Spatial variations in the decay coefficients of forest ecosystems in East and Southeast Asia

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ABSTRACT

We assessed spatial variation in the decay coefficients of fine wood litter on the forest floor in four forest formations in East and Southeast Asia. We used a novel approach to incorporate fragmentation loss in the decomposition process within four plots, each several hectares in area. The spatial patterns showed significant correlations with some biotic, edaphic, topographic, and climatic factors. Variation in the lowland tropical rainforest was driven largely by the feeding behaviors of termites. Variation in the hill dipterocarp forest exhibited no clear correlations with topographic parameters due to complementarity of decay activities by fungi and termites through segregation of their habitat between concave and convex sites, respectively. The subtropical rainforest showed variations associated with habitats distinguished by understory communities, reflecting edaphic conditions. Variation in the warm-temperate lucidophyll forest showed a clear negative correlation with slope convexity. The maximum area of spatial autocorrelation for the decay coefficient was used as the unit area for identification of significant relationships between decay coefficients and net primary productivity for aboveground coarse woody organs in terms of spatial variations, except in the subtropical forest plot. The ecological features of the four research plots were assessed based on spatial variation in structural and functional parameters over the unit areas or among the understory communities. Our results imply that 1) the positive correlations between decay coefficients and net primary productivity in two plots in a tropical zone were realized by spatial properties of the death rates of trees being higher or even at sites with higher decay coefficients and 2) the negative correlations in two plots in subtropical and warm-temperate zones were maintained by increasing the death rates on convex sites through frequent disturbance by typhoons. Inter- and intrasite variations in decay coefficients were evaluated using a probability density function of two-dimensional standard normal distributions regressed from data collected in the study area.

Key words: decay coefficient, NPP, slope convexity, spatial variations, termites

INTRODUCTION

Spatial variation in decay coefficients may affect the structural and functional parameters of a forest ecosystem through direct and indirect impacts on nutrients and other abiotic factors in soils. In this study, we explored the spatial variations in decay coefficients and other ecosystem features for different forest formations in East and Southeast Asia.

The decay coefficients of the forest floor are affected not only by various local biotic and abiotic factors in the soil (Swift et al. 1979) but also by the quality of litter (Weedon et al. 2009). Mori (2014) identified 16 factors, including 9 environmental factors and combinations thereof, that were significantly related to spatial variations in decay coefficients in a 52-ha tropical-rainforest plot in Sarawak. That study found that the decay coefficient in unit areas based on autocorrelation was significantly correlated with biomass, net primary productivity, and species diversity. That was the first study to assess spatial variation in ecosystem features in a large-scale research forest plot.

ITE (1988) assessed the decay ratio of soils globally using standardized cotton strips in various formations. However, few studies have explored spatial variations to
clarify the characteristics of each formation. Assessing the association of such characteristics using dimensional parameters based on long-term observations of a large-scale plot is essential (Yamakura, 1991). This study aimed to examine the relationship of spatial variation in forest-floor decay coefficients with the structural and functional parameters of four forest formations based on field observations over 6 to 11 years in 4- to 6-ha plots.

We assessed spatial variation in a mature forest of each formation. Standardized wood sticks were purchased commercially to remove the effect of differences in litter quality. We proposed newly developed decay coefficients to assess total weight loss with two decay processes of weight loss at remaining parts and length loss, separately. These decay coefficients were defined by three parameters: 1) the ratio of weight loss to initial total weight; 2) the ratio of weight loss to initial weight per remaining length; and 3) the ratio of length loss to initial length. From the definition (for details, see Materials and methods), these coefficients realize to be $1 = \frac{1}{2} + 3$. The third parameter is a measure of fragmentation due to the decay process. Removal of substrate from litter by termites influences the first decay ratio in tropical rainforests (Abe, 1979; Abe & Matsumoto, 1979). We examined the magnitude of the autocorrelation of the decay coefficient, which showed correlations with some variables of ecosystem structure and function. Inter- and intrasite variations in decay coefficients were examined with regard to annual mean temperature.

MATERIALS AND METHODS

Study sites

This study was conducted in permanent research plots, one located in each of four different forest formations in East and Southeast Asia: a lowland tropical rainforest in Pasoh Forest Reserve, Peninsular Malaysia (PS); a hill dipterocarp forest at Ulu Gadut, West Sumatra, Indonesia (UG); a subtropical rainforest at Tanpatsuyama on Tokunoshima in the Ryukyu Islands, southwest Japan (TP); and a warm-temperate lucidophyll forest in Kasugayama Forest Reserve, Nara, central Japan (KS). Their locations and general features are provided in Fig. 1 and Table 1. These four plots are all in humid climates without dry seasons; UG has a particularly high annual rainfall of about

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Fig. 1. Map of research plots used in this study and in previous referenced studies in the same area. Letters in the box at upper left indicate references and their positions on this map. They are a: Alhamd et al. (2004), b: Chairul & Yoneda (2002), c: Hirobe et al. (2004), d: Hou et al. (2005), e: Mori (2014), f: Mori et al. (2014), g: Nakane (1980), h: Tashiro et al. (2013), i: Yamashita & Takeda (1998), j: Yoneda (1975), k: Yoneda (1997), l: Yoneda et al. (1977), m: Yoneda & Kirita (1978), n: Yoneda et al. (1990), o: Yoneda et al. (1991) and p: Yoneda (unpublished).
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Table 1. General descriptions of four research plots and the litterbag experiment used in this study. The abbreviations LDF, HDF, SRF, and WLF represent a lowland mixed dipterocarp forest, a hill dipterocarp forest, a subtropical rainforest, and a warm-temperate deciduous forest, respectively. ABM is aboveground biomass of trees greater than 10-cm diameter at breast height,dbh.

