EFFECTS OF SOIL FAUNA ON EARLY-STAGE LITTER DECOMPOSITION ACROSS DIVERSE TROPICAL ECOSYSTEMS IN EAST MALAYSIA

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ABSTRACT

Litterbag studies from temperate zones have shown a significant effect of soil fauna on litter decomposition. However, understanding the decomposition dynamics in tropical regions remains limited compared to temperate regions. Here we investigated the impact of soil meso- and macrofauna on litter decomposition rates at three contrasting locations in tropical area of the Eastern part of Peninsular Malaysia (tropical forest near Tasik Kenyir, permaculture in Pahang and urban soils in Universiti Malaysia Terengganu campus). We conducted litterbag experiments with different mesh sizes and soil faunal sampling to investigate the effect of soil meso- and macrofauna on litter decomposition (Fig. 1). As decomposition is fast in the tropics, we expose litterbags for three months and collect them every month. Litter mass loss increased over time, with higher decomposition rates observed in tropical forests and permaculture compared to urban soils. Tropical forest soils host significantly more diverse communities of soil fauna than the other two sites. The principal component analyses (PCA) revealed divergence in the community structure of taxonomic and functional groups among different locations, with urban soils primarily comprising *Araneae*, *Protura*, and *Diplura*, while permaculture and tropical forests mainly consisted of *Acari* and *Collembola*. Size analyses revealed that soil macrofauna enhanced decomposition rates in permaculture, while mesofauna affected decomposition in urban soils. The C:N ratio of litter in litterbags increased after three months of incubation in permaculture and tropical forest without any significant differences among mesh sizes. Random forest analyses highlighted the importance of soil moisture and texture (content of sand, silt and clay) influencing soil biota associated with decomposition processes.

Keywords: decomposition rates; litterbags; litter quality; soil macrofauna; soil mesofauna

Introduction

Soil ecosystems host an immense diversity of organisms, ranging from microorganisms like bacteria, fungi and protists to larger soil animals such as termites and millipedes (Bardgett and van der Putten 2014). For instance, one single gram of soil harbors billions of microbial cells belonging to thousands of species (Fierer 2017). While soil microbes have received considerable attention during past decades (Fierer 2017; Mahé et al. 2017; Nilsson et al. 2018), soil animals have been often overlooked until recent years (Angst et al. 2024). Many studies have unveiled remarkable diversity and abundance of soil animals (Wall et al. 2008; Lavelle et al. 2022). For example, a single square meter of soil hosts hundreds of thousands of individuals of different groups of soil invertebrates, varying with soil type and microclimatic conditions (Petersen and Luxton, 1982; Wu et al. 2011; Heděnec et al. 2022). According to body size, we can recognize microfauna (< 0.2 mm), mesofauna (> 0.2 mm), and macrofauna (> 2 mm) (Swift et al. 1979). Soil microfauna (nematodes, tardigrades, and rotifers) contribute indirectly to litter decomposition via their grazing effects on fungal and bacterial communities (Cesarz et al. 2013; Devetter et al. 2017). In contrast, macrofauna (isopods, millipedes) and mesofauna (springtails and mites) contribute directly to litter decomposition by litter fragmentation and modifying conditions favorable for bacterial and fungal decomposers (Joly et al. 2020; Mrnka et al. 2020; Coq et al. 2022).

Despite their small size, soil animals play crucial roles in ecosystem functioning, particularly in complex processes, such as litter decomposition and nutrient cycling (Filser et al. 2016; Nielsen 2019). Litter decomposition is a fundamental process in terrestrial ecosystems, influencing soil fertility, carbon sequestration, and nutrient

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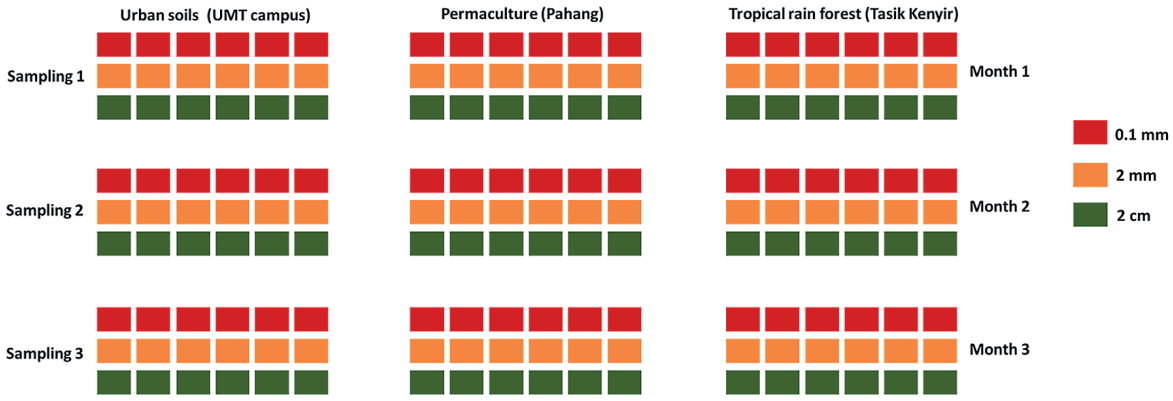

Fig. 1 Design of litterbag experiment.

cycling. In terrestrial ecosystems, more than 50% of the mean annual litterfall is returned to the soil via feeding activity of soil animals (Wall et al. 2008; García-Palacios et al. 2013; Heděnec et al. 2022). However, decomposition rates strongly vary between biomes, driven by multiple factors including climate, litter and substrate quality, and abundance and diversity of soil fauna (Wall et al. 2008; Heděnec et al. 2022). Soil macrofauna, such as isopods, millipedes, earthworms, and gastropods, are important drivers of leaf litter decomposition in temperate deciduous forests, while termites, millipedes, and ants are major decomposers in tropical regions (Petersen and Luxton 1982; Heděnec et al. 2022). However, the role of fauna in litter decomposition in tropical regions remains underexplored. For example, it remains unclear how land-use changes as well as differences in soil properties affect soil fauna communities and their role in litter decomposition. Land-use changes affect soil biodiversity in numerous ways (Jiangi and Purvis 2023), including pesticide use (Badani et al. 2023) and changes in soil properties (Oppong et al. 2023).

Many studies have revealed significant effects of soil fauna on litter decomposition rates (Barajas-Guzmán and Alvarez-Sánchez 2003; Wall et al. 2008; Zhang et al. 2008; García-Palacios et al. 2013; Heděnec et al. 2022). Soil macrofauna, such as isopods, millipedes, earthworms, gastropods, cockroaches and termites are responsible for litter fragmentation and colonization by microbial decomposers such as bacteria and fungi which enhance decomposition rates (Kheirallah 2004; Joly et al. 2018; Coq et al. 2022). Litterbags accessible or non-accessible for meso- and macrofauna provide a reliable tool to measure litter mass loss over time (Kampichler and Bruckner 2009; Frouz et al. 2015; Peguero et al. 2019; Peng et al. 2022b). Despite the increased number of litterbag studies (Kandeler et al. 1999; Kampichler and Bruckner 2009; Frouz et al. 2015; Peng et al. 2022b), most of these were performed in the temperate or subtropical zone while only a few studies were performed in tropical regions, especially in Peninsular Malaysia (Yamashita and Takeda 1998).

Most litterbag studies in temperate zones used relatively long incubation periods and infrequent litterbag sampling (Kandeler et al. 1999; Kampichler and Bruckner 2009; Peng et al. 2022b). If the same methodology were applied in tropical regions, there would be nothing left to study, as decomposition occurs more quickly than in temperate and subtropical regions. Significant mass loss occurs during the early period of incubation in tropical regions, which has been often overlooked in long-term studies (Yamashita and Takeda 1998; Frouz et al. 2015). Therefore, studying the early decomposition stages is crucial for capturing these rapid and distinct ynamics.

To fill this knowledge gap, we established a litterbag study to (i) assess the diversity and composition of soil meso and macrofauna in soils from various contrasting habitats with different land uses with different levels of anthropogenic pressure across peninsular Malaysia; (ii) to investigate the effect of soil meso and macrofauna on litter decomposition rates during three months of incubation and (iii) to investigate influencing factors shaping litter decomposition rates at various contrasting locations in peninsular Malaysia. We hypothesize that 1) soil in tropical rain forest will host the highest diversity and abundance of soil fauna via higher resource availability and stability. In contrast, permaculture and urban soils will host lower diversity and abundances of soil animals, due to lower availability of nutrients and higher anthropogenic disturbances; 2) we hypothesize that higher litter consumption in accessible litterbags incubated in tropical forest than in permaculture and urban soils due to stable microclimatic conditions and higher diversity of soil fauna 3) we expect that soil properties will shape litter decomposition via their effect on soil biota.

