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RESEARCH ARTICLE

Trade-offs between soil biodiversity and agricultural expansion: Evidence from litter decomposition dynamics in Madagascar

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Abstract

1. Home-Field Advantage (HFA) theory—positing that litter decomposes faster at its site of origin—allows us to disentangle the respective influences of litter quality, soil biota composition, and microclimate on shifts in litter decomposition following land use conversion. However, HFA remains poorly understood in tropical ecosystems with nutrient-poor soils.
2. We conducted a full in situ litterbag transplant experiment across land use conversion driven by agricultural expansion in Madagascar: secondary natural forests, two stages of slash-and-burn fallows, and Eucalyptus plantations. Litter mass loss, HFA and Functional Breadth (FB)—defined as the capacity of soil biota to decompose different litter types with varying properties at similar rates—was assessed to distinguish the influence of the whole soil food web (coarse mesh) versus micro- and mesofauna-driven processes (fine mesh). These indicators were compared across land uses in relation to soil properties, litter quality, and soil biota composition.
3. Forested land uses had lower microbial alpha-diversity but a higher proportion of specialist taxa than fallows. Natural forests showed markedly higher nematode and macrofauna alpha-diversity, as well as a greater proportion of omnivores and predator taxa, than all the other land uses.
4. Litter decomposition was higher in natural forests, for both litterbag mesh sizes, during the early stage of decomposition, leading to higher FB, but no evidence of HFA effects was observed. Conversely, higher FB in natural forests and positive HFA in Eucalyptus plantations were observed at the late stage of decomposition, but only in coarse-mesh litterbags. This suggests that the decline in ecosystem functioning following forest conversion is linked to the loss of larger-sized macrofauna.

5. Therefore, while Eucalyptus plantations caused less disturbance to microbial communities and early-stage decomposition processes than slash-and-burn fallows, they may not fully replace the multiple ecological roles of native forests, particularly for the functions requiring more specialised organisms and taxa.

KEYWORDS
deforestation, *eucalyptus* plantations, functional breadth, home field advantage, litter decomposition, slash-and-burn agriculture, soil fauna

1 | INTRODUCTION

Assessing the consequences of land use conversion on litter decomposition has been a major research focus for the past decades, especially in tropical ecosystems with low inherent soil fertility (Giweta, 2020; Vitousek & Sanford, 1986), where this function plays a key role in soil nutrient cycling (Wardle et al., 2004). However, it still remains insufficiently understood due to the interdependence of its key drivers—litter quality and soil biota composition within a given pedoclimatic context (Coûteaux et al., 1995; Aerts, 1997). First, litter quality, particularly its recalcitrance, affects litter decomposition rates (Jensen et al., 2005; Swift et al., 1979). Highly recalcitrant litter contains complex carbon compounds that require energy-costly extracellular enzymes to degrade. Second, the composition of soil biota significantly affects litter degradation (Wickings et al., 2012), as soil organisms are the primary agents of organic matter breakdown. Soil microbial community composition determines the types and efficiency of extracellular enzymes involved in decomposition (Sinsabaugh et al., 2002; Waldrop et al., 2000), while soil fauna affects decomposition both directly, through litter fragmentation and burial—mostly by macrofauna (Bradford et al., 2002; Setälä et al., 1996), and indirectly, by regulating microbial activities (A'Bear et al., 2014; Trap et al., 2016).

The tight interactions among abiotic conditions, biochemical litter quality and soil biota have been especially highlighted by the Home-Field Advantage (HFA) theory. The HFA theory posits that litter decomposition is often faster when litter is returned to its site of origin, reflecting the combined influence of site-specific environmental conditions and long-term plant–soil interactions (Miki, 2012). Early studies demonstrated that litter quality and local abiotic conditions strongly modulate decomposition rates (Gholz et al., 2000), suggesting the potential for site-specific litter decomposition patterns. Subsequent work provided empirical evidence that soil microbial communities can become functionally specialized to efficiently decompose the types of litter they recurrently encounter, thereby reinforcing the HFA (Ayres et al., 2009). However, despite two decades of research, substantial uncertainties remain. This is largely due to the strong variability of decomposition patterns observed across ecosystems worldwide, which complicates generalizations and mechanistic predictions (Ayres et al., 2009; Shi et al., 2025; Veen et al., 2015).

First, litter quality greatly modulates the magnitude of the HFA (Fanin & Bertrand, 2016; Veen et al., 2018; Pugnaire et al., 2023). Low-quality litter, which require more specialized decomposer communities, often leads to higher HFA compared to high-quality litter (Ayres et al., 2009; Shi et al., 2025; Veen et al., 2015). Second, HFA is mediated by soil biota Functional Breadth (FB), defined as their capacity to decompose a wide range of litter types with varying chemical and physical properties at similar rates (Keiser et al., 2011; Osburn et al., 2022; Zhu et al., 2024). Soil fauna impacts on HFA is variable and may lead to its reduction, likely by influencing microbial activity (Shi et al., 2025), although these effects can depend on its feeding preferences regarding litter quality (Yang et al., 2025). Third, the influence of soil biota on litter decomposition, FB, and HFA also greatly depends on the climate, with usually stronger effects under wetter climates that favour microbial activities (Handa et al., 2014; Wang et al., 2020). These tight interconnections make HFA outcomes greatly sensitive to the comparative framework used, that is, whether studies in contrasting ecosystems are ecologically similar or fundamentally different (Veen et al., 2015). These contexts are highly variable, because the strength and the nature of the contrasts being compared differ widely across studies, ranging from within-biome shifts (Hu et al., 2026; Yuan et al., 2019), to much stronger environmental changes (e.g. large altitudinal gradients, vegetation composition or land-use gradients) (Fanin & Bertrand, 2016; Veen et al., 2018; Wang et al., 2023). Furthermore, most of this evidence comes from temperate ecosystems, and their relevance for nutrient-poor tropical ecosystems remains poorly understood (Shi et al., 2025), despite their global importance and the multiple threats they face (Parr et al., 2014).

Deforestation through slash-and-burn agriculture and illegal logging is one of these major threats (Casse et al., 2004) and has been a major source of forest loss in Madagascar (Vieilledent et al., 2020). Slash-and-burn consists of harvesting and burning patches of forest, cultivating the land for a short period, and then leaving it fallow to promote soil and vegetation regeneration (Brady, 1996). However, growing land-use pressure has led to a widespread shortening of fallow periods, which no longer allow ecosystems to fully recover and result in land degradation that may become irreversible depending on its severity (Gay-des-Combes et al., 2017; Hands, 2021). These consequences are first and foremost observed through loss of crop yields (Kleinman et al., 1995; Bezerra et al., 2024), soil fertility (Styger et al., 2009; Mayor et al., 2016; Ferreira de Alencar Mendes et al.,

2023), and to a lesser extent soil biodiversity (Rossi et al., 2010; da Silva et al., 2025). Nonetheless, most of these studies have compared ecosystem resilience at different times following fire events, while the consequences of repeated short fallow cycles remain less studied (van Vliet et al., 2012).

In Madagascar, Styger et al. (2007) characterized this progressive degradation based on changes in fallow vegetation: the initial cycles support tree regrowth, but successive cycles lead to shrub fallows (or *Savoka*) after 2–5 cycles, and grass fallows (or *Tany Maty*) after 5–6 cycles. At later stages, these areas become permanent grassland, once soil fertility declines too much to support cultivation (Styger et al., 2009). Such degradation gradients are thus likely altering litter decomposition dynamics and the expression of HFA through the restitution of nutrient-impoverished litters, a reduction in soil biota diversity and FB, and diminished microclimate buffering following canopy and litter floor removals. However, this assumption remains to be tested. Non-native forest species—especially eucalyptus plantations—were introduced in Madagascar during the last century, as an alternative land-management strategy to meet timber and energy demand and reduce the illegal logging of natural forests (Kull et al., 2012). These plantations have been preferentially established on natural pseudo-steppes (Verhaegen et al., 2014) or on degraded natural forests (Aubréville & Bossanyi, 2015). The lower level of disturbance (no recurring fires, presence of a tree canopy and litter floor) should hence have less harmful consequences on soil biota, HFA and FB. However, this assumption remains uncertain, as the loss of above-ground biodiversity following the conversion of natural forest to eucalyptus, and the regular removal of biomass from plantations through tree harvesting (every 7 to 10 years), continue to raise concerns about the environmental sustainability of this land use (Bayle, 2019).

In this study, we assessed litter decomposition, HFA and FB across a land use conversion gradient in Madagascar. We aimed to disentangle how degradation-related biodiversity loss affects decomposition through changes in soil biota functional capacity (FB) and shifts in the degree of local specialization of decomposer assemblages, as reflected by HFA. We conducted a full in situ litterbag transplant experiment across secondary natural forests, two stages of slash-and-burn fallows (shrub fallows 'Savoka' and grass fallows 'Tany Maty'), and Eucalyptus plantations. Two litterbag mesh sizes were used to quantify decomposition outcomes mediated by the whole soil food web (coarse mesh) versus micro- and mesofauna-driven processes (fine mesh). We hypothesized that (i) conversion from secondary natural forest to slash-and-burn systems or Eucalyptus plantations decreases soil biota abundance and diversity; (ii) conversion impacts on soil biota will be mirrored by a decline in litter decomposition rates and FB, while HFA will remain more similar between the forested land uses due to their stronger microclimatic buffering, and (iii) the contribution of macrofauna to litter decomposition and FB will be higher in forested land uses, where canopy cover and forest floor provide more favourable conditions for macrofauna activity.

2 | MATERIALS AND METHODS

2.1 | Site description and sampling strategy

The study site is located in Andasibe, on the East coast of Madagascar (18°57′ S & 48°24′ E). The soils are classified as Ferralsols (FAO classification), with a sandy clay loam texture. The area experiences a subtropical highland climate (Cfb in the Köppen-Geiger classification). Between 1985 and 2014, the average annual temperature was 18.3°C, with low variation throughout the year, while annual rainfall averaged 2059 mm, with higher precipitations occurring between September and February. The native ecosystem consists of secondary natural forests, resulting from selective timber harvesting, which has reduced biodiversity (Makana & Thomas, 2006). The surrounding landscape is a mosaic of land uses, including slash-and-burn fallows with 3–5-year rotation cycles at various degradation stages (Figure 1a), and *Eucalyptus robusta Sm.* (Myrtaceae) plantations (Figure 1b).

