

Article

Effects of Topographical Differences on Macroinvertebrate Access and Litter Decomposition in a Temperate Broad-Leaved Forest

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Abstract

Geodiversity, particularly topographical gradients, significantly influences ecosystem function by creating heterogeneous environmental conditions. This study examined how local-scale microtopography and litter bag perforation affected leaf litter decomposition rates in a humid-temperate secondary forest. We categorized microtopography into ridge, valley, southwest slope, and northeast slope, with relative height differences of around 20 m. Using the litter bag method comparing non-perforated (1 mm mesh) and perforated (with 6 mm holes) bags, we measured leaf litter mass loss and moisture content of *Quercus serrata* over 6 and 12 months. While microtopography caused only slight differences in leaf litter moisture content, it significantly influenced decomposition rates. Leaf litter mass loss was lower in valley microtopography compared to the southwest slope and ridge microtopography. We infer that topographical differences in unmeasured microclimatic factors, such as solar radiation and soil temperature, may have potentially driven these spatial variations in decomposition. Furthermore, because the litter bag perforation did not significantly promote further mass loss, our results suggest that baseline decomposition driven by organisms capable of passing through the 1 mm mesh (e.g., microbes and meso/microfauna) might have been sufficiently high in this environment. These findings highlight that local-scale microtopographical differences enhance the spatial heterogeneity of leaf litter decomposition in forest ecosystems.

Keywords: litter decomposition; topography; spatial variability



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1. Introduction

Geodiversity, specifically topographical and geological gradients, is a pivotal factor influencing ecosystem function [1]. It dictates the range of environmental and abiotic conditions across different locations within an ecosystem, fostering heterogeneity in species richness, abundance, traits, and distribution of biological communities. Consequently, geodiversity shapes ecosystem function across spatial scales from regional to local [2]. At the local scale, geodiversity, such as microtopography, can influence both aboveground and

belowground processes, including predation pressure on invertebrates and organic matter decomposition, by amplifying fluctuations in abiotic conditions [3,4].

In forest ecosystems, topography creates various gradients due to slope aspect and gravity [5,6], altering the distribution and function of both aboveground and belowground communities [7–9]. Generally, soil moisture is lower on ridges than in valleys [10], and in the Northern Hemisphere, south-facing slopes tend to be drier due to greater solar radiation. Furthermore, forests exhibit nested relative height differences ranging from hundreds of meters down to a few meters, where topographical variations enhance the spatial heterogeneity of biological community distribution and function. For example, soil animal community structures [7,11] and organic matter decomposition rates [12] differ between ridges and valleys separated by approximately one hundred meters. Even microtopographical differences of around 10 m in relative height can lead to variations in soil respiration and N₂O fluxes [9]. However, such microtopographical differences have received less attention compared to larger-scale topographical variations, and quantitative assessments of their impact on forest ecosystem functions are rare. Investigating how these local topographical differences affect biological communities and ecosystem functions within forests is crucial for understanding the spatial heterogeneity of ecosystem functions driven by geodiversity.

Litter decomposition proceeds through mineralization by soil microorganisms (fungi and bacteria) and the fragmentation of substrate by soil microfauna and macrofauna [13,14]. However, the effect of soil animal communities on litter decomposition can be context-dependent, as they can also disturb soil microfauna [15]. At a global scale, the contribution of soil animal communities to litter decomposition is higher in tropical forests [16,17] but smaller in boreal regions [17]. At a local scale, the composition of soil animal communities varies with environmental factors and litter quality [18–20], and the contribution of macroinvertebrates to the decomposition of low-quality litter is small [21]. Moreover, soil macrofauna tend to play a larger role in litter decomposition under dry conditions and in environments with low soil microfauna activity [22,23]. This suggests that environmental heterogeneity controls the structure and function of soil macrofauna, and forest microtopography is expected to influence differences in litter decomposition rates and the contribution of soil macrofauna to this process. However, few studies have isolated the relationship between local-scale environmental factors like microtopography and litter decomposition by considering the size of soil invertebrates (but see [20,21]).

Across this size spectrum, soil fauna contribute to decomposition primarily through the physical fragmentation of litter, which increases the surface area available for microbial colonization and thereby facilitates subsequent mineralization by fungi and bacteria [15,16]. Because body size determines which soil animals can access litter through pores or openings of a given diameter, litter-bag designs that restrict entry according to mesh or perforation size have long been used to isolate the relative contribution of differently sized faunal groups to decomposition [24–26]. Microtopography is expected to shape these size-differentiated contributions indirectly, by generating local heterogeneity in moisture, solar radiation, and soil temperature that influences the activity and distribution of decomposer communities across the microfauna-to-macrofauna size spectrum [7,9,11].

This study aims to deepen the understanding of the spatial heterogeneity of ecosystem functions driven by geodiversity by clarifying how local-scale microtopography affects ecosystem functions, specifically litter decomposition, considering the size of soil invertebrates. The objectives of this study were to clarify the effects of microtopography on leaf litter decomposition rates and the contribution of macroinvertebrates to leaf litter decomposition in a forest ecosystem. To investigate these effects, we proposed two directional hypotheses, grounded in the environmental gradients described above: Hypothesis (1) Be-

cause soil moisture is generally higher in valleys than on ridges or south-facing slopes [10], and litter moisture promotes microbial decomposition, we hypothesized that leaf litter moisture content and decomposition rates would be higher in valley microtopography than on ridges or southwest slopes; Hypothesis (2) Because soil macrofauna are expected to play a larger role in litter decomposition under drier conditions [23,27], we hypothesized that the effect of macroinvertebrate access on leaf litter decomposition would be greater on ridges and southwest slopes than in valleys.

