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Litter Decomposition of a Deciduous *Tectona philippinensis* and an Evergreen *Parashorea malaanonan* Across Contrasting Sites

Jonathan Ogayon Hernandez*, Lerma San Jose Maldia, Crusty Estoque Tinio, Marilyn Sabalvaro Combalicer

Department of Forest Biological Sciences, College of Forestry and Natural Resources, University of the Philippines Los Baños, Laguna, Philippines
* Corresponding Author. E-mail address: johernandez2@up.edu.ph

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ABSTRACT

Litter traits and site conditions alter nutrient inputs from deciduous and evergreen forests by influencing litter decomposition processes. Here, we investigated the leaf and stem mass loss rate (MLR) of a deciduous (*Tectona philippinensis*) and an evergreen (*Parashorea malaanonan*) tree species and the factors influencing it through an intersite experiment and litterbag method in secondary forests in Lobo, Batangas and Mount Makiling Forest Reserve (MMFR). Variations in initial litter quality (leaf area, specific leaf area (SLA), leaf thickness, vein density), and site factors (light intensity and temperature) were assessed. *P. malaanonan* has a lower SLA and vein density than *T. philippinensis*. The leaf and stem MLR were significantly higher in the mixed litter (44.09–57.83%) than that of a single-species litter of either *T. philippinensis* (28.16–41.83%) or *P. malaanonan* (33.60–47.66%). The leaf MLR of *T. philippinensis* was greater when placed in Lobo (where the litter originated) than at a different site (i.e., MMFR). Moreover, leaf litter decomposition was faster in *T. philippinensis* than in *P. malaanonan*, particularly during the rainy season. Overall, the study showed that litter decomposition in deciduous and evergreen differed across sites due to variations in litter quality and environmental variables.

1. Introduction

Stem and leaf litter, which are products of plant metabolism, are essential for nutrient cycling in terrestrial ecosystems and serve as the link between forest and soil systems (Berg and McClaugherty 2020; Thalib et al. 2021). However, decaying litter contains a lot of carbon, which is released into the atmosphere as CO_2 is respired, leading to global warming (Didion et al. 2016). More frequent extreme weather events are also projected in the context of climate change, potentially increasing litter inputs (Li et al. 2021). Climate change can influence litter input and decomposition by altering air temperature, precipitation patterns, soil moisture availability (Figueroa et al. 2021), and litter chemistry (Song et al. 2023), impacting carbon cycling and ecosystem processes. Litter decomposition is important in nutrient and carbon cycles, which are fundamental ecosystems regulated by biotic and abiotic factors. Consequently, investigating litter decomposition in different species (e.g., deciduous and evergreen) and the factors influencing it can help us better understand forest ecosystem dynamics and functioning amid a changing climate.

Litter decomposition rates vary depending on the magnitude of the influence of different biotic and abiotic factors, such as site conditions (e.g., temperature), litter quality (e.g., leaf area), and season (wet vs. dry). For example, field and laboratory experiments showed a positive correlation between decomposition and temperature due to the increased metabolic activity of decomposers and litter consumption by invertebrate detritivores (Bradford et al. 2016; Migliorini and Romero 2020). However, variations in microclimate among studies have resulted in a mechanistic understanding and, thus, underdeveloped knowledge of what controls the decomposition process (Li et al. 2020). These variations in site conditions are addressed using intersite experiments, which allow researchers to explore how site-specific factors influence decomposition across diverse environmental and site conditions (Park et al. 2021). To the best of our knowledge, however, in-situ decomposition experiments are poorly explored due to logistical constraints and complexities of monitoring decomposition patterns in tropical settings. Thus, while the site condition-decomposition interaction is well documented in the literature, there is a need for more localized studies as site conditions vary significantly from one local site to another.

The decomposition rate is also determined by litter quality, interacting with extrinsic factors (e.g., environmental conditions) to regulate decay processes by providing nutrition and energy for decomposer organisms. Litter quality, such as biochemical composition (e.g., nutrient concentration) and physical structure (e.g., specific leaf area (SLA)), corresponds to nutritional value, palatability, and digestibility for decomposers (Barbe et al. 2017). Some studies reported that the presence of high lignin content and SLA may either accelerate or impede the decomposition process, depending on the concentration of nitrogen (N), phosphorus (P), and the lignin: N ratio in litter (Park et al. 2021; Yan et al. 2020). Moreover, litter from evergreen tree species decomposes slower than that from deciduous trees due to higher toughness, lower nutrient content, and higher concentrations of structural phytochemicals (Lidman et al. 2017). Evergreen leaves have a longer lifespan and slower growth rate than deciduous ones; hence, their litter input is also lower than those of deciduous species. This tendency highlights the need for additional research to fully understand the disparities in litter decomposition results across different tree species. Specifically, studies explaining how plant traits differ between Philippine evergreen and deciduous tree species still need to be studied in the context of litter decomposition dynamics.