Material and Methods

Study site description

Three contrasting habitats (tropical rainforest, permaculture, and urban soil at the campus of the Universiti Malaysia Terengganu) with different land uses, vegetation covers, soil properties, and composition and diversity of soil fauna were selected in the Terengganu and Pahang states in Malaysia. The tropical rainforest is locat-

ed near Kenyir Lake in the Hulu Terengganu district of Terengganu State in Malaysia (5.145357° N, 102.760592° E). The area is characterized by dominant tree vegetation with a canopy cover of 80–90%. The dominant trees are *Dipterocarpus*, *Shorea*, *Lithocarpus*, *Pometia*, *Artocarpus*, and *Maniltoa*, while dominant understory vegetation is from the family of *Zingiberaceae* and *Annonaceae*. The permaculture is situated next to the Delimah Guest House of Taman Negara in Pahang State (4.383298° N, 102.40406° E). The permaculture area is approximately 150 m^2. The main crops are papayas, bananas and other vegetables such as okra and cucumbers. The permaculture is managed without any inorganic fertilizers and pesticides. The permaculture is fertilized by chicken manure every three months. The post-harvest residuals are left on the site as organic biofertilizers to support natural soil decomposers. The campus of the Universiti Malaysia Terengganu (UMT) is situated in the coastal area of Kuala Nerus district of the Terengganu State (5.407046° N, 103.092333° E). The campus has approximately 26 km^2 and its vegetation consists of different coastal tree species, such as *Swietenia macrophylla*, *Cyrtophyllum fragrans*, and *Casuarina equisetifolia*.

Experimental design

We used three types of litterbags with different mesh sizes – those accessible for soil mesofauna (nylon net with 2 mm mesh size), macrofauna (nylon net with 2 mm mesh size and with 2 cm holes), and litterbags made from fabric with 0.1 mm mesh size as a control to test the effect of soil animals on decomposition of leaf litter. Each bag was filled with freshly fallen litter of various tree species found on the UMT campus which are also common in tropical forests across Malaysia. The leaf litter from different trees collected in the botanical garden at the UMT campus (*Agathis*, *Artocarpus*, *Cyrtophyllum*, *Dipterocarpus*, *Mangifera*, *Melaleuca*, *Milettia*, and *Shorea*) was oven-dried at 65°C for three days and equally mixed to include all dominant tree species characterized for both natural and anthropogenic habitats in tropical areas. The experiment was conducted at three sites, each containing three subplots. In each subplot, 6 litterbags containing 5 g of oven-dried leaf litter (dried at 60 °C for 48 hours) accessible to macrofauna, 6 accessible to mesofauna, and 6 control litterbags were deployed simultaneously. The litterbags were incubated and collected in three phases: after one month, 6 macrofauna-accessible, 6 mesofauna-accessible, and 6 control litterbags were retrieved from each subplot. After two months, another set of 6 litterbags from each category were collected, and finally, after three months, the remaining 6 litterbags of each type were retrieved. In total, 162 litterbags were retrieved (Supplementary file S1). The total mass of consumed litter was measured gravimetrically in the laboratory by subtraction of dry litter weights before and after incubation. The percentage of litter consumed, decomposition constant (*k* value), and effect size (based on the *k* value) of soil mesofauna and macrofauna were measured for each litterbag. Three litterbags of each mesh size category were randomly taken from each location to measure litter TOC, TN and C:N ratio after three months of incubation. The same number of replicates before incubation was measured as a control.

Soil fauna sampling and identification

Soil samples for mesofauna were collected using a shovel from a 10 × 10 cm square to a depth of 5 cm. A total of three compact soil blocks were taken from each location at each of the three months of incubation, resulting in a total of 27 samples. Soil mesofauna was extracted by dry extraction method using a modified Berlese-Tullgren extractor for three days (Pande and Berthet 1973). Soil mesofauna specimens were trapped in water with detergent and further stored in 70% ethanol for later identification (Peng et al. 2022a). Soil macrofauna was collected using the hand-sorting method. At each location, a soil block (25 × 25 cm and 5 cm in depth) was collected together with soil samples for mesofauna. In total, 27 monoliths were taken from all locations and sampling times. Soil monoliths were transferred to the lab and immediately processed using hand sorting of all soil fauna in size class larger than 2 mm (Swift et al. 1979; Ruiz et al. 2008). Soil animals were classified into 16 taxonomic groups at the family, order, subclass, or class level, including *Collembola*, *Acari*, *Diplura*, *Symphylla*, *Pauropoda*, *Protura*, *Lumbricidae*, *Diplopoda*, *Isoptera*, *Isopoda*, *Araneae*, *Chilopoda*, *Formicidae*, *Coleoptera*, Insect others, *Blattodea* (without *Isopotera*). Furthermore, soil fauna was classified into 7 functional groups, namely Predators, Omnivores, Saprophages: Macrofauna, Saprophages: Mesofauna, Macrofauna total, Mesofauna total and Total fauna (Swift et al. 1979; Artz et al. 2010; Filser et al. 2016; Orgiazzi et al. 2016).

Soil physico-chemical properties and litter chemistry

Soil samples were collected using a shovel from a 25 × 25 cm square to a depth of 5 cm. A total of three compact soil blocks were taken from each location. Soil moisture was measured gravimetrically, before and after drying at 65 °C for 72 hours using a drying oven at the Ecological laboratory of the Faculty of Science and Marine Environment (FSSM) at UMT. The pH was determined using a Horiba LAQUA PH210, obtained from the Plant Biotechnology Lab of FSSM, at a soil-to-water ratio of 1:5. Soil texture was determined as a percentage of sand, silt, and clay after sieving through the sieve of size 2 mm, 0.02 mm and 0.002 for sand, silt, and clay respectively. Available phosphorus (P) was analyzed using the Bray-1 extraction method with the Shimadzu UV Spectrophotometer, UV-1800 model. The percentage of organic matter (OM) in soil was measured by loss of ignition method using a muffle furnace at a temperature of 375 °C for 8 hours. Total Organic Carbon (TOC), Total Nitrogen (TN), and the Carbon-to-Nitrogen (C/N) ratio were determined

for soil and selected litter samples using the Elementar UNICUBE® organic elemental analyzer at the Organic Chemistry Laboratory of the Faculty of Marine Engineering and Technology at UMT, with helium as a carrier gas.

Statistical analyses

We used logarithmic regression to fit the temporal trend of mass loss for each species and mesh size across three sampling locations. The decomposition rate (decomposition constant) (k value) was calculated according to the single exponential model for comparisons among different litterbags and sampling locations (Peng et al. 2022b, 2022c). Specifically, we calculated the k value (months^{-1}) using Eq. (1):

$$k = -\frac{1}{t}\ln\left(\frac{M_t}{M_0}\right) \quad (1)$$

where M_0 is the initial litter dry mass (g) and M_t is the dry mass at sampling time t (month). Alpha diversity indices (Species Richness (S), Shannon Index (H'), and Simpson's Index (D)) based on the number of taxonomic groups were calculated using the "vegan" R package (Oksanen 2015). Richness refers to the number of different species (or taxa) present in a given sample, site, or community, without considering their abundance. The principal component analyses (PCA) were employed to visualize distribution of population density of various taxonomic and functional groups of soil fauna and soil physico-chemical properties. Random forest analyses using "rfPermute" package were used to test the importance of different physico-chemical properties on litter mass loss and decomposition rate (Liu et al. 2020). The effects of litterbag mesh size, sampling locations, sampling times and their interactions on the percentage of mass loss were assessed using a linear regression model. The Analyses of Variance (ANOVA) were used to compare the mean percentage of mass loss, decomposition rate, alpha diversity indices and densities of taxonomic and functional groups of soil fauna between three different sampling locations, followed by post hoc test (Tukey's Honest Significant Difference) for observed means. To test how access of meso- and macrofauna modulates litter decomposition rate (k) as assessed using different litterbag mesh sizes, effect sizes were calculated as a proxy. The effect sizes for mesofauna, macrofauna, and all total soil fauna were calculated as the normalized effects using the natural log response ratio (lnRR) as follows:

$$lnRR_{mesofauna} = ln\left(\frac{k_{2\ mm}}{k_{0.2\ mm}}\right) \quad (2)$$

$$lnRR_{macrofauna} = ln\left(\frac{k_{2\ cm}}{k_{2\ mm}}\right) \quad (3)$$

$$lnRR_{total} = ln\left(\frac{k_{2\ cm}}{k_{0.2\ mm}}\right) \quad (4)$$

where $k_{0.2mm}$, k_{2mm}, and k_{2cm} are the k values in the litterbags with mesh sizes of 0.1 mm, 2 mm, and 2 cm holes, respectively. The two-way ANOVA followed by Tukey's HSD test was run to test the effect of sampling location and incubation time on response ratio. The paired t-test was used to compare litter TOC, TN and C:N ratio in litterbags before and after three months of exposure in various sampling locations. Pearson correlation coefficient was used to test correlations of soil properties with litter mass loss and decomposition rates. All statistical analyses and graphical representations were conducted using the R-Studio program (R Core Team 2025) with the assistance of the "vegan" and "ggplot2" packages (Oksanen et al. 2012; Wickham 2014).

Table 1 Soil physico-chemical properties among various sampling locations.