Within this site, we relied on the vegetation stand analyses of Styger et al. (2007) to identify three plots of the following land uses: (i) secondary natural forests (henceforth referred to as "natural forest"), dominated by *Cryptocaria acuminata* Merr. (Lauraceae), (ii) shrub fallows ("Savoka") dominated by *Psiadia altissima* (DC.) Drake (Asteraceae), (iii) grass fallows ("Tany Maty") dominated by *Imperata cylindrica* L. Raeusch (Poaceae), and (iv) *E. robusta* plantations, in unfertilized rotations of 7 to 10 years since the 1970s (Figure 1). Eucalyptus plantations and grass fallows were mostly exclusively covered by *E. robusta* and *I. cylindrica*, respectively. More species could be found in the natural forest and the shrub fallows, but the dominance of *C. altissima* and *P. acuminata* of these land uses, as observed in the same zone (Ghimire et al., 2022; Styger et al., 2007, 2009), was ensured and used as one of the main selection criteria of the plots. All plots from each land use (natural forest, eucalyptus plantation, shrub fallow and grass fallow) were selected within a radius of about 5 km for this experiment (Table S1), amounting

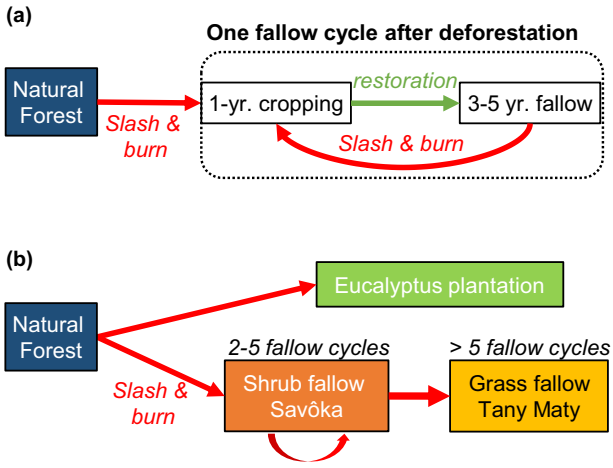

FIGURE 1 Description of one fallow cycle (a) and of the land uses studied (b).

to 4 land uses x 3 plots = 12 plots in total. Prior to the experiment, we spoke with representatives from the Mitsinjo association which manages, on a community basis, the natural forests and eucalyptus plantations in the Andasibe region. We explained the objectives of the study to them. We did the same with the owners of the fallow plots. These stakeholders helped us to find representative locations to place the litter bags in each of the ecosystems studied.

At the beginning of the experiment, in February 2017, litter floor samples were collected by including all of the organic horizon not adhering to the soil. In each plot, three collection points were randomly selected within a 4-meter radius, and repeated two times, the repetitions being approximately 10 meters apart. Within each plot, sampling was carried out for each replicate using a 20 cm square quadrat. One composite sample was made from the three collection points of each replicate. A total of 24 litter floor samples were collected for the 12 plots. At the same date, two soil composite samples were taken in each plot on the 0–10 cm layer with an auger, to determine soil properties, bacterial, fungal and nematode communities' abundance and composition. Soil macrofauna was also sampled, using the TSBF method (Anderson & Ingram, 1994). Briefly, one soil cube of 25 cm side was taken from each plot, and all the visible macrofauna individuals from the cube were collected and stored in 100% ethanol solution. Soil and macrofauna individuals were subsequently brought to the laboratory for further analyses. Soil samples were then split into two subaliquots: one subaliquot sieved at 2 mm and air-dried for the analyses of soil physico-chemical properties, and two fresh subaliquots for the extraction and analyses of soil microbial and nematodes communities.

2.2 | Litterbag experiment set up

Leaf litter representative of each land use was collected in September and October 2016 in each of the 12 selected plots. Litter of *C. acuminata* and of *E. robusta*, representative respectively of the natural forests and eucalyptus plantations studied, was collected shortly after leaf fall; the flexibility of the leaves was used as the criterion to assess the freshness of the litter collected. Senescent leaves of *P. altissima*, representative of shrub fallow, were collected directly on the plants. Finally, dry *I. cylindrica* above-ground biomasses were cut in the plots, and represented grass fallow main litter species. All samples were then sorted out to only keep the healthy (entire leaves, ungrazed without visible spot of rots or fungal colonization) litters of each species, air-dried and stored in the dark for 3 months until use. Their residual moisture was then estimated after oven-drying, for each species, 10 sub-samples of 5 g per species at 45°C for 72 h. In February 2017, 9 g of each land use representative litter was added in 30 cm x 20 cm litterbags with either coarse-mesh size (4 mm x 6 mm) or fine mesh size (0.5 mm x 0.5 mm), to study the impacts of the whole soil food web or only microorganisms, microfauna and mesofauna. The litterbags were set on the soil surface and secured at their corners with stainless steel nails (Figure S1). At each of the 12 plots, litterbags included the four litter types (from natural forest, *Eucalyptus* plantation, shrub fallow or grass fallow) for two litterbags mesh sizes (coarse or fine); two litterbags of each modality were randomly sampled after 4 and 12 months of decomposition, corresponding to 48 litterbags sampled at each date. Litters from each bag were removed, gently brushed to remove as much adherent soil as possible, and oven-dried at 45°C for 72 h. They were then weighed with a 10^{-2} g precision scale. A subaliquot of 0.5 g was then taken to determine their ashes content.

2.3 | Leaf litter, litter floor and soil analyses

A subaliquot of leaf litter collected from each plot was used to perform the following biochemical analyses (Table 1). Total C and N

TABLE 1 Main initial properties of the leaf litterfall of the representative species of each land use ($n = 6$).

	Representative species litter of each land use			
	E. robusta **(eucalypt. plantation)**	***C. acuminata*** **(natural forest)**	***P. altissima*** **(shrub fallow)**	***I. cylindrica*** **(grass fallow)**
C ($mg.g^{-1}$ DM)	**501 ± 6 a**	480 ± 1 b	**504 ± 1 a**	**450 ± 5 c**
N ($mg.g^{-1}$ DM)	**5.5 ± 0.8 bc**	12.1 ± 1.3 a	**7.6 ± 0.1 b**	**3.4 ± 0.8 c**
P ($mg.g^{-1}$ DM)	**0.20 ± 0.03 b**	0.56 ± 0.09 a	0.28 ± 0.17 ab	0.23 ± 0.04 ab
C:N ratio	93 ± 14 ab	40 ± 5 b	66 ± 1 b	**137 ± 38 a**
C:P ratio	*2573 ± 487 a*	*879 ± 157 a*	*2315 ± 1306 a*	*1994 ± 339 a*
N:P ratio	*28 ± 4 a*	*22 ± 2 a*	*35 ± 20 a*	*15 ± 2 a*
Soluble ($mg.g^{-1}$DM)	**475 ± 3 b**	71 ± 13 c	**654 ± 13 a**	61 ± 1 c
Cellulose ($mg.g^{-1}$ DM)	237 ± 37 bc	284 ± 68 b	**164 ± 13 c**	**476 ± 19 a**
Hemicellulose ($mg.g^{-1}$ DM)	**168 ± 22 b**	124 ± 13 c	**60 ± 8 d**	**305 ± 16 a**
Lignin ($mg.g^{-1}$ DM)	**186 ± 33 b**	488 ± 33 a	**109 ± 2 c**	**159 ± 30 b**
Lignocellulose Index (LCI)	**0.31 ± 0.04 b**	0.55 ± 0.04 a	**0.33 ± 0.01 b**	**0.17 ± 0.02 c**

Note: Values significantly different from the natural forest are in bold. Significant differences (mean ± standard deviation) were tested by ANOVA followed by Tukey HSD post hoc tests and bear different letters for p-value <0.05. LCI represent the proportion of lignin within the cell wall.

contents were determined by dry combustion using a CHN micro-analyser (Carlo Erba NA 2000, Milan, Italy), while total P content was obtained after acid mineralization and quantified by colorimetry with the yellow vanadomolybdate reagent (Neves et al., 2008) with modification. Soluble, hemicellulose, cellulose and lignin contents were obtained by the van Soest method (Van Soest, 1963) with a Fibersac 24 fibre analyser (Ankom, Macedon, NJ, USA). It allowed us to calculate the lignocellulose index LCI (LCI = lignin/[lignin + holocellulose]) as described in Whittinghill et al. (2012). Litter ash content was determined by combustion at 500°C and used to correct chemical composition on an ash-free dry mass basis. On the other hand, the litter floor was sorted into different categories (unfragmented leaf litter, fragmented litter, wood, and roots), oven-dried at 45°C for 72 h and weighed (Figure S2). The litter collected from litterbags after 4 and 12 months was processed following the same before being weighed; then a subaliquot was used to determine their ash content to correct the mass loss estimation.

Similarly, a subaliquot of the soil collected from each plot was used to characterize their physico-chemical properties after being sieved at 2 mm and dried. Soil texture was determined with the Robinson pipette method (NF X 31–107; AFNOR, 2003). Total C and N contents were determined by dry combustion using a CHN micro-analyser (Carlo Erba NA 2000, Milan, Italy). Soil pH was determined in water and in KCl (1 M) following NF ISO 10390 (AFNOR, 2005). Exchangeable Ca was extracted with the cobalt-hexamine chloride method and quantified by microwave plasma osmic emission spectrometry (MP-AES 4210 Agilent; NF ISO 23470, AFNOR, 2018). The soil cation exchange capacity (CEC) was determined by saturating the soil with an excess of cobalt-hexamine (NF X 31–130; AFNOR, 1999) and quantified by flame atomic absorption spectrometry. Phosphorus Olsen P (Olsen, 1954) was extracted from the soil using a 0.5 M sodium bicarbonate solution (pH 8.5) and quantified by colorimetry using the Malachite Green method according to Rao et al. (1997).

2.4 | Soil community analyses

A fresh soil subaliquot from each plot was used to determine soil microbial and nematodes communities' composition. Microbial DNA was extracted from 3 g of soil sub-samples using the DNA Kit with modification (initial procedure described in Plassart et al., 2012) at DP Forêts et Biodiversité laboratory (Antananarivo, Madagascar). Banks of 16S and 18S ribosomal sequences were prepared prior to pyrosequencing analyses as described in Maron et al. (2011). Pyrosequencing was carried out on a GS FLX Titanium (Roche 454 Sequencing System). Biocomputering analysis of the sequences was performed using the GnS-PIPE (Terrat et al., 2012), as described in detail in Tardy et al. (2015). In order to compare the data sets efficiently and avoid biased community comparisons, the sample reads were reduced by random selection close to the lowest data sets (3000 reads for 16S and 18S-rRNA gene sequences respectively for each soil sample). Richness and diversity indices (number of OTUs, Evenness index) were determined at a dissimilarity threshold of 5%. DNA sequences were deposited in the European Nucleotide Archive, under the study accession number PRJEB19651.

Nematodes were extracted from 200 g soil samples (fresh weight) by elutriation with the cotton–wool filter method (Seinhorst, 1962; Townshend, 1963) and counted under a binocular microscope. After fixation in formaldehyde (4%), 100–150 specimens per sample were randomly selected in mass slides and identified to family, genus and species levels under a microscope. The taxa were then assigned to a trophic group (Yeates et al., 1993). Macrofauna individuals were counted and identified under the binocular to the morphotype level (Gibb & Oseto, 2006).