2. Materials and Methods

2.1. Study Sites

The study site was an experimental field station at the Tokyo University of Agriculture and Technology (35°38' N, 139°22', elevation 155 m) in Hachioji City, Tokyo. The region experiences an Asian monsoon climate with wet and dry seasons occurring from June to September and December to January, respectively. The average temperature and annual precipitation in this area during 2019 were 15.3 °C and 1448.5 mm, respectively [28]. This study was conducted in a 1-ha plot in a secondary temperate forest with a horizontal spacing of 100 × 100 m, divided into 10 m × 10 m quadrats (Figure 1). This plot contained a deciduous broadleaved forest zone dominated by *Quercus serrata* and an evergreen coniferous forest zone planted with *Cryptomeria japonica* and *Chamaecyparis obtusa*. The understory and shrub layers of the deciduous forest zone also contained the evergreen trees *Eurya japonica* and *Ilex crenata*. The plot had been mown multiple times yearly; therefore, understory vegetation was undeveloped, but *Pleuroblastus chino* was dense around the plot. Trees with a diameter at breast height (DBH) exceeding 5 cm were measured and identified at this study site [29].

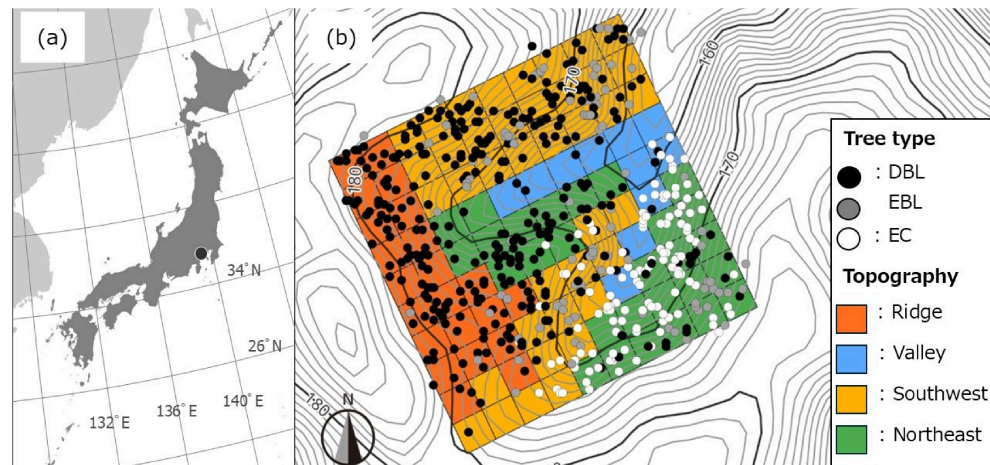


Figure 1. (a) Sampling area in Japan (b) and 1-ha plot (100 m × 100 m; site of the Japan Long-Term Ecological Network; JaLTER) of Field Museum Tamakyuryo, Hachioji, Tokyo, Japan. The topography of each quadrat was classified according to Bellingrath-Kimura et al. [9]. Tree type; DBL, deciduous broadleaf tree; EBL, evergreen broadleaf tree; and EC, evergreen conifer tree. Topography; Ridge: red, valley: blue, southwest slope: yellow, and northeast slope: green. In (a), grey shading indicates land area and the marker denotes the location of the study site. In (b), grey lines indicate topographic contours.

The 1-ha permanent plot features continuous ridges and valleys with an elevation difference of 20 m (Figure 1). Following Bellingrath-Kimura et al. (2015) [9], who conducted research at the same study site, we categorized the microtopography of each quadrat into four types: (1) ridge, (2) valley, (3) southwest slope, and (4) northeast slope. Ridges were defined as areas with an elevation of 170 m or higher and a measured slope angle of less

than 20°. Valleys were defined as areas outside of ridges with an elevation below 160 m and a measured slope angle of less than 12°. Southwest slopes were defined as areas outside of ridges and valleys with a slope aspect greater than or equal to 180°, while northeast slopes were defined as areas outside of ridges and valleys with a slope aspect less than 180°. Based on these classifications, the study plots included 22 quadrats categorized as ridge, 11 as valley, 39 as southwest slope, and 28 as northeast slope (Figure 1). The overall tree density across all study plots was 6.98 trees per quadrat (10 m × 10 m). Notably, the valley microtopography exhibited a lower tree density of 2.62 trees per quadrat compared to other locations. For the soil respiration (CO₂ flux) data used as an explanatory variable, we utilized existing data previously measured within the same 1-ha plot by Bellingrath-Kimura et al. (2015) [9]. Briefly, soil respiration was measured using the closed-chamber method, and the CO₂ concentrations were analyzed using gas chromatography to calculate the emission fluxes.

2.2. Litter Mass Loss (%) Surveys

In this study, we employed the litter bag method [30] to quantify decomposition rates by placing litter in mesh bags and retrieving them after a set period. To investigate the contribution of macroinvertebrates to litter decomposition, we prepared two types of litter bags: “macroinvertebrate access bags” (10 cm × 10 cm, 1 mm mesh size), which had 20 holes (6 mm in diameter) punched into them, and “macroinvertebrate exclusion bags” which were left untreated (10 cm × 10 cm, 1 mm mesh size). Each litter bag was filled with 2.0 g (air-dry weight) of *Quercus serrata* leaf litter, the dominant tree species at the study site. It has been reported that the initial C:N ratio of freshly fallen leaves from *Quercus serrata* is 67.4 [31]. This indicates that the substrate is relatively nutrient-poor and decomposes slowly, which is typical of this species. The *Quercus serrata* leaf litter was collected using litter traps installed within the 1-ha plot in 2010, 2012, and 2020. Before deployment, we determined the initial dry weight of a subset of 2.0 g air-dry litter samples by drying them in a constant temperature oven (70 °C for 48 h) to calculate a correction factor. This correction factor was then used to estimate the initial dry weight of the litter in each bag. In June 2021, a total of 3200 litter bags were deployed across all 100 quadrats (10 m × 10 m) within the 1-ha plot. A 1 m × 1 m sub-quadrat was established near the center of each of the 100 quadrats. The litter bags were placed on the F layer (fermentation layer) after removing the litter layer within these sub-quadrats, then covered with litter. In each sub-quadrat, 14 access bags (including 4 spares in case of damage or loss) and 18 exclusion bags (including 8 spares) were installed.