Mixing litter from deciduous (nutrient-acquisitive) and evergreen (nutrient-conservative) trees can cause synergistic effects on decomposition (Liu et al. 2016). Consequently, we investigated the leaf and stem mass loss rate (MLR) of a deciduous (*Tectona philippinensis*) and an evergreen (*Parashorea malaanonan*) tree species and the factors influencing it through an intersite experiment and litterbag method in secondary forests in Lobo, Batangas and Mount Makiling Forest Reserve (MMFR). Here, the MLR is expected to be higher at "high-quality" litter and at sites with high air temperature and light intensity, particularly in deciduous litter. The present study's findings are important for predicting carbon and nutrient fluxes and assessing the vulnerability of *T. philippinensis* and *P. malaanonan* habitats.

2. Materials and Methods

2.1. Study site description

The intersite litter decomposition experiment was conducted in two contrasting sites (Lobo and the Mount Makiling Forest Reserve (MMFR)) in the Philippines (**Fig. 1**) from December 2022 to December 2023. Our observation shows that these sites differ in species composition, dominance, stand structure, and climate. The Lobo site is dominated by deciduous to semi-deciduous species such as *T. philippinensis*, *Vitex parviflora*, and *Terminalia polyantha* (Hernandez et al. 2016). The MMFR site is dominated by evergreen to semi-deciduous species, including *Diplodiscus paniculatus*, *Celtis luzonica*, *Mallotus cumingii*, and *Swietenia macrophylla* (Malabrigo et al. 2016; Ebale et al. 2023). Based on our previous work, the importance value (IV) of *T. philippinensis* ranged from 45% to 67% in Lobo (Hernandez et al. 2016). Although not the most dominant species, *P. malaanonan* was ranked among the top 10 tree species based on IV (Castillo et al. 2015). The forest canopy in the Lobo site, with a daily mean light intensity of 1510-1800 lux during summer, is generally more open than in the MMFR, with a daily mean light intensity of 405–861 lux during summer. The MMFR and Lobo study sites have approximately 2500 trees ha^{-1} and 650 trees ha^{-1}, respectively. The average basal area (BA) of *P. malaanonan* was 3.76 $m^{2,}$ whereas *T. philippinensis* has an average BA of 18.18 m^2 (Castillo et al. 2015; Caringal et al. 2019). The mean annual air temperature (MAT) and mean annual precipitation (MAP) in the MMFR site are 26°C and 1,307 mm, respectively. The MAT is 27–32°C at the Lobo site, and the MAP is 1,140 mm. The soil pH at the Lobo site ranges from 5.27 to 5.95, whereas MMFR ranges from 6.22 to 9.2.

