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Roles of *Chromolaena odorata,* macrofauna, and forest edge on the decomposition rate of tree leaf litter in two types of seasonally dry tropical forest

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Background: The forest edge of seasonally dry tropical forests (SDTF) is commonly invaded by *Chromolaena odorata,* which could affect the leaf-litter decomposition (LLD) rate through the litter fauna and the litter chemistry. We tested the effects of positions (edge vs. interior), *C. odorata* inclusion, and macrofauna inclusion using litterbags containing the two most dominant tree species from each forest type of SDTF (a dipterocarp deciduous forest and a mixed deciduous forest [MDF]), in northern Thailand.
Results: The results showed that leaf litter decayed at the same rate between the forest edge and interior. A difference in the decomposition rate between the edge and interior was only found in the MDF and only when the composition of the litter contained a high nitrogen (*C. odorata*) and phosphorous content (*Pterocarpus macrocarpus* – a native tree of MDF). Exclusion of macrofauna resulted in slower decomposition rates, but this effect was not significant when combined with the edge condition.
Conclusions: Our findings indicated that the forest edge condition has no directly significant effect on the LLD rate but is mediated through changes in the litter chemistry by inclusion of *C. odorata* litter.

Keywords: forest edge, invasive herbaceous species, leaf-litter decomposition, seasonally dry tropical forest

Introduction

Seasonally dry tropical forests (SDTF) are a widespread forest ecosystem in southeastern Asia (Dexter et al. 2015) that have been subject to significant degradation and fragmentation due to anthropogenic activities (Delang 2002; Wanthongchai et al. 2008). These disturbances have led to the emergence of forest edges, which create microclimate variations between the interior and exterior of forest borders (Ewers and Didham 2006; Laurance et al. 2011). The forest edge causes a significant change in the forest biodiversity, such as increased levels of herbaceous plants (Szigeti et al. 2022) and soil fauna (De Smedt et al. 2016; De Smedt et al. 2019; Lacasella et al. 2015), which can lead to several adverse impacts on the forest ecosystem functions (Ewers et al. 2011; Sodhi et al. 2010).

Leaf-litter decomposition (LLD) is a critical process that contributes to carbon (C) and nutrient cycling and so ecosystem productivity in tropical forest ecosystems (Hätten-

schwiler et al. 2005; Zhang and Zak 1995). The decomposition of leaf litter is a complex process that is mediated by both biotic and abiotic factors (Cornwell et al. 2008; Krishna and Mohan 2017). In tropical forests that share a similar climate, variations in the LLD rate are primarily due to the chemical composition of the litter species and the activity of soil organisms (García-Palacios et al. 2013; González and Seastedt 2001; Meyer et al. 2020; Njoroge et al. 2023). It is known that these two factors are possibly altered along the edge-interior gradient in tropical forests (De Smedt et al. 2016; Salles et al. 2018).

Litter faunae, mainly arthropods, on the forest floor are categorized depending on their size into macro- and meso-fauna, and these could have different effects on the ecosystem function. In tropical forests, macrofaunae are the most important group of detritivores that control the LLD rates (González and Seastedt 2001). The activity and density of these groups are known to be sensitive to habitat changes (Wang et al. 2023), such as at forest edges, where

soil moistures are generally low (Birkhofer et al. 2015; Didham 1998; Ferguson 2004). When the distance from the forest edge in a dry forest increases, the canopy cover and soil humidity decrease (Dambros et al. 2013). These drier conditions may restrict the activity of litter macro-arthropods, which could retard the rate of LLD caused by these organisms (Didham 1998; Paudel et al. 2015).

Forest edges may also impact the litter quality by promoting the recruitment of numerous invasive herbaceous species, such as *Chromolaena odorata*, where such invasive species have been frequently reported in southern and southeastern Asia, especially in dry forests (Sharma et al. 2022; Wei et al. 2017). The presence of leaf litter from *C. odorata* could affect the chemical composition of the litter near the forest edges (Banful et al. 2008; Mboukou-Kimbatsa et al. 2007) because its leaves show a high nitrogen (N) content while the leaves of native tree species in SDTF generally have a low N content that can take more than a year to decompose (Hanpattanakit and Chidthaisong 2012). Mixing leaf litter from species that differ in their litter quality and structure changes the physio-chemical properties of the decomposition environment via nutrient transfer from high-quality (labile) litter to low-quality (recalcitrant) litter, resulting in an increased LLD rate (Bonanomi et al. 2014; Yang et al. 2022). Moreover, the mixed leaf litter can create more heterogeneous microenvironments due to leaf toughness and debris size, which can affect soil fauna activity and subsequently impact decomposition rates (Njoroge et al. 2022; Wang et al. 2024). As in SDTFs, which contain the majority of tree species and a few herbaceous species at the understory level (Bunyavejchewin 1983; Bunyavejchewin et al. 2011; Myo et al. 2016), forest edges heavily invaded by *C. odorata* have altered soil properties, such as soil moisture and organic matter (OM) content (Koné et al. 2012; Norgrove et al. 2000; Wei et al. 2017).