	Sampling locations			
	Urban soil	**Permaculture**	**Tropical forest**	**ANOVA**
Moisture (%)	7.0±1.0c	16.9±1.9b	26.8±2.7a	***
pH	5.9±0.2b	6.1±0.2a	6.3±0.1a	***
Conductivity (uS cm^{-1})	36.0±8.7c	45.7±8.8b	55.4±8.9a	**
TOC (g kg^{-1})	13±2c	16±3b	19±5a	***
TN (g kg^{-1})	0.5±0.0c	0.6±0.0b	0.7±0.0a	***
C:N ratio	26±3b	27±4a	27±5a	***
Plant available P (mg kg $^{-1}$)	11.8±3.0a	8.9±1.9b	5.9±0.8c	***
C:P ratio	1100±980	1800±1100	3220±3200	ns
N:P ratio	42±10c	67±11b	118±28a	***
C:N:P ratio	2.3±1b	2.8±1b	4.4±0a	*
OM (%)	3.8±1.0c	5.5±1.4a	6.2±1.9a	***
Sand (%)	35.0±8.8c	45.0±11.3b	55.0±13.8a	***
Silt (%)	50.0±12.5a	37.5±9.4b	25.0±6.3c	***
Clay (%)	15.0±3.8c	17.5±4.4b	20.0±5.0a	***

One-way ANOVA; *P < 0.05, **P < 0.01, ***P < 0.001. Letters indicate statistical homogenous groups.

Results

Soil properties and soil fauna community composition

Soil physico-chemical properties differed significantly among the three sampling locations (Table 1). For instance, soil moisture, conductivity, TOC, TN, N:P, and percentage of organic matter were higher in the tropical forest, intermediate in permaculture, and lowest in urban soil. The percentage of clay particles and sand was highest in the soils of the tropical forest, intermediate in permaculture, and lowest in urban soil, while the highest proportion of silt particles was found in the urban soil. The concentration of phosphorus was highest in urban soils, intermediate in permaculture, and lowest in soils of the tropical forest. The soil C:P ratio did not show any significant differences.

Table 2 Alpha diversity of soil faunal community among various locations and sampling times.

		Richness (S)±SD	Shannon index (H')±SD	Simpson index (D)±SD
Locality	Urban soil	6±1b	1.48±0.2b	0.725±0.04b
	Permaculture	6±1b	1.30±0.1b	0.610±0.04b
	Tropical forest	8±0.4a	1.75±0.1a	0.792±0.02a
	ANOVA	*	*	**
Sampling time	Month 1	6±0.9b	1.52±0.2	0.718±0.04
	Month 2	5±0b	1.39±0.1	0.709±0.02
	Month 3	8±0a	1.62±0.1	0.700±0.06
	ANOVA	**	ns	ns

Alpha diversity indices are based on the number of taxonomic groups. Two-way ANOVA; *P < 0.05, **P < 0.01. Letters indicate statistical homogenous groups.

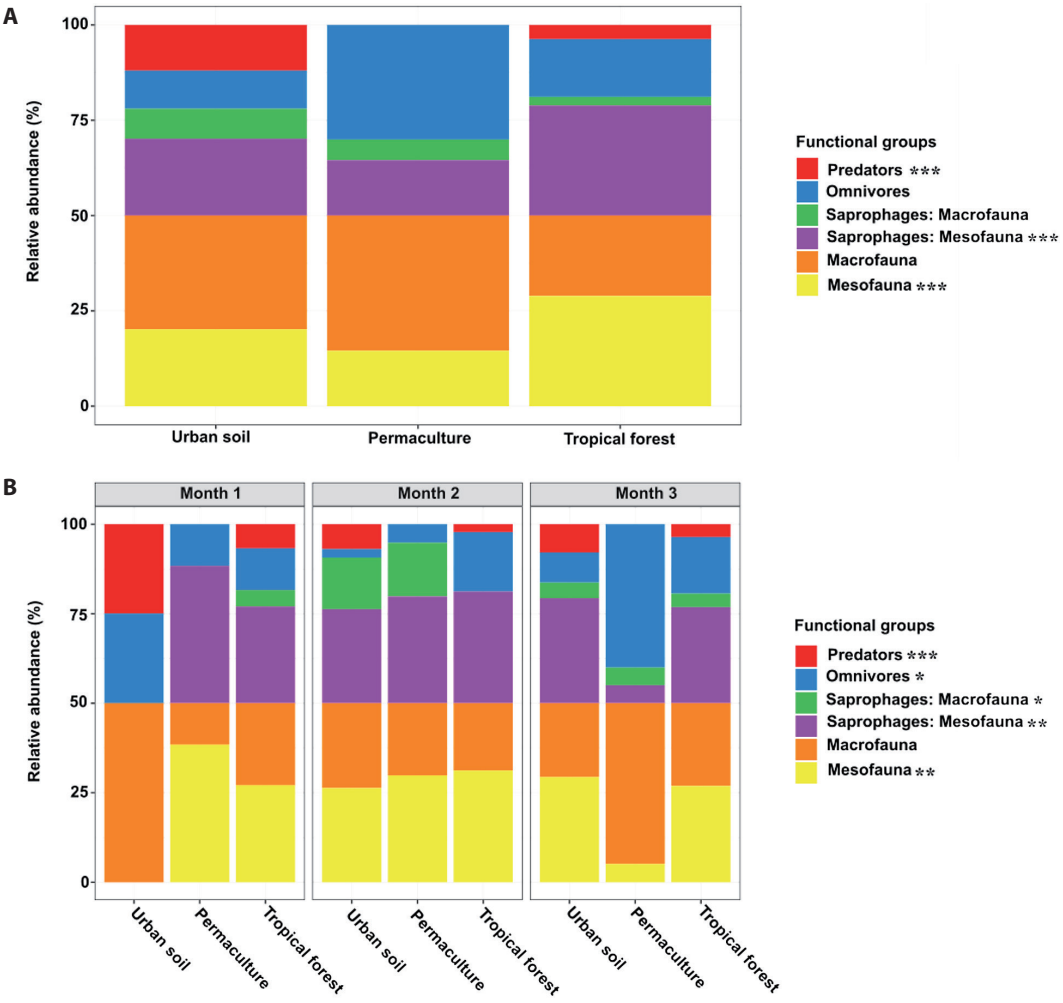

Fig. 2 Relative abundance of functional groups of soil fauna among different locations (A) and sampling times (B). Two-way ANOVA; *P < 0.05, **P < 0.01, ***P < 0.001.

Table 3 Abundance of taxonomic and functional groups of soil fauna (individuals per m2) among various locations and sampling times.

Group		Locations				Sampling times			
		Urban soil	Permaculture	Tropical rain forest	ANOVA	Month 1	Month 2	Month 3	ANOVA
Collembola		33.0±10b	17±1.8c	84±15a	***	20±6c	74±18.9a	40±8b	***
Acari		20±6c	46±4b	74±15a	***	27±9c	70±13a	44±9b	**
Diplura		0.±0b	0±0b	20±10a	*	20±10a	0±0b	0±0b	*
Symphylla		0±0b	3±2a	0±0b	*	3±2a	0±0b	0±0b	*
Pauropoda		0±0b	4±2a	0±0b	*	4±2a	0±0b	0±0b	*
Protura		7±4a	0±0b	0±0b	*	0±0b	0.0±0b	7±4a	*
Lumbricidae		20±10a	19±5a	0±0b	*	0±0c	30±9a	9±5b	***
Diplopoda		4±2	0±0	3±2		3±2	0±0	4±2	
Isoptera		0±0c	4±2b	11±3a	***	4±2b	0±0c	11±3a	***
Isopoda		0.0±0.0b	3±2a	0±0b	*	0±0b	0±0b	3±2a	*
Araneae		29±8a	0±0c	19±3b	***	30±9a	12±3b	6±2b	***
Chilopoda		7±2a	0±0c	3±2b	***	0±0b	3±2a	7±2a	***
Formicidae		20±8	124±60	50±15		30±6	40±18	124±60	
Coleoptera		3±2b	0±0b	20±6a	***	3±2	7±3	13±7	
Insect others		3±2c	13±2b	20±5a	***	7.6±2b	6.4±2b	22±4a	***
Blattodea		4±2	8±2	3±2		7±2a	0±0b	8±2a	**
Predators		36±6a	0±0c	23±2b	***	30±9a	16±4b	13±3b	***
Omnivores		30±8	145±63	93±12		48±4b	53±22b	168±58a	*
Sapro-phages	Macrofauna	24±9	26±7	14±4		7±3b	30±9a	27±6a	*
	Mesofauna	60.7±16b	70.±8b	177±21a	***	74.±19b	144±30a	91±15b	**
Total	Macrofauna	90±10	171±68	130±8		84±14	100±17	208±60	
	Mesofauna	61±16b	70±8b	177±21a	***	74±19b	144±30a	91±15b	**
Total fauna		150.±15b	242±63a	307±29a	*	158±16b	243±47a	298±53a	*

Two-way ANOVA; *P < 0.05, **P < 0.01, ***P < 0.001. Letters indicate statistical homogenous groups.