2.5 | Data analyses

Litter mass loss was calculated as the mass difference between the initial dry mass of litter added and the remaining dry mass at each sampling date. For each mesh size, we assessed the relative contribution of the litter quality, functional breadth and home-field advantage in explaining litter mass loss dynamics with the DART model developed by Keiser et al. (2014). This model states that litter mass loss (Y_i) is equal to the sum of litter ability ($ß_l$), soil ability (γ_s), and a home interaction parameter (η_h):

$$Yi = \alpha + \sum_{l=1}^{N} ß_l \text{ Litter } l_i + \sum_{s=1}^{M} \gamma_s \text{ Soil } s_i + \sum_{h=1}^{K} \eta_h \text{ Home } h_i + \varepsilon_i$$

where Yi is the litter mass loss for observation i, $ß_l$ the ability of litter species l (from species 1 to N), γ_s the ability of the soil community s (from community 1 to M), η_h the HFA of h (from home combinations 1 to K), and $\text{Home}_h = Litter_l \times Soil_s$ when l and s are home-field pairings. The parameters to be estimated are $ß_l$, γ_s, and η_h. The intercept term is defined by α and represents the average litter mass loss for all litterbags decomposition after controlling for litter, soil and home-field pairings. Negative parameter estimates indicate lower litter mass loss than the average rate observed across all litterbags in this design. The error term is defined by ε. Using this model, we calculated a quality index (Litter Quality: LQ—increasing with overall litter decomposability across land uses), the ability of soil microbial communities (Functional Breadth: FB—increasing with overall decomposition rates across litters), and the interactions between litter and soil (Home Field Advantage: HFA—indicating whether the land use degrades better its own litter) on litter mass loss.

Differences in soil and litter initial properties were first assessed using one-way ANOVAs, followed by Tukey HSD post Hoc tests. For soil biota community composition, we used Nonmetric Multidimensional Scaling (NMDS) based on Bray–Curtis distances (10,000 permutations) at the genera (bacteria, fungi and nematodes) or the morphotype level (macrofauna). These analyses were complemented with analysis of similarity (ANOSIM) tests (vegan R package) based on the Bray–Curtis distances with 999 permutations. The main community indicators (phyla relative abundance for microorganisms, and trophic group abundance for fauna taxonomic richness,

Shannon index and Evenness) were then fitted to each NMDS along with diversity indicators (R function envfit, vegan package), by performing multiple linear regressions between these indicators and the NMDS coordinates as explanatory variables. Decomposition indicators (raw or differential mass loss between the coarse and fine mesh size, and DART model outputs) were then assessed per sampling date using one-way ANOVAs, followed by Tukey HSD post Hoc test. The interactive effect of litter identity and land use per mesh size and sampling date were further assessed with two-way ANOVAs in Table 3, with the exception of litter mass loss in coarse-mesh litterbags after 12 months, which did not meet the criteria of homoscedasticity; this specific modality was analysed with a linear model coupled with ANOVA with White correction (White, 1980) with the ANOVA function of the {car} R package. All statistical analyses were performed using R software (R-4.4.3) and the following packages: agricolae, car, ggplot2, stats, vegan and viridis.

3 | RESULTS

3.1 | Initial litter quality, litter floor and soil physico-chemical properties

Litter N and P contents declined with increasing land use degradation, with the highest values in natural forests, and the lowest in grass fallows (p-values <0.05 for N). Consequently, initial litter C:N and C:P ratios ranged from 40 ± 5 to 137 ± 38 and 879 ± 157 to 1994 ± 339, respectively (Table 1). Among the species studied, litters from *P. altissima*, and to a lesser extent *E. robusta*, had higher soluble contents than *C. acuminata* and *I. cylindrica*, respectively from natural forest and grass fallow. *C. acuminata* litter had the highest lignin content, while *I. cylindrica* litter had the lowest lignocellulose index (LCI = lignin/(lignin + hollocellulose)), owing to high contents in both cellulose and hemicellulose in this species. Litter floor mass was markedly higher in the forested systems, with the highest values under eucalyptus plantation (1147 ± 255 g DM m^{-2}), than under the fallows (454 to 595 g DM m^{-2}, Figure S2). Soils from the different land uses exhibited modest differences in their texture, with significantly higher clay and lower sand contents in natural forests than shrub fallows (Table 2). An increase in both pH_{H2O} and pH_{KCl} was observed under shrub and grass fallows compared with under natural forest and eucalyptus plantations. No significant differences were observed among land uses for other soil physico-chemical properties, including soil C, N or P content, CEC or exchangeable P.

3.2 | Soil communities

Soil biotic communities' analyses at the genus or morphotype levels revealed marked differences between land uses, with contrasting patterns for soil microorganisms versus fauna (Figure 2; Figure S3). Overall, bacterial and fungal community compositions under natural forest were more similar to those under eucalyptus plantations than those under fallows (Figure S3). These trends were mostly driven by an overall lower taxonomic richness (Figure 2a), Shannon index and evenness (Table S2), along with a shift in relative abundances of genera within the *Acidobacteria* phylum in forested systems toward those within the *Actinobacteria* phylum in fallows (Figure 2a,e). Similarly, forested land uses were characterized by lower taxonomic richness yet a higher relative abundance of genera from the *Basidiomycota* phylum, whereas fallows presented higher relative abundances of the *Ascomycota*, *Glomeromycota*

TABLE 2 Main properties of the 0–10 cm layer of each land use (n = 6).

	Land uses			
	Eucalyptus plantation	Natural forest	Shrub fallow (Savoka)	Grass fallow (Tany maty)
Clay (mg.g^{-1}soil)	322 ± 68 ab	442 ± 34 a	**251 ± 28 b**	382 ± 79 ab
Silt (mg.g^{-1} soil)	*140 ± 20 a*	*149 ± 14 a*	*130 ± 16 a*	*154 ± 44 a*
Sand (mg.g^{-1} soil)	538 ± 77 ab	409 ± 43 b	**619 ± 27 a**	463 ± 120 ab
Soil Organic C (mg.g^{-1} soil)	*45.3 ± 14.9 a*	*42.8 ± 2.6 a*	*43.5 ± 7.5 a*	*42.6 ± 15.6 a*
Soil N (mg.g^{-1} soil)	*3.41 ± 1.00 a*	*4.17 ± 0.15 a*	*3.52 ± 0.59 a*	*3.29 ± 1.34 a*
Soil P (mg.g^{-1} soil)	*0.33 ± 0.09 a*	*0.30 ± 0.12 a*	*0.28 ± 0.03 a*	*0.31 ± 0.09 a*
Soil C:N ratio	*13.9 ± 4.9 a*	*10.3 ± 1.0 a*	*12.5 ± 1.9 a*	*13.6 ± 4.7 a*
Soil C:P ratio	*138 ± 8 a*	*159 ± 61 a*	*158 ± 16 a*	*137 ± 27 a*
Soil N:P ratio	*10.9 ± 4.1 a*	*15.3 ± 5.5 a*	*12.9 ± 2.7 a*	*11.1 ± 4.6 a*
pH H_2O	4.66 ± 0.37 bc	4.27 ± 0.08 c	**5.19 ± 0.10 a**	**4.83 ± 0.03 ab**
pH KCl	3.81 ± 0.28 ab	3.75 ± 0.02 b	4.14 ± 0.07 ab	**4.22 ± 0.13 a**
CEC (cmolc.kg^{-1} soil)	*1.77 ± 0.46 a*	*2.40 ± 0.53 a*	*2.04 ± 0.05 a*	*2.71 ± 0.77 a*
Exchangeable P (mg.kg^{-1} soil)	*0.57 ± 0.33 a*	*1.15 ± 0.23 a*	*1.03 ± 0.21 a*	*0.54 ± 0.08 a*

Note: Values significantly different from the natural forest are in bold. Significant differences (mean ± standard deviation) were tested by ANOVA followed by Tukey HSD post hoc tests and bear different letters for p-value <0.05.

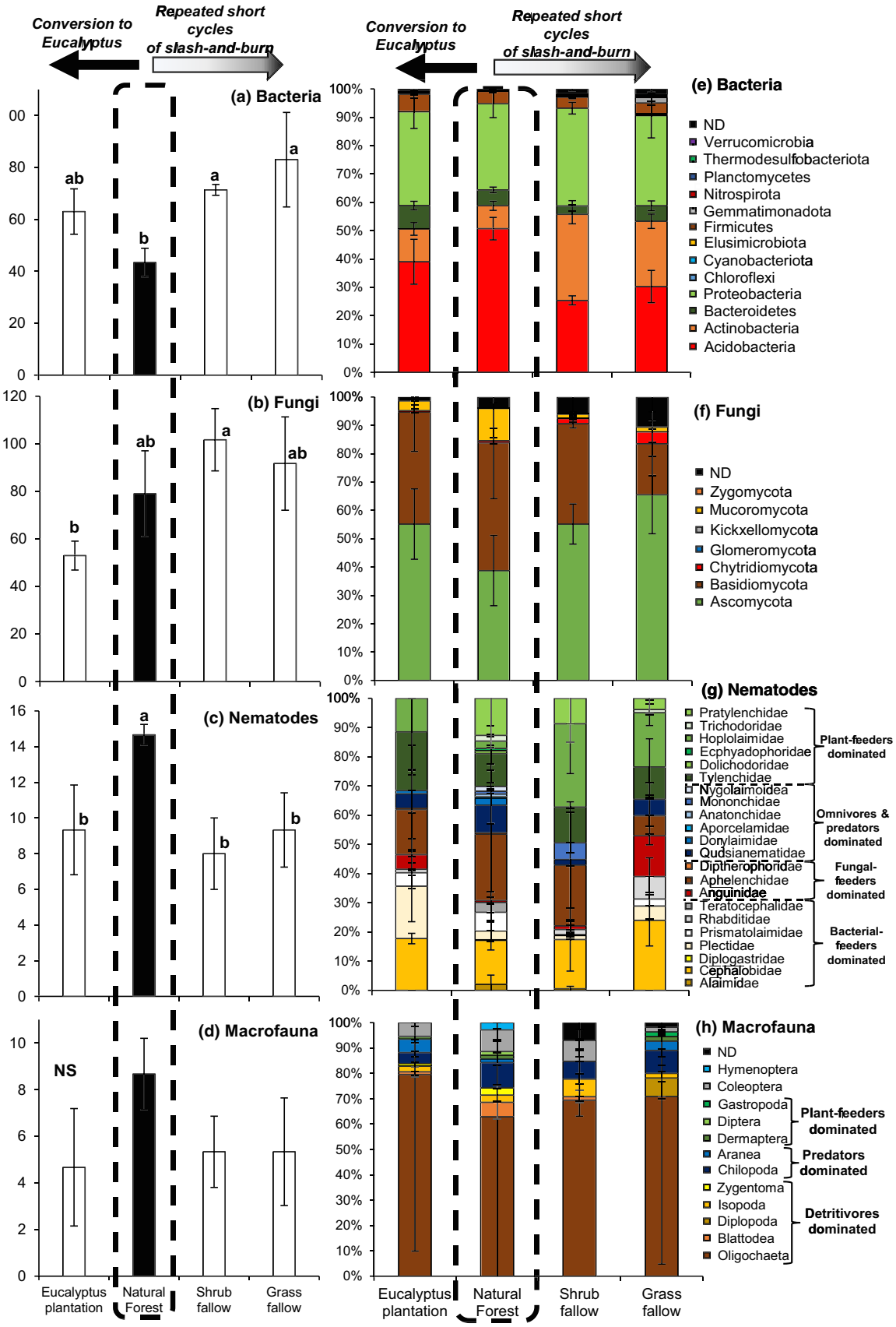

FIGURE 2 Soil community taxonomic richness (a–d) and composition (e–h) across land uses. Community composition for microorganisms, nematode and macrofauna groups is represented at the phylum, family and order level, respectively. ND, non-determined.

and *Chytridiomycota* phyla (Figure 2b,f). By contrast, both nematode and macrofauna communities were highly dissimilar between natural forest and the other land uses (Figure S3), with an overall higher taxonomic richness (Figure 2c,d) and a higher proportion of predatory and omnivores taxa (Figure 2g,h) in the forest. Macrofauna community composition also differed in the higher diversity of detritivores taxa under the natural forest (Figure 2h), and the presence of an endemic earthworm taxon *Kinotus* spp. (data not shown).