In Thailand, SDTFs are mainly dominated by deciduous tree species (Bunyavejchewin 1983; Bunyavejchewin et al. 2011). Mixed deciduous forests (MDF) and dipterocarp deciduous forest (DDF) are two commonly found types in northern Thailand that exist at similar elevations and experience regular disturbances from forest fires and human activities (Wanthongchai et al. 2008). The two forest types show a different species dominance (Bunyavejchewin 1983; Bunyavejchewin et al. 2011). Moreover, previous research has suggested that the soil environment of these two forest types is distinct, with MDFs showing a higher moisture and OM content in the soil while DDFs show a more sandy soil with less moisture, which could impact both the distribution and composition of the soil fauna and herbaceous species, leading to a different LLD rate between the two forest types in the same climatic region (Asanok et al. 2020; Myo et al. 2016).

Despite these potential factors that suggest that the LLD rates in fragmented SDTFs could be affected by the forest edges through the distribution of soil fauna and composition litter chemistry, there has been insufficient empirical studies to support or refute this. Therefore, we studied how the forest edge affects the LLD rate in a STDF by examining the relationships between the litter fauna and plant leaf chemistry in a MDF and DDF in northern Thailand. The experiment was conducted over 18 months as a litter bag experiment, which considered the contribution of herb litter and access to the litter fauna between the forest edge and interior. We hypothesized that the forest edge changes the composition of the leaf litter and litter fauna and these in turn increase the LLD rate compared to in the forest interior.

Materials and Methods

Study site
The study was carried out in a 350-ha SDTF in Nan province, northern Thailand (18.55 N, 100.79 E, 200 m above mean sea level). The climate is highly seasonal, with the rainy season lasting six months from May to October and the dry season lasting from December to mid-April. The precipitation in the area was 2,314 mm on an annual average basis, with a minimum–maximum temperature of 21.3°C–35.2°C. The dry season has an average temperature of 35.3°C and rainfall of 312.5 mm, whereas the rainy season has an average temperature of 29.4°C and rainfall of 1,935 mm. The area's forests are classified into two types of SDTFs – MDF and DDF – according to their zone of distribution. The DDF is located in the east part of the study site and covers about 200 ha, whereas the MDF is located in the west part of the site (Fig. 1) (Dumrongrojwatthana 2004). *Pterocarpus macrocarpus, Aporosa villosa*, and *Xylia xylocarpa* are the most prominent tree species in the MDF, whereas *Shorea obtusa* and *Dipterocarpus tuberculatus* are the dominant species in the DDF (Dumrongrojwatthana 2004). Around the fragment, various anthropocentric lands surround the forest remnants, including residential development, agriculture, abandoned fields, and transportation infrastructure.

Litter bag experiment
The leaf litter from the two most dominant tree species were selected from each type of forest (*P. macrocarpus* and *A. villosa* for MDF; and *S. obtusa* and *D. tuberculatus* for DDF) along with the herbaceous *C. odorata* from the forest edge. During the leaf-falling season, around February to March 2020, freshly senesced leaf material from these five species were collected within the forest remnant. The collected litter was dried at 80°C for 48 hours and then stored at 4°C before mixing at the given proportion and filling in litter bags. All samples of the five species were analyzed for
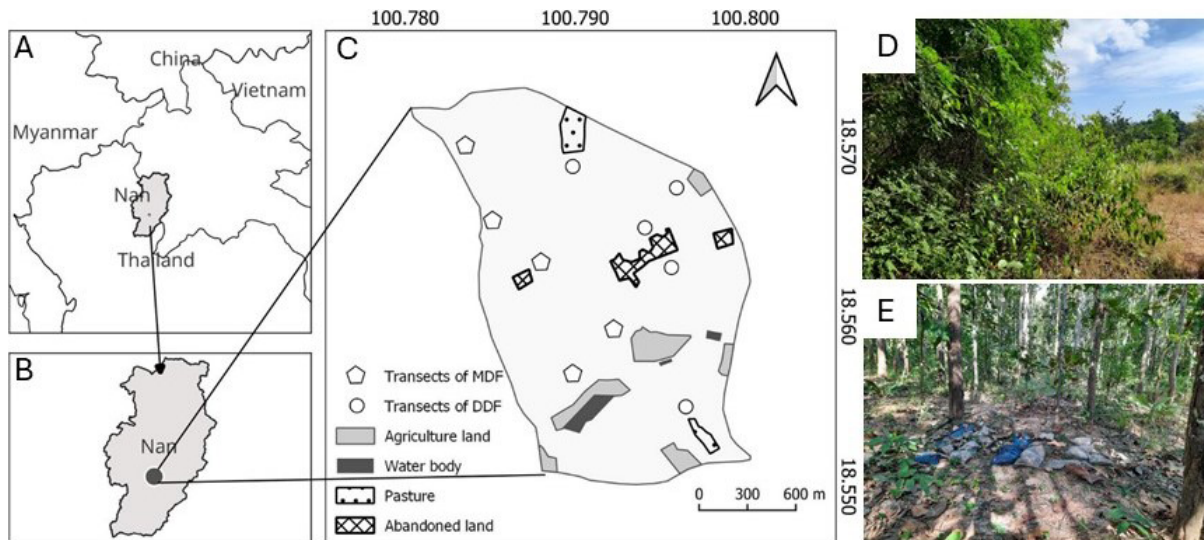
Fig. 1 Maps of the study area of a fragmented seasonally dry tropical forest in Nan province, northern Thailand (A, B). Shown are the two forest types and location of the study transects (C), landscape of forest edge (D), and experimental plot (E). DDF stands for dipterocarp deciduous forest and MDF stands for mixed deciduous forest.