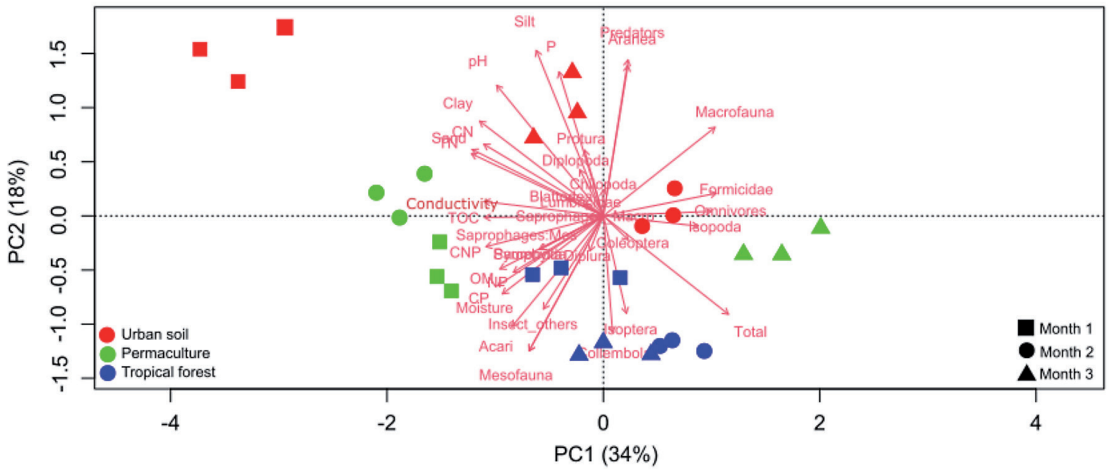

Fig. 3 Principal component analyses (PCA) of community structure of taxonomic and functional groups of soil fauna and soil physico-chemical properties among various sites and sampling times.

The alpha diversity of soil faunal groups, based on the number of taxonomic groups, differed among various locations and sampling times (Table 2). Soils in tropical forests hosted significantly higher taxonomic richness, Shannon index, and Simpson index than those in permaculture and urban areas. Taxonomic richness, Shannon index, and Simpson index did not differ between urban soils and permaculture. Furthermore, the taxonomic richness of soil fauna differed significantly among sampling times, showing an increasing trend over time. In

contrast, the Shannon index and Simpson index did not show any significant differences among sampling times.

The abundance of various taxonomic and functional groups differed among locations and sampling times (Table 3; Fig. 2). For example, *Acari* exhibited the highest abundance in tropical soils, intermediate abundance in permaculture, and the lowest abundance in urban soils. Furthermore, the abundance of *Acari* varied among sampling times. The total abundance of soil fauna was higher in tropical soils and in permaculture than in urban soils. Both soil mesofauna and saprophagous mesofauna showed significantly higher densities in tropical forests compared to permaculture and urban soil. In contrast, soil macrofauna and saprophagous macrofauna did not

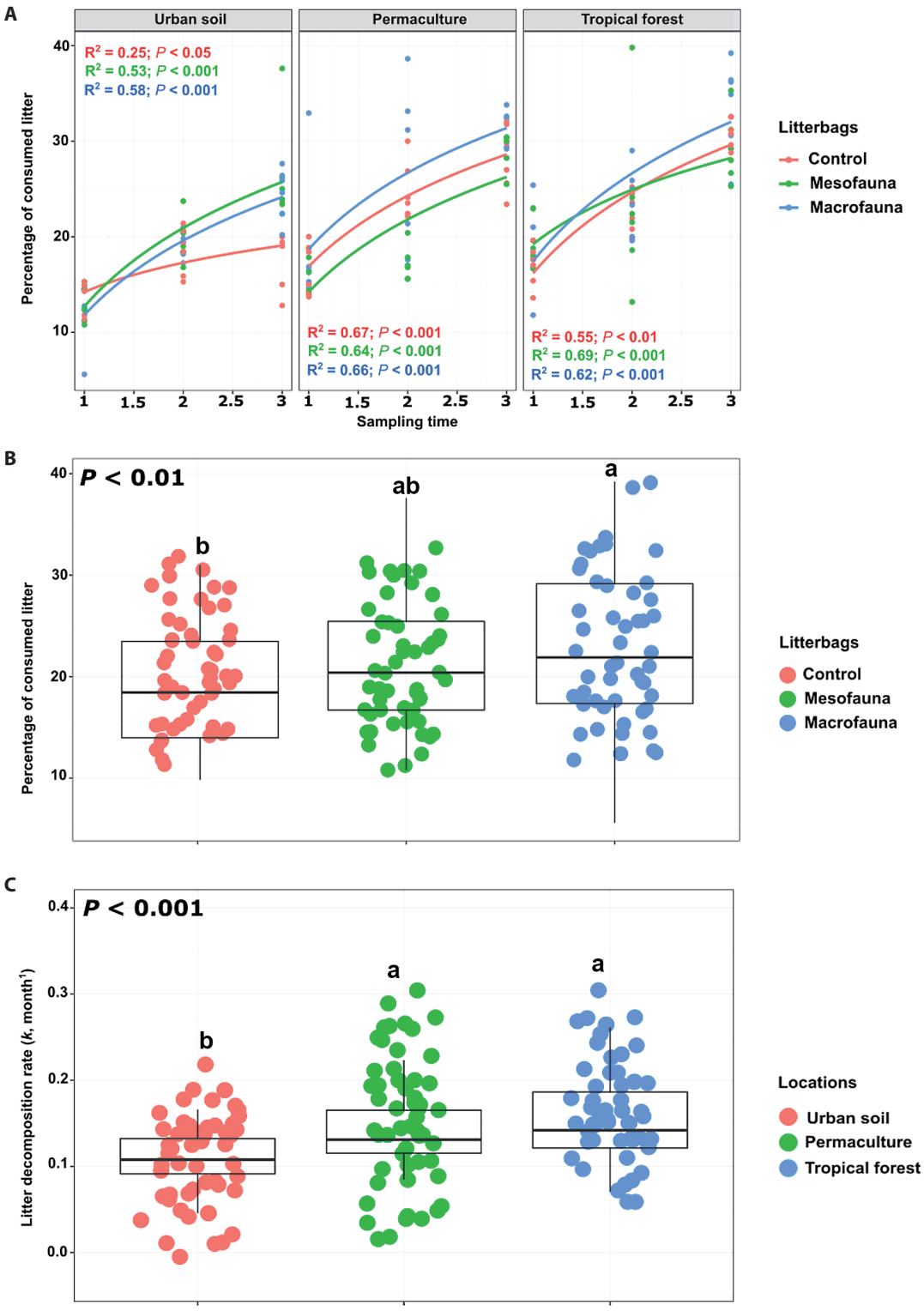

Fig. 4 Percentage of litter mass loss among sampling times (A) and different mesh sizes (B) and decomposition rates among different sampling sites (C). Letters indicate statistical homogenous groups.

show any significant differences among sampling sites. However, both soil macrofauna and saprophagous macrofauna exhibited differences among samplingtimes.

The PCA diagram revealed divergence in the community structure of taxonomic and functional groups among different locations and sampling times (Fig. 3). In urban soils, the community of soil fauna primarily comprised *Aranea*, *Protura*, and *Diplura*, and was associated with high pH, silt content, and P content. Conversely, the structure of soil fauna in permaculture and tropical forests mainly consisted of Acari and Collembola, with their community composition associated with a high C:N:P ratio, organic matter content, and soil moisture.

Effect of soil fauna on litter decomposition

Our results revealed an increase in litter mass loss in all types of litterbags over the course of increased incubation time (Fig. 4A). The litter mass loss was lowest after one month of incubation and highest after three months. The percentage of litter mass loss differed among litterbags with varying accessibility to soil meso- and macrofauna (Fig. 4B). Litterbags accessible to macrofauna exhibited a significant difference from control litterbags but did not show any significant differences compared to those accessible to mesofauna. Litterbags accessible to mesofauna did not show any significant difference in litter mass loss compared to control litterbags. Litterbags accessible to macrofauna in tropical forest and permaculture exhibited a higher percentage of mass loss than those in urban soils. Litter decomposition rates (*k* values) differed significantly among litterbags incubated at different locations (Fig. 4C). Litterbags in tropical forests and permaculture exhibited higher decomposition rates than those in urban soils. The litter chemistry in litterbags incubated for three months in different locations differed significantly among sampling locations but was not affected by mesh size. The TOC and CN ratio of litter in litterbags incubated in tropical forest and permaculture increased while urban soils showed no significant changes (Figs 5A–B). In addition, TN of litter incubated in all locations decreased significantly after three months of incubation (Fig. 5C).

Effect size measurement revealed that accessibility to soil mesofauna significantly increased decomposition