After about six months of deployment (December 2021) and twelve months after deployment (June 2022), five access bags and five exclusion bags were retrieved from each quadrat. The six-month collection period covered the spring to autumn seasons, while the twelve-month period encompassed all seasons. The wet and dry weights of the litter within the bags were measured using a microbalance (AS PRO ASP402F, AS ONE, Osaka, Japan). We then calculated leaf litter mass loss (%) and litter moisture content from the wet and dry weight values of the leaf litter in the bags. After collection, litter bags were immediately placed in zip-lock bags and sealed to prevent changes in wet weight. For the first collection, the wet weight of all leaf litter was measured. For the second collection, three litter bags were randomly selected from each quadrat, and their leaf litter wet weights were measured. All collected leaf litter from the bags was then oven-dried (70 °C for 48 h) to determine the dry weight. Leaf litter mass loss (%) was calculated as a percentage (%) using the formula: (mass loss/initial mass (g)) × 100. Bags where the mass after collection was greater than the initial mass were excluded from the analysis. Furthermore, we investigated whether

there was a significant difference in mass loss rates among the *Quercus serrata* leaf litter collected in different years (2010, 2012, and 2020).

2.3. Statistical Analysis

We used Generalized Linear Models (GLMs) to elucidate the effects of environmental factors on litter decomposition rates within the forest. Because microtopography and vegetation type were themselves quadrat-level variables, a quadrat-level random effect was not considered appropriate for this design. Instead, residual spatial autocorrelation among quadrats was directly assessed using a DHARMA (Version 0.47 [32]) Moran's I test for distance-based autocorrelation, based on quadrat centroid coordinates; no significant spatial autocorrelation was detected for either the 6-month model (observed = 0.0044, expected = −0.0102, sd = 0.0106, $p = 0.168$) or the 12-month model (observed = −0.0075, expected = −0.0104, sd = 0.0108, $p = 0.784$). First, we used Tukey's HSD test to examine the relationship between leaf litter collection year and leaf litter mass loss (%), confirming that the collection year did not significantly influence decomposition rates. We constructed two separate models, one for each retrieval period (6-month and 12-month). Because the 6-month and 12-month samples experienced distinct seasonal conditions—specifically, the latter included a cold winter period during which decomposition likely stagnated—we analyzed them independently to avoid obscuring the seasonal context. In these models, leaf litter mass loss (%) served as the response variable, and environmental factors were included as explanatory variables, assuming a beta error distribution with a logit link function. For the 6-month model, these explanatory variables comprised presence/absence of macroinvertebrate access (treatment), CO₂ flux, microtopography, leaf litter moisture content, and vegetation type. For the 12-month model, the same explanatory variables were used except CO₂ flux, which was not measured at this retrieval and was therefore excluded. Following Hasegawa et al. [29], vegetation types for each quadrat were categorized into three groups: “deciduous broadleaf”, “evergreen conifer”, and “other.” The “other” category included areas with no dominant vegetation type or mixed compositions. Any leaf litter decomposition resulting in negative mass loss values was excluded from the statistical analysis. Microtopography was treated as a categorical variable with four levels: ridge, valley, southwest slope, and northeast slope. To address potential multicollinearity among explanatory variables, we assessed the Variance Inflation Factor (VIF); all VIF values were below 5, indicating low collinearity. Additionally, we constructed a linear model to examine the relationship between leaf litter moisture content and microtopography, and differences were tested using Tukey's HSD. We also fitted a model including the interaction term between the macroinvertebrate exclusion treatment and microtopography, but because this interaction did not have a significant effect, it was excluded from the final model. Likelihood ratio tests ($p < 0.05$) were performed on the GLMs. When a categorical variable was found to be significant, differences in decomposition rates among its categories were further examined using Tukey's HSD. Because microtopography may itself determine other environmental variables such as tree density (e.g., tree density is lower in valleys), we additionally fitted a model including tree density as a covariate, using only the 6-month dataset ($n = 925$, after excluding 10 bags from a quadrat lacking tree density data), in order to isolate the effect of tree density from that of microtopography; tree density was not a significant predictor ($p = 0.240$), and microtopography remained highly significant after its inclusion (Supplementary Table S2). All statistical analyses were performed using R ver. 4.1.2 [33], and figures were generated using the ggplot2 package [34].

3. Results

In this study, a total of 2199 litter bags were retrieved after 6 and 12 months of placement. Across all retrieval periods and microtopographic types, 151 of 2199 retrieved litter bags (6.9%) were excluded due to negative or unmeasurable mass loss values. The exclusion rate was notably higher on northeast slopes (16.5%) than on southwest slopes (2.8%), ridges (1.7%), or in valleys (9.0%); however, the number of retained bags on northeast slopes (492) remained substantial (Table S1). The year of *Quercus serrata* leaf litter collection (2010, 2012, or 2020) had no significant effect on leaf litter mass loss (%) (Likelihood ratio test, $p > 0.05$). The average leaf litter mass loss (%) were 39.3% for exclusion bags and 38.0% for access bags after 6 months, and 38.3% for exclusion bags and 37.1% for access bags after 12 months. There was no significant difference in leaf litter mass loss (%) between the 6-month and 12-month retrieval periods. For both retrieval periods, the interaction term between microtopography and the presence/absence of macroinvertebrate access did not show a significant effect on leaf litter mass loss (%) (Likelihood ratio test, $p > 0.05$).