their chemical components, including C, N, potassium (K), and phosphorous (P). The C and N contents were analyzed using the Dumas method with a CN Analyzer (CN CORDER MT-700; Yanaco, Kyoto, Japan), while the P and K contents were evaluated using the wet ashing method with a 5:1:2 molar ratio of HNO_3: H_2SO_4: $HClO_4$. The analysis of P (vanadomolybdate yellow color) was conducted at a wavelength of 440 nm in a spectrophotometer, while the analysis of K was performed using atomic absorption spectrophotometry.

The dried leaf-litter were enclosed in mesh bags (20×20 cm^2, 30 g of litter weight) and placed on the ground, where they were collected at 5 periodic intervals (3, 6, 9, 12, and 18 months) to determine the remaining mass. Two mesh sizes of nylon-litter bags were chosen: 2 mm (micro- and meso-fauna pass through) and 5 mm (micro-, meso-, and macro-fauna pass through) (Dossa et al. 2016; Paudel et al. 2015). The litter quality (variations in chemical components of each species) along each transect was ascertained using the two dominant tree species for each forest type and one herbaceous species. Therefore, the litter bags contained tree litter (1:1 weight mixture of two tree species) and mixed herbaceous litter (1:1:1 weight mixture of leaves from the two dominant tree species and *C. odorata*). Leaves of *D. tuberculatus* were trimmed into 20×20 m^2 to fit into the litter bags, while the other leaf species remained untrimmed.

Five transects from each forest type were selected in the study site and were located 300 m away from each other. Within each transect, two 10×10 m^2 plots were set up in the field, one was located near the forest edge (0–5 m from the physical forest edge), and another were located in the forest interior (100–120 m from the physical forest edge). The environmental factors (soil moisture, canopy, and *C.*

odorata cover, leaf litter, and the soil type, N, and C content) were ascertained in the plots within August of the year 2020 and 2021. The average soil moisture, C, and N content was determined at the four corners and center using a 100 cm^3 volume of the collected topsoil layer. The soil OM (Walkley and Black 1934) and N (Bremner 1960) were measured by Department of Soil Science, Faculty of Agriculture, Kasetsart University, Thailand. The fresh to dry weight ratio was used to determine the soil moisture content. Densitometers were used to determine the average canopy cover per plot at the same location as the previous measurement. Five quadrats (20×20 cm^2) per plot were used to collect the leaf litter on the forest floor, then dried and weighed. The *C. odorata* cover was estimated as an average from three subplots of 1×1 m^2.

Litter bags were placed on the soil surface at center of each plot (10×10 m^2). We designed an evenly spaced four rows of five column sampling-grids and placed one litterbag for each mesh size and each plant species at each sampling point along the grid. A total of 400 litter bags (two types of plant species combination × two mesh sizes × two locations of plot × two forest types × five replicated plots × five sampling months) were placed in the forest. Litter bags were spread as flat as possible to maintain contact with the soil during the entire decomposition period in the incubation plots. To mimic natural decomposition conditions, litter bags were covered with a natural litter layer (Paudel et al. 2015). To avoid the litter bags being carried away by wind, a large mesh net was (12.7 cm mesh size) was laid on top of the litter bags after being placed on the soil surface. During the experimental period, a total of 31 of the 2-mm litter bags were removed from the analysis due to traces of termite destruction.

A set of eight litter bags (two plant species treatments ×

two mesh sizes × two locations) was removed from each transect for each of five sampling months (3, 6, 9, 12, and 18 months) and brought to the lab in a sealed plastic bag for further analysis. The outside of the litter bags was thoroughly inspected, and any foreign debris or plant matter was removed using forceps. The macrofauna found visually were collected by hand, and then the litter was extracted for fauna (macro- and meso-fauna) using Tullgren funnels. A 70% (v/v) ethanol solution was used to collect the soil fauna samples. The samples were sorted into broad taxonomic categories and counted under a stereoscopic light microscope. The relative density of the soil fauna was determined by comparing the number of groups and individuals collected from particular litterbags to the total dry weight of the litter in those bags. Following removal of the soil fauna, the litter was thoroughly rinsed with distilled water to remove any remains of soil or organic material. After being oven-dried at 60°C for 72 hours, the remaining mass of litter in all the collected litter bags was measured.

