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Research Article

Seasonal Decomposition Rates of Broadleaf and Conifer Wood Litter in Far Eastern Tropical Forest Communities

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Studies on wood litter decomposition sometimes show conflicting results. While low temperatures and humidity during winter in temperate climates are reported to halt the activity of decomposing agents, in the warmest and wettest tropical regions of the Far East, peat accumulates on the forest floor, indicating that the decomposition process is not proceeding well. In this study, we compared the inter-seasonal and inter-forest communities' decomposition rate constant (k) of jabon (*Anthocephalus macrophyllus* (Roxb.) Havil.) and tusam (*Pinus merkusii* Jungh. & de Vriese) woods in three forest communities (Karst, Lowland, and Pine) on the Indonesian island of Sulawesi. We placed 1,200 wooden planks (600 jabon logs and 600 tusam logs) measuring 10 cm × 10 cm × 1.5 cm on the ground in each forest community during different seasons: dry season and wet season. k was observed seasonally. We also observed the decomposing agent diversity, soil properties, and chemical content of the wood sample to examine factors affecting k values. The results showed the tendency of jabon wood k to be higher in the dry season than in the wet season, and the opposite trend was noted for tusam wood. k of both wood samples was highest in Karst, followed by Lowland and Pine forests. However, except for bacterial diversity and abundance of *Odontotermes* sp., there was no clear correlation between k and the diversity and abundance of decomposing agents. The k values varied distinctly, even among samples within the same forest community in the same season, causing the data not to be normally distributed. These findings indicate that decomposition processes in tropical forests vary at the microsite scale due to the high diversity of decomposing agents and their complex reciprocal association.

1. Introduction

The process of litter decomposition, also known as litter mineralization, refers to the physical, chemical, and biological processes involved in breaking down litter into simpler chemical elements [1]. Litter decomposition is the most important process in the nutrient cycle to restore soil fertility in most forest ecosystems [2]. Wood is one of the components of litter that takes longer to decompose [3].

Many studies of forest litter decomposition have been conducted, especially in temperate regions [4, 5]. However, information on the pattern of litter decomposition, in particular wood litter, among forest communities, and the factors that could potentially determine the rate of the decomposition process are insufficient, unclear, and ambiguous [6]. While low temperatures during winter in temperate regions are reported to halt the activity of decomposing agents [7], temperature changes in the tropics, especially around the equator, are less noticeable throughout the year [8]. Many studies have also shown that the rate of decomposition is directly proportional to rainfall [9, 10]. Meanwhile, the facts reflect that in the warmest and wettest tropical regions around the equator in the Far East, such as on the Indonesian islands of Sumatera and Kalimantan

(Indonesian Borneo), many forest ecosystems where peat accumulates on the forest floor indicate that the decomposition process is not going well [11].

Several studies in temperate climates have also revealed that due to the allelopathic content of leaf litter, the decomposition process in coniferous forests is slower than that in broadleaf forests [12, 13]. However, such research in the tropics is lacking, as conifer species are not common in the tropics. As with fine litter, there are multiple factors that have the potential to determine the rate of decomposition of wood litter [7]. These factors mutually influence and may have different impacts on litter decomposition rates in certain forest community. The factors controlling the rate of decomposition may differ in different climate regions and different forest communities [14], whereas in tropical climates, rainfall is a major determinant of seasonal patterns. Therefore, the rate of decomposition will be different in different forest types and seasons.

In this study, we compared the rate of decomposition of broadleaf wood with coniferous wood between seasons in three tropical forest communities on Sulawesi Island, Indonesia: secondary broadleaf karst forest, secondary broadleaf lowland forest, and *Pinus merkusii* Jungh. & de Vriese plantation. We designed a wood decomposition experiment using wood from two species of trees: *Anthocephalus macrophyllus* (Roxb.) Havil. (jabon) wood as a representative of broadleaf wood and *Pinus merkusii* (tusam) wood as a representative of coniferous wood. By examining the decomposition of tusam wood outside of Pine forests and broadleaf wood within Pine forests, we intend to find out whether tusam wood also decomposes slowly in broadleaf forests, and conversely whether broadleaf wood decomposes slowly in Pine forests. We also intend to examine the intrinsic and extrinsic factors that play a role in the decomposition process of the two wood samples in the three forest communities.

Given that many studies have reported that pine leaves contain allelopathic substances [15, 16], we predicted that the diversity of decomposing agents, especially of microorganisms in Pine forests, is lower than that in Karst and Lowland forests. This may have implications for the slower rate of wood decomposition in the Pine (*P. merkusii*) forest compared to broadleaf forests for both jabon wood and tusam wood. However, since no studies report that tusam wood contains allelopathic substances, unlike its leaves, we predicted that there would be no difference in the rate of decomposition between jabon wood and tusam wood either in the Pine forest or broadleaf forest communities. Since soil pH is positively related to the diversity and abundance of microorganisms, especially bacteria [17], we predicted that the rate of decomposition in Karst forests would be the highest among the three studied forests.

2. Materials and Methods

2.1. Study Site. We conducted this study in three secondary forests regenerated after shifting cultivation on Sulawesi Island, Indonesia: a 45-year-old secondary karst forest (Karst forest hereafter), a 54-year-old secondary lowland forest (Lowland forest hereafter), and a 58-year-old *P. merkusii* plantation forest (Pine forest hereafter). Previously, Putra et al. [18] assigned permanent plots of 1 ha in each forest community to analyse the structure and species composition of the forest community (Table 1). We carried out this research in the same plots.

Among the five most dominant species in the Karst forest plot, four species were pioneer species: *Kleinhovia hospita* (20% basal area), *Cananga odorata* (12% basal area), *Pterospermum celebicum* (6% basal area), and *Dracontomelon dao* (5% basal area). Another species was a climax species, *Diospyros celebica* (8% basal area). Of the five most dominant species in the Lowland forest plot, *Areca catechu* (23% basal area) and *Arenga pinnata* (13% basal area) were palms, while the other three species were climax species: *Diospyros celebica* (11% basal area), *Palaquium obovatum* (10% basal area), and *Mangifera* sp. (5% basal area). Meanwhile, *Pinus merkusii*, an introduced species in Sulawesi, is the dominant species in the Pine forest plot, covering 88% of the total basal area.

