattodea	4.6	\pm	0.6	4.2	\pm	0.8	5.0	\pm	0.7	86
Thysanoptera	0.5	\pm	0.2	0.2	\pm	0.2	0.2	\pm	0.2	5
Hemiptera	16.3	\pm	4.0	8.0	\pm	1.7	7.4	\pm	2.1	198
Lepidoptera (larvae)	0.0			0.3	\pm	0.2	0.5	\pm	0.2	5
Diptera (larvae)	1.9	\pm	1.0	1.8	\pm	0.5	1.1	\pm	0.4	30
Coleoptera										
Pselaphinae	10.9	\pm	4.6 ^a	7.2	\pm	2.1 ^a	1.3	\pm	0.5 ^b	121
Staphylininae	7.8	\pm	3.1	5.8	\pm	1.3	1.9	\pm	0.6	97
Other Coleoptera (larvae)	10.9	\pm	2.0	6.2	\pm	1.4	6.6	\pm	0.8	148
Other Coleoptera (adult)	15.0	\pm	4.6	11.0	\pm	2.2	7.4	\pm	1.1	209
Hymenoptera										
Formicidae (larvae)	7.5	\pm	3.2	15.0	\pm	9.2	16.2	\pm	6.5	242
Formicidae (adult)	300.8	\pm	72.0	320.2	\pm	66.7	360.5	\pm	31.7	6134
Others	2.9	\pm	0.7	3.2	\pm	1.2	1.9	\pm	0.5	50
Total N	4604			4142			7334			16080

Different letters indicate significant differences in mean density of each taxonomic group among forest types.

Appendix 3. Mean frequency of occurrence (points / plot) and total occurrences of litter termites at each forest type.

Family	Genus	Species	Young fallow	Old fallow	Primary forest	Total
Rhinotermitidae	<i>Coptotermes</i>	<i>sepangensis</i>	0.2	0.0	0.0	1
	<i>Schedorhinotermes</i>	<i>javanicus</i>	0.2	0.6	0.6	7
		<i>medioobscurus</i>	0.4	0.0	0.0	2
	<i>Heterotermes</i>	<i>tenuior</i>	0.8	1.0	1.0	14
	<i>Parrhinotermes</i>	<i>aequalis</i>	0.2	0.0	0.0	1
	Unknown		0.2	0.0	0.0	1
Termitidae	<i>Odontotermes</i>	<i>mathuri</i>	0.2	0.0	0.2	2
	<i>Bulbitermes</i>	<i>borneensis</i>	0.0	0.0	0.2	1
		<i>sarawakensis</i>	0.0	0.4	0.0	2
		sp. 1	0.2	0.0	0.0	1
	<i>Longipeditermes</i>	<i>longipes</i>	0.0	0.0	0.2	1
	<i>Nasutitermes</i>	sp. 1	0.0	0.0	0.2	1
	<i>Microcerotermes</i>	<i>serrula</i>	0.0	0.2	0.6	4
		<i>sabahensis</i>	0.4	0.4	0.0	4
	<i>Homalotermes</i>	<i>exiguus</i>	0.0	0.0	0.2	1
	<i>Globitermes</i>	<i>globosus</i>	0.0	0.0	0.2	1
	Unknown		0.0	0.6	0.6	6
	Total		14	16	20	50

Appendix 4. Mean frequency of occurrence (points / plot) and total occurrences of soil termites at each forest type.

Family	Genus	Species	Young fallow	Old fallow	Primary forest	Total
Rhinotermitidae	<i>Schedorhinotermes</i>	<i>javanicus</i>	0.8	0.4	0.2	7
		<i>medioobscurus</i>	0.2	0.0	0.0	1
	<i>Heterotermes</i>	<i>tenuior</i>	0.2	0.2	0.4	4
	<i>Parrhinotermes</i>	<i>aequalis</i>	0.4	0.0	0.0	2
		<i>microdentiformisoides</i>	0.0	0.0	0.2	1
	<i>Macrotermes</i>	<i>malaccensis</i>	0.0	0.4	0.2	3
Termitidae	<i>Odontotermes</i>	<i>mathuri</i>	0.4	0.0	0.0	2
	<i>Bulbitermes</i>	sp. 1	0.0	0.0	0.2	1
	<i>Longipeditermes</i>	<i>longipes</i>	0.2	0.0	0.0	1
	<i>Oriensubulitermes</i>	<i>inanis</i>	0.0	0.4	0.2	3
	<i>Malaysiotermes</i>	sp. 1	0.0	0.0	0.4	2
	<i>Microcerotermes</i>	<i>serrula</i>	0.0	0.0	0.6	3
		<i>sabahensis</i>	0.0	0.2	0.0	1
		<i>connectens</i>	0.0	0.2	0.0	1
	<i>Pericapritermes</i>	<i>semarangi</i>	0.2	0.6	1.6	12
		<i>dolichocephalus</i>	0.0	0.2	0.2	2
	<i>Procapritermes</i>	<i>prosetiger</i>	0.0	0.2	0.2	2
	Unknown		0.0	1.2	0.8	10
	Total		12	19	26	58

proper soil conditions and to allow the recovery of the soil termite community. Different recovery rates between litter and soil communities were also reported in Brazilian ant assemblages, and soil ants exhibited lower resilience than did litter ants (Bihn et al., 2008). In studies of belowground fauna, invertebrates from litter and soil are often pooled and treated as one unit, except for studies focusing on vertical distribution. Further separate analyses of litter and soil communities will reveal the vertical recovery process after disturbance, which is essential for evaluating the potential role of fallows in the biodiversity conservation of invertebrates following swidden cultivation.

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