Macroinvertebrate access was associated with significantly lower leaf litter mass loss (Likelihood ratio test, $p < 0.05$; Tables 1 and 2). Furthermore, a significant relationship was observed between microtopography and leaf litter mass loss (%) for both the 6-month and 12-month deployment periods (Likelihood ratio test, $p < 0.05$). Leaf litter mass loss (%) was lower in valley microtopography compared to southwest slope and ridge microtopography (Figures 2 and A1, Tables 1 and 2). For instance, after 6 months, the mass loss rates in the valley microtopography were 32.0% for access bags and 33.8% for exclusion bags, whereas those on the ridge reached 38.8% for access bags and 38.2% for exclusion bags (Figure 2).

Table 1. Results of the beta-distribution generalized linear model (GLM; logit link) for leaf litter mass loss (proportion) of litter bags retrieved after 6 months. The model structure was: leaf litter mass loss ~ litter bag treatment + leaf litter moisture content + soil respiration (CO₂ flux) + microtopography (4 categories) + vegetation type (3 categories). Bold text indicates $p < 0.05$. Estimates (Est.) and standard errors (SE) are on the logit scale; χ^2 and p -values were obtained from likelihood ratio tests. Model fit was assessed using Ferrari's pseudo- $R^2 = 0.252$.

Variable	df	Est. $\pm$ SE	χ^2	p
(Intercept)		-0.775 ± 0.045	-	-
Litter bag treatment	1		10.89	0.00097
Exclusion (ref)		0.00	-	-
Access		-0.082 ± 0.025	-	-
Litter moisture content	1	0.194 ± 0.013	211.99	$<2.2 \times 10^{-16}$
CO ₂ flux	1	0.008 ± 0.013	0.41	0.520
Topography	3		41.76	4.50×10^{-9}
Northeast slope (ref)		0.00	-	-
Southwest slope		0.096 ± 0.035	-	-
Ridge		0.092 ± 0.040	-	-
Valley		-0.172 ± 0.047	-	-
Vegetation type	2		49.79	1.55×10^{-11}
Evergreen conifer (ref)		0.00	-	-
Deciduous broadleaf		0.340 ± 0.049	-	-
Other		0.308 ± 0.055	-	-

Table 2. Results of the beta-distribution generalized linear model (GLM; logit link) for leaf litter mass loss (proportion) of litter bags retrieved after 12 months. The model structure was the same as in Table 1, except that soil respiration (CO₂ flux) was not measured at this retrieval and was therefore excluded. Bold text indicates $p < 0.05$. Estimates (Est.) and standard errors (SE) are on the logit scale; χ^2 and p -values were obtained from likelihood ratio tests. Model fit was assessed using Ferrari's pseudo- $R^2 = 0.177$.

Variable	df	Est. $\pm$ SE	χ^2	p
(Intercept)		-0.777 ± 0.076	-	-
Litter bag treatment	1		3.53	0.060
Exclusion (ref)		0.00	-	-
Access		-0.064 ± 0.034	-	-
Litter moisture content	1	0.223 ± 0.019	134.38	$<2.2 \times 10^{-16}$
CO ₂ flux	-	not included	-	-
Topography	3		13.97	0.00295
Northeast slope (ref)		0.00	-	-
Southwest slope		-0.010 ± 0.048	-	-
Ridge		0.036 ± 0.052	-	-
Valley		-0.200 ± 0.066	-	-
Vegetation type	2		18.06	0.00012
Evergreen conifer (ref)		0.00	-	-
Deciduous broadleaf		0.340 ± 0.080	-	-
Other		0.287 ± 0.088	-	-

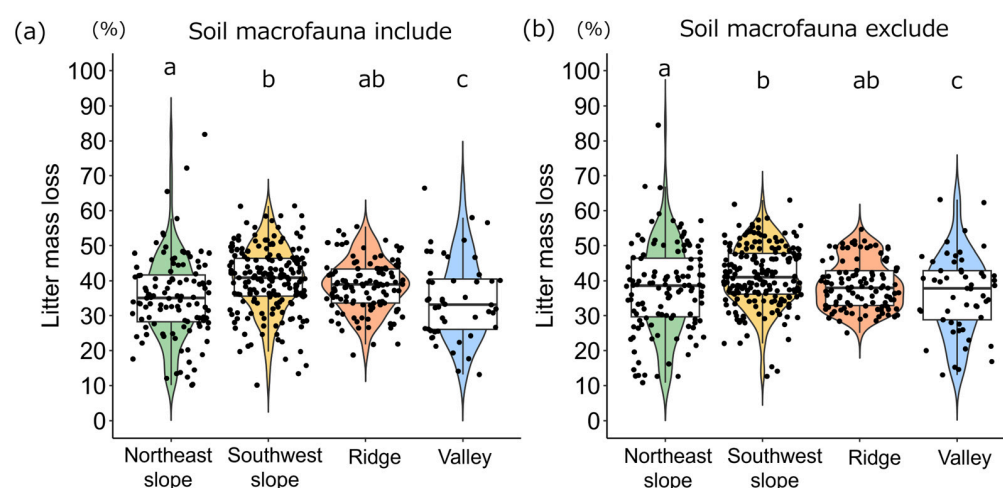


Figure 2. Leaf litter mass loss (%) of litter bag; (a) Soil macrofauna access bags, (b) Soil macrofauna exclusion bags. Different letters indicate a significant difference as determined by Generalized Linear Models (GLMs). For litter mass loss rates of bags deployed for 12 months, please refer to Figure A1.