The three forest communities are in the same climate type (climate type C), characterized by two distinct seasons in a year: the dry and wet seasons [19]. The dry season normally occurs from May to October and the wet season from November to April. However, due to El Niño and La Niña, the dry season and wet season may be longer or shorter than usual (Figure 1).

2.2. Wood Decomposition Experiments. To observe the rate of wood decomposition in each forest community, a decomposition experiment was carried out using two materials: (a) jabon (*Anthocephalus macrophyllus*; Rubiaceae) wood planks as a representative of broadleaf tree wood and (b) tusam (*Pinus merkusii*; Pinaceae) wood planks as a representative of coniferous wood. Each wooden plank was made into a square with dimensions of 10 cm on all sides and a thickness of 1.5 cm.

A total of 1,200 wooden planks consisting of 600 jabon planks and 600 tusam wood planks were dried in an oven at 60°C. The oven-dried wooden planks were weighed individually, and the figures were recorded as the initial weight. Each wooden plank was tagged with a numbered label made of Dymo tape. Pairs consisting of one jabon wood plank and one tusam wood plank each were connected using a 20 cm long nylon rope, so that there were 600 pairs of jabon wood-tusam wood planks.

At the beginning of the dry season (1-2 May 2019), 100 pairs of jabon wood-tusam wood planks were placed in 50 experimental points and were systematically and evenly distributed in each plot. There were two pairs of wooden planks at each experimental point. The nylon rope connecting each pair of wooden planks was tied to a peg, which was driven into the ground to keep the planks from moving. Once a month, at the beginning of each month, every wood plank sample was monitored, and any changes found were recorded. Hereafter, this first experiment will be referred to as Wood Plank jabon 1 (WPJ1) and Wood Plank tusam 1 (WPT1) (Table 2).

Table 1: Plot description (adapted from [18]).

Description	Karst forest	Lowland forest	Pine forest
Geographical coordinate	119°44′14.9″E 05°01′46.8″S	119°46′35.0″E 04°58′06.9″S	119°45′56.7″E 05°00′17.3″S
Soil type and texture	Rendzina with clay texture and exposed limestone rocks	Cambisol with silty clay mixed with small, medium, and large stones	Luvisol with loamy texture
Altitude (masl)	271	563	501
Age (years)	45	54	58
Density of tree diameter >5 cm/ha	1,125	1,672	1,273
Basal area (cm^2/ha)	295,555.91	467,459.63	600,070.03

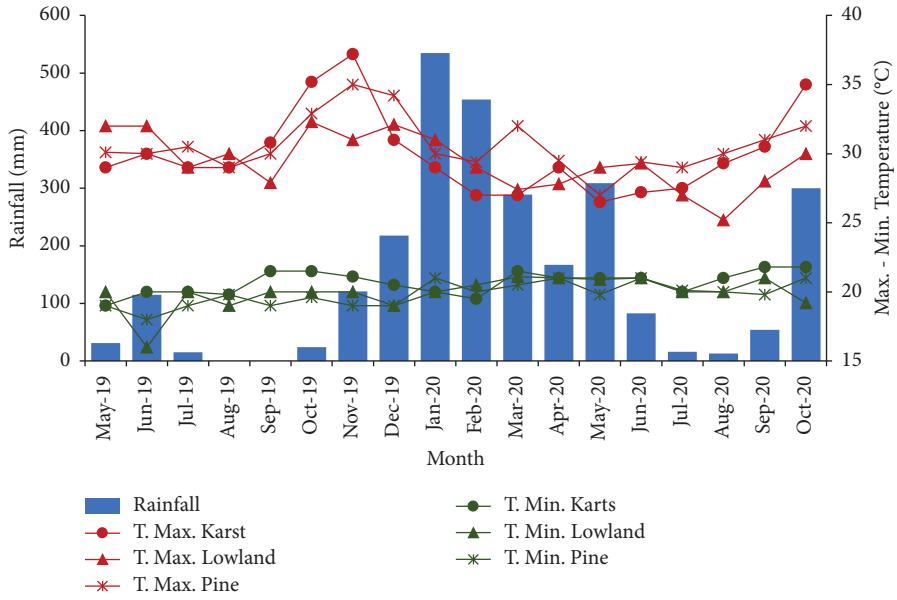

Figure 1: The dynamics of climate elements during the study period (source: Meteorology, Climatology, and Geophysics Council of the Republic of Indonesia).

Table 2: Experimental time period.

Time length (mos)	Season Period	Experiment Code	Season		
			Dry	Wet	Dry
6	Dry (1)	WPJ1-6; WPT1-6			
12	Dry toward Wet (1-12)	WPJ1-12; WPT1-12			
6	Wet (2)	WPJ2-6; WPT2-6			
12	Wet toward Dry (2-12)	WPJ2-12; WPT2-12			

Six months later, at the end of the dry season (1-2 November 2019), 50 pairs of wooden planks (one pair from each point) were collected and brought to the laboratory. The wooden planks collected from the field were carefully cleaned of adhering soil using a soft brush and then dried in an oven at 60°C. The oven-dried weight of each remaining non-biodegradable wood sample (hereafter referred to as WPJ1-6 for jabon planks and WPT1-6 for tusam planks) was recorded according to the tag number as the undecomposed residual weight. When the 50 pairs of planks from each experimental point were collected on 1-2 November 2019, 100 new pairs (two pairs at each point) were placed for a similar experiment, starting in a different season: the beginning of the wet season. Hereafter, this second experiment will be referred to as Wood Plank jabon 2 (WPJ2) and Wood Plank tusam 2 (WPT2) (Table 2).

On 1-2 May 2020 (12 months after the first experiment placement), the remaining 50 pairs of WPJ1-WPT1 (hereafter referred to as WPJ1-12 and WPT1-12) were collected. At the same time, 50 pairs of WPJ2-WPT2 (hereafter referred to as WPJ2-6 and WPT2-6) were collected. After being cleaned carefully using a soft brush and dried in an oven at 60°C, the remaining wood plank samples that had not been decomposed were weighed individually and recorded as the weight of the undecomposed residue after 12 months for WPJ1-12 and WPT-12, or after six months for WPJ2-6 and WPT2-6.