3.3 | Litter decomposition

Decomposition within fine-mesh litterbags was affected by both litter identity and the land use in which decomposition occurred, with their respective impacts varying over time (Table 3). Early-stage decomposition after 4 months averaged 42 ± 9% of the initial litter mass, and was mainly driven by litter identity (F-value = 56.7), rather than the land use where it decomposed (F-value = 16.8, Table 3), with no significant interaction between litter identity and land use was observed at this stage. *E. robusta* and *P. altissima* litters decomposed faster at this stage (Figure 3a), and decomposition after 4 months was overall higher under natural forest than the other land uses (Table 4). Late-stage decomposition after 12 months had progressed to an average of 48 ± 7% of the initial litter mass, with similar litter quality impacts as after 4 months—that is, higher decomposition of *E. robusta* and *P. altissima* litters, (Figure 3b), and a slight land use impact, with lower decomposition under the grass fallow (Table 4).

Decomposition after 4 months presented no significant differences between coarse- and fine-mesh litterbags ($p > 0.05$), independently of the land use considered (Figure 4; Figure S4). After 12 months, significant differences appeared for all land uses except the Eucalyptus plantations, with increased decomposition with coarse- compared to fine-mesh litterbags of about 12% ($p < 0.001$) under the natural forest, and of about 8–9% ($p < 0.05$) under both fallows (Figure 4). These differential effects were mirrored by significant impacts of litter identity: land use interactive effects ($p < 0.001$) on litter decomposition in coarse-mesh litterbags at this stage (Table 3).

3.4 | Dart model outputs: LQ, FB And HFA

Implementation of fine-mesh litterbags decomposition into the DART model evidenced a higher Litter Quality index for both *Eucalyptus* and shrub fallow land uses both after 4 and 12 months of decomposition (Table 4). Functional Breadth index presented

TABLE 3 ANOVA results for the relative importance of litter identity and the land use where they decomposed on litter mass loss, for either fine-mesh or coarse-mesh litterbags.

	After 4 months		After 12 months	
	F-value	*p*-value	*F*-value	*p*-value
Fine-mesh litterbags				
Litter identity	**56.7**	**<0.001**	**11.5**	**<0.001**
Land use	**16.8**	**<0.001**	**3.5**	**0.03**
Litter id: Land use	0.9	0.51	0.6	0.81
Coarse-mesh litterbags				
Litter identity	**64.7**	**<0.001**	**71.2**	**<0.001**
Land use	**9.9**	**<0.001**	**66.8**	**<0.001**
Litter id: Land use	1.1	0.40	**10.9**	**<0.001**

Note: Coarse-mesh litter mass loss after 12 months was tested with linear model coupled with ANOVA with the white.adjust method to correct for heteroscedasticity. Significant effects (*p*-value < 0.05) are emphasized in bold.

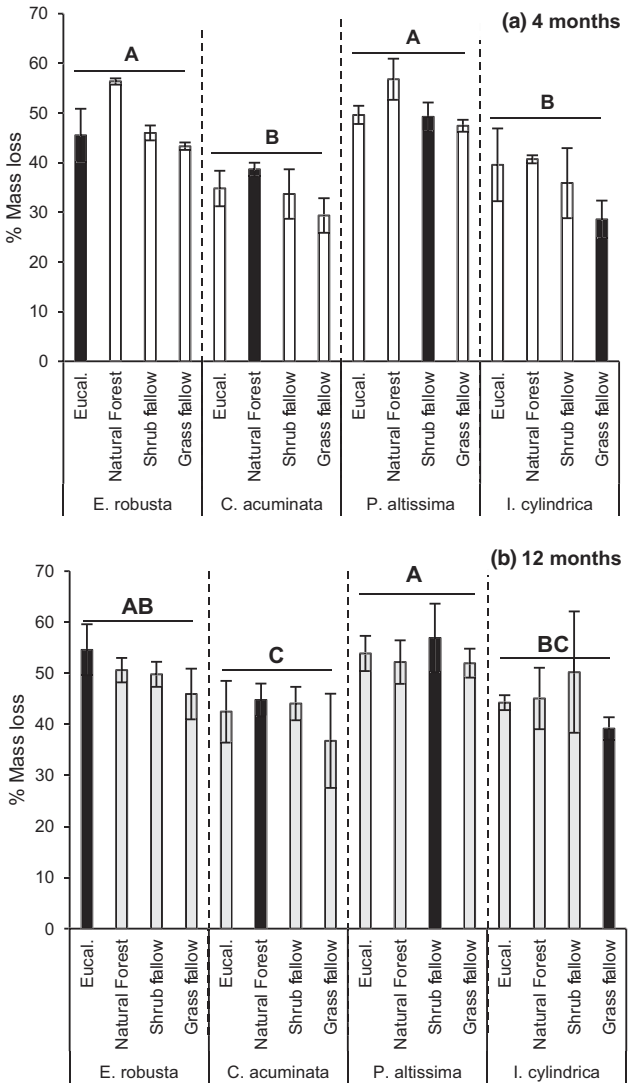

FIGURE 3 Fine-mesh litterbags litter mass loss after 4 and 12 months. Significant differences were tested between litter types, and bear different letters when $p < 0.05$. Black bars correspond to the litter species on its original land use.

TABLE 4 Averages litter mass loss and DART model outputs per land use.

	Fine-mesh litterbags		Coarse-mesh litterbags	
	4 months	12 months	4 months	12 months
Litter mass loss (%)				
Eucalyptus plantation	**42 ± 7 b**	49 ± 7 ab	45 ± 11 ab	**52 ± 7 b**
Natural forest	48 ± 9 a	48 ± 5 ab	48 ± 8 a	60 ± 5 a
Shrub fallow (Savoka)	**41 ± 8 bc**	50 ± 8 a	**43 ± 9 bc**	58 ± 6 a
Grass fallow (Tany maty)	**37 ± 9 c**	43 ± 8 b	**39 ± 10 c**	**52 ± 16 b**
Litter quality (LQ)				
Eucalyptus plantation	**5.9 ± 1.8 a**	**1.5 ± 3.1 ab**	**6.3 ± 1.7 a**	−3.0 ± 2.7 b
Natural forest	−8.3 ± 0.5 b	−6.2 ± 2.7 c	−8.0 ± 0.2 b	−5.9 ± 2.6 b
Shrub fallow (Savoka)	**8.0 ± 2.2 a**	**6.4 ± 2.2 a**	**10.6 ± 1.5 a**	**10.5 ± 3.2 a**
Grass fallow (Tany maty)	−5.6 ± 2.8 b	−1.7 ± 3.5 bc	−8.8 ± 2.8 b	−1.5 ± 2.0 b
Functional breadth (FB)				
Eucalyptus plantation	0.5 ± 3.1 ab	0.1 ± 1.9 a	1.8 ± 1.7 ab	**−6.1 ± 1.7 b**
Natural forest	5.7 ± 2.4 a	0.0 ± 1.1 a	3.4 ± 3.3 a	3.5 ± 3.4 a
Shrub fallow (Savoka)	**−1.6 ± 2.3 b**	2.9 ± 4.2 a	−1.0 ± 3.2 ab	2.9 ± 1.7 a
Grass fallow (Tany maty)	−4.6 ± 0.6 b	−3.0 ± 3.6 a	**−4.2 ± 1.9 b**	−0.3 ± 1.7 ab
Home-field advantage (HFA)				
Eucalyptus plantation	*−3.7 ± 7.7 a*	*5.7 ± 9.5 a*	*−2.7 ± 3.9 a*	7.3 ± 5.9 a
Natural forest	*−1.6 ± 1.3 a*	*3.7 ± 4.8 a*	*2.0 ± 2.9 a*	2.4 ± 4.0 ab
Shrub fallow (Savoka)	*0.1 ± 3.8 a*	*0.4 ± 5.1 a*	*−1.9 ± 2.4 a*	−5.7 ± 6.2 ab
Grass fallow (Tany maty)	*−3.9 ± 6.6 a*	*−3.4 ± 1.4 a*	*−3.4 ± 5.9 a*	**−14.4 ± 9.7 b**

Note: Significant differences (mean ± standard deviation) were tested within each date by one-way ANOVAs followed by HSD Tukey tests, and bear different letters when p-value <0.05. Values significantly different from the natural forest are in bold.

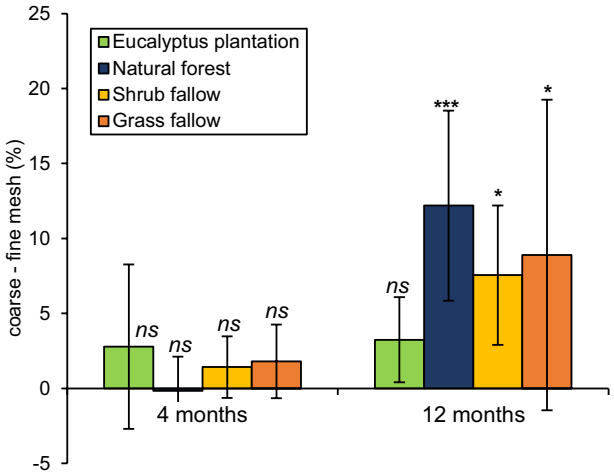

FIGURE 4 Litter mass loss differences between coarse and fine mesh size per land use. Significant differences were tested by comparing mass losses between coarse and fine mesh size within each land use. *, ** and *** represent p-values inferior to 0.05, 0.01 and 0.001, respectively.

significant differences ($p < 0.05$) after 4 months and was higher under natural forest and, to a lesser extent, for eucalyptus plantation. No significant differences were observed between land use for FB after 12 months, nor HFA for both dates.