| Location          | Area (ha) | Annual mean temperature (°C) | Annual rainfall (mm) | Altitude (m) | Inclination of 10 m × 10 m unit (mean ± sd) | Vegetation | Soils   |
|-------------------|-----------|-----------------------------|----------------------|--------------|---------------------------------------------|------------|---------|
| PS                | 02.58°N, 102.18°E | 200 × 300 m (6 ha) | 26.0                | 1182–2341 (1987–2005) | 0 ± 9.0                                      | LDF        | Typic Kanahapludults / Typic Paleudults*** |
| UG                | 00.55°S, 100.29°E | 140 × 280 m (3.92 ha) | 22.5                | 546–642      | 7 ± 9.0                                      | HDF        | Typic Dystropets***                     |
| TP                | 27.46°N, 128.56°E | 200 × 200 m (4 ha) | 20.2                | 79 ± 100     | 4 ± 9.8                                      | SRF        | Yellow soils****                        |
| KS                | 34.41°N, 135.51°E | 180 × 320 m (5.76 ha) | 13.7                | 24 ± 9.8     | 28 ± 9.8                                     | WLF        | Dry brown forest soils****              |

Litterbags

| Number | Spacing (m) | Collection (%) | Duration in fields |
|--------|-------------|----------------|--------------------|
| 1000   | 1           | 79             | Aug08-Sept09 (1.04 y) |
|        |             |                | Aug06-Aug07 (1.02 y) |
|        |             |                | May05-May06 (1.01y)  |
|        |             |                | Dec06-Dec07 (1.00 y) |

Table 2. Properties of topsoil at four understory communities in the Tanpatsuyama plot (TP). Each property was assessed according to the categories reported by Yagi (1993). Symbols + and ++ for humus indicate the “contained” and “rich” categories, respectively.

| Community No. | Layers | Depth (cm) | Humus | Structure |
|---------------|--------|------------|-------|-----------|
| G 1           | HA     | 0–2        | +     | grained   |
| G 2           | AB     | 0–2        | +     | nutty     |
| G 3           | AB     | 0–10       | +     | crumb/nutty |
| G 4           | A1     | 0–5        | ++    | crumb/blocky |
|               | A2     | 5–23       | +     | nutty/blocky |

6000 mm.

PS was a mixed dipterocarp forest, and sampling was conducted at a forest stand in an alluvial community (Davies et al. 2003) using a 50-ha plot. UG was part of a 6.55-ha permanent plot codominated by Fagaceae and Dipterocarpaceae (Nishimura et al. 2006, 2008). Overstory vegetation at TP was characterized by high dominance of Fagaceae (Castanopsis sieboldii and Quercus miyagii), and the understory species included many tropical elements (Nishi, 2005; Yoneda, 2016a, 2016b). KS exhibited high dominance of C. cuspidata, accompanied by a few evergreen needle-leaved tree species such as Abies firma and Tsuga sieboldii (Naka, 1982).

Intrasite variations in relative altitude (RA) and slope unevenness among these plots were calculated using data from a topographical survey collected at 10-m intervals. We assumed PS to be flat. Topography was characterized using the index of convexity (IC) introduced by Yamakura et al. (1995). The x- and y- coordinates of all trees greater than 10 cm in diameter at breast height (dbh) were measured.

The soil types of these four plots are shown in Table 1. Spatial variations in soil properties at TP were closely associated with four understory communities (G1–G4) identified through cluster analysis of vascular plants in 400 subplots of 4 m² each (Nishi, 2005). The sequence from G1 to G4 revealed gradients in plant life forms, habitat topography, and soil properties, namely diversification of life forms, changes in habitat topography from convex to gentle slopes or valleys (cf. Fig. 5–C), and maturity of soil properties (Table 2). Two canopy species, C. sieboldii and Q. miyagii, tended to dominate in poor soils on ridges or upper slopes and in mature soils on gentle slopes or in valleys, respectively. Nakane (1975) described a sequence of changes in brown forest soils from a ridge to a valley in a forest stand adjoining KS, which transitioned from a dry type (Bₐ) to an adequately wet type (B₇) via a semi-dry type (B₅), accompanying an increase in soil water content and soil porosity downslope.

Litterbag experiments

We assessed spatial variations in the decay coefficients on the forest floor through field observations using
litterbags holding small wooden sticks (2 × 95 × 115 mm). The sticks, commonly used as popsicle sticks in Japan, were purchased commercially, and their size was standardized such that the coefficient of variation in their dry weights was 3% (n = 5 sticks/set × 30 sets). Each set of five sticks was placed in a litterbag made from 3 × 3-mm nylon mesh, with the sticks enclosed separately in five pockets. Each litterbag was fixed to the forest floor with wire and then incubated for about 1 year (Table 1). We defined the initial total length of a set as 575 mm and the dry weight as 5.8 grams excluding the litterbag.

One thousand litterbags were set at PS at 1-m intervals, arranged in five 200-m lines (cf. Fig. 5A). The line at the southern end of PS was on the southern border of a 50-ha plot. Litterbags deployed at the other three plots were placed at 10-m intervals in the same positions as those used for the topographical survey, with 435, 441, and 627 bags deployed at UG, TP, and KS, respectively. The collected wood samples were rinsed, and then the total length and dry weight of each set of five sticks were measured. The percentages of the total deployed litterbags collected were 79% (PS), 92% (UG), 88% (TP), and 97% (KS).