Data analysis

Differences of environmental factors between the forest edge and forest interior were examined using the paired samples the related samples Wilcoxon signed rank test due to the data were asymmetrically distributed.

Initial litter weight (IL) and percentages of remaining litter weight (%RL) were calculated using a comparison of the weight of litter inside each bag prior to placement in the field at the onset of experiment. The RL was the weight of litter in each bag after each extraction was measured. The %RL, determined as shown in equation 1, was then used to determine the mean litter decomposition rate (k) for each forest site using the model (Olson 1963) as shown in equation 2.

$$\% \; Remaining \; litter \; (g) = \left(\frac{Remaining \; litter}{Initial \; Litter} \right) \times 100 \quad (1)$$

$$Remaining \; litter = Initial \; litter \times e^{-kt} \quad (2)$$

where t is the time in years and k is the decomposition rate.

This exponential model was linearized using the natural logarithm of the %RL in order to calculate the linearized decomposition rate, as shown in equation 3,

$$k = -ln \, (RL/IL)/t \quad (3)$$

All statistical analyses were separated between forest types and were performed using the R program (R Core Team 2022). Using the "nls" function of the R stats packages, the k value for LLD was calculated using sets of data representing replicates and incubation times for each treatment. We assessed normality using the "shapiro.test" in stats packages and homoscedasticity using the "bp.test" function (Zeileis and Hothorn 2002). Ordinary least square tests were conducted to determine if the initial leaf-litter characteristics could predict the k values for these treatments. We accounted for variations in k values for litter decomposition using multiple linear regression models comprised of the compositions of litter species, forest edge, mesh size of litter bags, and their interactions. The analysis was separated between forest types.

Results

Leaf litter chemistry and forest environmental factors

The *C. odorata* litter contained a significantly higher N content than the other four litter types (*S. robusta*, *D. tuberculatus*, *P. macrocarpus*, and *A. villosa*) but a similar amount of C as *P. macrocarpus* and *D. tuberculatus* litters (Table 1). The *A. villosa* and *D. tuberculatus* liters had more organic C than the other litters, while *S. robusta* had the lowest amount. The *C. odorata* and *P. macrocarpus* litter had a lower C:N ratio than the other litters, whereas *S. robusta, D. tuberculatus,* and *A. villosa* litter had a higher C:N ratio (Table 1).

The comparison of forest environmental factors between the forest edge and forest interior indicated that the leaf litter at forest floor and *C. odorata* cover was more pronounced at the forest edge. Conversely, canopy cover, OM, total N and soil water content exhibited no significant differences between the forest edge and the forest interior. This trend was observed consistently across both forest types (Table 2).

Litter faunae between forest edges and interior

A total of 24 distinct soil fauna groups were recorded in

Table 1 Initial concentration of mixed litter in two forest types

Litter species	OM (%)	Organic C (%)	N (%)	P (%)	K (%)	C:N ratio
Shorea obtusa	55.49 (0.59)	32.19 (0.12)	0.37 (0.49)	0.02 (0.25)	0.3 (0.11)	60.74 (0.22)
Dipterocarpus tuberculatus	58.68 (0.05)	34.04 (0.15)	0.31 (0.37)	0.03 (0.19)	0.27 (0.94)	77.36 (0.32)
Pterocarpus macrocarpus	57.26 (0.33)	33.21 (0.34)	0.37 (0.13)	0.24 (0.08)	1.87 (0.09)	63.87 (0.29)
Aporosa villosa	62.85 (0.13)	36.46 (1.15)	0.35 (0.07)	0.03 (0.39)	0.17 (0.07)	72.92 (0.04)
Chromolaena odorata	56.6 (0.24)	34.47 (0.03)	1.17 (0.04)	0.08 (0.69)	0.13 (0.34)	20.89 (0.04)

The leaf-litter species include native and invasive ones. Values in parenthesis are the standard errors.
OM: organic matter; C: carbon; N: nitrogen; P: phosphorous; K: potassium.

Table 2 Environmental factors between the edge and interior of two forest types

Environmental properties	DDF		MDF	
	Forest edge (0–5 m)	Forest interior (~120 m)	Forest edge (0–5 m)	Forest interior (~120 m)
Canopy cover	65.43 (2.56)	80.32 (4.23)	67.44 (4.32)	86.12 (3.94)
Soil water content	26.70 (5.68)	25.02 (0.96)	35.55 (2.18)	38.03 (2.56)
Organic matter (g/kg)	10.1 (1.23)	9.7 (1.90)	14.2 (1.11)	13.0 (1.75)
Total N (%)	0.48 (0.09)	0.39 (0.05)	0.73 (0.05)	0.65 (0.03)
Floor leaf litter (dried weight, g/m^2)	125.32 (5.34)[a]	105.11 (3.78)[a]	97.45 (6.41)[a]	85.64 (5.44)[a]
Chromolaena odorata cover (%)	23.3 (2.12)[a]	6.5 (1.86)[a]	26.3 (3.10)[a]	3.2 (0.73)[a]