On 1-2 November 2020 (12 months after being placed in the field), the remaining 50 pairs of WPJ2 and WPT2 (hereafter referred to as WPJ2-12 and WPT2-12) were collected from the field and brought to the laboratory, where they were cleaned, dried in the oven, and weighed. The oven-dried weight was recorded as the remaining weight that had not been decomposed after 12 months. The same experiment, but with different placement periods in the field, was designed to compare the rate of decomposition between seasons.

2.3. Chemical Analysis of Wooden Planks. Chemical analysis of the wooden planks was carried out at the Laboratory of Feed Chemistry, Faculty of Animal Husbandry, Hasanuddin University. The analysis began with 10 g wood samples taken from 10 jabon wood planks and 10 tusam wood planks. Jabon wood samples from 10 planks were mixed and dried.

The same was done for the tusam wood samples. Each dried sample of jabon wood and tusam wood was then crushed separately to obtain a fine powder sample of each. The analytical method used was different according to the chemical compound to be analysed. The content of lignin, cellulose, and hemicellulose was analysed using the Van Soest method and the appliance used was Fibertec. Carbohydrate content was analysed using the Luff–Schoorl method and the appliance used was Buret. Polyphenol and tannin contents were analysed using the Folin–Ciocalteu method and the appliance used was UV-Vis spectrophotometer. The methanol extraction method was used to analyse resin content. As for the determination of N, P, K, Ca, Mg, and Mn, the analytical method used was the atomic absorption spectrophotometer (AAS) method.

2.4. Decomposing Agent: Bacteria and Microscopic Fungi. Decomposing microorganisms, including microscopic fungi and bacteria, were inoculated from rotten wood samples collected randomly from each permanent plot. The inoculated fungal and bacterial samples were analysed through polymerase chain reaction (PCR) analysis at the Biotechnology Laboratory, Faculty of Forestry, Hasanuddin University. The results of the PCR analysis were then sent to PT Genetika Science Indonesia for sequencing analysis to determine the fungal and bacterial species. Only the species composition can be analysed, not the abundance of each species. Sampling of wood for microfauna analysis was only done once, during the transition from the dry season to the wet season, with the consideration that PCR analysis will detect the presence of genes for microorganisms that are active in the dry or wet season, or both.

2.5. Decomposing Agent: Macroscopic Fungi. In addition to using the PCR method, the diversity of macroscopic fungi was also surveyed from their visible fruiting bodies, which are commonly called mushrooms (hereafter referred to as macroscopic fungi). The survey was conducted once per season (i.e., in the dry season and wet season) on 25 subplots measuring 10 m × 10 m that were systematically distributed throughout the permanent plot of each forest community. Surveys in the wet season were carried out within three to five days after heavy rain. Each species was identified directly in the field using several digitally illustrated mushroom guidebooks, and each species name was recorded. Species that could not be identified in the field were photographed for identification in the laboratory or by a mushroom specialist. As with microscopic fungi, we did not measure the abundance (cover area) of macroscopic fungi. This is because different fungal species did not grow into mature fruiting bodies simultaneously. In one survey, there were clumps that had just grown to the hyphal knot stage and were expanding their area cover, clumps that were already at the pinhead stage, clumps that had grown into fully developed mushrooms, and clumps that were mostly rotten. Therefore, the fungal colony cover data from the instantaneous survey did not reflect the conditions throughout the year.

2.6. Decomposing Agent: Macrofauna in the Soil. The survey of the diversity and abundance of macrofauna in the soil was carried out using a rectangular sampling ring made of 1.00 mm thick metal plates measuring 20 cm wide × 20 cm long × 10 cm deep. One side of the sampling ring surface was made sharp so that it could be easily plugged into the ground. The sampling ring was plugged into the ground until the upper sides were flush with the ground. The soil in the sampling ring was dug up and placed into a plastic pot, and all macrofaunas found in the soil were collected. Macrofaunas collected from the sample rings were separated by species and placed into small specimen bottles containing 70% ethanol. In each plot, sampling was carried out 10 times, with each sample located near the experimental points. The survey was conducted once per season, in the dry season and the wet season. Identification of the macrofauna specimens was carried out at the Integrated Forest Laboratory and Forest Protection Laboratory, Faculty of Forestry, Hasanuddin University.

2.7. Decomposing Agent: Macrofauna on the Forest Floor. The diversity and abundance of macrofauna on the forest floor were surveyed using pitfall traps. Each trap consisted of a plastic cup with a surface area of 56.72 cm^2 (diameter 8.5 cm) and a depth of 15 cm. A total of 10 traps were installed in each plot and placed adjacent to the position of the wood sample for decomposition experiments. Macrofauna specimens captured in each pitfall trap were collected every 24 hours for 7 days. Macrofauna specimens were separated by species and placed into small specimen bottles containing 70% ethanol and brought to the Integrated Forest Laboratory and Forest Protection Laboratory, Faculty of Forestry, Hasanuddin University, for species identification. The survey was conducted once per season, in the dry season and the wet season.

2.8. Soil Properties. A total of 4 surface soil samples were taken from every plot purposively representing the most common soil conditions in each plot. Soil samples were taken using a ring sample with a diameter of 7 cm and a depth of 10 cm. Soil samples were brought to the Laboratory of Chemistry and Soil Fertility, Faculty of Agriculture, Hasanuddin University, to analyse several chemical properties such as pH (H_2O), TOC, N, C/N, P, Ca, Mg, K, Na, cation exchange capacity (CEC), and base saturation (BS) which may affect the diversity and abundance of decomposing organisms on the forest floor. CEC and BS were analysed using AA and AAS methods, respectively. Soil chemical analysis was carried out once per season, in the dry season and the wet season.

2.9. Maximum-Minimum Temperature. A maximum-minimum thermometer was placed in each plot to measure the monthly maximum and minimum air temperature. These data are needed to clarify whether there are differences in local air temperature between plots and, if there are differences, whether these differences affect the rate of

decomposition. Therefore, the thermometer was placed at a height of about 1 m from the ground rather than placing it directly above the ground. It was assumed that the temperature at the ground's surface was not purely the ambient temperature that could potentially affect the rate of decomposition but the temperature created by the decomposition process itself. Monthly maximum and minimum temperatures were recorded on the 1st or 2nd day each month (Figure 1).

