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Impact of tree litter identity, litter diversity and habitat quality on litter decomposition rates in tropical moist evergreen forest

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ABSTRACT

Background: Attempts to restore degraded highlands by tree planting are common in East Africa. However, up till now, little attention has been given to effects of tree species choice on litter decomposition and nutrient recycling.
Method: In this study, three indigenous and two exotic tree species were selected for a litter decomposition study. The objective was to identify optimal tree species combinations and tree diversity levels for the restoration of degraded land via enhanced litter turnover. Litterbags were installed in June 2019 into potential restoration sites (disturbed natural forest and forest plantation) and compared to intact natural forest. The tested tree leaf litters included five monospecific litters, ten mixtures of three species and one mixture of five species. Standard green and rooibos tea were used for comparison. A total of 1,033 litters were retrieved for weight loss analysis after one, three, six, and twelve months of incubation.
Results: The finding indicates a significant effect of both litter quality and litter diversity on litter decomposition. The nitrogen-fixing native tree *Millettia ferruginea* showed a comparable decomposition rate as the fast decomposing green tea. The exotic conifer *Cupressus lusitanica* and the native recalcitrant *Syzygium guineense* have even a lower decomposition rate than the slowly decomposing rooibos tea. A significant correlation was observed between litter mass loss and initial leaf litter chemical composition. Moreover, we found positive non-additive effects for litter mixtures including nutrient-rich and negative non-additive effects for litter mixtures including poor leaf litters respectively.
Conclusion: These findings suggest that both litter quality and litter diversity play an important role in decomposition processes and therefore in the restoration of degraded tropical moist evergreen forest.

1. Introduction

Although restoring degraded tropical forest land has received some attention in the past (Lamb, 1998; Holl et al., 2000; Lamb et al., 2005), much additional restoration work is needed to achieve the global protection area target (Mappin et al., 2019). So, efforts are still underway to restore tropical forests on human-disturbed lands across the globe (Fagan et al., 2020). In East Africa, Ethiopia has taken an ambitious commitment to restore 22 million ha of degraded land (Kassa, 2018). However, the success of secondary forest development will largely depend on soil fertility (Uriarte et al., 2015).

Tropical forest soils often function with a limited budget of essential nutrients, with the sustainable availability of these scarce resources largely depending on the efficiency of the nutrient recycling process. Undisturbed tropical forest soils can show nutrient recycling rates up to 2 to 5 times faster than grassland soils (Ochoa-Hueso et al., 2019). In tropical forests, plant leaf litter is the major source of nutrients (Xue et al., 2019), supplying more than 70% of the tropical forest nutrient demand (Chapin et al., 2011). This shows both the efficiency and degree of dependency of tropical forest ecosystems on litter decomposition in order to sustain their exceptional biodiversity (Vitousek, 1984; Powers et al., 2009; Krishna and Mohan, 2017). In that regard, litter decomposition is a crucial process to rebuild soil organic matter on degraded tropical forest land and to ensure sustainable availability of nutrients for the recovering secondary forest (Cleveland et al., 2006; Tang et al., 2010). Despite its importance, there is still a limited knowledge on the factors affecting the

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litter decomposition process in tropical forest ecosystems (Giweta, 2020).

Specifically for the tropical forests of Ethiopia, the majority of previous research on nutrient cycling focused on monospecific litter decomposition (e.g. Demessie et al., 2012; Birhane et al., 2019; Bekele et al., 2020; Negash and Starr, 2021), which may not be sufficient to understand the *in situ* decomposition patterns of these forests (Hättenschwiler et al., 2011; Jacob et al., 2010). Indeed, high diversity of litter types has been shown to enhance litter decomposition rate via positive diversity effects, e.g. by promoting fungal diversity (Mori et al., 2020; Song et al., 2010). Furthermore, overall litter quality and diversity, climatic variation, decomposer community (Zhang et al., 2008; Pei et al., 2017; He et al., 2019; Song et al., 2019; Desie et al., 2020), and the type of ecosystem where the litter is deposited (Mayer, 2008; Lu et al., 2017; Ochoa-Hueso et al., 2019) may have a strong effect on litter decomposition rates. Thus, it is crucial to understand which tree species, and in which composition, can stimulate the nutrient cycling in the Ethiopia Afromontane forest ecosystem, where there is currently active replacement going on of native tree species with exotics for economic purposes. Restoring the forest with species having contrasting leaf litter combinations might help to enhance the decomposition rate of the recently introduced exotic trees through induced functional traits that change antagonistic mechanisms into synergistic. In other words, competitors could become a facilitator of resource acquisition that increases leaf litter quality (Helsen et al., 2018, 2020). Finally, studies that have compared both native and exotic tree leaf litter mixtures with the standardized tea litters in both natural and strongly disturbed forest ecosystems are rare (Peh et al., 2012; Cizungu et al., 2014).

In this study, we compared litter decomposition rates of native tree litter (*Croton macrostachyus*, *Millettia ferruginea*, *Syzygium guineense*), exotic tree litter (*Eucalyptus globulus*, *Cupressus lusitanica*) and the standard litter types of the 'tea bag index' (Keuskamp et al., 2013) during a one-year incubation period in the Afromontane moist evergreen forests of the Gerese district of SW- Ethiopia. The objectives were fourfold: (1) to measure the impact of species identity on litter decomposition rate, (2) to evaluate the effect of litter diversity on litter decomposition rate, (3) to examine the impact of local habitat quality on litter decomposition rate, and (4) to compare the litter decomposition rates of the indigenous and exotic trees with the standard green and rooibos tea. We hypothesize that (a) litter identity, litter diversity, and habitat quality play a significant role in litter decomposition rate and that (b) litter decomposition can be enhanced by restoring the degraded land with native rather than with exotic tree species.