Values in parenthesis are the standard errors.
DDF: dipterocarp deciduous forest; MDF: mixed deciduous forest; N: nitrogen.
[a]Significant difference at $p < 0.05$.

the litter bags. Acari comprised 47.2%–55.2% of the total number of litter fauna individuals across the forest types and forest edge location. Collembola, Hymenoptera (ants), and Isoptera were, respectively, the second, third, and fourth most abundant components of the litter fauna in each of the two forest types. Compared to the 2-mm mesh bags, the 5-mm litter bags decreased the individual abundance of total fauna (individuals per plot) by 24.31% and 20.46%, respectively, in the DDF and MDF as well as the taxonomic diversity.

Leaf litter mass loss and decomposition rate (k)

The 18-month litter mass loss ranged from 33 to 62% of the total mass loss. The logarithmic regressions of mass loss for each treatment (mesh size, contribution of *C. odorata*, and forest edge) and forest type all showed good fits (all $p < 0.001$), indicating that the use of a single exponential model for calculation and comparison was reasonable. The mesh size, forest edge, and contribution of *C. odorata* and their interactions all significantly affected the litter k (Figs. 2 and 3). In the two forest types, the application of 5-mm mesh bags resulted in a higher mass loss at the end of the incubation period (month 18) than in the 2-mm mesh bags (16.6% in DDF and 17.2% in MDF). In addition, there were significant effects of mixing in *C. odorata* in only the MDF (DDF: $t = 0.656$, $p = 0.516$; MDF: $t = 2.104$, $p = 0.043$). The location of litter bags installed at the forest edges had no significant difference in the k value (DDF: $t = -1.219$, $p = 0.231$; MDF: $t = -0.180$, $p = 0.858$). However, the treatment interaction between the forest edge and litter mixing was found to be significantly different only in the MDF, but not in the DDF (DDF: $t = 0.425$, $p = 0.673$; MDF: $t = 2.001$, $p = 0.050$) (Table 3).

Discussion

Effect of forest edge on the community of fauna

Overall, the litter fauna density and assemblage were different across the two forest types. This indicated the important effect of tree species on the soil environment and microclimate in a similar climatic region (Li et al. 2022; Seidelmann et al. 2016; Tedersoo et al. 2016), which in turn affects the density of some fauna groups. However, within each forest type, no differences between the two plot locations (forest edge and forest interior) were observed (except for Acari). This was because there was very little change in the abiotic variables (i.e., air temperature, evaporation rate, and moisture content) due to the forest edge interior gradient. Similarly, previous studies on the succession of tropical forests revealed that the forest's physical environment due to forest edge had little or no effect on the detritivore community (Moreno et al. 2014; Moreno et al. 2020). Out of various types of disturbances, only high disturbance levels, such as anthropogenic clearance (Bloemers et al. 1997; Coyle et al. 2017; Paudel et al. 2015), resulted in microclimate changes that were significant enough to limit the activity of detritivores species in tropical forests (Coyle et al. 2017; Dossa et al. 2016; Paudel et al. 2015).