2.10. Data Analyses. The decomposition rate is expressed in terms of the decomposition rate constant (k) calculated using the model:

$$Yt = Yo.e^{-kt}, \quad (1)$$

where Yl = the lost mass of wood sample, Yt = litter weight at time t (months), Yo = initial litter weight, k = decomposition rate constant, e = natural logarithm, and t = decomposition time [20].

Mean abundance of soil macrofauna and mean value of soil chemical properties were compared between seasons in each forest community and between forest communities using analysis of variance (ANOVA) with Tukey's honest significant difference (HSD) method.The k values between seasons and between forest communities were compared using the independent sample non-parametric K with Kruskal–Wallis as the data were not normally distributed. The distribution normality of our data was tested using the Shapiro–Wilk test.

The associations between k of each wood sample and microorganism diversity, k of each wood sample and macrofauna abundance, and k of each wood sample and soil properties were analysed using Pearson's correlation analysis for normally distributed data and Spearman's correlation analysis for non-normally distributed data. All statistical analyses were performed using the R version 4.2.1 application [21].

3. Results

3.1. Comparison in Decomposition Rate between Seasons and between Forests. The mean k values varied inter-seasonally and between forest communities. The mean k value of WPJ1-6 was significantly greater than that of WPJ2-6 across forest communities ($P = 0.0383$; $P < 0.001$; and $P < 0.001$, respectively, in Karst, Lowland, and Pine forests; Figure 2 (top left)). Compared with WPT2-6, the mean k value of WPT1-6 was not significantly different in the Karst forest ($P = 0.9204$) but was significantly smaller in Lowland forests ($P = 0.0182$) and conversely significantly greater in the Pine forests ($P = 0.01$; Figure 2 (top right)).

The mean k value of WPJ1-12 was not significantly different compared to WPJ2-12 in the Karst forest ($P = 0.1914$). However, in the Lowland forest and Pine forest, the mean k value of WPJ1-12 was significantly greater compared to WPJ2-12 ($P < 0.001$ in Lowland forest and $P < 0.001$ in Pine forest) (Figure 2 (bottom left)). There was no significant difference in the mean k value between WPT1-12 and WPT2-12 in all forest communities ($P = 0.0672$; $P = 0.1060$; and $P = 0.6666$, respectively, in the Karst, Lowland, and Pine forests) (Figure 2 (bottom right)).

Comparison between forest communities showed that the mean k value of all experiments (except for WPT1-6) was significantly highest in the Karst forest. For WPJ2-6, WPT2-6, WPJ1-12, WPJ2-12, WPT1-12, and WPT2-12, the second-highest mean k value was in the Lowland forest and the lowest was in the Pine forest ($P < 0.001$ for all WPJ2-6 (Figure 2 (top left)); WPT2-6 (Figure 2 (top right)); WPJ1-12 and WPJ2-12 (Figure 2 (bottom left)); and WPT1-12 and WPT2-12 (Figure 2 (bottom right))). The mean k value of WPJ1-6 was also highest in the Karst forest but second-highest in the Pine forest and lowest in the Lowland forest ($P = 0.0091$, Figure 2 (top left)). Meanwhile, no significant difference was noted in mean k value among forest communities for WPT1-6 ($P = 0.7605$).

3.2. Decomposition Rate Constants between Different Sample Materials. The mean k value between jabon wood samples and tusam wood samples varied between forest communities in each season (Figure 3). However, it was generally noted that in the dry season, the mean k value of jabon wood sample was significantly greater than that of tusam wood sample ($P < 0.001$ in Karst forest and in Pine forest), except in the Lowland forest where there was no significant difference ($P = 0.3125$). During the wet season, the mean k value of jabon wood sample was similar to that of tusam wood sample in the Karst and Pine forests ($P = 0.1060$ in Karst forest and $P = 0.6319$ in Pine forest). However, in the Lowland forest, the mean k value of jabon wood sample was significantly lower than that of tusam wood sample ($P < 0.001$).

For the 12-month experiment starting from the dry to the wet season, the mean k value of jabon wood was not significantly different from that of tusam wood sample in all forest communities ($P = 0.2568$; $P = 0.0830$; and $P = 9259$, respectively, in the Karst, Lowland, and Pine forests), although numerically, the value was higher for jabon. However, in the experiment starting from the wet to the dry season, the mean k value of jabon wood sample was significantly smaller than that of tusam wood sample in all forest communities ($P = 0.0416$; $P < 0.001$; and $P = 0.0340$, respectively, in the Karst, Lowland, and Pine forests).

3.3. Chemical Traits of Sample Wood Experiment. The chemical content varies in a complex manner between wood samples. The content of carbohydrates, lignins, and tannins in the jabon wood samples was greater than that in the tusam wood samples (Table 3). Alternatively, the content of cellulase, hemicellulose, resin, and polyphenols in jabon wood samples was lower than that in the tusam wood samples. The content of N, Ca, P, Mg, and K was greater in jabon wood samples than in tusam wood samples, while the content of Mn was lower in jabon wood samples than in tusam wood samples.

Unfortunately, the difference in chemical traits between the two wood samples could not be statistically analysed, as the data lack replication. To analyse the chemical traits of