We assumed that loss processes of dry weight and length could be described as exponential decreases with time (t) of incubation (Ogawa et al. 1961; Olson, 1963), and assessed them using the following equations with three kinds of decay coefficient, μ1, μ2 and μ3.

\[ w = w_0 \times \exp^{-\mu_1 t}, \]
\[ w = w_0 \times \left( \frac{L}{L_0} \right) \times \exp^{-\mu_2 t}, \]
\[ L = L_0 \times \exp^{-\mu_3 t}, \]

where the parameters \( w, w_0, L, \) and \( L_0 \) are the dry weight and length at a given time (t) and at \( t = 0 \). From this definition, \( \mu_1 = \mu_2 + \mu_3 \). Thus, this newly developed method could evaluate the decay coefficient of total weight loss (μ1) by considering the effects of weight loss per remaining length (μ2) and fragmentation (μ3).

**Evaluation of spatial variations in the decay coefficients**

We assessed the spatial autocorrelation of the decay coefficients using Moran’s I. The index was calculated with a distance (lag) of 2 m or 5 m using the statistical package R with the function `moran.mc` installing Monte Carlo simulation on the Windows platform, and the magnitudes of spatial autocorrelations were examined from the spatial correlograms of Moran’s I (Zhang, 2010).

**Calculation of aboveground biomass, net primary productivity, and death rate**

We calculated the aboveground biomass (ABM), net primary productivity (NPP), and death rate (DR) of aboveground coarse woody organs using dbh census data collected during a period including the year of the litterbag experiment at each plot. This census was conducted four times over 11 years at PS, six times over 11 years at UG, seven times over 10 years at TP, and three times over 6 years at KS. Structural dimensions such as ABM and stem number (N) were assessed from the census data collected just before and after the experiment in each plot, and functional dimensions such as NPP and DR were assessed for the whole dataset to analyze their large temporal variances. NPP and DR were calculated as a growth rate of aboveground woody organs of living trees throughout the period and a death rate of dead trees during the period, respectively. NPP and DR do not include fluxes through dynamics of consumable fine organs such as leaves and small branches.

These dimensional parameters were calculated using a coarse wood-based biometric method (CWBBM) (Yoneda et al. 2016) with allometric equations. Tree height (H) was calculated following the following equation (Ogawa et al. 1965).

\[ \frac{1}{H} = \frac{1}{a \cdot \text{dbh}} + \frac{1}{H^*}, \]

where the coefficients \( a \) and \( H^* \) were estimated for each plot using the least squares method (Table 3). TP showed differing dbh-H relationships among the four understory communities, so we applied different coefficients to each community. We corrected estimated tree heights of trees having observed values with ratios of observed height/estimated one at observed year for their temporal changes.

The weights of the stem and branches of broad-leaved trees were calculated through regression for Pasoh Forest Reserve (Kato et al. 1978; Yoneda et al. 2016) independent of forest formations, and those of needle-leaved trees in KS were calculated using regressions for only A. firma and T. sieboldii, having one parameter of dbh without tree height, obtained in a temperate fir and hemlock forest in Shikoku, Japan (Ando et al. 1977). The equation of these regressions was \( L = c \cdot \text{dbh}^h \), with the two coefficients of \( c \) and \( h \) for each species and for two dbh groups.
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Table 3. Coefficients of the dbh-tree height (H) curves for the allometric equation (provided in the text) of four plots. The abbreviations N, R², and B indicate the number of trees used for calculation, coefficient of determination, and broad-leaved trees, respectively.

| Plot | a   | H*  | N   | R²  | Note                                      |
|------|-----|-----|-----|-----|-------------------------------------------|
| PS   | 2   | 61  | -   | -   | Kato et al. (1978)                        |
| UG   | 1.34| 52.2| 782 | 0.704| from trees in dbh ≥ 5 cm, observed by Suzuki & Khoyama (unpublished) |
|      | G1  | 1.68| 18.6| 256 | 0.347                                     |
|      | G2  | 1.44| 21.1| 310 | 0.440                                     |
| TP   | G3  | 1.12| 25.6| 137 | 0.462                                     |
|      | G4  | 0.98| 27.3| 107 | 0.479                                     |
| KS   | B   | 2.33| 24.1| 349 | 0.024 from trees in dbh ≥ 35 cm            |

Analysis of correlations among decay coefficients and dimensional parameters

We analyzed correlations among unit areas in each plot. Correlations in PS were examined for four different unit areas. These areas were 40 m in width and were located at four different lengths (20 m, 40 m, 100 m, and 200 m) along a 200-m line for the litterbag experiment. The width was set to 20 m on each side of the central line. Four lines were measured for this analysis; the line at the southern end of the site was excluded due to a lack of dbh census data in half of the unit area. Then we have 20 units (4 lines × 5 units) at a unit of 40-m width × 40-m length. The other three plots had 5–7 unit areas measured for this analysis, with a minimum unit area of 10 × 10 m based on the topographical survey.

The decay coefficient of 10 × 10-m basic unit was estimated by averaging the measured values from four observed points, and the coefficient of each unit was estimated to be an average value of consisting basic units such as an average value of 16 basic units for 40 × 40-m unit. Structural and functional parameters were estimated for all trees within a unit. These parameters, including the decay coefficient, were obtained in every unit, whereas the topographical parameter IC could not be estimated for units at the perimeter of a plot, based on its definition. Then, correlations between IC and other parameters were analyzed using the available IC data for inner units. Correlations between two parameters were assessed based on the correlation coefficient (R) or coefficient of determination (R²), and statistical significance was set at P < 0.05.