On the other hand, the DART model for coarse-mesh litterbags presented a similar land use hierarchy for LQ, FB and HFA to that of the fine-mesh litterbags after 4 months (Table 4). However, these outputs differed between coarse- and fine-mesh litterbags after 12 months of decomposition. First, the LQ index was the highest for shrub fallow, but not for Eucalyptus at this date, while FB differed significantly between land use at this date, with the highest value under natural forest and the lowest under Eucalyptus. Finally, coarse-mesh litterbags decomposition showed significant HFA effects after 12 months, with positive HFA under the eucalyptus plantation and negative HFA under the grass fallow (Table 4).

4 | DISCUSSION

4.1 | Land use conversion impacts on soil biodiversity

In partial agreement with our first hypothesis, natural forest presented higher biota diversity and abundance than the other land uses for soil fauna, but not for microbial communities. Soil microbial communities presented high similarity in their alpha- and beta-diversity between the natural forest and eucalyptus plantations, consistent with Lan et al. (2017). These similarities could be linked to both the presence of a closed canopy (Kaspari & Yanoviak, 2009)

and the absence of fire in both ecosystems (Brinkmann et al., 2019; Gongalsky et al., 2012; Renčo et al., 2022). The similar acidic conditions of soils under eucalyptus plantations and natural forests also likely exerted similar environmental filtering on microbial communities (Kalam et al., 2020; Kielak et al., 2016). In line with this assumption, microbial community dissimilarities were greater between the natural forests and the fallows, but unexpectedly through lower alpha-diversity under the forests, due to the dominance of taxa belonging to *Acidobacteria* and *Basidiomycota* phyla for bacterial and fungal communities, respectively. This dominance could be linked with the acidic conditions of the natural forest soils, more suitable for *Acidobacteria* taxa (Kalam et al., 2020; Kielak et al., 2016), than the increased soil pH observed in the fallows, commonly observed following fire due to calcium-rich wood ash and the associated release of cations in the soil solution (Demeyer et al., 2001; Fachin et al., 2021; Juo & Manu, 1996). In parallel, the restitution of lignin-rich litter in the natural forest likely supported *Basidiomycota*, a fungal group with lignolytic capacities (Osono, 2007). Furthermore, the development of these phyla, which include many slow-growing specialist taxa (Philippot et al., 2010), may have been more constrained in the fallows due to the stress caused by recurring fires (Brinkmann et al., 2019). Overall, these microbial communities' shifts are coherent with the Y-A-S strategies described by Malik et al. (2020), but we lack studies of the microbial ecology of these systems to draw robust conclusions.

Contrastingly, soil fauna showed comparable diversity loss under both eucalyptus plantations and slash-and-burn compared with the natural forests, especially within nematodes and macrofauna omnivores, predators and plant-feeders' trophic groups. These changes also involved the loss of an endemic earthworm, *Kinotus* sp., regardless of the land use conversion. These patterns are commonly observed with fire occurrence (Pen-Mouratov et al., 2012; Renčo et al., 2022), but also during forest conversion to eucalyptus plantations or pastures, where macrofauna diversity loss has been observed in eastern Amazonia and was negatively correlated with disturbance (de Vasconcelos et al., 2020). We assumed these decreases to be associated with the higher sensitivity to disturbance of omnivores and predators due to their bigger size and lower resilience (Gongalsky et al., 2012; Kladivko, 2001; Postma-Blaauw et al., 2010; Rossi et al., 2010), and to the higher exposure and sensitivity to plant community composition changes of the plant-feeders (Sauvadet et al., 2025), respectively.

4.2 | Land use conversion impacts on litter decomposition by the soil micro-food web

In partial agreement with our second hypothesis, litter decomposition and FB in the fine-mesh litterbags were higher in the natural forests than in the other land uses, but only during the early stage of decomposition. These litterbags allowed access to litter not only by microorganisms, but also by nematofauna and part of the mesofauna, corresponding to the soil micro-food web (Potapov et al., 2021). Considering the great similarities between natural forests and eucalyptus plantations in terms of microbial communities, soil properties, and microclimatic regulation, we assume that improved decomposition ability under the natural forest compared with all other land uses is linked with the greater diversity and structure of the higher trophic levels of the nematode community.

The benefits of nematodes on litter decomposition have long been recognized (Freckman, 1982) through their stimulation of microbial activities and nutrient turnover (A'Bear et al., 2014; Trap et al., 2016). It is also expected to observe higher impacts of this community at the early stage of decomposition (García-Palacios et al., 2016), that correspond to the phase of the decomposition of the most labile parts of the litter (Berg & McClaugherty, 2008), where microbial growth, turnover rates and activities are at their peak (Hättenschwiler et al., 2005). The absence of HFA in the fine-mesh litterbags suggests that the lower micro-food web disturbance under natural forests led to increased decomposition ability for the range of litter quality found in this degradation gradient.

4.3 | Macrofauna impacts on litter decomposition and HFA vary with land use

In partial agreement with our third hypothesis, macrofauna presence—assessed by comparing the patterns observed between coarse- and fine-mesh sized litterbags—strengthened site effects on litter decomposition, FB and HFA, yet only at the late stage of decomposition. They especially promoted decomposition in the natural forest (+12% on average) and to a lesser extent in the fallows (+8% on average) with no significant benefits under eucalyptus plantations, which led to significantly lower FB in this land use after 12 months. We expect the higher contribution of macrofauna to decomposition at the later stages, a common pattern in literature (Bradford et al., 2002; Handa et al., 2014), to be due both to (i) their benefits on litter fragmentation and burial (Setälä et al., 1996), important to put litter in contact with their microbial decomposers, now that most soluble compounds have already been leached and degraded (Berg & McClaugherty, 2008), and (ii) the stimulation of lignolytic fungi activities, driving late-stage litter decomposition (Osono, 2007; Purahong et al., 2016)—these top-down effects are known to be higher for the larger fauna than for nematodes (A'Bear et al., 2014). The higher benefits of macrofauna in natural forest compared to the other land uses were likely favoured by both a more diversified and endemic macrofauna community (Handa et al., 2014; Inkotte et al., 2022). The absence of macrofauna effects under eucalyptus plantation was more unexpected, as favourable climatic conditions tend to favour their impacts on litter decomposition (Handa et al., 2014; Pugnaire et al., 2023; Shi et al., 2025) and led to a positive HFA for this land use after 12 months. This could indicate that soil macrofauna have adapted to eucalyptus litter, resulting in lower decomposition efficiency for substrates other than eucalyptus litter. This assumption is consistent with observations of reduced activity under plantations compared with natural forests (Rivas et al., 2023; Roy & Chakrabartty, 2004; Zhang et al., 2016). Consequently, while

planting eucalyptus in degraded land appears as a promising way to allow natural forest regeneration (Brancalion et al., 2020; Fernandes et al., 2024; Rakotoarisoa et al., 2025) thanks to the ability of eucalyptus to preserve forest seed banks and promote the initial growth of native trees (Granzotto et al., 2024; Randriamalala et al., 2023), our study highlighted significant drawbacks in terms of soil biodiversity and late-stage decomposition capacity. Forest restoration in Madagascar's eastern coast should hence lean on the plantation of more diversified tree communities, such as mixing *Eucalyptus* with N_2-fixing species, for instance with *A. dealbata* Link (Kull et al., 2007), to improve both ecosystem functionality and soil biodiversity (Bini et al., 2013; Pereira et al., 2019).

5 | CONCLUSION

Our findings imply that while planted forests cause less disturbance of microbial communities and early-stage decomposition compared to fallows from slash-and-burn agriculture, they may not fully replace the multiple ecological roles played by native forests, particularly for the functions requiring more specialized organisms and taxa. The simplification of plant diversity, periodic wood harvesting and poorer litter quality likely constrain both belowground biodiversity and ecosystem functionality. Nevertheless, given the increasing land-use pressure in Eastern Madagascar, more diversified planted forests should be further explored as a potential land use for restoring early-stage degraded slash-and-burn fallows, offering a compromise between human needs and partially preserving belowground ecosystem functions.

AUTHOR CONTRIBUTIONS

Jean Trap and Jean-Pierre Bouillet conceived the study and designed the methodology. Seydina Mohamad Ba, Malalatiana Razafindrakoto, Marie-Paul Razafimanantsoa and Jean-Michel Leong produced the data. Marie Sauvadet, Jean Trap and Seydina Mohamad Ba analysed the data; Marie Sauvadet led the writing of the manuscript, and Jean-Pierre Bouillet and Jean Marc Bouvet provided the funding for the study. Marie Sauvadet, Seydina Mohamad Ba, Malalatiana Razafindrakoto, Tantely Maminiaina Razafimbelo, Marie-Paul Razafimanantsoa, Jean Marc Bouvet, Jean-Michel Leong, Jean Trap and Jean-Pierre Bouillet all contributed critically to the draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data from this article are available in the FigShare repository https://doi.org/10.6084/m9.figshare.30665573 (Sauvadet et al., 2026).

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REFERENCES

A'Bear, A. D., Jones, T. H., & Boddy, L. (2014). Size matters: What have we learnt from microcosm studies of decomposer fungus–invertebrate interactions? *Soil Biology and Biochemistry*, *78*, 274–283. https://doi.org/10.1016/j.soilbio.2014.08.009

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos*, *79*, 439–449. https://doi.org/10.2307/3546886

AFNOR. (1999). NF X31-130. Capacité d'échange cationique (CEC), méthode de Metson, unité cmol+/kg.

AFNOR. (2003). NF X31-107. Qualité du sol—Détermination de la distribution granulométrique des particules du sol—Méthode à la pipette.

AFNOR. (2005). NF ISO-10390. Qualité du sol–Détermination du pH.

AFNOR. (2018). NF ISO-23470. Qualité du sol—Détermination de la capacité d'échange cationique (CEC) effective et des cations échangeables à l'aide d'une solution de trichlorure de cobaltihexammine.

Anderson, J. M., & Ingram, J. S. (1994). Tropical soil biology and fertility: A handbook of methods. *Soil Science*, *157*(4), 265.