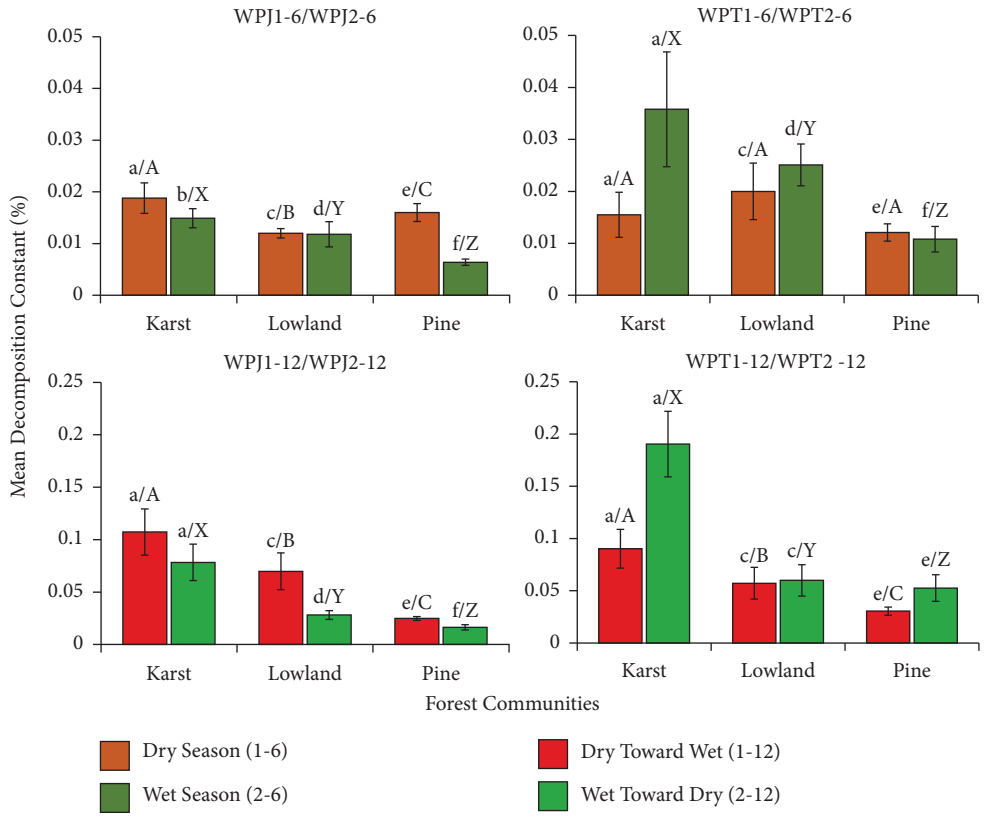

Figure 2: The mean k value of wood samples for six months of the experiment (top row) and 12 months of the experiment (bottom row). Different lowercase letters to the left of the slash above each bar indicate inter-season intra-forest community significant differences (a and b for Karst, c and d for Lowland, and e and f for Pine), while different uppercase letters to the right of the slash above each bar indicate forest communities significant differences in the dry season (A, B, and C) and in the wet season (X, Y, and Z). The bars indicate the standard of error.

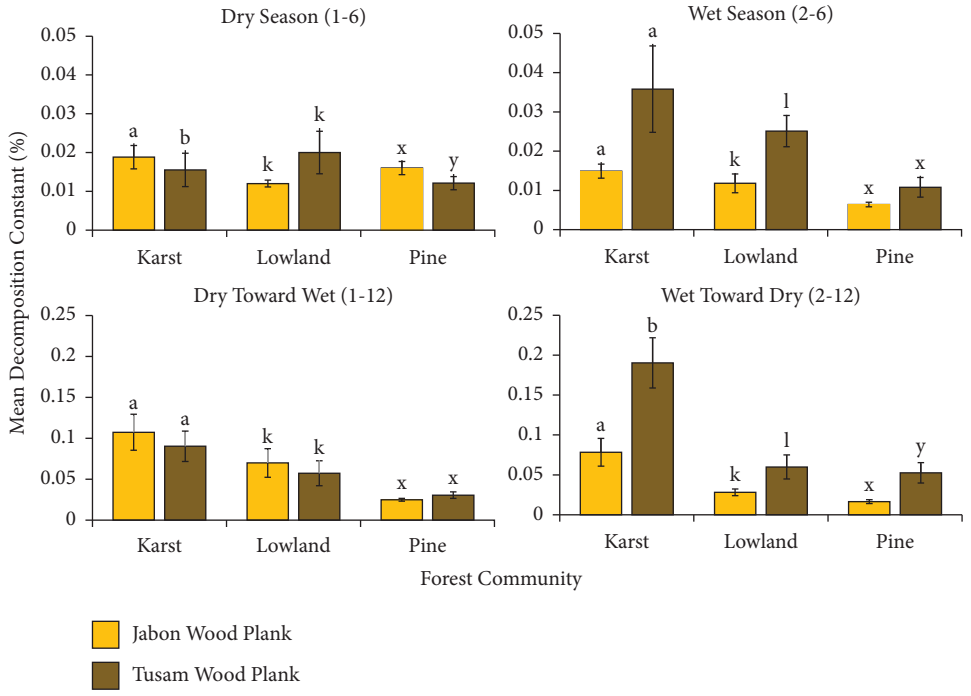

Figure 3: The mean value of k between different sample materials. Different letters on the stem in each forest type indicate a significant difference between the two wood sample materials.

Table 3: Chemical compound content of wood samples.

Chemical compound (%)	WP jabon	WP tusam
Carbohydrate	70.63	68.37
Cellulose	43.50	44.50
Hemicellulose	3.97	9.68
Lignin	27.10	23.80
Tannin	0.60	0.56
Resin	0.61	5.25
Polyphenol	0.07	0.24
N	0.49	0.33
Ca	0.39	0.01
P	0.16	0.04
Mn	0.01	0.03
Mg	0.21	0.04
K	0.99	0.27

each wood sample, samples were collected from 10 planks each of jabon and tusam wood. The wood samples from each species were then mixed for one analysis.

3.4. Diversity of Decomposing Bacteria and Fungi vs. Decomposition Rate Constant. Through PCR analysis of rotted wood samples collected from the plots, the identities of microscopic bacterial and fungal species could be discerned, but not their abundance. As predicted, there were fewer microbial species in the Pine forest than in the broadleaf forests (Karst and Lowland). A total of six bacterial species were confirmed in the three forest communities studied. Among them, four species were found in the Karst forest, two in the Lowland forest, and two in the Pine forest (Table 4). *Burkholderia cepacia* was confirmed in the Karst and Pine forests, and *Burkholderia cenocepacia* was confirmed in the Lowland and Pine forests. Three species (*Bacillus cereus, Burkholderia* sp., *and Burkholderia ubonensis*) were specialists in the Karst forest. *Bacillus thuringiensis* was a specialist in the Lowland forest. Meanwhile, no specialist bacterial species were found in the Pine forest.