2. Methods

2.1. Study area

The study area is located in the SW of Ethiopia, close to the city of Arba Minch and the town of Gerese. It is geographically located in the range of 37.30°–37.33° E and 5.92°–5.95° N at an elevation between 2,100 and 2,525 m above sea level. The area is characterized by year-round rainfall, estimated at 1,700 mm per year by Friis et al. (2010). Heavy rainfall starts in March and extends up to May. The average monthly minimum and maximum temperature during the cold and warm months are 11 °C and 24 °C, respectively (EMA, 2018).

The forest in our study area is categorized as Afromontane moist evergreen forest (Friis et al., 2010) and covers an area of 363 ha. The forest consists of three different forest habitat types, intact natural forest, disturbed natural forest, and plantation forest. The natural forest is characterized by a closed canopy dominated by old-growth trees and an abundance of smaller sized understory plants. The dominant tree species include *Syzygium guineense*, *Macaranga capensis*, *Ocotea kenyensis* and *Ilex mitis*. In the disturbed forest, native trees are scattered and mixed with planted exotic *Eucalyptus globulus*, *Cupressus lusitanica* and *Grevillea robusta* trees. This forest is characterized by large canopy gaps and the forest floor is partly covered by pioneer weeds and grasses. The local foresters use the gaps for exotic tree plantation as a restoration measure. As a result, the species composition in the degraded forest changed from natural to semi-natural. The plantation forest resulted from an attempt to protect the natural forest from human disturbance by an exotic tree plantation buffer (Eshetu and Högberg, 2000; Eshetu, 2014). This mature plantation is 46 years old and is mainly composed of *Eucalyptus globulus*. As it also serves as a source of wood for the local community, this buffer zone is not uniform and some parts are highly disturbed.

2.2. Litter collection and decomposition assessment

Undamaged senescent leaves were collected between February and April 2019 from three indigenous (*Croton macrostachyus*, *Millettia ferruginea* and *Syzygium guineense*) and two exotic (*Cupressus lusitanica* and *Eucalyptus globulus*) tree species. The senescent leaves were picked by hand from accessible branches of multiple mother trees of each species that were randomly distributed across the three forest types. Both ecological and socio-economical criteria were used for the species selection. *S. guineense* is a dominant keystone species in the Gerese highland forest. *C. macrostachyus* is a fast growing pioneer tree species with big leaves, and *M. ferruginea* is a nitrogen fixing tree. Both *C. macrostachyus* and *M. ferruginea* have been used by local people as agroforestry trees in the northern and southern parts of Ethiopia, respectively (Lelamo, 2021). The other two exotic trees are both present in the study area, where they were mainly planted for their economic value. Standard Lipton green (EAN: 87 22700 05552 5) and rooibos teas (EAN: 87 22700 18843 8) were used for decomposition rate comparison with the selected indigenous and exotic tree leaf litters, following the standard 'tea bag index' of Keuskamp et al. (2013).

All litter samples were transported to the Arba Minch University botany lab (hereafter AMU) in tagged plastic bags and were dried at 70 °C for a minimum of 48 h. The dried litter was subsequently ground and sieved with a 2-mm and 500-μm mesh size sieve. The 2-mm sieve was put on top of the 500-μm sieve. Litter that passed the 2-mm sieve but was trapped by the 500-μm sieve was used. For each individual leaf litter (3 indigenous and 2 exotic tree species), 2-g ground leaf litter was transferred into empty nylon mesh tea bags and sealed with a plastic sealer. In addition, 2-g mixture litters of two diversity levels were prepared from the 5 selected species (all ten possible 3-species combinations and the single 5-species combination). In the litter mixtures, all involved species contributed with an equal amount of litter. Together with the Lipton green and rooibos teas, this resulted in a total of 1,080 litterbags from the 18 different litter types. Before installation, all litterbags were labeled with aluminum metal sheets indicating litter types, incubation period, and forest type. In each of the three forest types we subsequently selected five random 3 m × 3 m plots where we installed four litterbags per litter type on June 12, 2019, at 30-cm intervals. Initial P, K, Ca, Mg, Na, Fe, Cu, Zn and Mn content of the grounded litter of each study species were quantified using Inductively Coupled Plasma Atomic Emission Spectroscopy. Laboratory procedure details are available in Appendix 1.

One litterbag of each litter type was then retrieved after respectively one, three, six, and twelve months. Of the 1,080 litterbags, only 1,033 were successfully recovered. The other 47 litterbags were damaged by earthworms, termites or root penetration. All retrieved litterbags were transported to AMU for further processing. Adhering soil was manually removed from the litterbags with a test tube brush. The cleaned litterbags were dried for 48 h at 70 °C. After drying, the litterbags were opened and their content was transferred to an aluminum foil cap for weight loss analysis with a 0.01-g precision electronic balance.

2.3. Environmental data collection

In each plot, soil samples were taken from three points at 30-cm depth from the surface, which were merged into a composite sample for further analysis at AMU. The soil samples were air-dried at room temperature for a week and ground with mortar and pestle to pass through a 2.5-mm

sieve. Ten grams of the sieved soil sample was used to prepare a 1:2.5 soil/water suspension to measure soil pH and electric conductivity using an HACH HQ40d digital multi-meter. The remaining soil macro- (i.e., P, K, Ca, Na, Mg) and micronutrient (i.e., Cu, Fe, Mn, Zn) analyses were carried out at KU Leuven, Belgium using an ICP-OES (Appendix 1). Other environmental parameters like soil temperature and moisture were measured once per month using a digital soil thermometer and TDR 150 soil moisture meter, respectively. Since soil moisture content was uniform across the three forest types during the study period, it was not used in the final analyses. Location, elevation and aspect were collected for each plot using a Garmin handheld GPS 64S.