Aubréville, A. A., & Bossanyi, I. (2015). No to the "eucalyptus war" in Madagascar! *Bois & Forêts des Tropiques*, *323*, 49–53. https://doi.org/10.19182/bft2015.323.a31242

Ayres, E., Steltzer, H., Simmons, B. L., Simpson, R. T., Steinweg, J. M., Wallenstein, M. D., Mellor, N., Parton, W. J., Moore, J. C., & Wall, D. H. (2009). Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biology and Biochemistry*, *41*(3), 606–610. https://doi.org/10.1016/j.soilbio.2008.12.022

Bayle, G. K. (2019). Ecological and social impacts of eucalyptus tree plantation on the environment. *Journal of Biodiversity Conservation and Bioresource Management*, *5*(1), 93–104. https://doi.org/10.3329/jbcbm.v5i1.42189

Berg, B., & McClaugherty, C. (2008). *Plant litter—Decomposition, humus formation, carbon sequestration* (2nd ed.). Springer. http://www.springer.com/life+sciences/ecology/book/978-3-642-38820-0

Bezerra, J. S., Arroyo-Rodríguez, V., Arasa-Gisbert, R., & Meave, J. A. (2024). Multiscale effects of slash-and-burn agriculture across the tropics: Implications for the sustainability of an ancestral agroecosystem. *Sustainability*, *16*(22), Article 22. https://doi.org/10.3390/su16229994

Bini, D., dos Santos, C. A., Bouillet, J.-P., de Morais Goncalves, J. L., & Bran Nogueira Cardoso, E. J. (2013). Eucalyptus grandis and Acacia mangium in monoculture and intercropped plantations: Evolution of soil and litter microbial and chemical attributes during early stages of plant development. *Applied Soil Ecology*, *63*, 57–66. https://doi.org/10.1016/j.apsoil.2012.09.012

Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H., & Newington, J. E. (2002). Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos*, *99*(2), 317–323. https://doi.org/10.1034/j.1600-0706.2002.990212.x

Brady, N. C. (1996). Alternatives to slash-and-burn: A global imperative. *Agriculture, Ecosystems & Environment, Alternatives to Slash-and-Burn*

Agriculture, *58*(1), 3–11. https://doi.org/10.1016/0167-8809(96)00650-0

Brancalion, P. H. S., Amazonas, N. T., Chazdon, R. L., van Melis, J., Rodrigues, R. R., Silva, C. C., Sorrini, T. B., & Holl, K. D. (2020). Exotic eucalypts: From demonized trees to allies of tropical forest restoration? *Journal of Applied Ecology*, *57*(1), 55–66. https://doi.org/10.1111/1365-2664.13513

Brinkmann, N., Schneider, D., Sahner, J., Ballauff, J., Edy, N., Barus, H., Irawan, B., Budi, S. W., Qaim, M., Daniel, R., & Polle, A. (2019). Intensive tropical land use massively shifts soil fungal communities. *Scientific Reports*, *9*(1), 3403. https://doi.org/10.1038/s41598-019-39829-4

Casse, T., Milhøj, A., Ranaivoson, S., & Romuald Randriamanarivo, J. (2004). Causes of deforestation in southwestern Madagascar: What do we know? *Forest Policy and Economics*, *6*(1), 33–48. https://doi.org/10.1016/S1389-9341(02)00084-9

Coûteaux, M.-M., Bottner, P., & Berg, B. (1995). Litter decomposition, climate and litter quality. *Trends in Ecology & Evolution*, *10*(2), 63–66. https://doi.org/10.1016/S0169-5347(00)88978-8

da Silva, J. V. C. d. L., Silva, D. G., Monteiro, Í. I., Cares, J. E., & Esteves, A. M. (2025). Effects of slash-and-burn agriculture on soil properties and nematode assemblages in the Caatinga dry forest (SSRN scholarly paper No. 5080220). Social Science Research Network. https://doi.org/10.2139/ssrn.5080220

de Vasconcelos, W. L. F., Rodrigues, D. D. M., Silva, R. O. C., & Alfaia, S. S. (2020). Diversity and abundance of soil macrofauna in three land use systems in eastern Amazonia. *Revista Brasileira de Ciência do Solo*, *44*, e0190136. https://doi.org/10.36783/18069657rbcs20190136

Demeyer, A., Voundi Nkana, J. C., & Verloo, M. G. (2001). Characteristics of wood ash and influence on soil properties and nutrient uptake: An overview. *Bioresource Technology*, *77*(3), 287–295. https://doi.org/10.1016/S0960-8524(00)00043-2

Fachin, P. A., Costa, Y. T., & Thomaz, E. L. (2021). Evolution of the soil chemical properties in slash-and-burn agriculture along several years of fallow. *Science of the Total Environment*, *764*, 142823. https://doi.org/10.1016/j.scitotenv.2020.142823

Fanin, N., & Bertrand, I. (2016). Aboveground litter quality is a better predictor than belowground microbial communities when estimating carbon mineralization along a land-use gradient. *Soil Biology and Biochemistry*, *94*, 48–60. https://doi.org/10.1016/j.soilbio.2015.11.007

Fernandes, M. M., José, M. B., Pereira, M. G., Vieira, M. V. A., Morais, I. S., Silva, T. P., & Araújo Filho, R. N. (2024). Edaphic attributes in different successional ecological restoration models consortium with eucalyptus in the Brazilian Atlantic Forest. *Floresta e Ambiente*, *31*, e20230042. https://doi.org/10.1590/2179-8087-FLORAM-2023-0042

Ferreira de Alencar Mendes, B. T., Pinheiro, M. R., Barretto, E. H. P., Barreiros, A. M., Correia Furquim, S. A., & Junqueira Villela, F. N. (2023). Impacts of slash-and-burn cultivation on the soil and vegetation of the Atlantic Forest in southeastern Brazil. *Human Ecology*, *51*(4), 655–669. https://doi.org/10.1007/s10745-023-00429-6

Freckman, D. W. (1982). *Nematodes in soil ecosystems*. University of Texas Press.

García-Palacios, P., Shaw, E. A., Wall, D. H., & Hättenschwiler, S. (2016). Temporal dynamics of biotic and abiotic drivers of litter decomposition. *Ecology Letters*, *19*(5), 554–563. https://doi.org/10.1111/ele.12590

Gay-des-Combes, J. M., Sanz Carrillo, C., Robroek, B. J. M., Jassey, V. E. J., Mills, R. T. E., Arif, M. S., Falquet, L., Frossard, E., & Buttler, A. (2017). Tropical soils degraded by slash-and-burn cultivation can be recultivated when amended with ashes and compost. *Ecology and Evolution*, *7*(14), 5378–5388. https://doi.org/10.1002/ece3.3104

Ghimire, C. P., (Ilja) van Meerveld, H. J., Zwartendijk, B. W., Bruijnzeel, L. A., Ravelona, M., Lahitiana, J., & Lubczynski, M. W. (2022). Vapour pressure deficit and solar radiation are the major drivers of transpiration in montane tropical secondary forests in eastern Madagascar. *Agricultural and Forest Meteorology*, *326*, 109159. https://doi.org/10.1016/j.agrformet.2022.109159

Gholz, H. L., Wedin, D. A., Smitherman, S. M., Harmon, M. E., & Parton, W. J. (2000). Long-term dynamics of pine and hardwood litter in contrasting environments: Toward a global model of decomposition. *Global Change Biology*, *6*(7), 7. https://doi.org/10.1046/j.1365-2486.2000.00349.x

Gibb, T. J., & Oseto, C. Y. (2006). *Arthropod collection and identification: Laboratory and field techniques*. Academic Press.

Giweta, M. (2020). Role of litter production and its decomposition, and factors affecting the processes in a tropical forest ecosystem: A review. *Journal of Ecology and Environment*, *44*(1), 11. https://doi.org/10.1186/s41610-020-0151-2

Gongalsky, K. B., Malmström, A., Zaitsev, A. S., Shakhab, S. V., Bengtsson, J., & Persson, T. (2012). Do burned areas recover from inside? An experiment with soil fauna in a heterogeneous landscape. *Applied Soil Ecology*, *59*, 73–86. https://doi.org/10.1016/j.apsoil.2012.03.017

Granzotto, F., Matiello, J., Silva Junior, J. C. C. D., Milagre, J. C., da Silva, R. P., Sulzbach, P., da Silva, P. S., Nunes, P. B., & Rovedder, A. P. M. (2024). Eucalyptus productive matrix influences the soil seed bank in southern Brazil. *Canadian Journal of Forest Research*, *54*(6), 674–685. https://doi.org/10.1139/cjfr-2023-0256

Handa, I. T., Aerts, R., Berendse, F., Berg, M. P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M. O., Jabiol, J., Makkonen, M., McKie, B. G., Malmqvist, B., Peeters, E. T. H. M., Scheu, S., Schmid, B., van Ruijven, J., Vos, V. C. A., & Hättenschwiler, S. (2014). Consequences of biodiversity loss for litter decomposition across biomes. *Nature*, *509*(7499), 218–221. https://doi.org/10.1038/nature13247

Hands, M. (2021). The search for a sustainable alternative to slash-and-burn agriculture in the World's rain forests: The Guama model and its implementation. *Royal Society Open Science*, *8*(2), 201204. https://doi.org/10.1098/rsos.201204

Hättenschwiler, S., Tiunov, A. V., & Scheu, S. (2005). Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *36*(1), 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932

Hu, D., Zhu, G., Wu, P., Zhang, S., & Cheng, D. (2026). High-quality litter drives a stronger home-field advantage of leaf decomposition in young plantations. *Functional Ecology*, *40*(1), 97–112. https://doi.org/10.1111/1365-2435.70219

Inkotte, J., Bomfim, B., da Silva, S. C., Valadão, M. B. X., da Rosa, M. G., Viana, R. B., D'Ângelo Rios, P., Gatto, A., & Pereira, R. S. (2022). Linking soil biodiversity and ecosystem function in a Neotropical savanna. *Applied Soil Ecology*, *169*, 104209. https://doi.org/10.1016/j.apsoil.2021.104209

Jensen, L. S., Salo, T., Palmason, F., Breland, T. A., Henriksen, T. M., Stenberg, B., Pedersen, A., Lundström, C., & Esala, M. (2005). Influence of biochemical quality on C and N mineralisation from a broad variety of plant materials in soil. *Plant and Soil*, *273*(1), 307–326. https://doi.org/10.1007/s11104-004-8128-y

Juo, A. S. R., & Manu, A. (1996). Chemical dynamics in slash-and-burn agriculture. *Agriculture, Ecosystems & Environment, Alternatives to Slash-and-Burn Agriculture*, *58*(1), 49–60. https://doi.org/10.1016/0167-8809(95)00656-7

Kalam, S., Basu, A., Ahmad, I., Sayyed, R. Z., El-Enshasy, H. A., Dailin, D. J., & Suriani, N. L. (2020). Recent understanding of soil Acidobacteria and their ecological significance: A critical review. *Frontiers in Microbiology*, *11*, 580024. https://doi.org/10.3389/fmicb.2020.580024

Kaspari, M., & Yanoviak, S. P. (2009). Biogeochemistry and the structure of tropical brown food webs. *Ecology*, *90*(12), 3342–3351. https://doi.org/10.1890/08-1795.1

Keiser, A. D., Keiser, D. A., Strickland, M. S., & Bradford, M. A. (2014). Disentangling the mechanisms underlying functional differences among decomposer communities. *Journal of Ecology*, *102*(3), 603–609. https://doi.org/10.1111/1365-2745.12220

Keiser, A. D., Strickland, M. S., Fierer, N., & Bradford, M. A. (2011). The effect of resource history on the functioning of soil microbial

communities is maintained across time. *Biogeosciences*, *8*(6), 1477–1486. https://doi.org/10.5194/bg-8-1477-2011