The presence of *C. odorata* has been shown to have significant impacts on soil properties and microbial activities (Koné et al. 2021). In invaded areas, soil microbial biomass carbon, carbon mineralization, enzymatic activities, and available N and phosphorus generally increased compared to non-invaded areas (Koné et al. 2021). This suggests that a lower coverage of *C. odorata* in forest interiors might result in reduced soil microbial activity and nutrient availability compared to forest edges with higher invasion. Moreover, the effects of *C. odorata* on soil properties appear to be more pronounced in MDF compared to DDF. MDF sites generally have higher soil fertility, with greater soil moisture, OM, total N, available phosphorus, and exchangeable K than DDF sites (Charoonphong and Suwanwaree 2014). This higher initial fertility in MDF may provide a more favorable environment for *C. odorata* to establish. The litter quality of *C. odorata* has a low lignin/N ratio (Mboukou-Kimbatsa et al. 2007), which can lead to faster decomposition and nutrient release (Koné et al., 2021), as soil conditions are generally more favorable for soil fauna. A study showed that the presence of *C. odorata* increases earthworm density and promotes soil aggregate formation (Mboukou-Kimbatsa et al. 2007). The increased
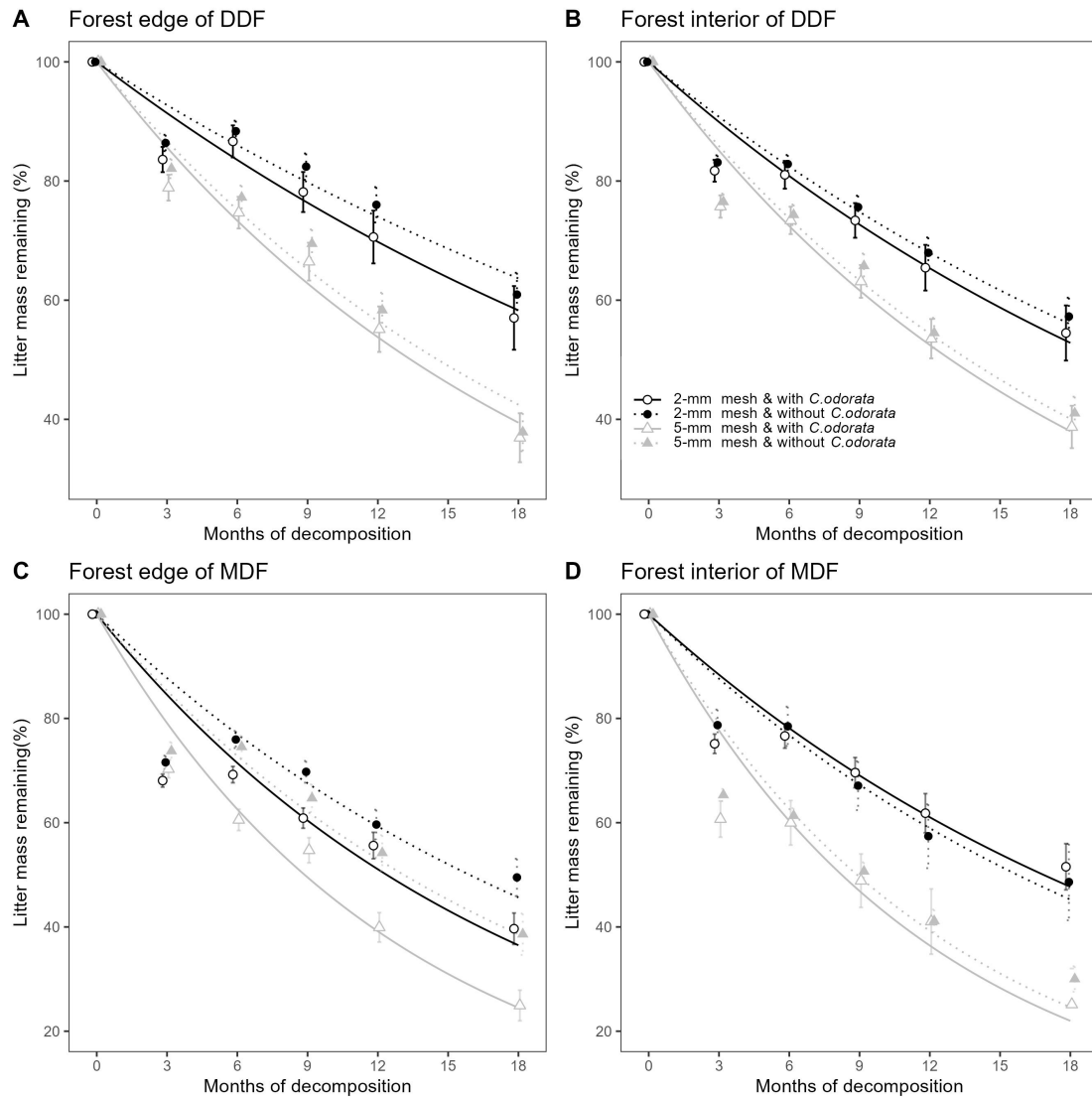
Fig. 2 Litter mass loss (% initial dry mass) of different species in litter bags with different mesh sizes and litter mixture across sampling sites. (A) Forest edge of DDF. (B) Forest interior of DDF. (C) Forest edge of MDF. (D) Forest interior of MDF. Values are the means ± standard error, and a logarithmic fitting for each treatment is given. DDF stands for dipterocarp deciduous forest and MDF stands for mixed deciduous forest.
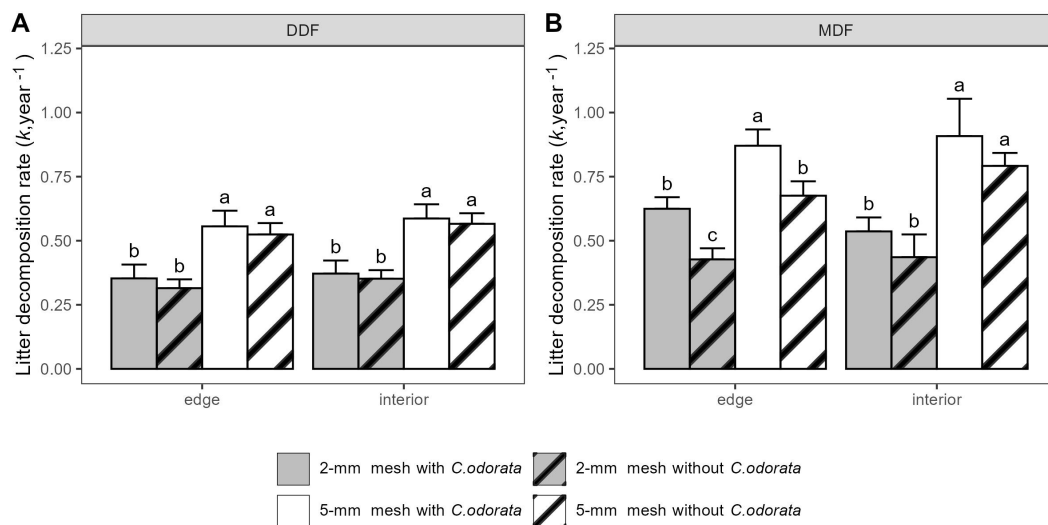