2.4. Data analysis

We first performed a principal component analysis (PCA) on all measured soil variables for all plots, to visualize potential differences in the soil chemical composition of the three forest types. Moreover, we estimated 'litter quality' of each litter mixture, prior to the decomposition experiment, as the percentage of evergreen leaves in the mixture (Table 1), since evergreen species are theoretically expected to have lower litter quality than deciduous species (Silva et al., 2015). Thus 'litter quality' acts as a predictor variable with five levels (0%, 1/3 = 33%, 2/5 = 40%, 2/3 = 67%, 100%). For example, a litter mixture that contains litter from one evergreen and two deciduous tree species received a 'litter quality' of 33%.

Before statistical analysis, the remaining litter mass was log-transformed for all litter types (Appendix 2), to satisfy model assumptions. We constructed an initial linear mixed model (LMM) for the log-transformed remaining litter mass of only the monospecific litter types (response) as a function of forest type (plantation, degraded and natural), litter type (7 monospecific litter types), observational period (after 1, 3, 6 and 12 months), and the interactions between litter type and forest type, and between litter type and observational period. Tukey multiple mean comparisons were also carried out among the seven litter types and the three forest types. A second LMM modelled the log-transformed remaining litter mass of all 17 litter types as a function of forest type, observation period, litter quality and litter diversity, including all first-order interaction terms.

Since four litter mass measurements were taken from the same plot during the one-year incubation period, plot ID was included as a random factor in both LMMs. Both LMMs were performed with the lme function from the lme4 R package (Bates et al., 2015). Multicollinearity among the explanatory variables was assessed by computing variance inflation factors, using the vif function from the lme4 R package. Stepwise model structure optimization was employed to select the best-fitted model following the procedure of Zuur et al. (2009).

Next, we performed a general linear model, with log-transformed remaining litter mass of all litter types after one year (thus only including the last time point) as a response and species richness (number of tree species in the litter), litter quality, forest type and all first-order interactions as predictors.

In order to evaluate the effect of litter mixture on decomposition rate, the relative individual performance (RIP) of the three indigenous and two exotic tree leaf litters were calculated following the procedure recommended by Barantal et al. (2011) and Lin and Zeng (2018).

$$RIP = \frac{Mixture - Single}{Single} \times 100 \quad (1)$$

where Mixture represents the mean mass loss of each mixture litter and Single the mean mass loss of unmixed, monospecific litters.

One sample Student t-tests to mean zero were carried out to reveal the significance of potential non-additive effects of each monospecific litter, where zero represents the additive effect in which both synergistic and antagonistic nonadditive effect cancel each other out.

The net diversity effect (NDE) was calculated by subtracting the expected value (Exp.) from the observed litter mixture value (Obs.) (Rubio-Ríos et al., 2021) to measure how much litter mass is lost or remaining due to the presence or absence of nutrient-rich indigenous tree leaf litter in the mixture. The mean mass loss observed and the expected value were obtained from the average value of the mass loss of each litter mixture and the individual monospecific litters included in the mixture, respectively.

$$NDE = Obs. - Exp. \quad (2)$$

3. Results

3.1. Description of forest and litter types

The three forest types differed in their soil chemical composition (Fig. 2) (see Fig. 1). Especially the natural forest showed larger variation and higher nutrient concentrations compared to both plantation and disturbed forest (Fig. 2).

The initial leaf litter nutrient composition varied strongly among the five selected tree species (Table 1). Litter mass loss after one year incubation revealed significant correlation with the initial leaf litter concentration of macronutrients P ($r = 0.55$, $p = 0.035$), K ($r = 0.86$, $p < 0.001$) and Na ($r = 0.61$, $p = 0.016$), and micronutrients Cu ($r = 0.67$, $p = 0.007$) and Zn ($r = 0.65$, $p = 0.008$).

3.2. Monospecific litter decomposition

Decomposition of the 402 retrieved monospecific litter bags varied considerably, both within and across the four observational periods and 7 litter types. The litter mass remaining during the first observational period ranged from 84.2% to 49.4% (Fig. 3a, Table S1). Litter type (species) had a significant effect on the remaining mass over time (Table 2). Among the selected five tree species, *M. ferruginea* demonstrates the fastest mass loss (Fig. 3a, Table S1). Compared to the standard green and rooibos teas, only *M. ferruginea* had a fast decomposition comparable to green tea (Fig. 3a, Table S1). Both *C. lusitanica* and *S. guineese* had slower decomposition than the slowly decomposing rooibos tea, whereas the decomposition rates of *C. maycrostachyus* and *E. globulus* were intermediate between the above two groups (Fig. 3a). The linear mixed model further showed that monospecific litter decomposition was not different across the three forest types (Table 2).

Table 1
Initial chemical composition ($mg \cdot kg^{-1}$) for the selected three indigenous and two exotic tree leaf litters in the Gerese highland Afromontane moist evergreen fragmented forest SW Ethiopia.