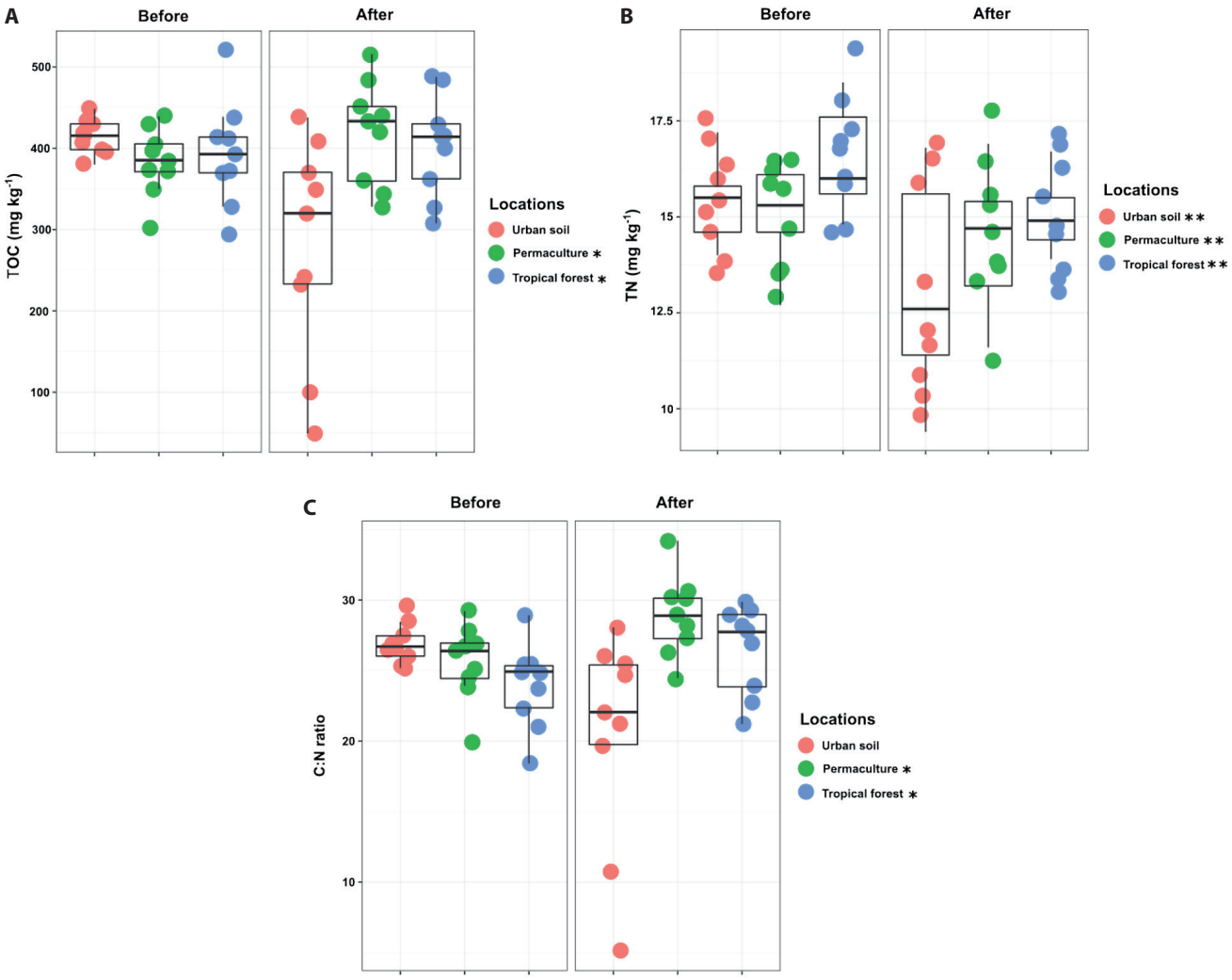

Fig. 5 Total Organic Carbon (A), total Nitrogen (B) and C:N ratio (C) of litter in litterbags incubated in different sampling locations. Asterisks indicate statistically significant differences (Paired t-test; *P < 0.05, **P < 0.01).

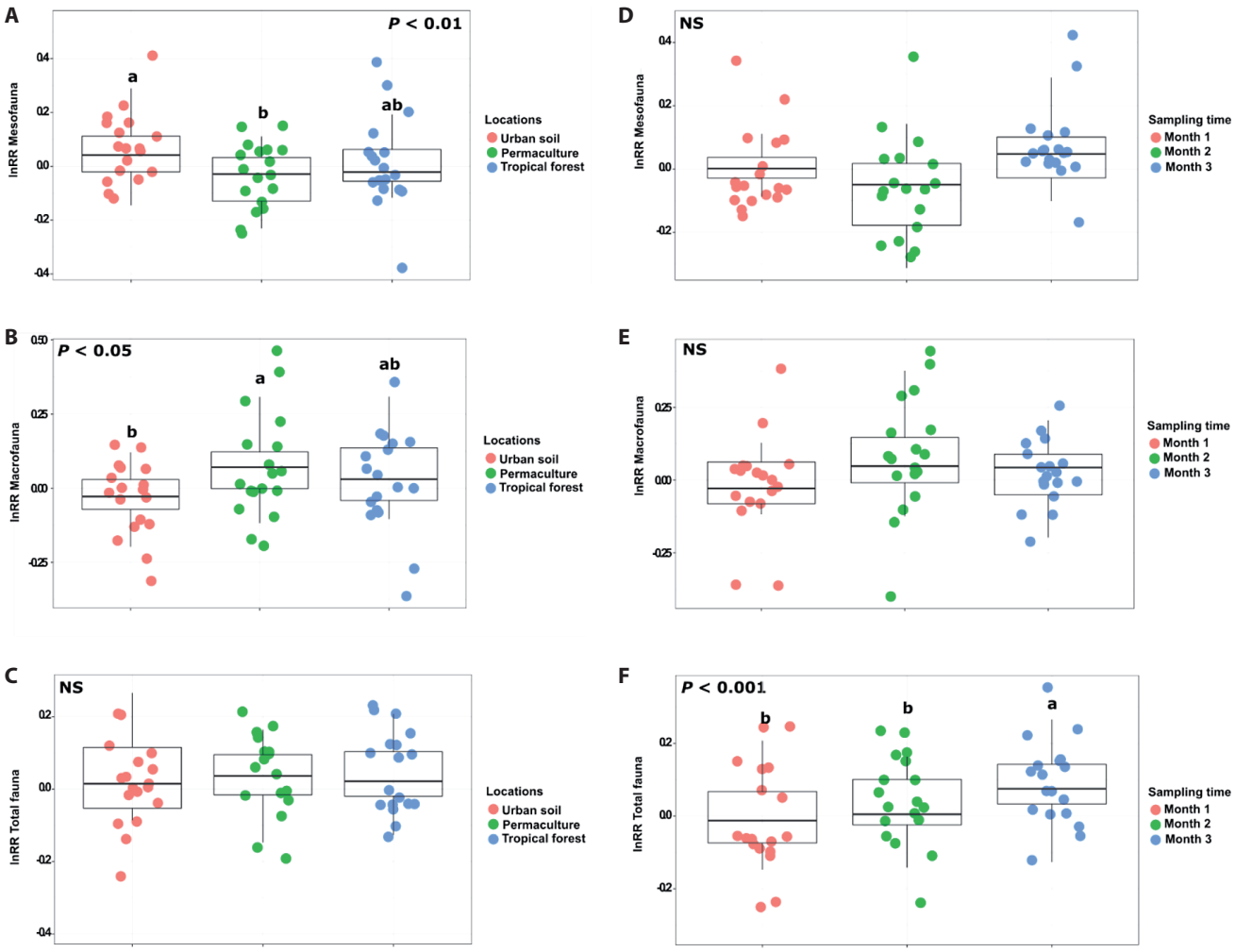

Fig. 6 Effect of soil mesofauna, macrofauna and total fauna on litter decomposition rates among locations (A–C) and sampling times (D–F). Letters indicate statistical homogenous groups.

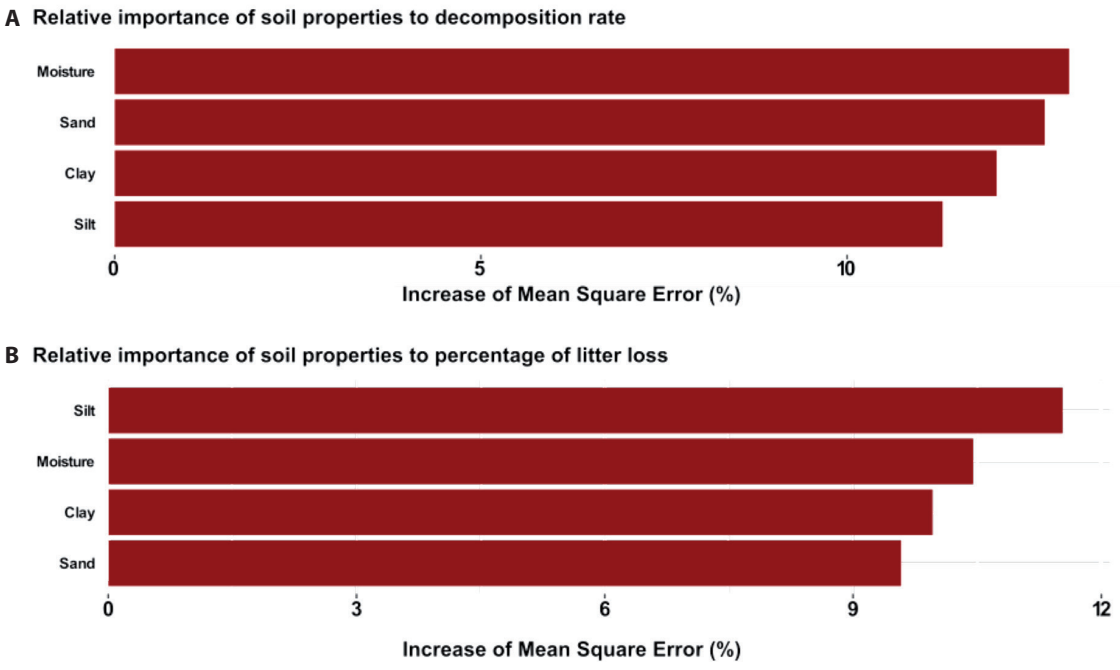

Fig. 7 Relative importance of soil physico-chemical properties to decomposition rates (A) and percentage of litter mass loss (B).

Table 4 Pearson correlation coefficients of soil physico-chemical properties and litter decomposition expressed as percentage of litter mass loss and decomposition rate.

