

## Effects of land use across Southwestern Madagascar on soil faunal feeding activity and litter decomposition

Roger Andriamparany<sup>1†</sup>, Jean Robertin Rasoloariniaina<sup>2†\*</sup>, Simone Cesarz<sup>3,4</sup> and Aristide Andrianarimisa<sup>1</sup>

<sup>1</sup> Department of Zoology, Faculty of Science, University of Antananarivo, P.O. Box 906. 101 Antananarivo, Madagascar

<sup>2</sup> Department of Environment, Institut Universitaire de l'Innovation Technologique, University of Vakinankaratra, P.O. Box 180. Vatofotsy, 110 Antsirabe, Madagascar

<sup>3</sup> German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

<sup>4</sup> Institute of Biology, Leipzig University, Leipzig, Germany

† These authors share first authorship

\* Corresponding author, email: ratsim17@gmail.com

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### Abstract

Soil fauna play a central role in organic matter turnover, yet their activity and contribution to decomposition remain poorly understood in tropical drylands. We assessed how climate, land use, and soil fauna jointly shape soil biological functioning in the semi-arid southwest of Madagascar. Across two contrasting regions (Coastal Plain and Plateau), nine land-use types, and two seasons, we measured soil faunal feeding activity using bait-lamina strips and litter decomposition using fine- and coarse-mesh litterbags. Feeding activity was strongly controlled by season, being nearly absent during the dry period and peaking in the wet season, whereas regional differences were minor. Land-use intensity affected feeding activity but not decomposition: surprisingly, the highest feeding activity occurred in strongly managed systems such as new crop fields and cattle pen hedges. Feeding activity increased with soil depth during the wet season, likely reflecting higher and more stable moisture conditions below the surface. Litter decomposition showed no significant effects of region, land use, or mesh size, suggesting that microbial processes dominated under prevailing dry conditions. Our findings highlight that soil faunal activity in semi-arid Madagascar is highly sensitive to short-term moisture availability but only weakly structured by land use or region. Understanding these temporal dynamics is crucial for predicting the resilience of soil biota and decomposition under increasing climatic variability.

**Keywords** Bait-lamina | Litter-bags | Land use | Feeding activity | Soil fauna | Southwestern Madagascar

## 1 Introduction

In Madagascar, 74% of the population lives in rural areas, of which 78% are considered poor (WRI 2005). In particular, the sub-arid southwest of Madagascar suffers from exceptional poverty and a high risk of further temperature increase, which aggravates the living and health conditions of the local human population that mostly depends on the direct exploitation of natural resources for

their livelihoods (Neudert et al. 2015; Rasoloariniaina et al. 2015; Navaez & Eberle 2021). The subsistence production of the local population mainly includes agriculture, livestock husbandry, and the collection of forest resources (Andriamparany et al. 2014; Ralambomanantsoa et al. 2023). Because rural livelihoods in southwestern Madagascar rely heavily on soil fertility and vegetation productivity, understanding the biological drivers of decomposition is critical for sustainable resource use and

climate adaptation. Soil biota are essential components that regulate fundamental ecosystem functions such as nutrient cycling, decomposition, and soil formation. These functions underpin key ecosystem services, including soil fertility, forage provision, and forest productivity (Van Straalen 1998; Wardle et al. 1998; Walther et al. 2002) that sustain local agriculture, livestock husbandry, and the collection of forest resources (Lavelle et al. 2006; Wall et al. 2012; Bardgett & Van der Putten 2014). Despite their central importance, quantitative information on soil biological processes in Madagascar remains scarce. In particular, data on litter decomposition, a key pathway through which organic matter and nutrients are recycled, are very limited for the country and entirely lacking for the dry southwest (Powers et al. 2009; Seibold et al. 2021). Likewise, little is known about the feeding activity of soil fauna, even though it provides a direct measure of the contribution of soil organisms to decomposition and nutrient turnover.