There were ten confirmed microscopic fungal species in the three forest communities. Among them, only one species (*Talaromyces pinophilus*) was found in all forest communities; two species (*Trichoderma virens* and *Aspergillus aculeatus*) were found only in Karst forests; three species (*Penicillium pinophilum*, *Trichoderma* sp., and *Aspergillus* sp.) were found only in Lowland forests; two species (*Penicillium citrinum* and *Cladosporium tenuissimum*) were found only in Pine forests; and two other species (*Aspergillus terreus* and *Aspergillus japonicus*) were found in Karst and Lowland forests (Table 4).

For macroscopic fungi, we found a total of 130 species across forest communities: 65 species in Karst forest (7 in the dry season, 48 in the wet season, and 10 shared in both seasons), 67 in Lowland forest (12 in the dry season, 41 in the wet season, and 14 shared in both seasons), and 42 species in Pine forest (10 in the dry season, 29 in the wet season, and 3 shared in both seasons) (Figure 4). Of the 65 species found in the Karst forest, 39 species were specialists in this forest community. In the Lowland forest, 32 of the 67 species found were specialists only in this forest community. Meanwhile, 24 of 42 species found in the Pine forest were specialists only in this forest community. In all forest communities, macroscopic fungal species were more diverse in the wet season than in the dry season.

The mean number of macroscopic fungi species per $100\,m^2$ (sub-plot) during the dry season was the highest in the Lowland forest (3.88 ± 0.28), the second highest in the Karst forest (2.20 ± 0.28), and the lowest in the Pine forest (1.32 ± 0.28) ($P < 0.001$). In the wet season, the mean number of macroscopic fungi species per $100\,m^2$ was similar between the Karst forest (7.20 ± 0.61) and Lowland forest (7.84 ± 0.61) but significantly lower in the Pine forest (3.64 ± 0.61) ($P < 0.001$). Correlation analyses only detected a significant association between the number of species of bacteria and the k of the 12-month experiment on tusam wood (WPT2-12).

3.5. Decomposing Agent Macrofauna vs. Decomposition Rate Constant. Through observations using rectangular sampling rings and pitfall traps, 39 species of macrofauna were found in the soil and on the forest floor, including termites, ants, cockroaches, centipedes, earthworms, and the larvae of several insect species. In Table 5, only the seven dominant species potentially associated with wood decomposition, such as feeding on wood or utilising rotted wood as a nest, were listed. *Odontotermes* sp. (termites) was the most common macrofauna species caught in the rectangular sampling ring, while *Odontomachus* sp. was the most common macrofauna species caught in the pitfall traps. ANOVA analysis with Tukey's HSD method showed that *Odontotermes* sp. was caught more in the dry season, while *Eudrilus eugeniae*, *Willowsia* sp., and *Xyleborus* sp. were more caught in the wet season. Other species did not show significant differences in abundance between seasons.

Correlation analysis showed that the mean value of k only significantly correlated with the abundance of several macrofauna species in a particular season. For the macrofauna caught from rectangular sampling rings, a significant association was only noted in the dry season between mean k value of WPJ1-6 and the abundance of *Odontotermes* sp. ($P = 0.0364$). However, for the macrofauna caught by pitfall trap, significant correlations were noted only in the 12-month experiments started in the dry season toward the wet season between WPJ1-12 and *Solenopsis geminata* ($P < 0.001$), between WPJ1-12 and *Ips* sp. ($P = 0.0398$), and between WPT1-12 and *Odontomachus* sp. ($P = 0.0188$).

3.6. Soil Properties vs. Decomposition Rate Constant. Among the examined soil properties, C, N, P, K, and CEC values were consistently higher in the dry season than in the wet season across forest communities (Table 6). Correlation analysis showed no significant relationship between any of the 11 soil properties examined and the mean k value of the two wood samples over the six-month experiment. This insignificant relationship occurred across forest communities both in the dry season and the rainy season.. For a 12-month experiment starting from the onset of the dry season, a significant correlation was found only between Na and the

Table 4: Existence of microscopic decomposing agents in the three forest communities (√ = exist).

Species	Existence			Degraded compound
	Karst	Lowland	Pine	
Bacteria				
Bacillus cereus	√			Cellulose, hemicellulose[a], lignin[b]
Burkholderia sp.	√			Cellulose[c], hemicellulose[d], lignin[e]
Burkholderia ubonensis	√			Phosphor[f]
Burkholderia cepacia	√		√	Cellulose[g], lignin[h]
Bacillus thuringiensis		√		Cellulose[i], hemicellulose[j]
Burkholderia cenocepacia		√	√	Phosphor, potassium[k]
Number of bacterial species	4	2	2	
Fungi				
Trichoderma virens	√			Cellulose, hemicellulose[l]
Aspergillus aculeatus	√			Cellulose, hemicellulose[m]
Aspergillus terreus	√	√		Cellulose[n], hemicellulose[o], lignin[n]
Aspergillus japonicus	√	√		Cellulose[p]
Penicillium pinophilum		√		Cellulose[q], hemicellulose[r], lignin[s]
Trichoderma sp.		√		Cellulose[r], hemicellulose[t], lignin[r]
Aspergillus sp.		√		Cellulose[r], lignin[u]
Penicillium citrinum			√	Cellulose[p] lignin[v]
Cladosporium tenuissimum			√	Cellulose, hemicellulose, lignin[w]
Talaromyces pinophilus	√	√	√	Cellulose[x], phosphor[y]
Number of fungal species	5	6	3	
Total bacteria and fungi	9	8	5	

a = [22]; b = [23]; c = [24]; d = [25]; e = [26]; f = [27]; g = [28]; h = [29]; i = [30]; j = [31]; k = [32]; l = [33]; m = [34]; n = [35]; o = [36]; p = [37]; q = [38]; r = [39]; s = [40]; t = [41]; u = [42]; v = [43]; w = [44]; x = [45]; y = [46].