	Percentage	Decomposition rate (k, months)
Moisture	0.33*	0.34*
pH	0.11	0.14
Conductivity	0.06	0.12
TOC	0.07	0.10
TN	0.25	0.27
CN	−0.04	−0.01
P	−0.17	−0.16
CP	0.20	0.20
NP	0.27	0.27
CNP	0.16	0.16
OM	0.13	0.16
Clay	0.35*	0.37*
Silt	−0.35*	−0.36*
Sand	0.35*	0.37*

Asterisks indicate statistically significant differences, *P < 0.05, Bonferonni corrections were used to adjust multiple correlations.

rates in litterbags incubated in urban soils more than in permaculture without any other significant differences (Fig. 6A). Soil macrofauna increased litter decomposition rates in permaculture compared to urban soil but did not show any differences between urban soils and tropical forest or tropical forest and permaculture (Fig. 6B). Accessibility to both macrofauna and mesofauna together did not show any effect on decomposition rates (Fig. 6C). The effect of accessibility to mesofauna or macrofauna on litter decomposition did not differ among different sampling times, however, accessibility to both mesofauna and macrofauna together had a significantly larger effect on litter decomposition three months after incubation (Figs 6D–F).

Random forest analyses revealed the importance of soil moisture, sand content, clay content, and silt content, respectively, for decomposition rates (Fig. 7A). Similarly, silt content, soil moisture, clay content, and sand content, respectively, significantly contributed to litter mass loss (Fig. 7B). Pearson correlation coefficient revealed that litter decomposition rates and the percentage of mass loss increased significantly with soil moisture and with the content of clay and sand, while they decreased with silt content (Table 4).

Discussion

Soil fauna variation across locations

Our results revealed more diverse communities of soil fauna in tropical rainforest than in permaculture and urban soils. We hypothesize that variations in the diversity of soil fauna are mediated by abundant and diverse resources in tropical forest, stable environmental conditions, low levels of disturbance, and complex ecological interactions. For example, the structural complexity of rainforests creates numerous microhabitats, from the mineral soils to the forest floor, which supports different soil fauna species adapted to specific niches and thus increasing overall soil biodiversity (Korboulewsky et al. 2016). In agreement with Korboulewski et al. (2016), we suggest that soil fauna is directly affected by the physical characteristics (microhabitats) and chemical composition (resource quality) of the litter specific to each tree species. In addition, soil communities are also affected by humus characteristics which are strongly linked with the litter chemistry of aboveground vegetation and often vary at different site locations (Korboulewsky et al. 2016; Schelfhout et al. 2017).

The relative abundances of various taxonomic and functional groups differed among locations and sampling times. We expect that abundances of various taxonomic and functional groups are linked to resource availability. We suggest that high nutrient content related to rapid decomposition processes in tropical habitats further supports growth and reproduction of soil organisms (Wall et al. 2008; Zhang et al. 2008; Peguero et al. 2019; Schaefer et al. 2009). Our results indicate changes in the composition of various taxonomic and functional groups of soil fauna with significantly higher densities of soil mesofauna and saprophagous mesofauna in the tropical forest compared to permaculture and urban soil. We suggest that changes in the composition of various groups of soil fauna are driven directly by aboveground vegetation via the feeding preferences of different animals. For example, a study by Gerlach et al. (2014) revealed different feeding preferences of isopods for various native and introduced plants. Moreover, a laboratory study by Heděnec et al. (2023) showed a higher consumption rate of high-quality leaf litter consumed by soil macrofauna. Similarly, a field study by Peng et al. (2022a) from the temperate zone revealed a shift in community structure of soil meso- and macrofauna in soils beneath different tree species which also differed in litter chemistry.

Our study revealed that the community structure of soil fauna in urban soils was associated with soil pH, silt content, and P content while the structure of soil fauna in permaculture and tropical forests mainly was primarily shaped by C:N:P ratio, organic matter content, and soil moisture. In addition, community structure diverged between different sampling locations. The sampling locations showed differences in soil physico-chemical properties, as well as by vegetation cover. We expect that soil physico-chemical properties are shaped by parent material and dominant vegetation (Birkhofer et al. 2012; De Schrijver et al. 2012). We expect that soil physico-chemical properties shape various groups of soil fauna indirectly via their direct effect on soil microbiota. For example, soil pH or moisture can stimulate bacterial or fungal growth

and thus can stimulate the abundance of bacterial or fungal feeders (Rousk and Bååth 2011; Heděnec et al. 2024).

Soil fauna accessibility enhances litter decomposition

Our results revealed an increase in litter mass loss for three months of incubation. We hypothesize that soil fauna would affect litter decomposition even at the early decomposition stage within three months of litterbag exposure. Increased decomposition over time can be attributed to the progressive colonization and activity of soil animals, which intensify decomposition during time. We suggest that warm and humid tropical climate supports litter decomposition in comparison with drier and colder biomes (Wall et al. 2008; Frouz et al. 2015; Heděnec et al. 2022). We also expect that stable moisture and temperature in tropical climates can accelerate the physiological activity of soil animals as well as soil microbiota, which can potentially result in high decomposition rates (Powers et al. 2009; Peguero et al. 2019).

Our study showed that litterbags accessible to macrofauna exhibited a significantly higher litter mass loss than control litterbags but did not show any significant differences compared to those accessible to mesofauna. This indicates the crucial role of macrofauna in breaking down litter, likely due to their ability to fragment larger pieces of organic matter, thereby increasing the surface area available for microbial decomposition (García-Palacios et al. 2013; Frouz 2018; Fujii et al. 2018). Our results partly corroborate with similar litterbag studies across different habitat types with various dominant vegetation (Peguero et al. 2019; Peng et al. 2022b), however, our results showed significant litter mass loss only in litterbags accessible for macrofauna. We hypothesize that body size can affect litter decomposition rate via a higher consumption rate per body weight. For instance, a study by Ardestani et al. (2019) showed that big-size animals consumed more leaves per unit of body weight than small-sized animals.

Interestingly, litterbags in tropical forests and permaculture did not differ significantly in decomposition rates, suggesting that both environments provide favorable conditions for decomposers, possibly due to higher resource availability, moisture levels, and more stable microclimatic conditions compared to urban soils. However, our results based on effect size showed that soil macrofauna showed the highest effect on litter mass loss in permaculture. This suggests that in highly biodiverse tropical forests, other factors such as microbial activity and environmental conditions might play a more dominant role in driving decomposition (Wall et al. 2008; García-Palacios et al. 2013). In contrast, in permaculture systems, where biodiversity is managed and possibly less diverse than in natural forests, macrofauna might have a more pronounced effect.

Our effect size comparison showed that mesofauna exhibited the highest effect on litter mass loss in urban soils. This could be explained by the fact that urban soils typically have lower organic matter and nutrient levels compared to permaculture and tropical forests as shown by our data. Therefore, the presence and activity of mesofauna can have a disproportionately large impact on litter decomposition, as these organisms become critical drivers of the process (Peguero et al. 2019). Moreover, reduced biodiversity in urban soils means that mesofauna, which might otherwise be one of many decomposer groups, plays a more central role in the decomposition process in urban soils.

Our results indicated an increase of TOC and C:N ratio of litter in litterbags after three months of incubation while TN of litter in litterbags decreased significantly after three months of incubation. This suggests that soil fauna preferred the most palatable litter with a low CN ratio and left in litterbags only litter with a high C:N ratio. In addition, the passing of consumed leaf litter through the gut system also reduces the chemistry of feces which may affect the total C:N ratio of remaining litter in litterbags.

Soil properties shape fauna-mediated litter decomposition

The random forest analyses underscored the complex interplay of soil properties in shaping decomposition processes, revealing how different soil texture components, such as clay, sand, and silt, can significantly influence the rates and efficiency of litter decomposition. High clay content, for example, has been found to enhance moisture retention in soils, which is beneficial for the activity of decomposers such as microbes and soil fauna that require moist conditions to thrive (Cortez 1998; Butterly et al. 2010). Moisture is critical for enzymatic reactions involved in the breakdown of organic matter, and adequate moisture levels can facilitate the growth and activity of decomposing organisms, thereby accelerating decomposition processes (Brockett et al. 2012).

In contrast, the presence of clay in excessive amounts can also impede soil aeration, creating anaerobic conditions that are less favorable for many decomposers. In poorly aerated soils, the activity of these microorganisms is restricted, slowing down the decomposition process (Wang et al. 2021; Qian et al. 2022). Furthermore, anaerobic conditions can lead to the production of toxic substances such as methane and hydrogen sulfide, which can inhibit the activity of soil fauna and further inhibit microbial decomposition (van Agtmaal et al. 2015). Therefore, while clay content is beneficial for moisture retention, it must be balanced to avoid negative impacts on soil aeration. Furthermore, clay soils, with their fine particles, tend to be dense and compact, which can impede the movement and penetration of larger soil organisms like macrofauna (Swift et al. 1979; Frouz et al. 2006; Ruiz et al. 2008). These conditions are limiting factors for such fauna to create and maintain their own tunnels, potentially limiting their ability to forage and thrive.