Quadrats dominated by deciduous broadleaf trees (*Quercus serrata*) showed greater *Quercus serrata* leaf litter mass loss (%) than those dominated by evergreen conifers (*Cryptomeria japonica*) (Tukey's HSD, $p < 0.05$; Figures A2 and A3). After 6 months, the average mass loss rates were 38.4% for access bags and 39.5% for exclusion bags in the quadrats dominated by deciduous broadleaf trees, compared to 19.4% and 25.0% in the *Cryptomeria japonica* quadrats (Figure A2). Furthermore, leaf litter moisture content significantly promoted leaf litter mass loss (Likelihood ratio test, $p < 0.05$; Figures 3 and A4). Additionally, a significant relationship was found between leaf litter moisture content and microtopography, with valley microtopography exhibiting slightly higher leaf litter moisture content than other topographical types (Tukey's HSD, $p < 0.05$; Figure 4).

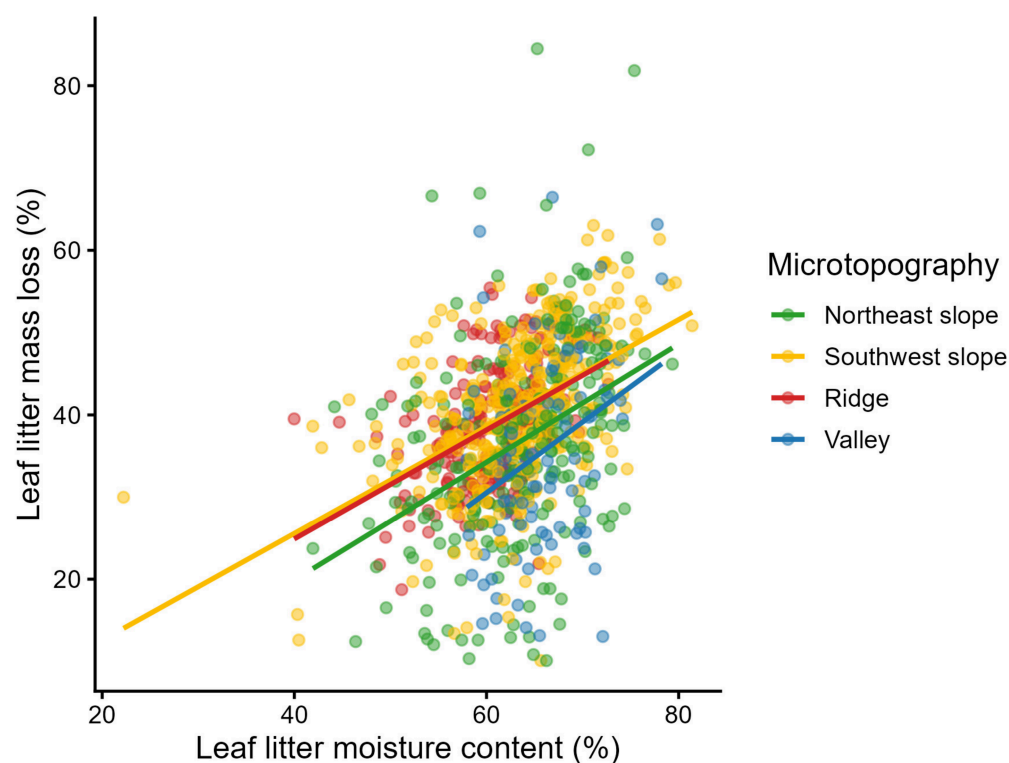


Figure 3. Relationship between leaf litter moisture content and leaf litter mass loss across microtopographical types, for litter bags deployed for 6 months. Each point represents an individual litter bag; lines show linear regression fits for each microtopographical type.

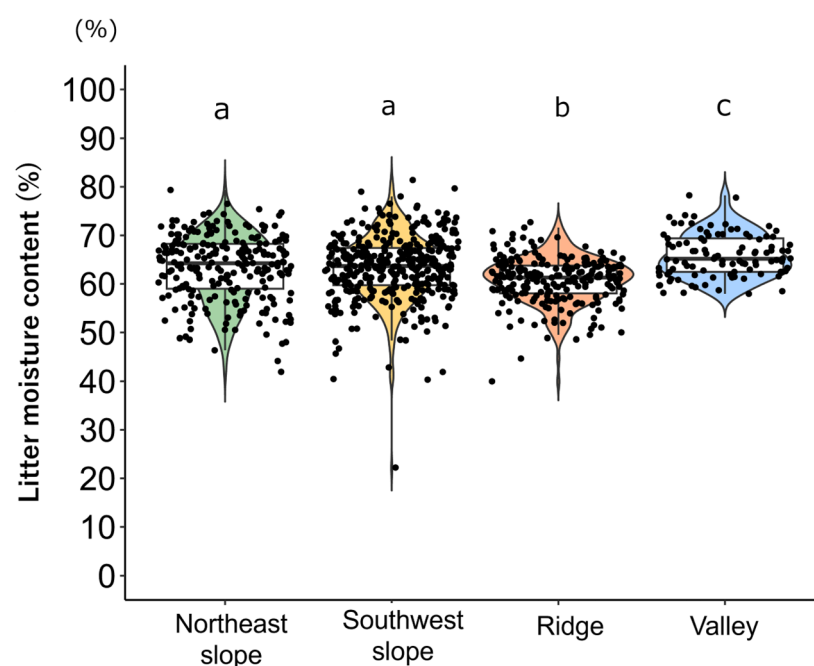


Figure 4. Leaf litter moisture content across microtopographical types for litter bags deployed for 6 months. Leaf litter moisture content was calculated from the difference between the wet and dry weights of the retrieved leaf litter. Different letters indicate significant differences as determined by Tukey's HSD. Each point represents an individual litter bag. Box plots show the median and interquartile range (IQR), with whiskers extending to $1.5 \times \text{IQR}$. Violin shapes depict the kernel density distribution of the data. Colors indicate microtopographical types: northeast slope (green), southwest slope (yellow), ridge (red), and valley (blue).