RESULTS

Characteristics of decay coefficients

Table 4 shows the basic statistics of the three decay coefficients (μ1, μ2, μ3) estimated for the four research plots. When we examined their frequency distributions in terms of skewness and kurtosis at each plot, the positive values indicated positively skewed and leptokurtic curves, respectively, except for μ2 at the Ulu Gadut plot (UG), which was normally distributed, with P < 0.05 (Fig. 2). The other coefficients tends to show normal distributions when log-transformed, but their normality was rejected (P > 0.05) except for log μ1 and log μ2 at KS (P < 0.05). The decay coefficients μ2 and μ3 showed weak correlations in all plots (P < 0.05, Table 5).

The arithmetic mean values of the three different decay coefficients tended to increase exponentially with increasing annual mean temperature of the plot, and μ3 exhibited a remarkably high rate of increase (Fig. 3–A). The coefficients of variation (CV) for μ1 and μ2 had maximum ranges of 0.38–0.86 and 0.38–0.72, respectively, among the four plots, with no clear dependence on annual mean temperature (Fig. 3–B). The decay coefficient of μ3, in contrast, generally showed a decreasing CV and accounted for an increasing proportion of the total decay coefficient, μ1 with increasing temperature (Fig. 3–C). Standard deviations of these three decay coefficients showed similar temperature-dependence to be nearly parallel with one of μ1 and μ2. This caused differences in a CV-temperature relationship between μ3 and the other two decay coefficients. Percentages of the number of collected samples of μ3 = 0 in one year of observation were 9 % (PS), 32 % (UG), 65 % (TP), and 87 % (KS). TP showed slightly larger μ3/μ1 ratio than UG, in contrast to the patterns found in μ1 and μ2.
Spatial patterns of decay coefficients

A correlogram of Moran’s I shows that the three decay coefficients at PS had significant continuous autocorrelations for $\mu_1$, $\mu_2$, and $\mu_3$ up to radial sizes of 10, 4, and 10 m, respectively, as well as separately at sizes of 18–20 m, and 18–22 m (Fig. 4). This finding shows that the spatial variation in $\mu_1$ was more strongly affected by $\mu_3$ than by $\mu_2$. Appendix 1–A illustrates the autocorrelation of $\mu_3$ along five 200-m lines as convex patterns with different amplitudes, which correspond to the size determined using Moran’s I. Their spatial patterns showed no clear correla-
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Table 5. Correlations between $\mu_2$ and $\mu_3$ in four plots. Abbreviations N, r, and P represent the number of samples, correlation coefficient, and level of significance, respectively.

| Plot | N  | r   | P   |
|------|----|-----|-----|
| PS   | 788| 0.298| 0.000|
| UG   | 397| 0.173| 0.001|
| TP   | 389| 0.213| 0.000|
| KS   | 624| −0.095| 0.017|

Fig. 3. Relationships between decay coefficients and annual mean temperature ($T$) at four plots. A: mean value ($\bar{\mu}$) - $T$ relationships. B: Coefficient of variation - $T$ relationships. Symbols are the same as in A. C: $\bar{\mu}_3$/$\bar{\mu}_1$ ratio - $T$ relationship. Symbols shown in two shades indicate supplemental data for 1-ha plots at Padang (P), West Sumatra, and Bangkirai (B), East Kalimantan in Indonesia, collected using the same methods as in this study.

Correlation between the decay coefficient and some parameters of topography, stand structure, and productivity

Fig. 6 shows the dependency of correlations with $\mu_1$ on the unit area over which the parameters were evaluated. Absolute values of correlation coefficient tended to increase with increasing unit area in all four plots. PS showed significant positive correlations ($P<0.05$) at a unit area of $40 \times 40$ m for both $\mu_1$ – net primary productivity (NPP) (Appendix 2–A) and $\mu_1$ – aboveground biomass (ABM), although these correlations were weak, with coefficients of determination that did not reach 0.3. UG had a significantly positive $\mu_1$ – NPP relationship only for a unit area of $70 \times 70$ m (Appendix 2–B) when we used NPP during the last 2 years of analysis rather than the entire period of 11 years.
We could not confirm any significant correlations at TP during this analysis period for any unit area. KS, in contrast, had a significantly negative $\mu_1 - NPP$ relationship over a wide range of a unit areas, from $10 \times 10$ m to $90 \times 80$ m. A higher significant level ($R^2 = 0.658, P < 0.001$: Appendix 2–D) was obtained for a unit area of $60 \times 60$ m, although the relationship at $90 \times 80$ m had a higher coefficient of determination ($R^2 = 0.724, P < 0.01$).

Fig. 7 shows a diagram of the correlation among these parameters, including an index of convexity ($IC$) for unit areas with significant correlations, as shown in Fig. 6. The diagram for TP (Fig. 7–C) shows the relationships among the four clustering communities of understory vegetation, reflecting the lack of significant relations in Fig. 6.

PS had stronger positive correlations ($P < 0.001$) among the three parameters of $ABM$, $NPP$, and tree density ($N$) than those determined using $\mu_1$. At UG, there was a significantly positive relationship only between $\mu_1$ and $NPP$. The coefficients of $\mu_2$ and $\mu_3$ in UG tended to exhibit opposite correlations with $IC$, positive and negative, over the range of unit areas up to $40 \times 40$ m (Fig. 8–A). This pattern resulted in inconsistent relationship between $\mu_1$ and $IC$ over the entire range.