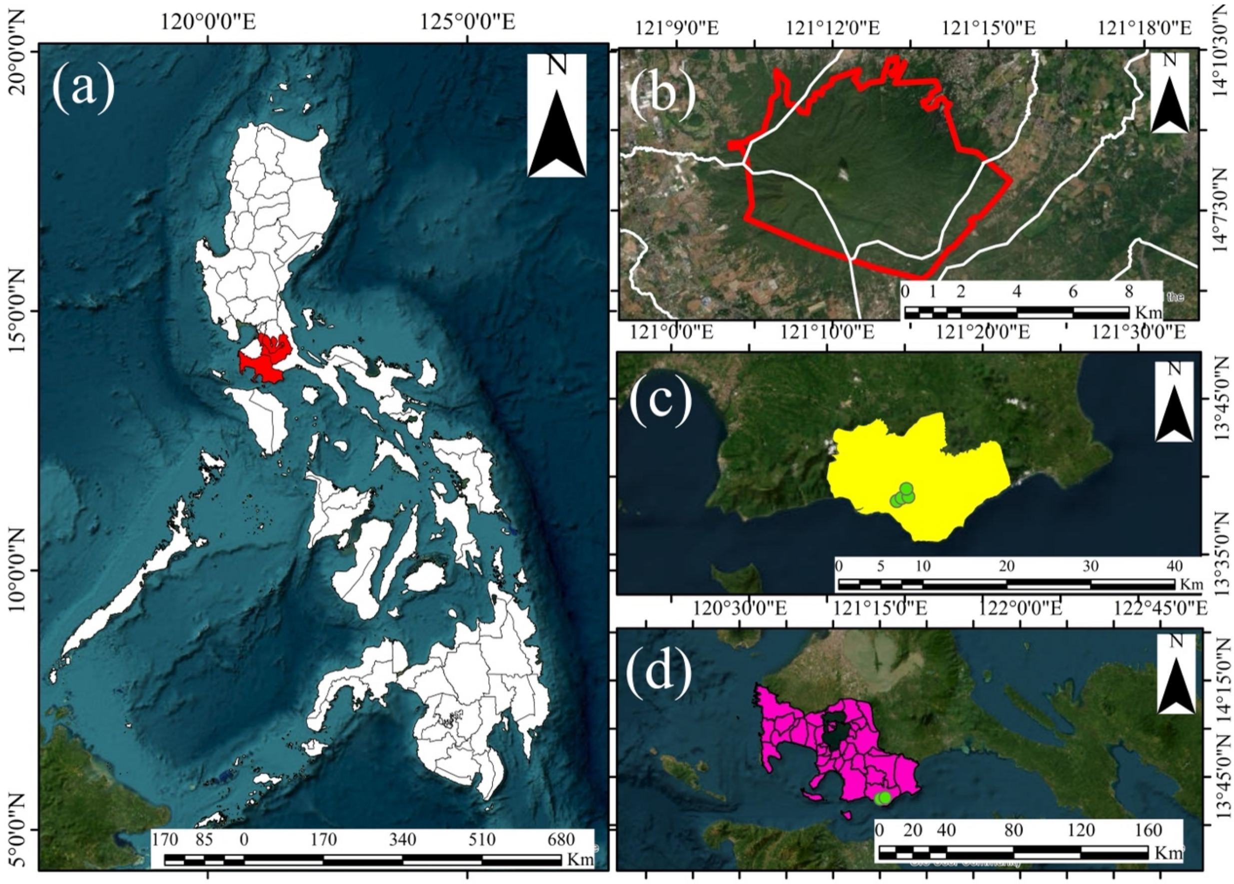

Fig. 1. (a) Philippine map showing the location of the study sites in (b) Mount Makiling Forest Reserve (MMFR) site in Laguna and (c) Lobo site located in (d) Batangas, Philippines.

2.2. Environmental Data Measurement and Monitoring

The mean daily air temperature and light intensity were measured in each study site using portable light and air temperature loggers (Onset, HOBO Pendant Optic USB Base Station and

Coupler). One week before sampling, these loggers were deployed in the field, securely sealed, and fastened to tree trunks (c.a., 2–4 m above ground). These loggers were retrieved and downloaded every three months via USB cable and exchanged with the loggers in place for the past three months.

2.3. Experimental Materials and Intersite Experiment

Freshly fallen, undecomposed leaf and stem litter from *T. philippinensis* and *P. malaanonan* were collected from mature trees (> 25 cm dbh) in native collection sites. These species were selected based on their contrasting leaf functional traits and distinct habitat characteristics, as earlier mentioned, to capture a broad range of ecological conditions. This approach is expected to further understand the intersite experiment's broader ecological implications.

Litter samples were cut and air-dried in an open paper bag for several days. Air-dried samples (6–7 g for leaf and 5–7 g for stem) were placed inside the terylene-made litterbags (c.a., 200 cm^2) with a mesh size of 0.5 mm. These bags were sealed, color-coded to distinguish between species, and tagged correctly.

Four study plots (144 m^2) were established at each research site, and the distance between plots was approximately 1 km. The intersite experiment had three sets of litterbags. The first and second sets contained monospecific litter for *T. philippinensis* and *P. malaanonan*. The third set comprised even mixtures of the two species. Following the modified procedure in Park et al. (2021), nine 5-m parallel lines with four points each for bag placement were laid out in each plot and site (**Fig. 2**). The distance between lines was approximately 1 m. A total of 192 bags (2 sites × 4 plots × 3 sets of litter × 2 bags per species × 4 collection times) were placed on the ground (**Fig. 2**). Each bag was supported by sturdy pegs/large nails. Collection of litterbags was done every three months depending on the season (wet and dry season) for one year. The collected litter bags were carefully packed to avoid the loss of fine particles and stored in a box until further analysis in the laboratory. Other extraneous materials attached to the bags were also removed carefully.