Kielak, A. M., Barreto, C. C., Kowalchuk, G. A., van Veen, J. A., & Kuramae, E. E. (2016). The ecology of Acidobacteria: Moving beyond genes and genomes. *Frontiers in Microbiology*, *7*, 744. https://doi.org/10.3389/fmicb.2016.00744

Kladivko, E. J. (2001). Tillage systems and soil ecology. *Soil and Tillage Research*, *61*(1–2), 61–76. https://doi.org/10.1016/S0167-1987(01)00179-9

Kleinman, P. J. A., Pimentel, D., & Bryant, R. B. (1995). The ecological sustainability of slash-and-burn agriculture. *Agriculture, Ecosystems & Environment*, *52*(2), 235–249. https://doi.org/10.1016/0167-8809(94)00531-I

Kull, C. A., Tassin, J., Moreau, S., Rakoto Ramiarantsoa, H., Blanc-Pamard, C., & Carrière, S. M. (2012). The introduced flora of Madagascar. *Biological Invasions*, *14*(4), 875–888. https://doi.org/10.1007/s10530-011-0124-6

Kull, C. A., Tassin, J., & Rangan, H. (2007). Multifunctional, scrubby, and invasive forests? *Mountain Research and Development*, *27*(3), 224–231. https://doi.org/10.1659/mrd.0864

Lan, G., Li, Y., Wu, Z., & Xie, G. (2017). Soil bacterial diversity impacted by conversion of secondary forest to rubber or eucalyptus plantations: A case study of Hainan Island, South China. *Forest Science*, *63*(1), 87–93. https://doi.org/10.5849/forsci.16-012

Makana, J.-R., & Thomas, S. C. (2006). Impacts of selective logging and agricultural clearing on Forest structure, floristic composition and diversity, and timber tree regeneration in the Ituri Forest, Democratic Republic of Congo. *Biodiversity and Conservation*, *15*(4), 1375–1397. https://doi.org/10.1007/s10531-005-5397-6

Malik, A. A., Martiny, J. B. H., Brodie, E. L., Martiny, A. C., Treseder, K. K., & Allison, S. D. (2020). Defining trait-based microbial strategies with consequences for soil carbon cycling under climate change. *The ISME Journal*, *14*(1), 1–9. https://doi.org/10.1038/s41396-019-0510-0

Maron, P.-A., Mougel, C., & Ranjard, L. (2011). Soil microbial diversity: Methodological strategy, spatial overview and functional interest. *Comptes Rendus Biologies*, *334*(5–6), 403–411. https://doi.org/10.1016/j.crvi.2010.12.003

Mayor, A. G., Valdecantos, A., Vallejo, V. R., Keizer, J. J., Bloem, J., Baeza, J., González-Pelayo, O., Machado, A. I., & de Ruiter, P. C. (2016). Fire-induced pine woodland to shrubland transitions in Southern Europe may promote shifts in soil fertility. *Science of the Total Environment*, *573*, 1232–1241. https://doi.org/10.1016/j.scitotenv.2016.03.243

Miki, T. (2012). Microbe-mediated plant–soil feedback and its roles in a changing world. *Ecological Research*, *27*(3), 509–520. https://doi.org/10.1007/s11284-012-0937-5

Neves, M. S. A. C., Souto, M. R. S., Tóth, I. V., Victal, S. M. A., Drumond, M. C., & Rangel, A. O. S. S. (2008). Spectrophotometric flow system using vanadomolybdophosphate detection chemistry and a liquid waveguide capillary cell for the determination of phosphate with improved sensitivity in surface and ground water samples. *Talanta*, *77*(2), 527–532. https://doi.org/10.1016/j.talanta.2008.03.014

Olsen, S. R. (1954). *Estimation of available phosphorus in soils by extraction with sodium bicarbonate*. U.S. Dept. of Agriculture.

Osburn, E. D., Hoch, P. J., Lucas, J. M., McBride, S. G., & Strickland, M. S. (2022). Evaluating the roles of microbial functional breadth and home-field advantage in leaf litter decomposition. *Functional Ecology*, *36*(5), 1258–1267. https://doi.org/10.1111/1365-2435.14026

Osono, T. (2007). Ecology of ligninolytic fungi associated with leaf litter decomposition. *Ecological Research*, *22*(6), Article 6. https://doi.org/10.1007/s11284-007-0390-z

Parr, C. L., Lehmann, C. E. R., Bond, W. J., Hoffmann, W. A., & Andersen, A. N. (2014). Tropical grassy biomes: Misunderstood, neglected, and under threat. *Trends in Ecology & Evolution*, *29*(4), 205–213. https://doi.org/10.1016/j.tree.2014.02.004

Pen-Mouratov, S., Ginzburg, O., Whitford, W., & Steinberger, Y. (2012). Forest fire modifies soil free-living nematode communities in the Biriya woodland of northern Israel. *Zoological Studies*, *51*, 1018–1026.

Pereira, A. P. A., Durrer, A., Gumiere, T., Gonçalves, J. L. M., Robin, A., Bouillet, J.-P., Wang, J., Verma, J. P., Singh, B. K., & Cardoso, E. J. B. N. (2019). Mixed *eucalyptus* plantations induce changes in microbial communities and increase biological functions in the soil and litter layers. *Forest Ecology and Management*, *433*, 332–342. https://doi.org/10.1016/j.foreco.2018.11.018

Philippot, L., Andersson, S. G. E., Battin, T. J., Prosser, J. I., Schimel, J. P., Whitman, W. B., & Hallin, S. (2010). The ecological coherence of high bacterial taxonomic ranks. *Nature Reviews Microbiology*, *8*(7), 523–529. https://doi.org/10.1038/nrmicro2367

Plassart, P., Terrat, S., Thomson, B., Griffiths, R., Dequiedt, S., Lelievre, M., Regnier, T., Nowak, V., Bailey, M., Lemanceau, P., Bispo, A., Chabbi, A., Maron, P.-A., Mougel, C., & Ranjard, L. (2012). Evaluation of the ISO standard 11063 DNA extraction procedure for assessing soil microbial abundance and community structure. *PLoS One*, *7*(9), e44279. https://doi.org/10.1371/journal.pone.0044279

Postma-Blaauw, M. B., de Goede, R. G. M., Bloem, J., Faber, J. H., & Brussaard, L. (2010). Soil biota community structure and abundance under agricultural intensification and extensification. *Ecology*, *91*(2), 460–473. https://doi.org/10.1890/09-0666.1

Potapov, A. M., Rozanova, O. L., Semenina, E. E., Leonov, V. D., Belyakova, O. I., Bogatyreva, V. Y., Degtyarev, M. I., Esaulov, A. S., Korotkevich, A. Y., Kudrin, A. A., Malysheva, E. A., Mazei, Y. A., Tsurikov, S. M., Zuev, A. G., & Tiunov, A. V. (2021). Size compartmentalization of energy channeling in terrestrial belowground food webs. *Ecology*, *102*(8), e03421. https://doi.org/10.1002/ecy.3421

Pugnaire, F. I., Aares, K. H., Alifriqui, M., Bråthen, K. A., Kindler, C., Schöb, C., & Manrique, E. (2023). Home-field advantage effects in litter decomposition is largely linked to litter quality. *Soil Biology and Biochemistry*, *184*, 109069. https://doi.org/10.1016/j.soilbio.2023.109069

Purahong, W., Wubet, T., Lentendu, G., Schloter, M., Pecyna, M. J., Kapturska, D., Hofrichter, M., Krüger, D., & Buscot, F. (2016). Life in leaf litter: Novel insights into community dynamics of bacteria and fungi during litter decomposition. *Molecular Ecology*, *25*(16), 4059–4074. https://doi.org/10.1111/mec.13739

Rakotoarisoa, M. V., Carrière, S. M., Randriambanona, H., Laques, A.-E., Rakotondrabe, T., & Randriamalala, J. R. (2025). Native tropical forest species regeneration in non-native eucalyptus tree plantations along the agricultural landscapes of south-eastern Malagasy highlands. *Global Ecology and Conservation*, *60*, e03631. https://doi.org/10.1016/j.gecco.2025.e03631

Randriamalala, J. R., Rabeniala, R., & Randriambanona, H. (2023). Native forest regeneration and eucalyptus plantations in the Malagasy Highland. *African Journal of Ecology*, *61*(1), 242–246. https://doi.org/10.1111/aje.13088

Rao, A. S., Reddy, K. S., & Takkar, P. N. (1997). Malachite green method compared to ascorbic acid for estimating small amounts of phosphorus in water, 0.01 M calcium chloride, and olsen soil extracts. *Communications in Soil Science and Plant Analysis*, *28*(6–8), 589–601. https://doi.org/10.1080/00103629709369813

Renčo, M., Adámek, M., Jílková, V., & Devetter, M. (2022). Post-fire recovery of soil nematode communities depends on fire severity. *Diversity*, *14*(12), 1116. https://doi.org/10.3390/d14121116

Rivas, Y., Aponte, H., Rivera-Salazar, D., Matus, F., Martínez, O., Encina, C., & Retamal-Salgado, J. (2023). Microbial community and enzyme activity of Forest plantation, natural forests, and agricultural land in Chilean coastal cordillera soils. *Forests*, *14*(5), 938. https://doi.org/10.3390/f14050938

Rossi, J. P., Celini, L., Mora, P., Mathieu, J., Lapied, E., Nahmani, J., Ponge, J.-F., & Lavelle, P. (2010). Decreasing fallow duration in tropical slash-and-burn agriculture alters soil macroinvertebrate diversity: A case study in southern French Guiana. *Agriculture, Ecosystems*

& *Environment*, *135*(1), 148–154. https://doi.org/10.1016/j.agee.2009.08.012

Roy, S., & Chakrabartty, P. K. (2004). Deterioration of soil physicochemical properties, microbial biomass C, and N-mineralization due to replacement of sal forest with exotic species and rain-fed agriculture in East India. *International Journal of Ecology and Environmental Sciences*, *30*, 67–75.