At TP, there were significant positive relationships between $IC$ and the three dimensional parameters of $ABM$, $NPP$, and $N$ when these relationships were compared among the four communities based on their average values (Table 6). Two communities (G1, G2) distributed on ridges and upper slopes (Fig. 5–C) had significantly higher values for these parameters than did the other two communities (G3, G4) located on gentle slopes or in valleys. These discrepancies were 1.2 fold in $ABM$, 1.3 fold in $NPP$, 1.8 fold in $N$, and 1.5 fold in $DR$. Both $\mu_1$ and $\mu_2$ had the opposite relation, with values for communities G3 and G4 as much as 1.3 times greater than those for G1 and G2. The decay coefficient of $\mu_3$, on the other hand, did not differ clearly among the four communities statistically, although it tended to be higher at G3 and G4.

At KS, there was a significant correlation between $\mu_1$ and $NPP$ only for a unit area of $60 \times 60$ m (Fig. 7–D). We confirmed significant correlations ($P < 0.05$) between $IC$ and some parameters of $\mu_1$ including $ABM$, $NPP$, and $NP$ for the tree density of two dominant pioneer species, *Symlocos purpurea* and *Acer rubinerve*, over a range of unit areas smaller than $40 \times 40$ m (Fig. 8–B). These relationships with $IC$ could be stably identified in a unit area of $60 \times 60$ m from their high coefficients of determination, despite the non-significant relationship at a $60 \times 60$-m unit due to the small number of calculable units ($n = 3, P > 0.05$). Spatial variations in both $\mu_1$ and $NPP$ were
associated with the ratio of the three dominant species to total species in terms of tree numbers in a unit area. The dominant species were *Castanopsis cuspidata*, *Abies firma*, and *S. prunifolia*, which accounted for 68% of the total tree number in this plot. The ratio showed negative and positive correlations with $\mu_1$ ($P<0.004$) and NPP ($P<0.001$), respectively. *A. firma* tended to have sympatric and allopatric distributions, respectively, with *S. prunifolia* and *C. cuspidata*. Higher ratios of total density of *A. firma* and *S. prunifolia* tended to be found at sites with higher IC values, around ridges, and throughout the whole range of altitude, while high density of *C. cuspidata* was observed at sites with slightly lower IC and on upper slopes (Fig. 9).

**DISCUSSION**

**Diversity of spatial variation in decay coefficients as an indicator of forest function**

*Lowland tropical rainforest ecosystem in Pasoh:* Spatial variation in $\mu_1$ at a 1-m interval on flat alluvial soils was strongly affected by $\mu_3$. Frequent chewing marks on wood samples indicated that termites were a major determinant of $\mu_3$. A spatial distribution pattern of $\mu_3$ showing frequent waves in Appendix 1–A should be derived from termite’s foraging patterns to expand a site from a central place of each wave radiately, central-place foraging (Abe, 1989; Yoneda et al. 1991). The size of a significant autocorrelation for $\mu_3$ was detected to be 10 m in radius continuously, and 18–22 m separately. This distribution pattern could cause high variance in the decay coefficient for leaf litter within a small area of $20 \times 20$ m in this forest reserve (Yamashita & Takeda, 1998). Feeding traces were observed in wood samples not only along the sides but also on the bottom faces that touched the soil. This implies that the most common termites in this study were *Macrotermes malaccensis* and *M. carbonarius*, which are the dominant wood feeders in this forest (Abe, 1979; Abe & Matsumoto, 1979). The average territories around their nests are equivalent in area to circles 5 and 15 m in radius, respectively, based on their nest densities (Abe &
Matsumoto, 1979), if their horizontal distributions are assumed to be random or uniform. These sizes as well as incubation periods of samples in field are an important factor driving autocorrelations. Thus, the spatial variations in two decay coefficients, $\mu_1$ and $\mu_3$, should be strongly affected by the feeding behaviors and distributions of termite nests within the forest. These two species approach foraging sites through tunnels from nests in or on the soil (Abe, 1989). Such feeding activities in tunnels sheltered from direct sunlight and diverse nesting habitats, both subterranean and epigeous, would cause unclear correlations of $\mu_3$ with canopy gaps (Tashiro et al. 2013) as well as with epigeous nests observed in this study (Appendix 1-A).

The decay coefficient of $\mu_1$ exhibited a significant positive correlation with NPP when evaluated within a unit area of $40 \times 40$ m, the size at which the maximum autocorrelation was observed. This suggests that a decay coefficient based on this unit area could be a useful indicator of material cycling in this forest ecosystem. The parameter NPP, on the other hand, was more strongly correlated with the structural parameters ABM and $N$ in the same unit area. This difference shows that structural parameters affected NPP more strongly than the functional parameter $\mu_1$ did in this plot, based on the general trend of NPP and its association with ABM in the process of regeneration (Kira & Shidei, 1967).