Species	Litter type	Deciduousness	P	K	Ca	Mg	Na	Fe	Mn	Zn	Cu
Croton macrostachyus	Native	deciduous	71.2	212.1	383.3	155.8	2.1	8.8	31.0	0.4	0.12
Cupressus lusitanica	Exotic	evergreen	14.2	45.9	316.0	25.7	1.2	9.6	1.6	0.2	0.05
Eucalyptus globulus	Exotic	evergreen	5.2	45.7	209.9	20.5	17.4	1.2	8.1	0.1	0.07
Millettia ferruginea	Native	deciduous	43.8	260.8	136.8	52.8	2.8	2.3	3.5	0.5	0.13
Syzygium guineense	Native	evergreen	12.6	45.6	136.5	59.7	1.7	2.8	10.8	0.2	0.11

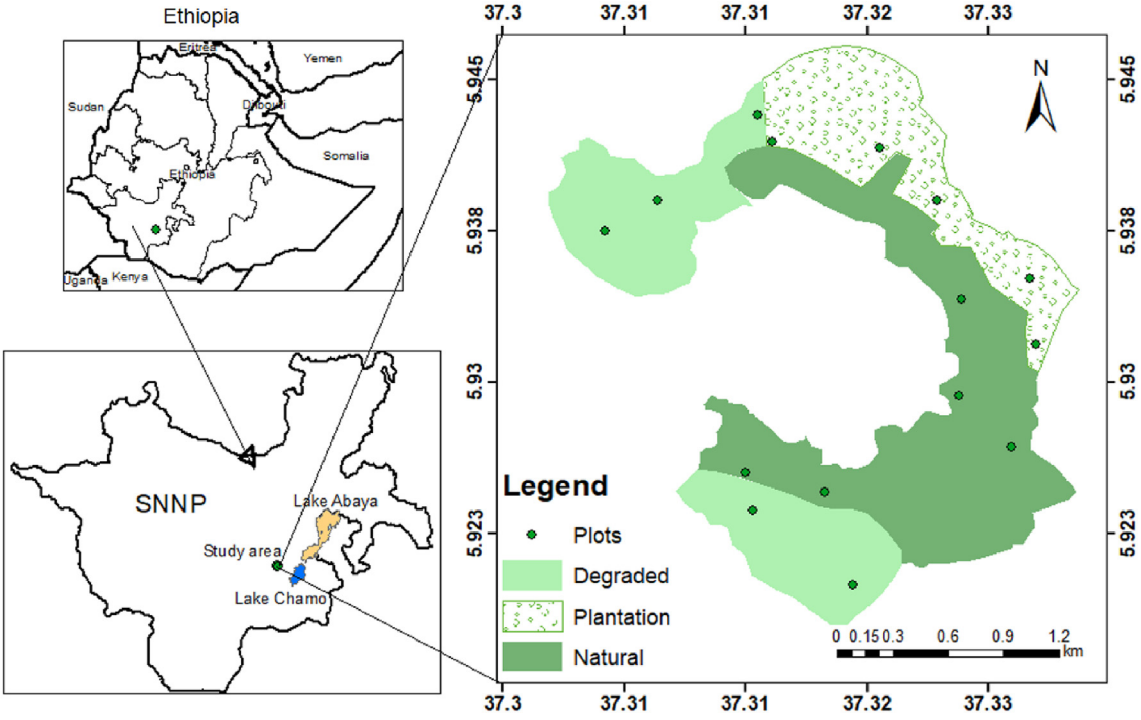

Fig. 1. Maps of the study area in the Afromontane moist evergreen fragmented forest of Gerese district SW Ethiopia, visualizing the three forest types (degraded, plantation and natural) and the location of our plots.

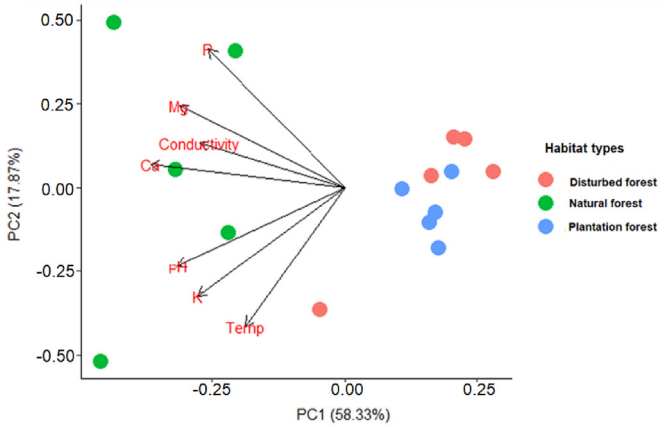

Fig. 2. Soil properties of the three forest types in the Gerese highland Afromontane moist evergreen forest SW Ethiopia. Where Temp = Average monthly temperature.

3.3. Effects of species richness and litter quality on decomposition

When including the 631 retrieval litter bags containing the species mixtures (11 additional litter types) to the linear mixed model, the overall remaining litter mass still decreased significantly with time, but at a varying pace for litter types of different litter quality (significant interaction). Decomposition was furthermore faster in the disturbed forest compared to the two other forest types (Table 3).

Low quality litters (e.g. *S. guineense* and *C. lusitanica*) that were mixed with both the two high quality litter species *C. macrostachyus* and *M. ferruginea* showed higher decomposition rates than the same species mixed with only one high quality litter species, except for the litter mixture of *M. ferruginea*, *E. globulus* and *C. lusitanica* (Fig. S1). Lower decomposition rates were revealed for litter mixtures that contained low quality litters (e.g., *S. guineense*, *C. lusitanica* and *E. globulus*) (Fig. S1).

A linear mixed model on decomposition of all litter types based on only the results after 1 year showed a clear positive litter diversity effect on decomposition. As the number of species in the litter mixture increased from one to five, the remaining litter mass significantly decreased (Fig. 4a). While the three forest types showed differences in litter decomposition in the model including all observational periods, decomposition was no longer significantly affected by forest type when considering only the last observational period (1 year) (Table 4 and Fig. 4c).