4. Discussion

The average proportion of leaf litter mass loss of *Quercus* genus species in temperate forests typically ranges from 30% to 40% per year [31,35–37]. Our observed average of 39.3% is consistent with this range. Furthermore, we observed no significant difference in the total mass loss between the 6-month and 12-month retrieval periods. This lack of continued decomposition indicates that the fragmentation and microbial mineralization processes nearly halted during the cold and dry winter months, limiting most of the annual mass loss to the active spring-to-autumn seasons.

While our finding that *Q. serrata* leaf litter decomposition was faster in broadleaf-dominated quadrats might appear consistent with the Home-Field Advantage (HFA) hypothesis [38], our single-species experimental design precludes a direct test of this mechanism. Rather than a specific adaptation of decomposer communities to conspecific litter (i.e., HFA), it is highly likely that the *Cryptomeria japonica* plantations experienced lower activity densities of soil animals. This reduction in decomposer activity could be driven by the accumulation of poor-quality coniferous litter (i.e., local litter matrix quality), past historical disturbances. Thus, in *C. japonica* plantations, the inhibition of broadleaf litter decomposition likely resulted from these combined environmental and biological constraints.

Leaf litter moisture content was slightly higher in valley microtopography than on ridges or southwest slopes, in the direction predicted by Hypothesis 1; however, contrary to this hypothesis, leaf litter decomposition was faster on ridges and southwest slopes than in valleys. Hypothesis 1 is therefore only partially supported: the predicted moisture gradient was observed, albeit weakly, but it did not translate into faster decomposition in the wetter valley microtopography as expected. Topography is a key factor that creates primary environmental gradients—such as slope position, slope aspect, and soil moisture—which influence material cycling. First, soil quality typically varies with slope position because gravity-driven down-slope fluxes of water and sediments transport nutrients from upper slopes to lower slopes, often leading to higher soil fertility in valleys [39]. This increased nutrient availability generally enhances microbial activity and accelerates litter decomposition. Second, slope aspect and fine-scale relief dictate the angle of incident sunlight, generating significant gradients in local solar radiation and ground temperature [40]. South-facing slopes and ridges receive more solar radiation and are generally warmer, which can directly accelerate the metabolic rates of decomposers. Third, differences in vertical position and slope aspect also lead to soil moisture gradients [10]. Previous studies at our research site indicated that soil core moisture content tended to be significantly higher in valleys than in other topographical types [9]. In contrast, while our results showed a statistically significant difference in leaf litter moisture content, the effect of microtopography on litter moisture content was only slight.

The unexpected finding that leaf litter moisture content within litter bags was not substantially higher in valleys could be attributed to differences in the measurement location of moisture and the effect of tree density at the study site. The surface layer of the forest floor tends to be drier than the more decomposed F layer [41], and the F layer has fewer pore spaces, allowing it to retain moisture through capillary action [42]. Therefore, the moisture content within litter bags, which were placed between the litter (L) layer and the F layer, may not have shown a clear difference between valleys and ridges. Additionally, a negative correlation can exist between tree density and soil moisture in the A horizon [43]. Similarly, because tree density was lower in the valley microtopography at our study site, it might have been less likely for the litter moisture content in the litter bags (placed between the L and F layers) to be high. Thus, in microtopographies with relative height differences of about 20 m, differences in leaf litter moisture content can be small due to multiple

interacting factors. This implies that in the relationship between litter decomposition rate and microtopography, our results allow us to focus on two key environmental gradients (e.g., solar radiation, soil temperature) while largely excluding the moisture gradient.

The effect of topography on leaf litter mass loss rate varies with topographical scale and climate. For instance, lower slope positions can receive nutrient inputs from upper slopes [39], promoting decomposition downslope [44]. Contrary to previous reports, our study found faster decomposition on ridges and southwest slopes, and slower decomposition in valleys. This suggests that at smaller topographical scales, nutrient reduction on ridges might not be severe enough to inhibit decomposer community function [45,46]. The effect of solar radiation and ground temperature gradients on litter mass loss rate differs by climatic zone. Even within temperate zones, in forests with low precipitation, litter decomposition is faster in valleys and on north-facing slopes and slower on ridges and south-facing slopes [3,47]. These reports suggest that in regions with low precipitation, soil moisture limits the function of decomposer communities. Our contrasting results are likely due to the scale of our study site and its climate. In regions where topographical changes lead to significant differences in soil moisture or where reduced litter moisture content inhibits decomposer community function [48], decomposition would be promoted in moisture-favorable areas like valleys. Ridges and south-facing slopes represent harsher environments for fungi, bacteria, and small soil animals due to sun exposure and high temperatures [11]. However, at a local scale, the positive effect of increased temperature on decomposition [49] may sometimes outweigh the negative effects of dryness on fungi and bacteria. Therefore, in the microtopographical scale of a humid temperate secondary forest, it is inferred that abundant solar radiation on ridges and southwest slopes promotes the function of decomposer communities, particularly fungi and bacteria.