Fig. 3 Effects of tree species, litter bag mesh size, and their interactions on the leaf litter decomposition rates (k, year^{-1}) in DDF (A) and MDF (B). Values are means ± standard deviation, and different letters indicate significant ($p < 0.05$) differences between treatments. DDF stands for dipterocarp deciduous forest and MDF stands for mixed deciduous forest.

Table 3 Summary of multiple regression analysis, showing the effect of forest type, location, mesh size, and presence of *Chromolaena odorata* on the linearized *k*-rate for the two different forest types

Treatments	DDF		MDF	
	t	*p*-value	*t*	*p*-value
Forest edge	−1.219	0.231	−0.180	0.858
Mesh size (5-mm)	7.073	< 0.01	7.447	< 0.01
Mixtures with *C. odorata*	0.656	0.516	2.104	0.043
Mesh size (5-mm) × forest edge	−0.109	0.913	−1.591	0.121
Mixtures with *C. odorata* × forest plot	0.425	0.673	2.001	0.050
Mesh size (5-mm) × mixtures with *C. odorata*	0.019	0.984	0.231	0.818
Mesh size (5-mm) × mixtures with *C. odorata* × forest edge	−0.119	0.905	−0.190	0.850

DDF: dipterocarp deciduous forest; MDF: mixed deciduous forest.

faunal activity can enhance litter incorporation into the mineral soil, potentially leading to greater changes in soil organic C distribution in MDF compared to DDF (Guidi et al. 2022).

Effect of litter fauna on the leaf-litter decomposition rates

Many previous studies have shown that the macrofauna had a higher impact on the LLD rates than the mesofauna did (Hättenschwiler et al. 2005; Peguero et al. 2019; Yang and Chen 2009). Our findings here showed that the LLD rates were faster when the macrofauna could gain access to the litter bags. However, the effect is not pronounced with respect to the forest edge. As termites were the majority macrofauna taxa found in this study and were present at the same density in both the forest edge and interior, the presence of the forest edge did not shift the LLD rate in our experiment regardless of the litter species chemistry. Termites can survive in dry conditions (Ashton et al. 2019), and indeed *Macrotermes* thrive in this condition (Arshad 1982). Moreover, the supplementing of leaf litter with *C. odorata* litter may not alter the termite feeding, as several studies have shown that termites show only a slight preference for the leaf litter of different species (Matsumoto and Abe 1979).

Macro- and meso-fauna responses differ from habitat conversion, such as forest edges, where the macrofauna density has been reported to be more affected by the habitat variation than the mesofauna, but the mesofauna community are more sensitive than the macrofauna (Wang et al. 2023). Our result shows the opposite trend, where the litter mesofauna contributed to the high density at the forest edge plot because colonization of herbaceous species shifted the soil physical factors, such as the soil moisture, N, and C contents, to provide a better food source and habitat complexity in the soil and litter layer (Sabatté et al. 2021; Zheng et al. 2022). As in SDTFs, which contain the majority of tree species and a few herbaceous species at the understory level (Bunyavejchewin 1983; Bunyavejchewin et al. 2011), forest edges heavily invaded by *C. odorata* alter the soil properties, such as the soil moisture and OM con-

tent (Koné et al. 2012; Norgrove et al. 2000; Wei et al. 2017), resulting in a higher density of Acari at the MDF edge. In contrast, the soil in the DDF was sandier than in the MDF (Myo et al. 2016), which may explain the reduced levels of C, N, and moisture, and so making it unfavorable for soil mesofauna.

Even though Acari are frequently mentioned as dominant fauna in litterbag experiments (Xin et al. 2012) and exhibit significant variations in response to environmental factors (Ahmed et al. 2020; Elmoghazy and Shawer 2013; Manu 2011), their contribution to decomposition appears limited. Because the feeding guilds of soil mites in tropical forests span a wide range—including detritivores, fungivores, omnivores, and predators (Díaz-Aguilar and Quideau 2013)—not all mites directly contribute to litter decomposition. The study on OM breakdown found no significant treatment-related effects when Acari abundances were reduced by up to 80% using insecticides (Pamminger et al. 2022). This suggests that other trophic levels, such as microorganisms or termites, may play a more crucial role in decomposition than the mesofauna community in tropical forests (Abe 2019; Fujii et al. 2016).