3.4. Relative individual performance (RIP)

The RIP was different across the five study species (Fig. 5). A significantly negative RIP was observed for *M. ferruginea* ($t_{27} = 12.5$, $p < 0.001$), indicating that this species has a higher decomposition rate as monospecific litter than in mixtures, and thus relatively high litter quality (Fig. 5). *C. macrostachyus* and *E. globulus* litter showed both synergistic and antagonistic effects across the different litter mixtures that seemingly canceled each other out, resulting in RIP values of zero ($t_{27} = -0.5$, $p = 0.623$ and $t_{27} = -1.1$, $p = 0.298$, respectively) (Fig. 5). *S. guineense* and *C. lusitanica* litter showed a higher decomposition rate in mixtures than alone, resulting in positive RIP values, thus indicating relatively low litter quality ($t_{27} = -13.0$, $p < 0.001$ and $t_{27} = -9.3$, $p < 0.001$, respectively) (Fig. 5).

3.5. Net diversity effect (NDE)

All litter mixtures except CDE (*S. guineense*, *E. globulus* and *C. lusitanica*) showed a positive net diversity effect (Fig. 6). The highest net diversity effect was observed for those litter mixtures that combine both high and low-quality leaf litter (e.g. BCD and BCE in Fig. 6). The lowest net diversity effect was observed for those litter mixtures that incorporate only poor-quality litter (CDE in Fig. 6). All other leaf litters that were combined intermediate-quality groups demonstrated moderate, but always positive net diversity effects (Fig. 6).

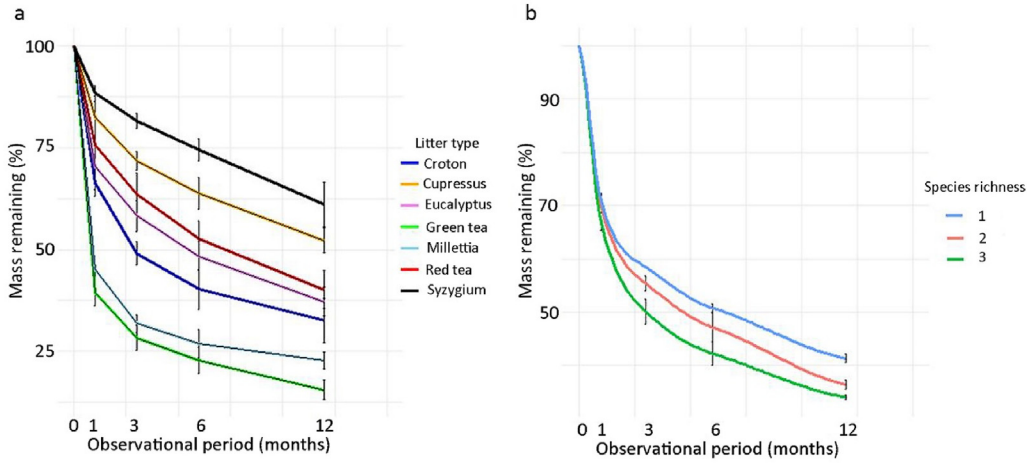

Fig. 3. Mass remaining (%) per litter type (a) and per species richness level (b) over time. Mean and standard deviations are indicated per time interval (after 1, 3, 6 and 12 months, respectively).

Table 2
F-statistics and associated *p*-values of the linear mixed model testing the impact of litter type, forest type, observational period and their interactions on remaining litter mass across 7 monospecific litter types. numDF = numerator degree of freedom, denDF = denominator degree of freedom.

	numDF	denDF	*F*-value	*p*-value
Intercept	1	359	357959	<0.001
Litter type	6	359	1270	<0.001
Observational period	1	359	2999	<0.001
Forest type	2	13	1	0.244
Litter type: Observational period	6	359	29	0.001
Litter type: Forest types	12	359	5	0.001
Forest types: Observational period	2	359	0.6	0.533

Table 3
F-statistics and an associated *p*-value of the linear mixed model testing the impact of litter quality (proportion of evergreen tree leaf litter in mixture), forest type, observational period and their interactions on remaining litter mass. numDF = numerator degree of freedom, denDF = denominator degree of freedom.

	numDF	denDF	*F*-value	*p*-value
Intercept	1	1008	28226	<0.001
Litter quality	1	1008	972	<0.001
Forest type	2	13	4	0.035
Observational period	1	1008	1349	<.001
Litter quality: Forest type	2	1008	0.4	0.653
Litter quality: Observational period	1	1008	10	0.002
Forest type: Observational period	2	1008	0.4	0.714

4. Discussion

4.1. Species identity

Species identity had a significant impact on the decomposition rate across all observational periods. The agroforestry species *C. macrostachyus* and *M. ferruginea* both showed fast litter decomposition, especially the nitrogen fixing *M. ferruginea*. Nitrogen fixing trees (NFTs) have been reported as reliable sources of nitrogen for the restoration of degraded tropical farmland (Munroe and Isaac, 2014). Crop and coffee production under the canopy of NFTs is indeed a common practice among the Ethiopian traditional farmers (Hailu et al., 2000; Zebene and Ågren, 2007; Hundera et al., 2015). For example, in the Sidama zone in south Ethiopia, the total N in the soil under the canopy of the NFT *M. ferruginea* was 24 times higher than under the canopy of *Eucalyptus camaldulensis* (Zebene and Ågren, 2007). Besides improving soil fertility

Table 4
Litter mass remaining after one year incubation as a function of litter identity, species richness (SR) and forest type.