Contrary to Hypothesis 2, macroinvertebrate access bags showed inhibited rather than enhanced leaf litter decomposition compared to exclusion bags. Hypothesis 2 is therefore rejected. Generally, except for high-quality leaf litter, macroinvertebrates contribute to leaf litter decomposition by fragmenting the litter, thereby promoting mineralization [13,14,50]. However, our study did not support this general trend. It should be noted that some meta-analyses conclude that the contribution of macroinvertebrates to leaf litter decomposition is small [51]. Additionally, it has been suggested that macroinvertebrate-driven litter decomposition is more likely to occur in temperate marine climate zones and is harder to detect in temperate monsoon climates [50]. In a humid temperate secondary forest, the negative effect or lack of positive contribution from macroinvertebrates might be because microbial activity was sufficiently high, masking any potential contribution from macroinvertebrates. If microbial (fungal and bacterial) decomposition is sufficiently rapid, the effect of fragmentation by macroinvertebrates on decomposition rate would be relatively small. In temperate forests, earthworms function as major macroinvertebrate litter feeders [52], but their fecal pellets decompose more slowly than leaf litter [53], which might have mitigated any positive effects. Furthermore, macroinvertebrates can also exert negative effects by consuming other decomposers or disturbing litter [54], and these negative effects might have outweighed any positive ones. The contribution of macroinvertebrates to decomposition is suggested to be higher in environments unsuitable for microbial and small soil animal inhabitants [27]. For example, in tropical rainforests, litter decomposition along drier forest roads is often dominated by feeding from macroinvertebrates like termites, more so than within the forest interior [55]. Moreover, when comparing climatic zones, the effect of macroinvertebrates on litter decomposition is significantly larger in arid regions [27]. Therefore, in warm and humid environments favorable for microbial communities, the contribution of macroinvertebrates to decomposition may be small, or even negative.

Although our experimental design did not measure the specific abundances of fungi, bacteria, mites, collembolans, or nematodes, the mass loss results from our litterbag treatments offer macroscopic insights into the decomposition process. We did not directly verify the body-size range of fauna entering through the 6 mm perforations. Based on the standard principles of the litterbag method, the 1 mm mesh effectively excludes macroinvertebrates (>2 mm) while allowing access to microorganisms, microfauna, and mesofauna [20,56]. By implementing this exclusion treatment, we detected no significant contribution of macroinvertebrates to leaf litter decomposition. Because a substantial baseline mass loss was observed within these exclusion bags, we infer that the combined activities of microorganisms and small- to medium-sized soil fauna primarily drove the decomposition in our study system, even though their individual contributions could not be separated. However, these microorganisms (fungi and bacteria) and small- to medium-sized soil animals (microfauna and mesofauna) might have been differentially affected by microtopography. Furthermore, the composition of fungi and bacteria varies with surrounding tree species [57,58], suggesting that there might be an interaction between the effects of environmental gradients on microbial communities and the surrounding tree species. To accurately clarify the relative contributions of microorganisms, microfauna, mesofauna, and macrofauna to decomposition, previous reports recommend conducting three-stage mesh size litter bag experiments (e.g., [51]). Future studies incorporating multiple mesh sizes and direct community analyses are necessary to fully elucidate these interactive effects on the litter decomposition process. Furthermore, the temporal scale of our litter bag retrievals might have influenced the detectability of the positive effects of macroinvertebrates. Because our first retrieval occurred at 6 months to evaluate the long-term overall decomposition dynamics, it is possible that their initial contribution to fragmentation was subsequently masked by the continuous mineralization activities of microorganisms and smaller soil fauna over the half-year period. Therefore, finer-scale temporal sampling in future studies would be helpful to fully disentangle the transient early-stage effects of macrofauna.

5. Conclusions

At the local scale of the studied humid temperate secondary forest, microtopographical differences of around 20 m in relative height were found to significantly affect the spatial heterogeneity of the litter decomposition process. Although we did not directly measure specific decomposer abundances or microclimatic variables, our results suggest that the combined activities of microorganisms and small- to medium-sized soil fauna (e.g., [20]) were enhanced on ridges and southwest slopes. This pattern likely reflects the overriding influence of generally warmer local microclimates, despite the relatively uniform litter moisture conditions across the topographical types. Conversely, the suppression of decomposition in the valleys and the *Cryptomeria japonica* plantations highlights the complex interplay between cold microclimates, vegetation-driven litter matrix quality, and decomposer activities [9,38]. While our findings are based on a single-species litterbag experiment over one year in a 1-ha plot, they clearly underscore the importance of considering fine-scale geodiversity and local vegetation structure when evaluating the spatial dynamics of material cycling in forest ecosystems.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/f17070783/s1>, Table S1: Number and percentage of litter bags excluded from the statistical analysis; Table S2: Comparison of GLM results with and without tree density as a covariate.

Author Contributions: Conceptualization, K.N.; methodology, T.Y.; validation, T.Y.; formal analysis, K.N.; investigation, K.N. and S.D.B.-K.; resources, T.Y.; data curation, K.N. and S.D.B.-K.;

writing—original draft preparation, K.N.; writing—review and editing, T.Y. and S.D.B.-K.; visualization, K.N.; project administration, T.Y. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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Appendix A