To measure feeding activity of soil organisms that can also inform litter decomposition processes, the bait-lamina test was introduced as a simple tool for assessing the activity of soil organisms that contribute to nutrient cycling in the soil (Von Törne 1990). It is an easily applicable and low-effort screening method for assessing the feeding activity of soil animals by comparing different locations (Larink & Sommer 2002; Römbke et al. 2006). It has been used in different areas. Ecotoxicological studies showed that bait-lamina sticks are sensitive indicators of soil disturbance, pollution, and stress, as feeding activity declines under such pressures (Larink 1993; Kula & Römbke 1998; Paulus et al. 1999; Keplin & Hüttl 2000). Ecological studies demonstrated that bait-lamina feeding reflects differences in soil biotic activity across habitats, with effects of plant diversity, land use, and climate drivers such as drought (Larink & Sommer 2002; Römbke et al. 2006; Asato et al. 2025; Thakur et al. 2018; Siebert et al. 2019). Feeding activity of soil organisms often shows strong variability along both horizontal and vertical gradients. Vertical gradients (soil depth) are relevant because resources such as organic matter, oxygen, and moisture typically decline with depth, thereby reducing food availability for soil fauna. At the same time, land use can shape soil conditions by altering vegetation cover, litter input, and microclimatic conditions. Consequently, we expect feeding activity to vary across land-use types and to decline with increasing soil depth. Seasonal differences may further modify these patterns, especially in regions with pronounced dry and wet periods. Understanding how feeding activity varies along depth profiles and among land-use systems is crucial for linking soil biodiversity to ecosystem functioning.

However, bait-lamina sticks do not capture the actual breakdown of organic matter, which is a key ecosystem function supporting soil fertility. For this reason, litterbag experiments have been developed to directly measure litter decomposition in situ (Bocock & Gilber 1957; Crossley & Hoglund 1962). Litterbag studies worldwide reveal that decomposition rates are strongly shaped by climate, soil texture, litter quality, and land management, with faster decomposition under moist, fine-textured conditions and slower breakdown in drylands and degraded systems (Swift et al. 1979; Powers et al. 2009; Seibold et al. 2021). Using litterbags with different mesh sizes provides additional insights into the biological mechanisms of decomposition by distinguishing the contributions of different decomposer groups (Bradford et al. 2002). Fine-mesh bags largely exclude meso- and macrofauna such as mites, springtails, isopods, and earthworms, thus reflecting decomposition primarily driven by microorganisms and microfauna (Hättenschiler et al. 2005). Coarse-mesh bags, in contrast, allow access to larger soil fauna, enabling the quantification of their relative contribution to litter breakdown (Garcia-Palacios 2013). Comparing mesh sizes across land-use and environmental gradients therefore helps to identify where and under which conditions larger soil animals enhance decomposition, information that cannot be captured by microbial activity measurements alone. Despite the widespread use of bait-lamina and litterbag methods globally, no study has jointly applied them in semi-arid tropical systems where climatic gradients and land-use mosaics strongly interact. This limits our ability to predict how soil organisms mediate fertility under the dual pressures of climate variability and land-use change.

In southwestern Madagascar, two contrasting regions provide a natural gradient for testing these processes: the elevated plateau, characterized by relatively higher rainfall and finer soils, and the low-lying coastal region, which is drier and more sandy (Battistini 1965; Guyot 2002; Dworak 2014). Differences in soil texture and water availability between these regions are expected to strongly influence both soil faunal feeding activity and litter decomposition. In addition, the climate is strongly seasonal, with a hot rainy season (typically November–March) and a prolonged dry season (April–October). Water availability therefore fluctuates markedly over the year, and such seasonal dynamics are expected to regulate soil organism activity and the rate of organic matter turnover. At the same time, human land use has created a fine-grained mosaic of habitats including forest-like pastures, field hedges, tamarind tree fields, fallow crop fields, half-open pastures, open pastures, old and new crop fields to cattle pen hedges. These land-use types differ in vegetation cover, litter input, and soil disturbance, and thus provide opportunities