**Hill dipterocarp forest ecosystem in Ulu Gadut:** The decay coefficient of $\mu_1$ showed no clear correlation with the topographic parameter IC due to the opposite responses of $\mu_2$ and $\mu_3$ within the calculable range of unit area. A convex spatial pattern of $\mu_3$, similar to that at PS, was obtained from supplemental observations on the main ridge of UG at 1-m intervals in the presence of termites (Appendix 1-B). This indicates that the differing correlations with IC were caused by decomposers with different habitats, such as fungal associations at wet (concave) sites and termites at dry (convex) sites, as these are separated topographically in the super-humid climate of the study site, which receives around 6000 mm of rainfall annually. Mori (2014) represented the complex spatial distribution of the decay coefficients of wood samples in a mixed dipterocarp forest at Lambir Hill (Fig. 1) and identified the influences of termite habitat selectivity on the distribution. This habitat segregation of decomposers can lead to high decay coefficients over a large area where soil conditions vary topographically in a hilly tropical rainforest.

Autocorrelation of $\mu_1$ was observed at a 60–65-m radius, equivalent to a square area of about $110 \times 110$ m. This area is larger than the $70 \times 70$-m unit area at which a
significant positive correlation was observed between $\mu_1$ and $NPP$ over 2 years excluding a period of severe dry weather (Yoneda et al. 2006). This disagreement may have been caused by restriction of the total area of this plot, 140 $\times$ 280 m, for statistical analysis. Mori (2014) detected a positive correlation between decay coefficients and the aboveground growth rate within a unit area of 100 $\times$ 100 m based on the magnitude of autocorrelation in a 52-ha plot in Lambir. That is, the disagreement observed at UG does not contradict the usefulness of the maximum area of autocorrelation for a unit as a parameter of forest function.

Subtropical rainforest ecosystem in Tanpatsuyama: The spatial variation in $\mu_1$ was strongly affected by $\mu_2$, which was associated with the habitats of four clustering communities of understory vegetation. Specifically, these two coefficients were significantly elevated in the habitats of G3 and G4 on well-developed soils compared to those of G1 and G2 on poor soils. The relative altitude and $IC$ based on a unit of 10 $\times$ 10 m also differed significantly between these two pairs of communities (Table 6). This suggests that topographic parameters affect the decay coefficients as well as soil properties. The coefficient $\mu_3$, in contrast, was not clearly associated with these communities. This is a different pattern of responses to soil properties from that observed at UG, although the $\mu_3/\mu_1$ ratios of the two plots were almost the same. This discrepancy might have been caused by a driver of $\mu_3$ other than termites acting at UG, despite the presence of termites in the Tokunoshima, where TP is located (Abe, 1989). Stoklosa et al. (2016) noted that
termites were important decomposers of woody debris in a subtropical mixed hardwood and pine forest in Mississippi, USA. Further observations are necessary to assess the contribution of termites to decay in this forest formation.

A negative correlation was confirmed between $\beta_1$ and $\text{NPP}$ among all four communities (Appendix 2 - C). We examined the mechanism through which higher $\text{NPP}$ was obtained under lower $\beta_1$ conditions. Higher $\text{DR}$ of G1 and G2 with lower $\beta_1$ could produce annual decomposition, $\text{DEC}$, nearly equivalent to those at G3 and G4, obtained as a value of one year multiplied by the product of $\beta_1$ and $\text{DR}$ (Table 6). The elevated $\text{DEC}$ of G1 may be temporally stable in comparison with that of G4, when we consider that the temporal variances in $\text{DR}$ were 55 % and 155 % of the coefficient of variation over 10 years, respectively. This stable high $\text{DEC}$ at a convex site that suffers frequent disturbances from typhoons might support nutrient cycling in this highly productive system as well as functional resilience of the vegetation in this type of habitat (Kubota et al. 2004). The higher biomass in this habitat was realized through high dry matter density, with higher tree density and suppressed canopy height due to chronic wind stress (Kira & Shidei, 1967). The strong sprouting ability of Castanopsis sieboldii and high recruitment of diverse species maintained these structural features of G1 and G2.

**Warm-temperate lucidophyll forest ecosystem in Kasugayama:** The $\mu_2$ decay coefficient had a weak

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**Table 6. Dimensional features of four communities in TP.** Index of convexity ($IC$) is a mean value based on a unit area of 100 m$^2$. RA is the relative altitude. Subscripts show periods of observation as the last two digits of the year after 2000 AD. Superscripts indicate significant differences ($P < 0.05$) between items marked with the same letters.

| Cluster of vegetation | Area (ha) | $IC$ | RA (m) | $u_1$ (1/yr) | $u_2$ (1/yr) | $u_3$ (1/yr) | $\text{ABG}_{2007}$ (t/ha) | $\text{NPP}_{07-12}$ (1/ha) | $\text{DR}_{02-12}$ (t/ha/y) | $\text{DEC}_{02-12}$ (t/ha/y) |
|-----------------------|-----------|------|--------|--------------|--------------|--------------|----------------------|-----------------|----------------|----------------|
| 1                     | 0.52      | 1.81 $^{ab}$ | 30$^{a}$ | 0.65$^{ab}$ | 0.48$^{a}$ | 0.17$^{a}$ | 377                   | 1235            | 6.63          | 6.01          | 3.87          |
| 2                     | 1.71      | 0.25$^{a}$ | 35$^{ab}$ | 0.64$^{a}$ | 0.47$^{a}$ | 0.17$^{a}$ | 348                   | 780             | 4.90          | 4.47          | 2.73          |
| 3                     | 1.06      | -0.62$^{a}$ | 40$^{a}$  | 0.80$^{a}$ | 0.57$^{a}$ | 0.23$^{a}$ | 311                   | 605             | 4.36          | 2.72          | 2.09          |
| 4                     | 0.71      | -0.82$^{a}$ | 45$^{a}$  | 0.91$^{a}$ | 0.70$^{ab}$ | 0.22$^{a}$ | 288                   | 528             | 4.45          | 4.37          | 3.40          |
| total                 | 4.00      | 0.02  | 37      | 0.73         | 0.54         | 0.19         | 331                   | 748             | 4.90          | 4.19          | 2.99          |

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![Fig. 8](image-url) Relationships between correlation coefficient and unit area used for analysis of correlations between the index of convexity, $IC$, and several dimensional parameters. A: UG, B: KS. Asterisks are the same as those in Fig. 6.