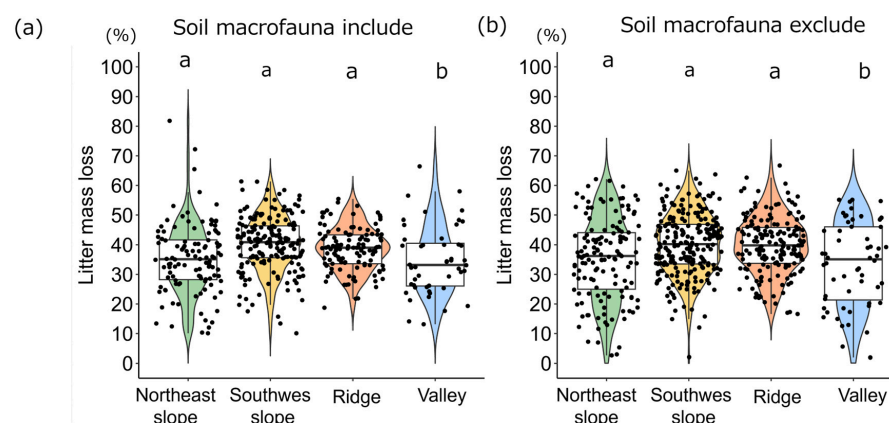


Figure A1. Leaf litter mass loss (%) of litter bag (12 months); (a) Soil macrofauna access bags, (b) Soil macrofauna exclusion bags. Different letters indicate a significant difference as determined by likelihood ratio tests.

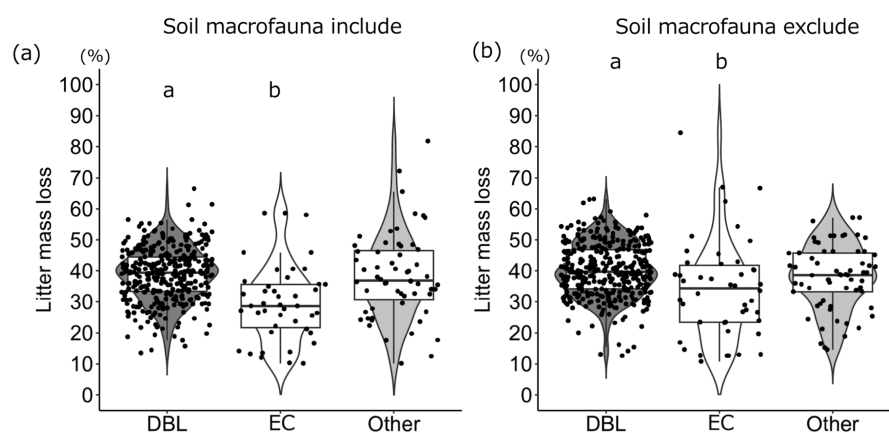


Figure A2. Decomposition rates of litter bags across different surrounding vegetation types after a 6-month deployment period. (a) Soil macrofauna access bags, (b) Soil macrofauna exclusion bags. For litter mass loss rates of bags deployed for 12 months, please refer to Figure A3. Different letters indicate a significant difference as determined by Tukey's HSD.

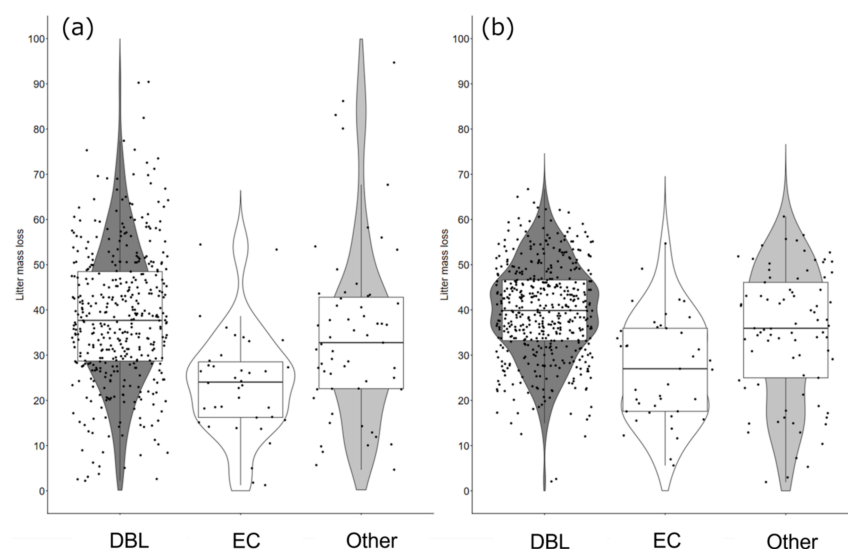


Figure A3. Leaf litter mass loss (%) of litter bag (12 months); (a) Soil macrofauna access bags, (b) Soil macrofauna exclusion bags. DBL = deciduous broadleaf, EC = evergreen conifer, Other = no dominant/mixed vegetation type.

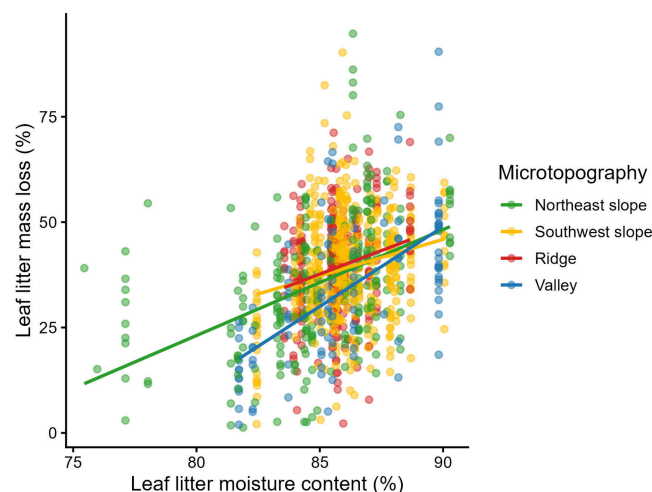


Figure A4. Relationship between leaf litter moisture content and leaf litter mass loss across microtopographical types, for litter bags deployed for 12 months. Each point represents an individual litter bag; lines show linear regression fits for each microtopographical type. Litter moisture was higher and more homogeneous among microtopographical types at this retrieval than at 6 months.

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