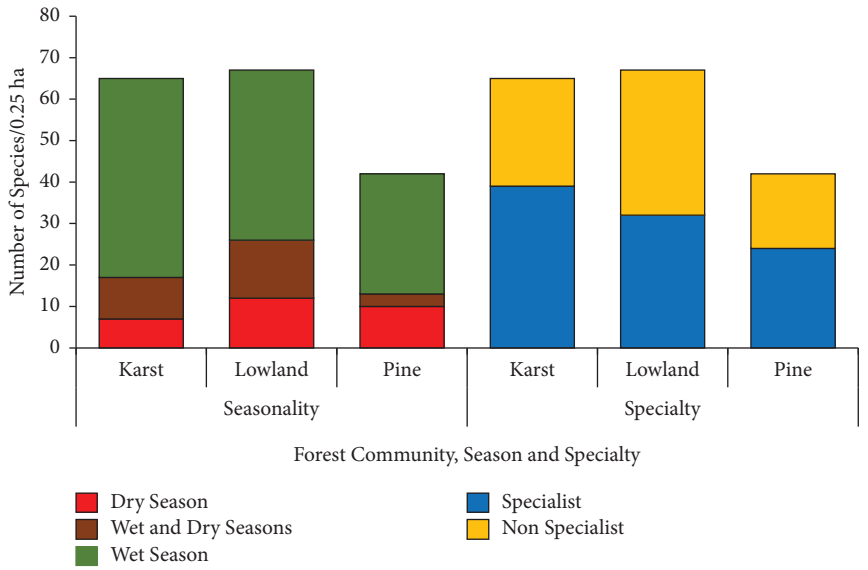

Figure 4: Macroscopic fungal species diversity by season (left) and habitat specialization (right).

mean k value of the two wood samples, WPJ1-12 ($P = 0.0455$) and WPT1-12 ($P = 0.0266$). Meanwhile, for the 12-month experiment starting from the onset of the wet season, a strong negative and significant correlation was detected between Mg and the mean k value of WPT2-12 ($P = 0.0026$).

4. Discussion

Our study aimed to determine the differences in the k value of jabon wood (broadleaf) and tusam wood (conifer) between two seasons and three forest communities. In addition, we intended to investigate the factors associated with

Table 5: Mean abundance of soil macrofauna in three forest communities.

Species	Family	Mean abundance of macrofauna in each forest community					
		Karst		Lowland		Pine	
		Dry	Wet	Dry	Wet	Dry	Wet
Captured using rectangular sampling ring in the forest soil (individuals/400 cm²)							
Odontotermes sp.	Termitidae	47.9 a	1.0 b	2.4 a	1.2 a	26.9 a	0.3 b
Odontomachus sp.	Formicidae	6.8 d	10.2 d	4.3 d	9.8 e	2.8 d	5.4 d
Solenopsis geminata	Formicidae	8.9 g	6.9 g	5.2 g	8.9 h	0.3 g	4.4 h
Eudrilus eugeniae	Eudrilidae	2.3 j	6.7 k	3.8 j	7.3 k	2.8 j	5.1 k
Paratrechina longicornis	Formicidae	1.0 m	2.3 m	1.4 m	1.6 m	0.6 m	1.0 m
Willowsia sp.	Entomobryidae	0.6 p	3.4 q	5.0 p	4.4 p	1.2 p	1.2 p
Philoscia sp.	Philosciidae	1.1 s	2.0 s	0.1 s	2.3 t	0.3 s	0.7 s
Total in the forest soil		68.6 v	32.5 v	22.2 v	35.5 w	34.9 v	18.1 v
Captured in the pitfall trap on the forest floor (individual/56.72 cm²/7 days)							
Odontomachus sp.	Formicidae	13.2 a	27.4 a	10.0 a	15.5 a	4.8 a	9.7 a
Willowsia sp.	Entomobryidae	6.5 d	13.6 e	7.0 d	13.0 e	4.0 d	12.5 e
Xyleborus sp.	Curculionidae	5.0 g	8.0 h	3.3 g	8.4 h	1.1 g	3.7 g
Paratrechina longicornis	Formicidae	2.8 j	7.1 j	7.7 j	7.9 j	3.7 j	4.6 j
Solenopsis geminata	Formicidae	5.1 m	5.8 m	2.8 m	6.1 m	2.0 m	4.5 m
Ips sp.	Scolytidae	2.1 p	5.6 p	2.4 p	3.1 p	1.0 p	1.2 p
Teleogryllus sp.	Gryllidae	1.1 s	0.9 s	0.1 s	2.7 t	0.3 s	1.1 s
Total on the forest floor		35.8 v	68.4 w	33.3 v	56.7 w	16.9 v	37.3 w

Different letters after the mean abundance value in the rows of each forest community column indicate significant differences between seasons in each forest community (ANOVA with Tukey's HSD method at $P < 0.05$).

Table 6: Chemical properties of soil in permanent plots at three research sites during the dry season and wet season.

Parameter	Mean value of seasonal soil chemical properties					
	Karst forest		Lowland forest		Pine forest	
	Dry	Wet	Dry	Wet	Dry	Wet
pH	6.23 a	6.33 A	6.51 b	6.28 A	5.95 c	5.90 B
C (%)	2.62 d	1.98 C	2.41 de	2.25 C	2.27 e	0.95 D
N (%)	0.24 f	0.20 E	0.24 f	0.21 E	0.24 f	0.10 F
C/N (%)	11.25 g	10.25 G	10.50 g	10.75 G	9.25 g	10.00 G
P (ppm)	13.33 h	10.90 HI	11.88 h	8.93 H	13.84 h	11.63 I
Ca (kg^{-1})	7.21 j	5.63 J	5.35 j	6.85 J	5.04 j	5.77 J
Mg (kg^{-1})	0.89 k	0.91 K	1.87 k	2.02 K	1.73 k	2.29 K
K (kg^{-1})	0.60 l	0.37 L	0.42 l	0.29 L	0.46 l	0.41 L
Na (kg^{-1})	0.52 m	0.43 M	0.34 m	0.49 M	0.34 m	0.38 M
CEC (kg^{-1})	20.53 n	19.06 N	22.41 n	18.24 N	18.53 n	17.77 N
BS (%)	44.75 o	38.50 O	35.50 o	54.25 O	42.00 o	49.25 O

Different lowercase letters after the mean values of soil properties in a row indicate significant differences between forest communities during the dry season (e.g., a, b, and c), while different uppercase letters after the mean values of soil properties in a row indicate significant differences between forest communities during the wet season (e.g., A, B, and C) (ANOVA with Tukey's HSD method at $P < 0.05$).

differences in k value. Although statistical analyses showed a sporadic pattern of mean k value between seasons, in general, there was a trend that for the jabon wood sample (WPJ), the mean k value in the dry season was higher than that in the wet season, and vice versa for tusam wood (WPT), for which the mean k value in the dry season was lower than that in the wet season.