to assess how soil organisms respond to different levels of resource supply and habitat alteration (Eckert et al 2025; Van Der Zanden et al 2025). Investigating soil faunal feeding activity and litter decomposition across climatic regions, seasons, and land-use types is essential because these factors jointly determine how soils function under changing environmental and management conditions. Differences between plateau and coastal regions highlight the role of climate and soil texture, seasonal contrasts capture the strong influence of rainfall variability, and land-use comparisons reveal how human practices shape the capacity of soils to sustain fertility and productivity.

The present study is the first attempt to jointly assess soil faunal feeding activity (bait-lamina) and litter decomposition (litterbags) in southwestern Madagascar across regions and land-use types. Given the semi-arid climate of this area (Battistini 1965), we expect that (H1) soil faunal feeding activity and litter decomposition are higher on the Plateau than in the Coastal region, because the Plateau receives more rainfall and has finer-textured soils that retain moisture. We further hypothesize (H2a) that feeding activity is higher in the rainy season and strongly reduced in the dry season due to water limitation. We further hypothesize (H2b) that in the Coastal region, which has a more humid climate, the potential negative effects of the dry season are less pronounced. We also expect (H3) that land-use intensification reduces feeding activity and decomposition. Along the gradient from least to most disturbed habitats, we predict the highest activity in systems with dense vegetation cover and litter input, such as forest-like pastures, field hedges and tamarind tree fields, followed by fallow crop fields, half-open pastures and open pastures with intermediate cover, and the lowest activity in old and new crop fields and cattle pen hedges, where vegetation cover is sparse and disturbance is highest. We further hypothesize (H4) interactions between region and land use are more pronounced on the Plateau, where higher productivity and organic matter inputs amplify differences between land-use types. Considering soil depth, we hypothesize (H5) feeding activity of soil organisms is highest near the surface and declines with increasing soil depth, but this depth-related pattern is modified by land-use intensity, season, and region. Systems with higher disturbance and reduced vegetation cover are expected to show stronger seasonal fluctuations and lower feeding activity across depths compared to less disturbed systems. Finally, (H6) the influence of mesh size on litter decomposition (i.e., the contribution of meso- and macrofauna) depends on region and land use. We expect the effect of coarse mesh (faunal access) to be strongest on the Plateau and in less disturbed land uses (e.g., forest-like pastures and field hedges), where soil moisture and litter input support abundant soil fauna. In contrast, in drier or

more disturbed systems (e.g., crop fields and cattle pen hedges), decomposition should rely more on microbial activity, resulting in smaller differences between mesh sizes. Taken together, these hypotheses address how climate (regional and seasonal gradients) and human land use jointly shape soil biological activity and decomposition processes in semi-arid Madagascar, with implications for soil fertility and sustainable land management.

## 2 Material and methods

### Study area

The study area is located in the Mahafaly Plateau and Coastal Plain of southwestern Madagascar (Fig. 1). It is located 90 km south of the town of Toliara (Tuléar), between 23°47'–24°40'S and 43°35'–44°40'E. According to the Köppen climate classification, the region is characterized by a dry semi-arid climate (BS) (Ohba et al. 2016). The annual rainfall varies from 300 mm on the Coastal plain to 600 mm on the Plateau, with a mean value of 400 mm, though primary productivity can vary substantially on very small spatial and temporal scales (Battistini 1965; Ratovonamana et al. 2011, 2024).