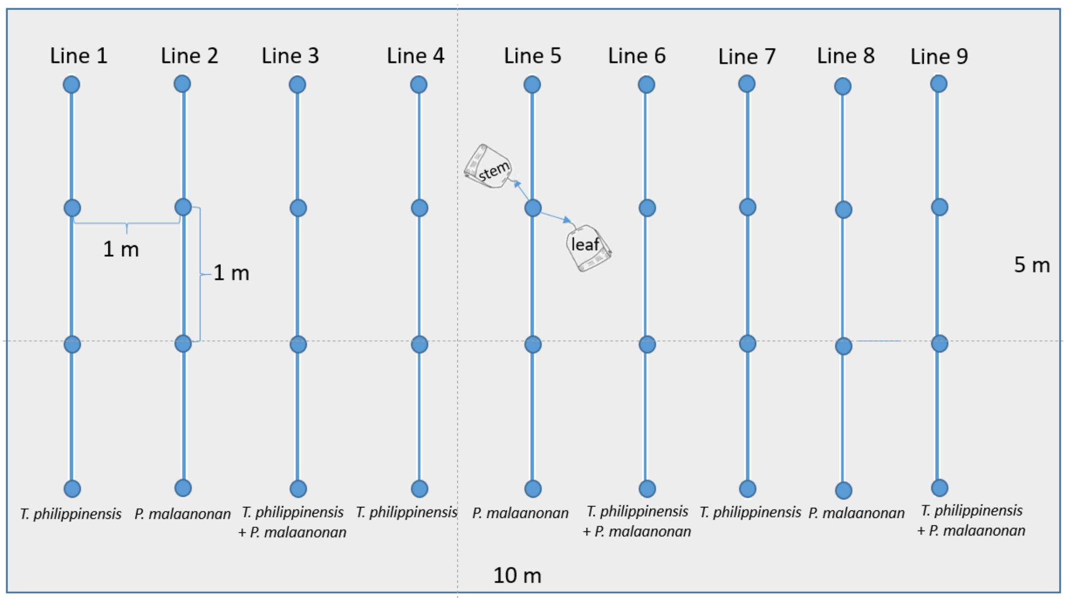

Fig. 2. Representation of the plot layout used in the intersite litter decomposition study conducted at Lobo, Batangas, and Mount Makiling Forest Reserve, Philippines.

2.4. Data and Statistical Analysis

For each litterbag set, the mean mass loss rate (MLR) of *T. philippinensis* and *P. malaanonan* across plots at each site and collection time was calculated using Equation 1 (Park et al. 2021).

$$MLR\ (\%) = \frac{(X - X_i)}{X} \times 100\% \qquad (1)$$

where X is the initial dry weight of the leaf litter, and X_i is the weight of the residual leaf litter after time t (year).

The data were first assessed for normal distribution. The inter-specific differences in litter traits between the two species and site variables (air temperature and light intensity) were evaluated using the Wilcoxon rank test. The Kruskal-Wallis rank sum test was used to examine whether there are statistically significant differences in MLR among the three litterbag sets and between sites and months. Principal component analysis (PCA) was conducted to determine the influence of initial litter quality and environmental factors and their interaction on the decomposition rates across species and sites. This study examined only principal components 1 (PC1) and PC2 with eigenvalues greater than one. All statistical analyses were performed using RStudio (version R 4.3.1) at $p < 0.05$ significance level.

3. Results and Discussion

3.1. Leaf and Stem Mean Mass Loss Rates Between Species and Sites

Litter decomposition rates in terrestrial ecosystems may differ depending on litter quality and plant life forms (Ramos et al. 2021). In the present study, the quarterly leaf and steam mean MLR was significantly higher in the mixed litter (44.09–57.83%) than that of a single-species litter of either *T. philippinensis* (28.16–41.83%) or *P. malaanonan* (33.60–47.66%) in both Lobo and MMFR sites (**Fig. 3**). Similarly, a faster decomposition was reported in the mixture of litter of the sclerophyllous *Phillyrea angustifolia* and *Pistacea lentiscus* with *Quercus ilex* in a Mediterranean maquis, a high-diversity, nutrient-poor, shrubby ecosystem (De Marco et al. 2011). In a mixed-species plantation of needle-leaf and broadleaf species, a higher MLR in mixed-litter than in the two single-litter treatments was also observed (Zeng et al. 2023). However, a meta-analysis challenged the concept that mixing litters often enhances decomposition rates, suggesting that additive and adverse effects could slow down the process (Porre et al. 2020). The result can be attributed to contrasting species functional types, which can influence decomposer functional diversity (Patoine et al. 2020), enzymatic activities, and decomposition pathways (García-Palacios et al. 2015). Mixed-species litters may have more diverse physical characteristics, which, when combined, may enhance synergistic interactions among decomposers, resulting in higher decomposition rates (Liu et al. 2020). This tendency indicates that more diversified ecosystems would have better litter inputs, decomposition processes, and carbon and nutrient cycling.