	Df	Sum Sq	Mean Sq	*F*-value	*p*-value
Litter quality	1	13076	13076	223	<0.001
Species richness	1	882	882	15	<0.001
Forest type	2	51	26	0.4	0.647
Litter quality: Species richness	1	72	73	1	0.266
Litter quality: Forest type	2	26	13	0.2	0.800
Species richness: Forest type	2	36	18	0.3	0.735

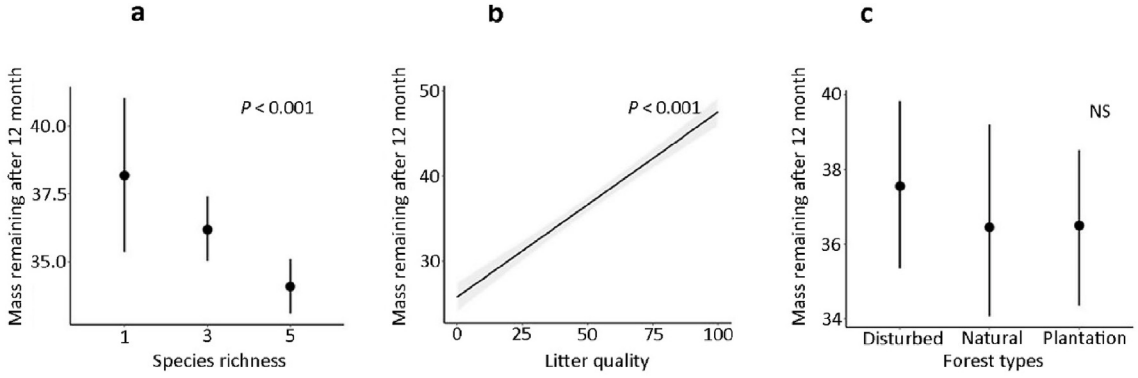

Fig. 4. Predicted mass remaining (mean and SE) after 1 year of incubation as a function of species richness (a), litter quality (b) and forest type (c) based on the linear mixed model accounting for site. The shade interval in b indicates the standard error interval.

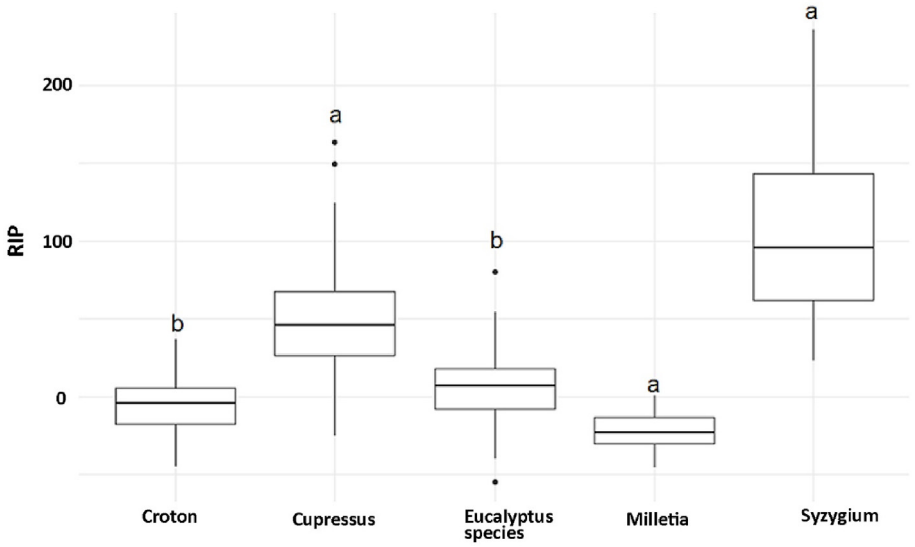

Fig. 5. Relative individual performance (RIP) of the leaf litter of three indigenous (*C. macrostachyus*, *M. ferruginea*, and *S. guineense*) and two exotic trees (*C. lusitanica* and *E. globulus*) in the Gerese forest. A RIP of zero represents an additive effect, positive and negative values represent nonadditive antagonistic and synergetic effect, respectively. Where **a** is significant and **b** is not significant at alpha = 0.05.

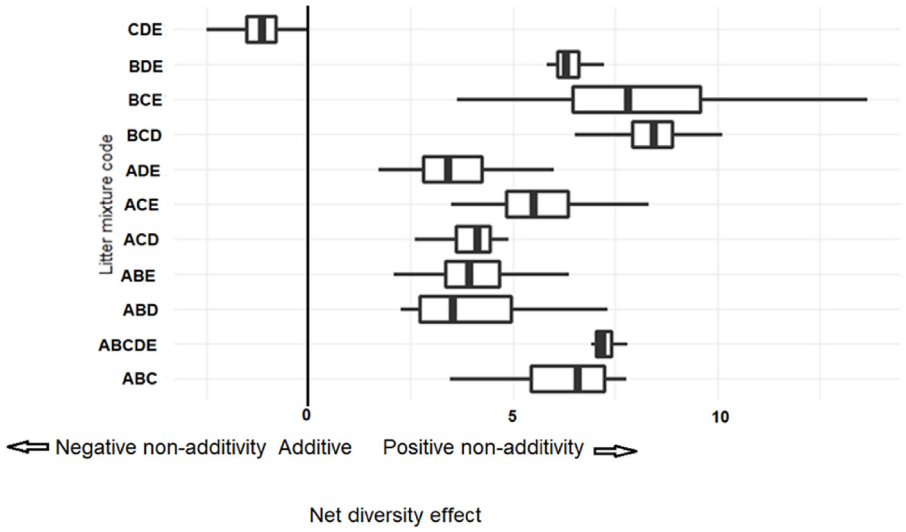

Fig. 6. Net diversity effect (NDE) of the eleven litter mixtures after one year incubation in moist Afromontane forest SW Ethiopia. *Millettia ferruginea* = B, *Croton macrostachyus* = A, *Eucalyptus globulus* = D, *Cupressus lusitanica* = E.