The jabon wood's higher mean k value in the dry season than in the wet season can be explained by the results of correlation analysis, which shows a significant association between the abundance of *Odontotermes* sp. and jabon wood mean k values in the dry season (WPJ1-6). Several previous studies, however, reported conflicting results regarding the correlation between the season and *Odontotermes* sp. attacks. While Cheik et al. [47] reported the beneficial impact of *Odontotermes* spp. on water infiltration in soil, several other studies found that the foraging activity of this termite species was lower in the hot-wet season [48, 49], although the abundance of workers was positively correlated with relative humidity [48]. The declining population of *Odontotermes* sp. during the wet season at the study site is thought to be related to the increase in the population of several ant species that often function as predators, such as *Odontomachus* sp., *Solenopsis geminata*, and *Paratrechina longicornis*.

The opposite trend was shown by tusam wood which shows a higher mean k value in the wet season than in the dry season. Tusam wood distinctly contains more

hemicellulose (9.68%) than jabon wood (3.97%). Hemicellulose significantly increases the water absorption behaviour and wettability of wood so that it can potentially reduce wood's resistance to microorganisms [50, 51]. Other studies also reported that the abundance of decomposing microorganisms was greater in humid and warm environmental conditions [52]. This study showed a significant positive correlation between the mean k value of WPT2-12 and the number of species of bacteria. In addition, this study showed that the number of species of macroscopic fungi was greater in the wet season than in the dry season. Unfortunately, we do not have data about the difference in the diversity of microscopic fungi between seasons.

Data that are not normally distributed and the insignificant difference of mean k values between the 12-month experiment starting at the onset of the dry season and the onset of the wet season, in particular for tusam wood samples, implies that the difference in the initial conditions of the decomposition process does not affect the process throughout the year. Wood that begins with a faster decomposition process in the dry season does not decompose faster in the following wet season. Conversely, wood that begins with a slower decomposition process in the wet season does not decompose more slowly in the following dry season. The presence of a suitable decomposing agent at a time seems to have a more significant effect on the rate of decomposition than the climatic conditions at the start of the wood decomposition process. This finding suggests that different woods may be favoured by different decomposing agents, each of which has different seasonal abundance patterns. The macrofauna *Odontotermes* sp. had a stronger influence than microorganisms in determining the rate of wood decomposition during the early process of decomposition (see also [53]). In a longer decomposition process, physical environmental factors can influence microbial activity more effectively than macrofauna either directly or indirectly [54].

As predicted, this study revealed that the highest mean k value of the two species of wood samples was recorded in the Karst forest and the lowest in the Pine forest, except for WPT1-6. This finding suggests that, just as in temperate regions [55, 56], the litter decomposition rate in the Pine forest in the tropics is also slower than that in broadleaf forests. Several previous studies have reported microbes' critical role in wood decomposition, especially fungi [57, 58]. In this study, differences in mean k value between forest communities are proportional to differences in the number of microbial species, especially macroscopic fungi, between forest communities. In addition, among soil chemical properties, pH and C were significantly lower in the Pine forest compared to the Karst and Lowland forests. However, correlation analyses showed that the disparity in the number of microbial species between forest communities was statistically not related to differences in mean k value among forest communities. This may be due to the insufficient number of variables analysed, in which only three forest communities were compared.

Lower k value in Pine forests occurred for both tusam and jabon wood samples. Kimura et al. [15] succeeded in isolating two main inhibitors determined by spectral data, namely, 9α,13β-epidioxyabeit-8(14)en-18-oic acid and abscisic acid-β-D-glucopyranosyl ester, from the foliage of red pine (*Pinus densiflora*). Thus, it can be assumed that the slow decomposition of tusam wood in Pine forests is not caused by intrinsic factors, but rather by extrinsic factors, one of which can be allelopathic substances contained in pine leaf litter on the forest floor.

While we can generally draw trends, statistical analysis of these studies showed sporadic and sometimes conflicting results. This would not likely be due to the insufficient number of replicates, considering that each treatment consisted of 50 replicates, with a total sample size of 1,200 wooden planks. The data disparity from one place to another is sometimes very high, which has implications for datasets that are not normally distributed. These results are in accordance with a previous study by Powers et al. [59], which states that the factors that influence the decomposition process are complex and may vary by site. Each of several previous studies reported various factors that affected the litter decomposition process, ranging from UV radiation and visible light [60]; mesofauna [59]; macrofauna, earthworms, and arthropod abundance [61]; wood substrate quality [58]; tree species, temperature, and precipitation [62]; bacterial species [63]; and rainfall [9]. Through very complex interaction patterns, all of these decomposing agents and environmental factors play a role in the decomposition of litter. In the tropics, this pattern of interactions can be more complex and mutual due to the high diversity of decomposing agents at the microenvironmental level, and this leads to differences in k values, even within the same forest community. Between two forest communities that do not differ in macro- and microclimatic conditions, biodiversity, or specimen richness, the communities of decomposing agents on the forest floor can differ significantly [64].

5. Conclusion

Although there is a tendency for the k value of jabon wood to be higher during the dry season than the rainy season, and vice versa for tusam wood, and a tendency for the k value of both wood samples to be higher in the broadleaf forest than in Pine forest, the data show high disparity even within the same season and forest community. The results of the statistical analysis show that most of the data are not normally distributed. This is due to the high diversity of decomposing agents and environmental factors in the tropics, where they work in very complex reciprocal associations. Environmental factors such as rainfall and soil chemistry can affect the k value directly and individually or indirectly and collectively through the activity of decomposing agents at different levels. The results of many controlled experimental studies conducted in the laboratory may be able to show how a single decomposing agent affects the rate of decomposition, but this may not be the case in the field. Therefore, field research on various forest communities in the tropics is still needed to determine the accumulative working patterns of decomposing agents and the influence

of environmental factors on the rate of decomposition of wood litter.

Data Availability

The data used to support the findings of this study are available from the corresponding author upon request.

Disclosure

The funder had no role in the research design, in data collection, in data analysis and interpretation, in writing the manuscript, and in the decision to publish the results.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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