The significantly higher MLR in mixed-litter than in single-litter was particularly pronounced during the rainy season from August to December. This tendency can be ascribed to the improved microenvironment and soil moisture content that may have promoted microbial activity. This tendency partially agrees with previous findings highlighting one of the synergistic effects of litter mixing, i.e., nutrient transfer from high-quality litter species (deciduous) to low-quality litter (evergreen), which may have supported more types of decomposers (Liu et al. 2020). Because of this nutrient transfer, mixed litter may have been more responsive to decomposition than single litter because it contained more organic components with variable chemical compositions that met the nutritional needs of different decomposers. The results indicate that any alteration in the precipitation patterns in either *T. philippinensis* or *P. malaanonan* forest stand will substantially affect litter decomposition dynamics.

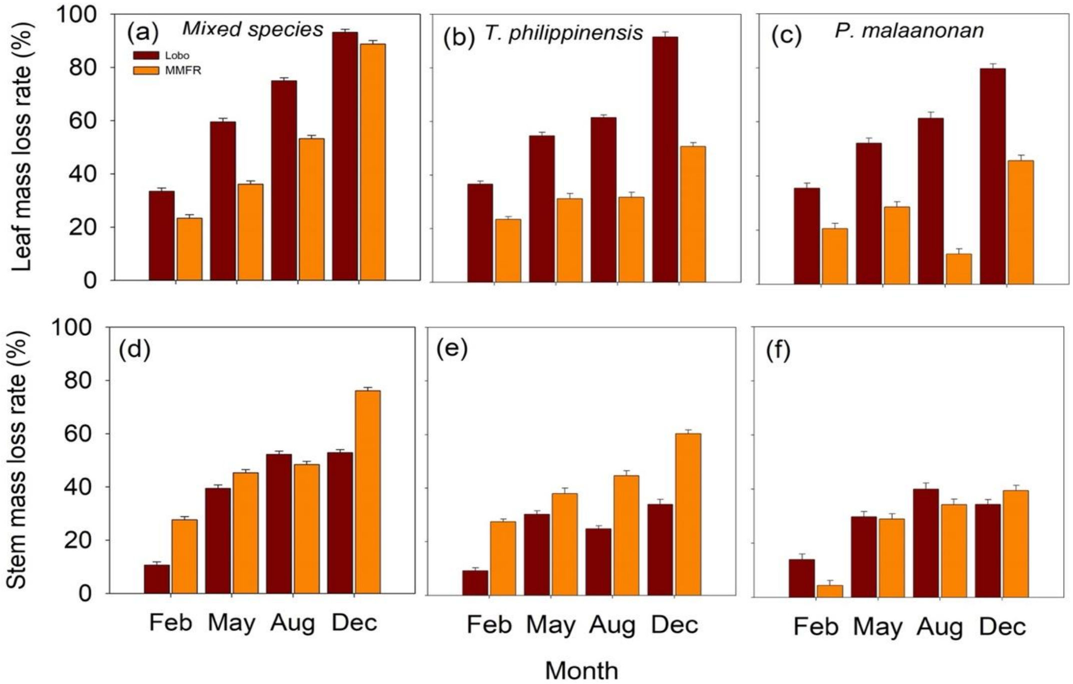

Fig. 3. Quarterly (a–c) leaf and (d–f) stem mean MLR of *T. philippinensis* and *P. malaanonan* via reciprocal litter transplant experiments in Lobo and Mount Makiling Forest Reserve sites.

The annual leaf MLR in *T. philippinensis* also varied significantly between sites ($p < 0.0001$, **Fig. 4**). It was greater when placed at Lobo, where the litter originated, than when it was placed at MMFR. The result agrees with the home-field advantage (HFA) hypothesis (Palozzi and Lindo 2018). Consequently, leaf litter from *T. philippinensis* may have adapted to environmental conditions, soil characteristics, and microclimate, all of which alter the composition of the microbial population, supporting the decomposition process at the Lobo site. In a previous study by Pugnaire et al. (2023), the HFA effect was also detected in low-quality litter, necessitating specialized fungal communities to maximize decomposition, implying that the HFA effect is linked to litter quality. A similar link was also observed in the most recalcitrant litter of *Pinus pinaster*, particularly during the mild years (Wang et al. 2020). Moreover, the HFA effect was more evident in hard-to-decompose litter and strongly dependent on water availability (Lam et al. 2021; Zhang et al. 2021). This result explains the reverse pattern observed in *P. malaanonan*, particularly in leaf MLR (i.e., faster decomposition even at the Lobo site). This reverse pattern suggests that factors other than the HFA may have influenced its decomposition as environmental variables, soil properties, and microbial activity may vary between sites depending on litter quality and the decomposer involved. Specifically, the annual air temperature was significantly higher in Lobo (27–32°C) than in MMFR (26°C). An incubation experiment revealed that temperature substantially impacts litter mass loss, and the magnitude of the impact varied by species (Bonanomi et al. 2023). Regarding forest structure, Lobo has fewer trees per hectare than MMFR, explaining the synergistic effect of litter mixing on the decomposition rate. This result also explains the significantly higher mean annual light intensity at the Lobo site (1,209–1,553 lux) than in MMFR (345–731 lux). A shading-decomposition experiment revealed strong light-intensity effects on litter mass loss, although the effects depended on tree species and season (Ma et al. 2017).