Sauvadet, M., Autfray, P., Rafenomanjato, A., Ripoche, A., & Trap, J. (2025). Conservation agriculture improves the balance between beneficial free-living and plant-parasitic nematodes for low-input rainfed rice crop. *Applied Soil Ecology*, *209*, 106029. https://doi.org/10.1016/j.apsoil.2025.106029

Sauvadet, M., Ba, S. M., Razafindrakoto, M., Maminiaina Razafimbelo, T., Razafimanantsoa, M.-P., Bouvet, J.-M., Leong Pock Tsy, J.-M., Trap, J., & Bouillet, J.-P. (2026). Data set from *Trade-offs between soil biodiversity and agricultural expansion: Evidence from litter decomposition dynamics in Madagascar*. (p. 23159 Bytes) [Dataset]. figshare. https://doi.org/10.6084/M9.FIGSHARE.30665573

Seinhorst, J. W. (1962). Modifications of the elutriation method for extracting nematodes from soil. *Nematologica*, *8*(2), 117–128. https://doi.org/10.1163/187529262X00332

Setälä, H., Marshall, V. G., & Trofymow, J. A. (1996). Influence of body size of soil fauna on litter decomposition and 15N uptake by poplar in a pot trial. *Soil Biology and Biochemistry*, *28*(12), 1661–1675. https://doi.org/10.1016/S0038-0717(96)00252-0

Shi, B., Zheng, J., Pugnaire, F. I., Behm, J. E., Zhuang, X., Meng, Y., & Liu, S. (2025). Home-field advantage of litter decomposition across biomes: A global meta-analysis. *Plant and Soil*, *515*(2), 2015–2026. https://doi.org/10.1007/s11104-025-07701-2

Sinsabaugh, R. L., Carreiro, M. M., & Repert, D. A. (2002). Allocation of extracellular enzymatic activity in relation to litter composition, N deposition, and mass loss. *Biogeochemistry*, *60*(1), 1–24. https://doi.org/10.1023/A:1016541114786

Styger, E., Fernandes, E. C. M., Rakotondramasy, H. M., & Rajaobelinirina, E. (2009). Degrading uplands in the rainforest region of Madagascar: Fallow biomass, nutrient stocks, and soil nutrient availability. *Agroforestry Systems*, *77*(2), 107–122. https://doi.org/10.1007/s10457-009-9225-y

Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M., & Bates, D. M. (2007). Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agriculture, Ecosystems & Environment*, *119*(3), 257–269. https://doi.org/10.1016/j.agee.2006.07.012

Swift, M. J., Michael, J., Heal, O. W., Anderson, J. M., & Jonathan, M. (1979). *Decomposition in terrestrial ecosystems*. Blackwell.

Tardy, V., Spor, A., Mathieu, O., Lévèque, J., Terrat, S., Plassart, P., Regnier, T., Bardgett, R. D., van der Putten, W. H., Roggero, P. P., Seddaiu, G., Bagella, S., Lemanceau, P., Ranjard, L., & Maron, P.-A. (2015). Shifts in microbial diversity through land use intensity as drivers of carbon mineralization in soil. *Soil Biology and Biochemistry*, *90*, 204–213. https://doi.org/10.1016/j.soilbio.2015.08.010

Terrat, S., Christen, R., Dequiedt, S., Lelievre, M., Nowak, V., Regnier, T., Bachar, D., Plassart, P., Wincker, P., Jolivet, C., Bispo, A., Lemanceau, P., Maron, P.-A., Mougel, C., & Ranjard, L. (2012). Molecular biomass and MetaTaxogenomic assessment of soil microbial communities as influenced by soil DNA extraction procedure. *Microbial Biotechnology*, *5*(1), 135–141. https://doi.org/10.1111/j.1751-7915.2011.00307.x

Townshend, J. L. (1963). A modification and evaluation of the apparatus for the Oostenbrink direct Cottonwool filter extraction Method1. *Nematologica*, *9*(1), 106–110. https://doi.org/10.1163/187529263X00205

Trap, J., Bonkowski, M., Plassard, C., Villenave, C., & Blanchart, E. (2016). Ecological importance of soil bacterivores for ecosystem functions. *Plant and Soil*, *398*(1), 1–24. https://doi.org/10.1007/s11104-015-2671-6

Van Soest, P. J. (1963). The use of detergents in the analysis of fibrous feeds. II. A rapid method for the determination of fiber and lignin. *Journal of the Association of Official Analytical Chemists*, *46*, Article 46.

van Vliet, N., Mertz, O., Heinimann, A., Langanke, T., Pascual, U., Schmook, B., Adams, C., Schmidt-Vogt, D., Messerli, P., Leisz, S., Castella, J.-C., Jørgensen, L., Birch-Thomsen, T., Hett, C., Bech-Bruun, T., Ickowitz, A., Vu, K. C., Yasuyuki, K., Fox, J., … Ziegler, A. D. (2012). Trends, drivers and impacts of changes in swidden cultivation in tropical forest-agriculture frontiers: A global assessment. *Global Environmental Change, Adding Insult to Injury: Climate Change, Social Stratification, and the Inequities of Intervention*, *22*(2), 418–429. https://doi.org/10.1016/j.gloenvcha.2011.10.009

Veen, G. F., Freschet, G. T., Ordonez, A., & Wardle, D. A. (2015). Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos*, *124*(2), 187–195. https://doi.org/10.1111/oik.01374

Veen, G. F. (C.), Keiser, A. D., van der Putten, W. H., & Wardle, D. A. (2018). Variation in home-field advantage and ability in leaf litter decomposition across successional gradients. *Functional Ecology*, *32*(6), 1563–1574. https://doi.org/10.1111/1365-2435.13107

Verhaegen, D., Randrianjafy, H., Rakotondraoelina, H., Trendelenburg Rakotonirina, M.-C., Andriamampianina, N., Montagne, P., Rasamindisa, A., Chaix, G., Bouillet, J.-P., & Bouvet, J.-M. (2014). Eucalyptus robusta pour une production durable de bois énergie à Madagascar: Bilan des connaissances et perspectives. *Bois et Forêts des Tropiques*, *320*, 15–30.

Vieilledent, G., Nourtier, M., Grinand, C., Pedrono, M., Clausen, A., Rabetrano, T., Rakotoarijaona, J.-R., Rakotoarivelo, B., Rakotomalala, F. A., Rakotomalala, L., Razafimpahanana, A., Ralison, J. M., & Achard, F. (2020). *It's not just poverty: Unregulated global market and bad governance explain unceasing deforestation in Western Madagascar* (p. 2020.07.30.229104). *bioRxiv*. https://doi.org/10.1101/2020.07.30.229104

Vitousek, P. M., & Sanford, R. L. (1986). Nutrient cycling in moist tropical Forest. *Annual Review of Ecology and Systematics*, *17*, 137–167.

Waldrop, M. P., Balser, T. C., & Firestone, M. K. (2000). Linking microbial community composition to function in a tropical soil. *Soil Biology and Biochemistry*, *32*(13), 1837–1846. https://doi.org/10.1016/S0038-0717(00)00157-7

Wang, L., Zhou, Y., Chen, Y., Xu, Z., Zhang, J., & Liu, Y. (2023). Home-field advantage and ability alter labile and recalcitrant litter carbon decomposition in an alpine forest ecotone. *Plant and Soil*, *485*(1), 213–225. https://doi.org/10.1007/s11104-022-05693-x

Wang, X., Gossart, M., Guinet, Y., Fau, H., Lavignasse-Scaglia, C.-D., Chaieb, G., & Michalet, R. (2020). The consistency of home-field advantage effects with varying climate conditions. *Soil Biology and Biochemistry*, *149*, 107934. https://doi.org/10.1016/j.soilbio.2020.107934

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., van der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science*, *304*(5677), 1629–1633. https://doi.org/10.1126/science.1094875

White, H. (1980). A Heteroskedasticity-consistent covariance matrix estimator and a direct test for Heteroskedasticity. *Econometrica*, *48*(4), 817–838. https://doi.org/10.2307/1912934

Whittinghill, K. A., Currie, W. S., Zak, D. R., Burton, A. J., & Pregitzer, K. S. (2012). Anthropogenic N deposition increases soil C storage by decreasing the extent of litter decay: Analysis of field observations with an ecosystem model. *Ecosystems*, *15*(3), 450–461. https://doi.org/10.1007/s10021-012-9521-7

Wickings, K., Grandy, A. S., Reed, S. C., & Cleveland, C. C. (2012). The origin of litter chemical complexity during decomposition. *Ecology Letters*, *15*(10), 1180–1188. https://doi.org/10.1111/j.1461-0248.2012.01837.x

Yang, C., Dossa, G. G. O., Atapattu, A. J., Xia, S., & Yang, X. (2025). Soil fauna explain the plant apparency effect on litter decomposition

in tropical rainforests. *Catena*, *257*, 109157. https://doi.org/10.1016/j.catena.2025.109157

Yeates, G. W., Bongers, T., De Goede, R. G. M., Freckman, D. W., & Georgieva, S. S. (1993). Feeding habits in soil nematode families and genera—An outline for soil ecologists. *Journal of Nematology*, *25*(3), 315.

Yuan, X., Niu, D., Wang, Y., Boydston, A., Guo, D., Li, X., Wen, H., Qin, Y., & Fu, H. (2019). Litter decomposition in fenced and grazed grasslands: A test of the home-field advantage hypothesis. *Geoderma*, *354*, 113876. https://doi.org/10.1016/j.geoderma.2019.07.034

Zhang, F.-Q., Pan, W., Gu, J.-D., Xu, B., Zhang, W.-H., Zhu, B.-Z., Wang, Y.-X., & Wang, Y.-F. (2016). Dominance of ammonia-oxidizing archaea community induced by land use change from Masson pine to eucalypt plantation in subtropical China. *Applied Microbiology and Biotechnology*, *100*(15), 6859–6869. https://doi.org/10.1007/s00253-016-7506-8

Zhu, M., Fanin, N., Wang, Q., Xu, Z., Liang, S., Ye, J., Lin, F., Yuan, Z., Mao, Z., Wang, X., & Hao, Z. (2024). High functional breadth of microbial communities decreases home-field advantage of litter decomposition. *Soil Biology and Biochemistry*, *188*, 109232. https://doi.org/10.1016/j.soilbio.2023.109232

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Sampling plot location.

Table S2. Soil biota main diversity indices per land use ($n=3$). Diversity indices were assessed at the genera levels for bacteria, fungi and nematodes, and at the order level for macrofauna. Significant differences (mean ± standard deviation) were tested within each mesh size class by one-way ANOVAs followed by HSD Tukey tests, and bear different letters when p-value <0.05. Values significantly different from the natural forest are in bold.

Figure S1. Coarse-mesh litterbags set up in one land use plot (Savoka). Personal picture taken by Seydina Mohamad Ba.

Figure S2. Main litter floor composition in each land use ($n=6$). Differences were tested with one-way ANOVA followed by post Hoc Tukey test, and bear different letters when significantly different (p-value <0.05).

Figure S3. Non-Metric Dimensional Scaling (NMDS) of soil bacterial (a), fungal (b), nematodes (c) and macrofauna (d) communities between land uses. NMDS are based on Bray–Curtis distances at the genera levels for bacteria, fungi and nematodes, and at the order level for macrofauna. Community variation between land uses was assessed using ANOSIM tests (based on Bray–Curtis distances and 999 permutations), with R-values ranging between 0 and 1, and increasing with the level of dissimilarity between land uses (noted above the NMDS panel of each sub-figure). Communities' main indicators are fitted on each graph, only significant fits (p-value <0.05) are drawn.

Figure S4. Litterbag mesh size impacts on litter mass loss ($n=48$ per date), after 4 months (in red) and 12 months (in blue) of decomposition, for all litter identity and land uses.

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