![Fig. 9](image-url) Distributions of units with abundances of Castanopsis cuspidata, Abies firma, and Symplocos prunifolia higher than the third quartile in the ratio of total stem density of these three species to total one of all trees in a 20 × 20-m unit area with coordinates of IC and relative altitude. Open circles and triangles show units characterized by C. cuspidata and by a combination of A. firma and S. prunifolia, respectively. Dots with gray shading show units with a ratio lower than the third quartile.
Spatial variations in the decay coefficients of forest ecosystems

Fig. 10. Relationships between decay coefficient and annual mean temperature of several forest formations in climatic zones ranging from the tropical to the cool-temperate zone in East and Southeast Asia (Fig. 1). Triangle and circle symbols indicate different decay coefficients: \( \mu \) from the exponential decrease model and \( \beta \) from the logistic decrease model (Yoneda, 1975). Open, closed, and gray-shaded triangles indicate different materials: the small wood sticks of this study, leaf litter, and accumulated fine litter in the Ao layer of soils, respectively. Four large open triangles show the results of this study, and two small ones indicate supplemental data (see Fig. 3). Open and closed circles show commercially available wood and natural dead wood, respectively. An open circle with the letter “a” is a value recorded at Lambir with Kapur (Dryobalanops aromatica) wood (Mori, 2014), and the others are referenced from a previous study with balsa (Ochroma lagopus) wood (Yoneda et al. 1991). Vertical lines show the range of the standard deviation. The two thick lines show the regressed \( \mu-T \) and \( \beta-T \) relationships.

A significant negative correlation between \( \mu_1 \) and NPP was observed within the unit area of \( 90 \times 80 \) m, which was almost equivalent to the maximum area of autocorrelation for \( \mu_1 \) in a \( 90 \times 90 \)-m unit. This negative correlation may have occurred through the same mechanism as that at TP, i.e., the association with frequent disturbance by typhoons, which occur at an average interval of 6.6-years in this forest (Naka, 1982), although we did not observe a significant negative relationship between \( \mu_1 \) and DR within 6 years of observations. Disturbance events should be biased toward forest stands on ridges and higher slopes facing west and southwest based on the major wind direction of typhoons in this area. This bias may have led to a positive correlation between IC and the density of pioneer tree species, NP, in this plot (Fig. 8). Nakane (1975) estimated the same topographical gradient of decay rates as that of the decay coefficients under an assumption of a constant supply rate of coarse woody litter irrespective of topographic position. However, the elevated DR of trees, which was biased toward convex sites, appears to be an important ecological feature of this forest. The negative correlations observed at KS and TP may indicate spatial variations in material cycling in forest ecosystems that suffer from frequent typhoons.

We observed habitat segregation between C. cuspidata and A. firma-S. prunifolia communities accompanying Tsuga sieboldii at topographically convex sites at KS, in contrast to the strong dominance of C. sieboldii, which has strong sprouting abilities, at TP. KS has thermal conditions of 106–111°C•month, as assessed with the warmth index, in the upper zone of warm-temperate climate, where mixed forest of these two evergreen needle-leaved species is often found in western Japan (Kira et al. 1976). This floristic feature of convex sites may affect the vegetation at KS; thus, these species’ tolerance of storm disturbances should be examined as one of the driving factors for their establishment.

Spatial \( \mu_1 \)-NPP relations: Spatial relations differed among the four plots when we assessed these parameters based on a unit area that was nearly equivalent to the maximum autocorrelation area for \( \mu_1 \) at each plot. We examined these relationships based on material cycling through the dynamics of coarse woody debris in a forest ecosystem (Yoneda et al. 2016, 2017). The annual decomposition, DEC, is an important parameter for assessing spatial variations in productivity under dynamic equilibrium conditions. The decay coefficient is affected primarily by abiotic and biotic environmental factors in soils (Swift et al. 1979; Mori, 2014) and the quality of litter (Hirobe et al. 1979; Mori, 2014)
2004; Weedon et al. 2009), whereas the DR of trees is largely influenced by density-dependent effects such as self-thinning (Yoda et al. 1963) and external disturbances such as storms (Yoneda et al. 1998) or drought (Nakagawa et al. 2000; Yoneda et al. 2006). Assuming that these two parameters, the decay coefficient and DR, are mutually independent, they can produce various spatial relationships between $\mu$ and DEC in a forest. Hereby, a negative $\mu$-DEC relationship could be realized when DR is spatially a negative relationship with $\mu$1 as well as a positive $\mu_1$-DEC relationship when DR is constant or has a positive relation with $\mu_1$. DR values that are highly biased against sites with lower $\mu_1$ could result in negative relationships throughout a wide range of $\mu_1$.

This bias could be a major reason for the negative relationships observed at TP and KS. The positive relationships at PS, UG, and Lambir (Mori, 2014) suggest that the spatial variations in their DR values satisfy the latter conditions. This implies that various $\mu_1$-NPP relations occur, depending on the DR-$\mu$ relationship of a forest ecosystem.