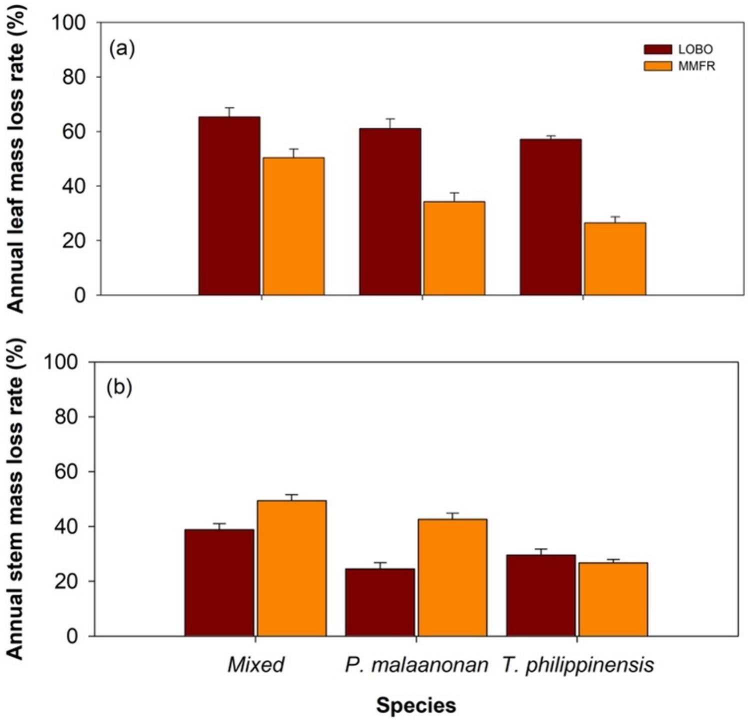

Fig. 4. Annual (a) leaf and (b) stem MLR of mixed-litter, *T. philippinensis* litter, and *P. malaanonan* litter via reciprocal transplant experiments in Lobo and Mount Makiling Forest Reserve sites.

Consequently, our results can be attributed to variation in leaf litter traits between *T. philippinensis* and *P. malaanonan* (**Fig. 5**). Leaves of *P. malaanonan* are significantly larger (74.71 cm, $p < 0.0001$) and thicker (0.21 mm, $p = 0.0001$) than those of *T. philippinensis*, implying that it may contain more phytocompounds (e.g., lignin and secondary metabolites) that resist the decomposition process within its "original" environment. A significantly lower SLA (143.94 cm g^{-1}) in *P. malaanonan* than *T. philippinensis* can explain the presence of more phytocompounds in their leaves, as a lower SLA indicates a greater dry leaf mass (**Fig. 5**). Thicker leaves tend to have multiple layers of structural components, such as cuticular and epidermal layers (Hernandez et al. 2024), which prevent microbial penetration and enzymatic breakdown (Siv et al. 2018). *P. malaanonan* has evergreen leaves, which may contain lower nutrient concentrations compared to the deciduous leaves of *T. philippinensis.* This result means that *P. malaanonan*'s leaves are low-quality food for decomposers. Nutrient availability in leaves, particularly nitrogen, limits the growth and activity of decomposers, influencing decomposition (Alonso et al. 2021). Generally, leaf litter with high nutrient content and low stoichiometric characteristics decomposes quickly (Hou et al. 2021; Kong et al. 2022). Furthermore, deciduous leaves have a shorter life span than evergreen leaves, further explaining the HFA effect in *T. philippinensis.* Deciduous species experience nutrient resorption before senescence, implying that the trees reabsorb most nutrients before leaf loss, resulting in more nutrient-rich litter for decomposers (Park et al. 2021).