and agricultural yield, NFTs also provide other ecosystem services such as provisioning of livestock fodder, reducing soil erosion, and firewood and timber production (Azene Bekele, 2007; Koutika et al., 2021). Although *S. guineense* was expected to show a higher percentage of litter mass loss in the natural forest where it is a dominant species (Kavvadias et al., 2001; Ayres et al., 2009; Lu et al., 2017; Li et al., 2020), our results indicated the contrary, this species was shown a lower percentage of litter mass loss (11.7%) than the slowly decomposing rooibos tea (24.4%) and the recently introduced exotic tree *C. lusitanica* (17.6%). There are two likely explanations for the observed decomposition differences among the five litter types. First, the initial leaf litter chemical composition, and second, the leaf litter physical structure. Especially macronutrients such as K, Na, P and the micronutrients Cu and Zn showed a significant correlation with litter mass loss. Many studies reported that initial leaf litter chemistry had a significant impact on individual leaf litter decomposition (Ayres et al., 2009; Cuchietti et al., 2014; He et al., 2019; Song et al., 2019; Desie et al., 2020). However, decomposition rate is also known to be strongly influenced by leaf litter lignin and phenolic compounds that determine the physical defense structures of the leaves (Zhang et al., 2008; Talbot and Treseder, 2012; Rahman et al., 2013). These recalcitrant compounds are usually more abundant in evergreen leaves, resulting in the lower overall litter quality of evergreen versus deciduous trees (He et al., 2019). Only two out of three monoculture native tree leaf litters support the hypothesis that litter decomposition can be enhanced by restoring the degraded land with native rather than with exotic trees. It is important to notice that the native tree *S. guineensis* demonstrated a lower decomposition rate than the two exotic tree species. Thus, species identity is clearly more important in mediating litter decomposition than the origin of the tree species.

4.2. Litter diversity

Species richness had a positive effect on the decomposition rate: mass loss increased as the number of species in the litter mixture increased. This may be related to resource partitioning along multiple niche axis for the microbial decomposer communities (Bracken, 2020). As reported by

Chapman and Newman (2010) microbial diversity increases proportionally with increasing leaf litter diversity. Especially mycorrhizal fungi and actinomycetes have a positive relationship with litter diversity (Pei et al., 2017). These mycorrhizal fungi are especially important during late-phase decomposition, when they can facilitate the active transportation of inorganic ions from nutrient-rich to nutrient-poor litter (Pei et al., 2017). A meta-analysis conducted by Mori et al. (2020) confirmed that diversifying litter from mono to mixed-species can enhance the litter decomposition rate by 34.7% in the forest biome. Additionally, such diversity effects can be attributed to leaf litter chemical heterogeneity that attracts different types of decomposers to the litter mixture. This result broadly supports the hypothesis that litter diversity enhances litter decomposition rates.

4.3. Litter composition

Among the eleven-litter mixtures, only one litter mixture CDE (*S. guineense*, *E. globulus*, *C. lusitanica*) showed an antagonistic litter mixture effect. This may be related to the high-lignin concentration of the leaves of three functionally homogenous evergreen trees (Augusto et al., 2015). According to Cuchietti et al. (2014) litter mixture with high-lignin is often demonstrated an antagonistic effect. On the other hand, the highest litter mixture decomposition rate was observed for the litter mixture ABD (73 ± 5) and ABE (68 ± 5) that have 67% deciduous tree (A & B) and 33% evergreen tree (D & E) leaves. It is thought that legume species like *M. ferruginea* (B) play a vital role to enhance ecosystem function (Zhang et al., 2014; Li et al., 2015; Wei et al., 2019) by amplifying microbial abundance, growth, and colonization on the component leaf litters in the litter mixture (Milcu et al., 2008; Song et al., 2010; Wei et al., 2019). Indeed, the top quality litter *M. ferruginea* introduced a significant synergistic non-additive effect while the two evergreen tree leaf litters (*S. guineense* and *C. lusitanica*) introduced a significant non-additive antagonistic effect in the litter mixture. The intermediate quality litters (*C. macrostachyus* and *E. globulus*) also introduced additive effects, however, these species introduce both synergistic and antagonistic effects that cancel each other so their RIP was not statistically significant. This indicates that all species involved in the litter mixture do not have equal performance to the nutrient turnover process. However, prior studies relate the non-additive litter mixture effect with leaf litter chemical heterogeneity (Sauvadet et al., 2019), species identity (Chen et al., 2013) and change of decomposer community (Chapman and Koch, 2007). The water media also enhance microbial activity (Gogo et al., 2021) but it is difficult to determine which factor affects microbial community (Cleveland et al., 2014). Evidence shows that substrate quality, environmental factors and decomposition stage play a crucial role in microbial community development (Chapman et al., 2013; Bani et al., 2018). Thus, the non-additive effect that we observe in this study is mainly determined by litter quality and associated change of decomposer community following the physical and chemical change of litter during the decomposition process (Sauvadet et al., 2019). In that regard, the number of nutrient-rich litters involved in the litter mixture has a considerable impact on the overall decomposition rate of the mixture. For example, litter mixtures that have two nutrient-rich species (*C. macrostachyus* (A) and *M. ferruginea* (B)), in the litter mixture ABD, demonstrate a higher decomposition rate than the litter mixture that have only one nutrient-rich leaf litters ADE. This predominant role of leaf litter trait in the litter mixture decomposition rate was also reported by Kou et al. (2020). However, determining an optimal number of nutrient-rich deciduous and nutrient-poor evergreen tree leaf litters in the litter mixture might need further research. It is also important to consider the proportion of functional groups. Given that the two deciduous litters (A & B) decomposed faster than the other three evergreen litter (C, D, E). This finding concords with the finding of Wang et al. (2020) which states that "mixing broad-leaved with coniferous species has the potential to promote nutrient recycling and ecosystem productivity". Zhang et al. (2020) also reported that adding 30%–40% broadleaf litter proportion in the conifers plantation accelerated the decomposition rate by increasing fungal diversity. This indicates that the ecosystem needs to be diverse both in species and functions (Scherer-Lorenzen, 2008; Laird-Hopkins et al., 2017; Grossman et al., 2020). Species diversity alone might not be a guarantee for stable nutrient availability and/or sustainable ecosystem productivity.