Seasonal variations also play a role in litter decomposition and fauna activity in tropical forests (González and Seastedt 2001), which could significantly impact decomposition rates in this study, regardless of the effect of litter quality. Tropical arthropods exhibit very high rates of intra-annual turnover in species composition, associated with seasonal changes in environmental variables (Beng et al. 2018) such as temperature, rainfall, and humidity (Krishna and Mohan 2017). The maximum leaf litter breakdown rate coincided with the rainy season (de Souza Rezende et al. 2016).

Effect of adding *C. odorata* on the leaf-litter decomposition rate

The results showed that the inclusion of *C. odorata* into the leaf litter did not change the LLD rate of the DDF tree leaf litter (*S. robusta* and *D. tuberculatus*) but sped up that of MDF tree leaf litter (*A. villosa* and *P. macrocarpus*) by approximately 15%. Despite the stronger influence on the

decomposition rate of low-quality litter seen in many previous studies (Fuqiang et al. 2010; Gartner and Cardon 2004; Steinwandter et al. 2019), the regulation of the LLD rates of the tree species was not affected by the mixing of high- and low-quality litter. Thus, adding high-quality litter from a different species may not necessarily drive the decomposition rates of the target litter (Santonja et al. 2017), as demonstrated by the opposite effects of adding *C. odorata* litter on the decomposition of tree litter, even though the soil contained a lower N content than in the leaf litter. The litter's potential regulating effect on the N and P concentrations and other environmental factors may be the cause (Feller et al. 2003). Rapid decomposition and a high initial concentration of N were observed in the *C. odorata* litter in the MDF due to the combined effect between the N and P concentrations. Mixing both *C. odorata* and *P. macrocarpus* leaf litter resulted in a significant rise in the P concentration in the total litter chemistry, which may have had a direct and positive impact on the LLD rate. Previous research has identified consistent patterns, where a higher N input only resulted in the inhibition of the decomposition of low-quality litter (Knorr et al. 2005), while a combination of N and P enrichment caused an enhanced LLD (Ochoa-Hueso et al. 2019; Tie et al. 2023).

Nutrient transfer dynamics between N and P differ significantly during decomposition. Under laboratory conditions, *C. odorata* attained 100% decomposition within 8 weeks (Okeke and Omaliko 1992). N from *C. odorata* could be rapidly released and depleted from the litter. Phosphorus is often strongly retained and released more slowly, particularly in recalcitrant litters (Ong et al. 2017; Robbins et al. 2019). The pattern of rapid N depletion and slower P release was observed in other study. In tropical peat swamp forests, leaf litter P content was rapidly depleted, while N release was more gradual (Ong et al. 2017).

Furthermore, our findings suggest that the antagonistic effects observed in DDF species may be attributable to the high lignin content of *D. tuberculatus* and *S. robusta* litter compared to that of *P. macrocarpus* (Osono 2020; Sarjubala Devi and Yadava 2007; Yang et al. 2020). Protein complexes, like those produced by lignin, are difficult for most organisms to degrade (Hättenschwiler and Vitousek 2000).

Effect of forest edge on leaf-litter decomposition between forest types

The MDF was suggested to have higher decomposition rates due to more favorable conditions for decomposer organisms, such as higher soil nutrient content and greater plant diversity (Asanok et al. 2022; Ishida et al. 2023). Moreover, the leaf traits of the MDF are dominated by species with higher specific leaf area and leaf dry matter content, while the DDF is characterized by species with higher wood density and thicker leaves (Asanok et al. 2022). Higher specific leaf area is generally associated with faster de-

composition rates, which could indicate more rapid decomposition. Additionally, the DDF experiences more frequent fires compared to the MDF (Khaing et al. 2019). Fire can also affect decomposition rates by altering soil properties and vegetation structure, as well as the amount of C transferred to the mineral soil (Campo and Merino 2016). This association between increased fire frequency and reduced decomposition rates could, in turn, impact the differences in C storage between the DDF and MDF (Campo and Merino 2016;, Mondal and Sukumar 2013).

Conclusions

The forest edge influenced the LLD rate of the native tree species of a SDTF in certain conditions, specifically by adding a higher N content in the litter composition (addition of *C. odorata* to *P. macrocarpus* litter). However, this effect was only found in the leaf litter that was not mixed with the hard to decompose species, such as *S. robusta* and *D. tuberculatus*. Moreover, the macrofauna had a robust impact on the LLD rate regardless of the forest edge conditions. Our finding emphasizes the importance of litter species in shaping the LLD under a forest edge condition to gain a better understanding of the impact of forest fragmentation on ecosystem function.

Abbreviations
DDF: Dipterocarp deciduous forest
LLD: Leaf-litter decomposition
MDF: Mixed deciduous forest
SDTF: Seasonally dry tropical forests

Authors' contributions
KR conceived the ideas, conducted field study, drafted the manuscript, designed the figures, and analyzed the data and results. MF and CC conceived the ideas and reviewed the manuscript. All authors discussed the results and commented on the manuscript.

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Competing interests

The authors declare that they have no competing interests.

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