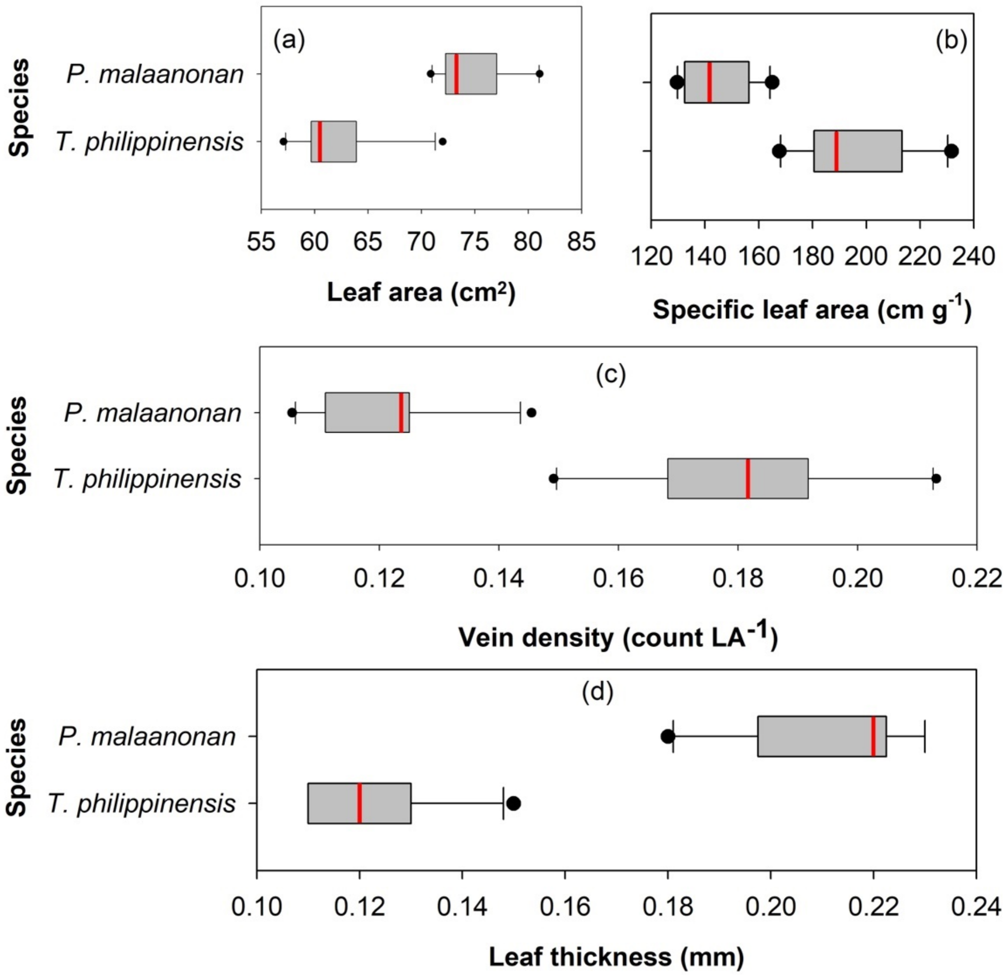

Fig. 5. (a) Leaf area, (b) specific leaf area, (c) vein density, and (d) leaf thickness of *T. philippinensis* and *P. malaanonan* from Lobo, Batangas, and Mount Makiling Forest Reserve, respectively.

3.2. Litter Quality and Environmental Factors Influencing Leaf and Stem Mean MLR of T. philippinensis and P. malaanonan

The influence of initial litter quality and site factors on the decomposition rates across species and sites is depicted through a PCA (**Fig. 6**). The first two axes (PC1 and PC2) explained 65.45% of the total variation, with PC1 contributing 46%. High negative factor loadings were observed for initial VD (-0.71), SLA (-0.83), and light (-0.91) on PC1. These findings suggest that any significant changes in these factors are strongly associated with fluctuations in the decomposition rate patterns of either species. Hence, a combination of light, SLA, and VD can be a dominant predictor of litter decomposition. This tendency explained a larger leaf MLR of *P. malaanonan* when its litter was transplanted in another site (i.e., Lobo). Notably, *P. malaanonan*'s leaves possess significantly fewer veins per unit leaf area (0.12 veins LA^{-1}, $p < 0.0001$) compared to *T. philippinensis*, implying a simpler leaf structure for *P. malaanonan*. Leaves with fewer veins may have more interveinal space or leaf material for microbial access and penetration, resulting in a faster decomposition rate. A comparable trend, where leaf veins resisted decomposition, was observed in two *Quercus* species (Pavlović et al. 2020). However, the environment (i.e., cooler climate, less microbial activities) where *Quercus* is naturally occurring is intrinsically different from *P. malaanonan*'s. This result highlights the interplay between environmental factors and species characteristics in shaping decomposition processes.