Overall our results indicate that both species richness and functional diversity accelerate decomposition rate. However, the negative complementarity effect that we observe in functionally homogenous evergreen tree stand CDE suggests the importance of functional diversity over species richness. On the other hand, recent work gives more emphasis to leaf chemical and physical traits, for both positive and negative complementarity effects than species and functional diversity (López-Rojo et al., 2021). Thus, further research is needed to differentiate the degree of importance among the three diversity levels (species, functional, and trait diversity).

4.4. Habitat quality

The natural forest was richer in soil macro and micronutrient content compared to the plantation and the disturbed forest. This may be related to the diverse native plant community, which provides nutrient-rich leaf litters and/or is adapted to recycle nutrients more efficiently (Meier et al., 2005). Other studies also showed that leaf litterfall from diverse old-aged natural forest trees is an important source of soil nutrients (Meier et al., 2005; Gessner et al., 2010). However, this variation was not a significant factor in the litter decomposition rate. Especially the replacement of natural forests with Eucalyptus plantations is known to inhibit litter decomposition (Kavvadias et al., 2001; Ferreira et al., 2016; Ferreira and Guérold, 2017). But in this study, both natural (disturbed and undisturbed) and plantation forests have comparable decomposition rates. Thus, we found no statistical evidence to support our third hypothesis that predicted habitat quality effects on litter decomposition rate - at least in the later decomposition stage. This may be explained by the combined effect of high nutrient leaching with the high amount of rainfall during the study period and/or the recently reemerging native trees and shrubs species under the canopy of plantation forest might neutralize the impact of pure monoculture plantation forest (Pandey et al., 2007; De Long et al., 2016; Chen et al., 2019). As reported by Mayer (2008), the impact of forest type might not be easily detected in a forest ecosystem that has a common historical background like the disturbed and undisturbed natural forests of the Gerese highland area, or the plantation forest which acts as a buffer zone for the natural forest. Thus, it is difficult to generalize here since we do not have scientific-based evidence about the history of the study area (Cowan and Anderson, 2019).

On the other hand, a strong significant interaction effect between litter types and forest types was observed. This indicates the presence of home-field advantage for the indigenous nutrient-rich leaf litters (Lin et al., 2020). Thus, combining the nutrient-rich indigenous tree leaf litter with both exotic and indigenous nutrient-poor litter enhances the litter decomposition rate. This supports our hypothesis that rehabilitating degraded forest land with native tree species enhances litter decomposition rates.

5. Conclusion and recommendation

The present study was designed to determine the impact of species identity, litter diversity and habitat quality on litter decomposition. Three native and two exotic tree leaf litters and their mixtures were incubated for one year in three different forest habitat types to investigate litter decomposition rates in comparison with green and rooibos tea references. The findings broadly support our hypothesis that both species identity and litter diversity have a significant impact on litter decomposition. The litter decomposition rate was proportionally increased as the litter mixture increased from monoculture to a mixture of five

species. The native nitrogen-fixing tree *M. ferruginea* contributes considerably to the decomposition rate of nutrient-poor litter species. However, caution needs to be applied to avoid forest stands that are rich in species but poor in function. Functionally redundant tree stand inhibit nutrient turnover and complementarity effect. Contrary to expectation the study did not find a significant impact of habitat quality on litter decomposition across all observational periods. This abiotic factor is probably important in relation to the short-term nutrient leaching processes in early-stage decomposition but in the latter stage, decomposition is mainly driven by species identity. It was also hypothesised that litter decomposition can be enhanced by restoring the degraded land with native rather than with exotic trees. Evidence obtained from the monoculture litter decomposition partly supports this hypothesis. Among the three native tree species, only two species promote litter decomposition rate. The native tree *S. guineense* revealed a lower decomposition rate than the slowly decomposed rooibos tea and recently introduced exotic species. This indicates that species identity itself is more important than whether the species is exotic or native. Furthermore, the study revealed the importance of functional diversity over species richness. Hence, functionally diverse native trees are strongly recommended while applying the commonly used tree plantation approach to restore degraded forest land. Still, further research is needed to determine the optimal proportion of different functional groups.

Authors contribution

Seyoum Getaneh: Developed the research design and carried out field and laboratory work, data collection and analysis. Developed the first draft of the manuscript and incorporated comments from the advisor and coauthors.

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Availability of data and materials

The data generated and used for analysis during this study are included in the manuscript.

Ethical approval and consents to participants

Not applicable.

Consents to publication

Not applicable.

Declaration of competing interest

The authors declared no competing interests.

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Appendix A. Supplementary data

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