Temperature dependence of decay coefficients in East and Southeast Asia

The mean values of the three types of decay coefficients used in this study had positive relationships with annual mean temperatures in the associated plots (Fig. 3-A). When we examined the dependency of $\mu_1$ on temperature, the geometric mean values at PS and UG tended to be similar to the decay coefficient ($\mu$) of fine litter in tropical forests in East and Southeast Asia, whereas TP and KS had values as low as those of balsa wood decomposed in Western Japan (Yoneda et al. 1991) (Fig. 10). High values observed at PS and UG were driven largely by fragmentation by termites. Differences in the decay coefficients between this study and a balsa-wood experiment conducted in tropical forests (Yoneda et al. 1991) might be the result of the short field incubation period of 1 year both used for assessment or of differing effects of fragmentation due to the larger size of the balsa samples ($2 \times 2 \times 15$ cm) compared to the samples used in the present study ($2 \times 95 \times 115$ mm). Fragmentation by termites may thus accelerate the rate of increase in the decay coefficient with increasing temperature in fine litter, such as in the samples used in this study, when the coefficient is obtained from short-term observations of up to 1 year. When we assume a positive linear correlation between the relationship of $\mu$ with temperature ($T$) on semilogarithmic coordinates, the regression line for fine litter in this study was $\mu = 0.102 \times 3.04^{0.10}$. This formula indicates that the rate of increase is fairly high, up to $\mu_{0.10} = 3$, due to the high activity of termites in tropical forests.

Most of the data examined fell within a range of mean value ($m_\mu$) / 1 standard deviation ($\sigma$) from the regression line. The variance of a regression indicates intersite variations in $\sigma$ among forests with the same annual temperature conditions. Most of these data were collected within a small area, making it difficult to evaluate them using mean values due to the spatial variations within each forest. When we assume that the variance of a regression shows intrasite variations within a forest, the probability of the occurrence of an observed value can be estimated from the regression. These probabilities are 39% at PS, 38% at UG, 24% at TP, and 28% at KS when we apply the probability density function of a normal distribution to the logarithmic values of the decay coefficient. When all values for the regression are assumed to represent the mean value of each forest with regard to spatial variations, it is necessary to estimate the overall probability as the product of the probabilities of intersite and intrasite variations. The overall probability can be represented with a probability density function showing a two-dimensional standard normal distribution. The calculated probabilities of $\mu$ within $m_\mu \pm \sigma$ were 26% at PS, 26% at UG, 17% at TP, and 19% at KS.

We still have insufficient data to calculate the regression with regard to spatial variations in the decay coefficients. Such calculations represent an important ecological issue, showing the need to evaluate the functions and structures of each forest formation in light of its spatial variations. Kira (1976, 1991) reported large variance in NPP among different forest types in East and Southeast Asia, accounting for 34–41% of coefficient variation for each type, and found stand maturity to be a parameter driving variations in energy efficiency for NPP based on gross productivity. The present study indicates that intrasite variance in decay coefficients are as large as intersite variations, affecting the spatial variations in NPP and DR. Therefore, the spatial variation in decay coefficients is a useful parameter for describing the functional and structural features of a forest ecosystem.

ACKNOWLEDGEMENTS This study was conducted under NIES-FRIM-UPM Joint Research Project on Tropical Forest Ecology and Biodiversity at Pasoh Forest Reserve, Field Biology Research and Training Project by JICA in Padang, and Research Project on Rehabilitation process of tropical forest ecosystem through the interaction
between plants and soil in Bukit Bangkirai and Padang. We sincerely thank Dr. Saw Leng Kuang, Dr. Syunzo Kawamura and Dr. Eiji Suzuki for their cooperation as the leaders of these projects. We also thank Dr. Sanae Mori, Dr. Akira Itoh, Dr. Katsutoshi Sakurai and Dr. Tsuguyuki Masunaga for their valuable comments for this manuscript, and Dr. Eiji Suzuki and Mr. Tadatsugu Hamada for their informations about research sites at Bukit Bangkirai and Pasoh. We also acknowledge all members to joint field observations for litterbag experiments and dbh-census of this study. We thank Kyushu Regional Forest Office, Forest Agency and Nara Park Office, Nara Prefecture for their permission of this study at TP in the present Amamigunto Forest Ecosystem Reserve and at KS in the Kasugayama Forest Reserve, respectively. This study was partially supported by the Ministry of the Environment, Japan through Global Environment Research and MEXT/JSPS KAKENHI Grant Number 19310149.

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Appendix 1. Horizontal changes in decay coefficients of wood sticks placed at 1-m intervals on five 200-m lines in PS (A) and two 50-m lines along the main ridge of the UG plot (B1 and B2), obtained from supplemental observations. Open and closed circles show $\mu_1$ and $\mu_3$, respectively. B1 and B2 are a mature forest stand in UG and a secondary forest neighboring UG, respectively. Gray-shaded triangles in A are locations of epigeous termite nests. Symbols of ** in A and B2 show canopy gaps.
Appendix 2. Correlations between the decay coefficient, $\mu_1$, and net primary productivity, $NPP$, in four plots. **A**: PS (40 x 40-m unit), **B**: UG (70 x 70-m unit), **C**: TP (four understory communities), **D**: KS (60 x 60-m unit). Figures in **C** correspond to four understory communities being a sequence from G1 to G4 in Fig. 5-C. $R^2$ is the coefficient of determination.