Sand, on the other hand, contributes to better aeration and drainage due to its larger particle size and greater pore spaces between particles (Lavelle et al. 2020). Soils

with higher sand content tend to be well-aerated, which supports the activity of aerobic decomposers and facilitates rapid organic matter breakdown (Coleman et al. 2004; Wang et al. 2021). However, sandy soils can suffer from poor moisture retention, especially in dry conditions, which can limit the availability of water to decomposers and slow down decomposition (Coleman et al. 2004; de Vries et al. 2012; Alster et al. 2013). Thus, the positive effects of sand on soil aeration need to be balanced with sufficient moisture retention to support continuous decomposition activity. Sandy soils, with larger particles and greater pore spaces, offer less resistance to movement and are more easily penetrated by both macrofauna and mesofauna (Swift et al. 1979; Wall et al. 2008; Xin et al. 2012). These conditions facilitate the creation of tunnels and burrows, enabling soil organisms to navigate and exploit their environment effectively.

Silt particles alter moisture retention and aeration (Coleman et al. 2004). Silt improves soil structure and thus the availability of nutrients to soil organisms. However, too much silt can lead to compaction and reduce soil pore spaces, negatively impacting both aeration and water infiltration (Hartmann et al. 2014). The optimal decomposition rates are achieved when soil texture maintains a balance between these components – clay for moisture retention, sand for aeration, and silt for nutrient availability and structure (Callesen et al. 2003; Coleman et al. 2004; Velasquez et al. 2007). This balance ensures that soil conditions remain conducive to the activity of decomposers, supporting efficient organic matter breakdown and nutrient cycling in various soil environments.

Implications, limitations and future perspective

Our study revealed that soil fauna has a large impact on litter decomposition. Efficient litter decomposition by soil fauna enhances nutrient cycling, thereby improving soil fertility and crop yields (De Vries et al. 2013; Edlinger et al. 2023). The implications of efficient litter decomposition extend beyond immediate soil fertility. The presence of a robust soil fauna community can also enhance crop resilience against pests and diseases, reducing reliance on chemical pesticides (Teixeira et al. 2019; Vannier et al. 2019; Griffiths et al. 2000; Delgado-Baquerizo et al. 2020). Furthermore, our findings emphasize the importance of understanding and conserving soil fauna diversity in urban and permaculture settings, as these ecosystems are often subject to anthropogenic disturbances which can impact soil fauna communities and, consequently, litter decomposition processes (Peng et al. 2022b). By recognizing the critical role of soil fauna in litter decomposition and ecosystem functioning, efforts can be made to integrate conservation and management practices that support soil fauna biodiversity and abundance.

We suggest that our study also includes several limitations but the methods used in our study make our results comparable to other studies. Firstly, decomposition was measured solely through mass loss from the litterbags, which does not fully capture the underlying mechanisms driving these processes. Mass loss can result from various factors, including microbial mineralization, leaching, and the fragmentation and washing out of small organic matter particles, making it difficult to distinguish the specific contributions of these processes (Kampichler and Bruckner 2009; Frouz 2018). Additionally, the role of soil fauna in litter decomposition is complex; fauna can both accelerate and slow down microbial activity through their consumption and transformation of litter (Frouz 2018; Angst et al. 2024). Furthermore, the use of litterbags with different mesh sizes may not perfectly replicate natural conditions where litter is freely accessible to all decomposers. We suggest that our study focused on specific sites and may not capture the full range of soil fauna diversity and dynamics in tropical ecosystems. Additionally, the short-term nature of the study may not fully represent long-term trends in litter decomposition dynamics. Despite the above-mentioned limitation, our study provides new insights into the initial dynamics of decomposition that are often neglected in long-term studies. We suggest that future research should employ more comprehensive methods to highlight the intricate mechanisms of litter decomposition and to fully understand the ecological roles of soil fauna. For example, combining litterbag experiments with laboratory cutting-edge methods, such as the stable isotope method, amplicon sequencing method or shotgun metagenomic method is promising to investigate specific groups of soil biota involved in specific decomposition processes (Baldrian 2017; Sultana et al. 2019; Zhang et al. 2020).

Conclusion

Our study revealed the complex interplay between soil properties, soil fauna composition, and environmental factors in shaping litter decomposition processes. For example, the significant variation observed in soil physico-chemical properties among different sampling locations highlights the diverse environmental conditions supporting various groups of soil fauna that litter decomposition. Furthermore, our results showed the impact of soil fauna on litter decomposition, with macrofauna playing a particularly significant role. Understanding the interactions between soil fauna and environmental factors, such as soil moisture and nutrient content, can provide valuable insights for ecosystem management and conservation strategies aimed at enhancing litter decomposition and nutrient cycling in terrestrial ecosystems.

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Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT – OpenAI version 3.2 in order to grammar check and edit English language since author(s) are not native English speakers. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

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Supplementary file S1

	Treatment	Locality	Time	Before	After	Percentage	k
A1	2 cm	Tropical_rain_forest	1	5,0	3,73	25,4	0,29
A2	2 cm	Tropical_rain_forest	1	5,0	4,41	11,8	0,13
A3	2 cm	Tropical_rain_forest	1	5,0	3,95	21,0	0,24
A4	2 cm	Tropical_rain_forest	1	5,1	4,20	17,6	0,19
A5	2 cm	Tropical_rain_forest	1	5,0	4,15	17,0	0,19
A6	2 cm	Tropical_rain_forest	1	5,1	4,18	18,0	0,20
A7	2 mm	Tropical_rain_forest	1	5,1	4,10	19,6	0,22
A8	2 mm	Tropical_rain_forest	1	5,1	3,93	22,9	0,26
A9	2 mm	Tropical_rain_forest	1	5,0	3,85	23,0	0,26
A10	2 mm	Tropical_rain_forest	1	5,0	4,06	18,8	0,21
A11	2 mm	Tropical_rain_forest	1	5,0	4,10	18,0	0,20
A12	2 mm	Tropical_rain_forest	1	5,1	4,25	16,7	0,18
A13	0.2 mm	Tropical_rain_forest	1	5,0	4,08	18,4	0,20
A14	0.2 mm	Tropical_rain_forest	1	5,0	4,23	15,4	0,17
A15	0.2 mm	Tropical_rain_forest	1	5,0	4,32	13,6	0,15
A16	0.2 mm	Tropical_rain_forest	1	5,0	4,02	19,6	0,22
A17	0.2 mm	Tropical_rain_forest	1	5,0	4,15	17,0	0,19
A18	0.2 mm	Tropical_rain_forest	1	5,0	4,12	17,6	0,19
B1	2 cm	Urban_soil	1	5,0	4,38	12,4	0,13
B2	2 cm	Urban_soil	1	5,1	4,36	14,5	0,16
B3	2 cm	Urban_soil	1	5,1	4,37	14,3	0,15
B4	2 cm	Urban_soil	1	5,1	4,45	12,7	0,14
B5	2 cm	Urban_soil	1	5,0	4,72	5,6	0,06
B6	2 cm	Urban_soil	1	5,1	4,46	12,5	0,13
B7	2 mm	Urban_soil	1	5,1	4,47	12,4	0,13
B8	2 mm	Urban_soil	1	5,0	4,44	11,2	0,12
B9	2 mm	Urban_soil	1	5,1	4,36	14,5	0,16
B10	2 mm	Urban_soil	1	5,1	4,32	15,3	0,17
B11	2 mm	Urban_soil	1	5,1	4,55	10,8	0,11
B12	2 mm	Urban_soil	1	5,1	4,36	14,5	0,16
B13	0.2 mm	Urban_soil	1	5,1	4,34	14,9	0,16
B14	0.2 mm	Urban_soil	1	5,1	4,32	15,3	0,17
B15	0.2 mm	Urban_soil	1	5,0	4,41	11,8	0,13
B16	0.2 mm	Urban_soil	1	5,1	4,37	14,3	0,15
B17	0.2 mm	Urban_soil	1	5,1	4,52	11,4	0,12
B18	0.2 mm	Urban_soil	1	5,1	4,34	14,9	0,16
C1	2 cm	Permaculture	1	5,1	4,35	14,7	0,16
C2	2 cm	Permaculture	1	5,1	4,37	14,3	0,15
C3	2 cm	Permaculture	1	5,1	4,32	15,3	0,17
C4	2 cm	Permaculture	1	5,1	4,24	16,9	0,18
C5	2 cm	Permaculture	1	5,1	3,42	32,9	0,40
C6	2 cm	Permaculture	1	5,1	4,26	16,5	0,18
C7	2 mm	Permaculture	1	5,1	4,14	18,8	0,21