Moreover, the sites (-0.5) and months (-0.68) displayed high positive loadings on PC2. Initial SLA and VD showed a strong positive correlation with light and site, suggesting that these traits are influenced by specific site conditions present at each site where *P. malaanonan* and *T. philippinensis* are grown. These traits interact with site microclimatic conditions, altering litter quality and affecting decomposition rates (Bernaschini et al. 2016). However, the magnitude of the effects depends on climate gradient and time (Canessa et al. 2020). It further explains the observed high MLR during the rainy season (**Fig. 2**) and a strong correlation between MLR and month (**Fig. 6**). A study also revealed higher decomposition rates of *Anadenanthera peregrina* in the rainy season, which was attributed to enhanced vegetative growth and the nutrient resorption (Valente et al. 2023). Moreover, a meta-analysis found a significant % reduction in litter decomposition by 43% depending on drought type and intensity, decomposer community, climate conditions, and litter quality (Ferreira et al. 2023). Litter decomposition is generally reduced during the dry season due to altered soil moisture and nutrient availability, which play an essential role in facilitating microbial and enzymatic processes for the degradation of organic matter (Hernandez and Park 2024). These results highlight the complex interactions between site, month, initial litter traits, and environmental factors influencing decomposition rates. Understanding this interaction is critical for predicting decomposition processes across different ecosystems.

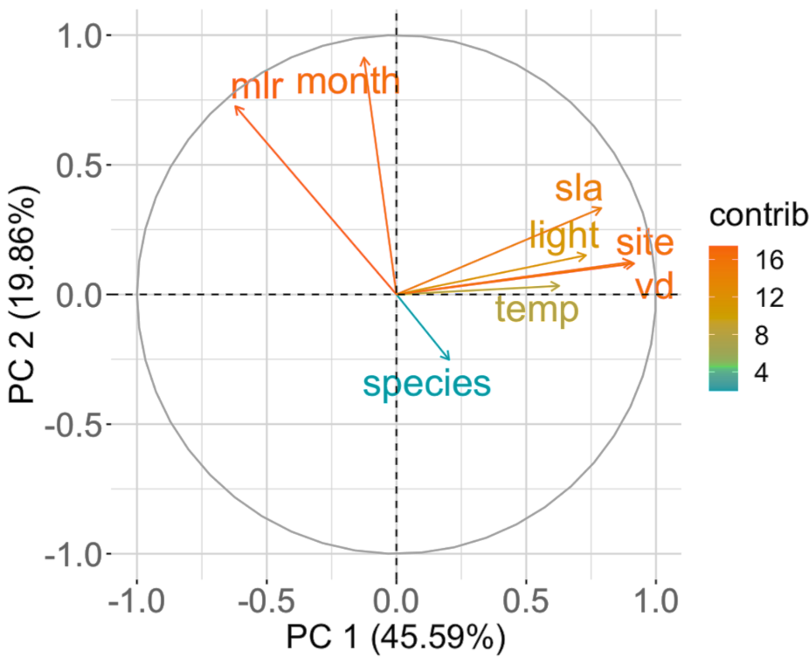

Fig. 6. Principal component analysis (PCA) based on the correlation matrix of initial leaf litter traits (sla, specific leaf area; vd, vein density), mass loss rate (MLR), and site conditions (light, air temperature), month, and species in Lobo, Batangas, and Mount Makiling Forest Reserve. The "contrib" denotes the contribution of the variables to principal components.

4. Conclusions

The present study showed that the litter decomposition rate of deciduous *T. philippinensis* or evergreen *P. malaanonan* differed between the two sites due to variations in litter quality and environmental variables. Litter mixing induced synergistic effects on decomposition rates across all sites. Leaf litter decomposition was shown to be faster in deciduous species than in evergreen species during the rainy season and slower during the dry season for both species and sites. Moreover, we demonstrated that the HFA effect on leaf and stem decomposition appeared to occur only in *T. philippinensis.* Our results confirmed the important role of initial litter quality and site conditions in regulating litter decomposition, enhancing our understanding of how they control carbon and nutrient fluxes in deciduous and evergreen tropical forest stands. Future efforts should explore additional factors such as litter chemistry, palatability and nutritional contents, decomposer communities, and their interactions to elucidate litter decomposition dynamics further.

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