	Treatment	Locality	Time	Before	After	Percentage	k
C8	2 mm	Permaculture	1	5,1	4,19	17,8	0,20
C9	2 mm	Permaculture	1	5,1	4,27	16,3	0,18
C10	2 mm	Permaculture	1	5,0	4,30	14,0	0,15
C11	2 mm	Permaculture	1	5,0	4,28	14,4	0,16
C12	2 mm	Permaculture	1	5,0	4,29	14,2	0,15
C13	0.2 mm	Permaculture	1	5,0	4,00	20,0	0,22
C14	0.2 mm	Permaculture	1	5,1	4,38	14,1	0,15
C15	0.2 mm	Permaculture	1	5,0	4,25	15,0	0,16
C16	0.2 mm	Permaculture	1	5,0	4,08	18,4	0,20
C17	0.2 mm	Permaculture	1	5,1	4,14	18,8	0,21
C18	0.2 mm	Permaculture	1	5,1	4,4	13,7	0,15
D1	2 cm	Urban_soil	2	5,0	4,03	19,4	0,11
D2	2 cm	Urban_soil	2	5,1	4,03	21,0	0,12
D3	2 cm	Urban_soil	2	5,1	4,09	19,8	0,11
D4	2 cm	Urban_soil	2	5,0	4,09	18,2	0,10
D5	2 cm	Urban_soil	2	5,1	4,16	18,4	0,10
D6	2 cm	Urban_soil	2	5,1	4,22	17,3	0,09
D7	2 mm	Urban_soil	2	5,1	4,06	20,4	0,11
D8	2 mm	Urban_soil	2	5,1	4,16	18,4	0,10
D9	2 mm	Urban_soil	2	5,1	4,05	20,6	0,12
D10	2 mm	Urban_soil	2	5,0	4,16	16,8	0,09
D11	2 mm	Urban_soil	2	5,1	3,89	23,7	0,14
D12	2 mm	Urban_soil	2	5,1	4,13	19,0	0,11
D13	0.2 mm	Urban_soil	2	5,0	3,93	21,4	0,12
D14	0.2 mm	Urban_soil	2	5,0	3,97	20,6	0,12
D15	0.2 mm	Urban_soil	2	5,1	4,32	15,3	0,08
D16	0.2 mm	Urban_soil	2	5,1	4,29	15,9	0,09
D17	0.2 mm	Urban_soil	2	5,1	4,16	18,4	0,10
D18	0.2 mm	Urban_soil	2	5,1	4,11	19,4	0,11
E1	0.2 mm	Tropical_rain_forest	2	5,0	4,01	19,8	0,11
E2	0.2 mm	Tropical_rain_forest	2	5,0	3,74	25,2	0,15
E3	0.2 mm	Tropical_rain_forest	2	5,0	3,82	23,6	0,13
E4	0.2 mm	Tropical_rain_forest	2	5,1	3,98	22,0	0,12
E5	0.2 mm	Tropical_rain_forest	2	5,1	3,85	24,5	0,14
E6	0.2 mm	Tropical_rain_forest	2	5,0	3,96	20,8	0,12
E7	2 cm	Tropical_rain_forest	2	5,0	4,00	20,0	0,11
E8	2 cm	Tropical_rain_forest	2	5,0	3,75	25,0	0,14
E9	2 cm	Tropical_rain_forest	2	5,0	4,02	19,6	0,11
E10	2 cm	Tropical_rain_forest	2	5,1	3,62	29,0	0,17
E11	2 cm	Tropical_rain_forest	2	5,1	3,91	23,3	0,13
E12	2 cm	Tropical_rain_forest	2	5,1	3,78	25,9	0,15
E13	2 mm	Tropical_rain_forest	2	4,9	2,95	39,8	0,25
E14	2 mm	Tropical_rain_forest	2	5,16	4,48	13,2	0,07
E15	2 mm	Tropical_rain_forest	2	5,0	4,07	18,6	0,10
E16	2 mm	Tropical_rain_forest	2	5,02	3,94	21,5	0,12

	Treatment	Locality	Time	Before	After	Percentage	k
E17	2 mm	Tropical_rain_forest	2	5,0	3,88	22,4	0,13
E18	2 mm	Tropical_rain_forest	2	5,1	3,87	24,1	0,14
F1	2 cm	Permaculture	2	5,1	3,51	31,2	0,19
F2	2 cm	Permaculture	2	5,1	4,01	21,4	0,12
F3	2 cm	Permaculture	2	5,0	3,88	22,4	0,13
F4	2 cm	Permaculture	2	5,0	4,12	17,6	0,10
F5	2 cm	Permaculture	2	5,1	3,41	33,1	0,20
F6	2 cm	Permaculture	2	5,1	3,13	38,6	0,24
F7	0.2 mm	Permaculture	2	5,1	3,73	26,9	0,16
F8	0.2 mm	Permaculture	2	5,0	3,88	22,4	0,13
F9	0.2 mm	Permaculture	2	5,1	3,97	22,2	0,13
F10	0.2 mm	Permaculture	2	5,1	3,90	23,5	0,13
F11	0.2 mm	Permaculture	2	5,1	3,87	24,1	0,14
F12	0.2 mm	Permaculture	2	5,0	3,50	30,0	0,18
F13	2 mm	Permaculture	2	5,0	4,16	16,8	0,09
F14	2 mm	Permaculture	2	5,1	4,19	17,8	0,10
F15	2 mm	Permaculture	2	5,0	4,15	17,0	0,09
F16	2 mm	Permaculture	2	5,0	4,22	15,6	0,08
F17	2 mm	Permaculture	2	5,0	4,22	15,6	0,08
F18	2 mm	Permaculture	2	5,0	3,98	20,4	0,11
G1	0.2 mm	Urban_soil	3	5,1	4,13	19,0	0,07
G2	0.2 mm	Urban_soil	3	5,1	4,11	19,4	0,07
G3	0.2 mm	Urban_soil	3	5,0	4,00	20,0	0,07
G4	0.2 mm	Urban_soil	3	5,0	4,36	12,8	0,05
G5	0.2 mm	Urban_soil	3	5,0	3,82	23,6	0,09
G6	0.2 mm	Urban_soil	3	5,0	4,25	15,0	0,05
G7	2 mm	Urban_soil	3	5,1	3,88	23,9	0,09
G8	2 mm	Urban_soil	3	5,0	3,88	22,4	0,08
G9	2 mm	Urban_soil	3	5,0	3,75	25,0	0,10
G10	2 mm	Urban_soil	3	5,0	3,83	23,4	0,09
G11	2 mm	Urban_soil	3	5,0	3,69	26,2	0,10
G12	2 mm	Urban_soil	3	5,0	3,12	37,6	0,16
G13	2 cm	Urban_soil	3	5,0	3,68	26,4	0,10
G14	2 cm	Urban_soil	3	5,1	3,69	27,6	0,11
G15	2 cm	Urban_soil	3	5,0	3,88	22,4	0,08
G16	2 cm	Urban_soil	3	5,1	4,07	20,2	0,08
G17	2 cm	Urban_soil	3	5,0	3,77	24,6	0,09
G18	2 cm	Urban_soil	3	5,1	3,78	25,9	0,10
H1	2 cm	Tropical_rain_forest	3	5,0	3,47	30,6	0,12
H2	2 cm	Tropical_rain_forest	3	5,0	3,18	36,4	0,15
H3	2 cm	Tropical_rain_forest	3	5,1	3,10	39,2	0,17
H4	2 cm	Tropical_rain_forest	3	5,0	3,19	36,2	0,15
H5	2 cm	Tropical_rain_forest	3	5,1	3,32	34,9	0,14
H6	2 cm	Tropical_rain_forest	3	5,1	3,80	25,5	0,10
H7	2 mm	Tropical_rain_forest	3	5,1	3,30	35,3	0,15

	Treatment	Locality	Time	Before	After	Percentage	k
H8	2 mm	Tropical_rain_forest	3	5,0	3,60	28,0	0,11
H9	2 mm	Tropical_rain_forest	3	5,1	3,74	26,7	0,10
H10	2 mm	Tropical_rain_forest	3	5,1	3,81	25,3	0,10
H11	2 mm	Tropical_rain_forest	3	5,1	3,61	29,2	0,12
H12	2 mm	Tropical_rain_forest	3	5,0	3,44	31,2	0,12
H13	0.2 mm	Tropical_rain_forest	3	5,0	3,56	28,8	0,11
H14	0.2 mm	Tropical_rain_forest	3	5,1	3,51	31,2	0,12
H15	0.2 mm	Tropical_rain_forest	3	5,1	3,59	29,6	0,12
H16	0.2 mm	Tropical_rain_forest	3	5,1	3,53	30,8	0,12
H17	0.2 mm	Tropical_rain_forest	3	5,1	3,44	32,5	0,13
H18	0.2 mm	Tropical_rain_forest	3	5,1	3,44	32,5	0,13
I1	2 cm	Permaculture	3	5,0	3,53	29,4	0,12
I2	2 cm	Permaculture	3	5,0	3,54	29,2	0,12
I3	2 cm	Permaculture	3	5,0	3,38	32,4	0,13
I4	2 cm	Permaculture	3	5,0	3,37	32,6	0,13
I5	2 cm	Permaculture	3	5,1	3,66	28,2	0,11
I6	2 cm	Permaculture	3	5,0	3,31	33,8	0,14
I7	0.2 mm	Permaculture	3	5,0	3,83	23,4	0,09
I8	0.2 mm	Permaculture	3	5,0	3,72	25,6	0,10
I9	0.2 mm	Permaculture	3	5,1	3,58	29,8	0,12
I10	0.2 mm	Permaculture	3	5,0	3,65	27,0	0,10
I11	0.2 mm	Permaculture	3	5,1	3,48	31,8	0,13
I12	0.2 mm	Permaculture	3	5,0	3,40	32,0	0,13
I13	2 mm	Permaculture	3	5,1	3,80	25,5	0,10
I14	2 mm	Permaculture	3	5,1	3,57	30,0	0,12
I15	2 mm	Permaculture	3	5,1	3,66	28,2	0,11
I16	2 mm	Permaculture	3	5,1	3,55	30,4	0,12
I17	2 mm	Permaculture	3	5,1	3,55	30,4	0,12
I18	2 mm	Permaculture	3	5,1	3,55	30,4	0,12