According to the soil classification system developed by the International Union of Soil Sciences (IUSS) Working Group on Soil Taxonomy (WRB 2022), the Plateau is characterised by shallow Lithosols with minimal weathering intensity and significant susceptibility to erosion (Alho et al. 2007; Hanisch 2015), as well as Chromic Luvisols with a loamy-clay texture that restricts their agricultural use (Oliveira et al. 2009; Hanisch 2015; Tab. 1). The soil type in the Coastal Plain is Calcareous Regosols, characterised by weak pedogenetic argillisation, an alkaline soil reaction, and a lack of exchangeable hydrogen (Reintam & Kaar 1999). It has a sandy-silty texture with a variable proportion of pebbles and gravel (Hanisch 2015).

### Bait-lamina test

The bait-lamina method introduced by Von Törne (1990) consists of vertically burying a PVC stick containing the bait substance to attract soil organisms. The bait lamina experiments were carried out in the wet and the dry seasons of 2013. In the present study, a bait-lamina stick was 165 mm long, 5 mm wide, and 1.5 mm thick to measure the feeding activity of the soil fauna. In each strip, 20 holes with a diameter of 1.5 mm were drilled 5 mm apart. These apertures were filled with a mixture of

cellulose powder, agar-agar, activated carbon, wheat bran, and whole wheat flour in a ratio of 5.2:1.2:0.8:0.8:2 and water (110 ml) using a knife and fingers. The prepared bait-laminas were dried in a drying oven (60°C) for 8 h, checked to ensure that the bait was secured in the holes, and wrapped in aluminum foil during transportation to the field (Reinecke et al. 2008). During the wet and dry season in 2013, the strips were inserted vertically into the soil such that the uppermost aperture was just below the soil surface. Thus, the bait extended  $19 \times 5 \text{ mm} = 95 \text{ mm}$  into the soil. The number of bait portions eaten (apertures from which the organic bait material had been removed) was considered as the feeding activity, expressed as a percentage of the total filled apertures. At the end of the exposure period of 14 days, bait laminae were retrieved from the soil and visually assessed by holding the strips against the light and counting the empty apertures.

### Litter bag experiment

Litter bags were carried out during the wet season (2011–2012), using two different types of mesh size, which allowed for the exploration of the role of litter fauna in litter decomposition: a mesh size of  $20 \times 20 \text{ }\mu\text{m}$  (fine) that avoided the entrance of meso and macrofauna, and a mesh size of  $5 \times 5 \text{ mm}$  (coarse) that allowed meso and macrofauna to feed on the litter. We chose *Typha* sp. leaves as litter because of their availability and high abundance in the study area. The leaf litter was dried in a solar oven (60°C), weighed into  $5.0 \pm 0.01 \text{ g}$  portions, and placed in fine- and coarse-mesh  $20 \times 20 \text{ cm}$  litter bags. The litter bags were harvested after four months of decomposition. After the removal and transport of samples to the laboratory, the leaves of each litter bag were cleaned, cut into small pieces, and dried at 80 °C for at least 12 h. The dried sample was placed in a numbered, pre-cleaned (at 1000°C) crucible, and incinerated in a muffle furnace at 550 °C for 1 h. After combustion, each sample was weighed again. The ash-free dry weight was calculated by subtracting the ash weight from the litter weights.

### Experimental design

Two different methods were used, i.e., bait lamina-strips to measure detritivore feeding activity and litter bags with two different mesh sizes to assess decomposition. We applied a factorial design to investigate the effects of two contrasting regions (Coastal Plain and Plateau) and land use (9 levels). For the assessment of detritivore activity (bait-lamina strips), we considered both seasons (wet and dry), whereas the litter bags were only deployed

during the wet season. Within each region, we selected five or six villages, respectively (Tab. 1; Figs S1 and S2). Villages were treated as random replicates nested within regions. Across these villages, we sampled nine land-use types representing a gradient of human disturbance and vegetation cover: forest-like pastures, field hedges, tamarind trees, fallow crop fields, half-open pastures, open pastures, old crop fields, new crop fields, and cattle pen hedges (Appendix 1). Not all land-use types were available in every village, resulting in an unbalanced but representative design (Tab. 1, Figs S1,S2).

### Statistical analyses

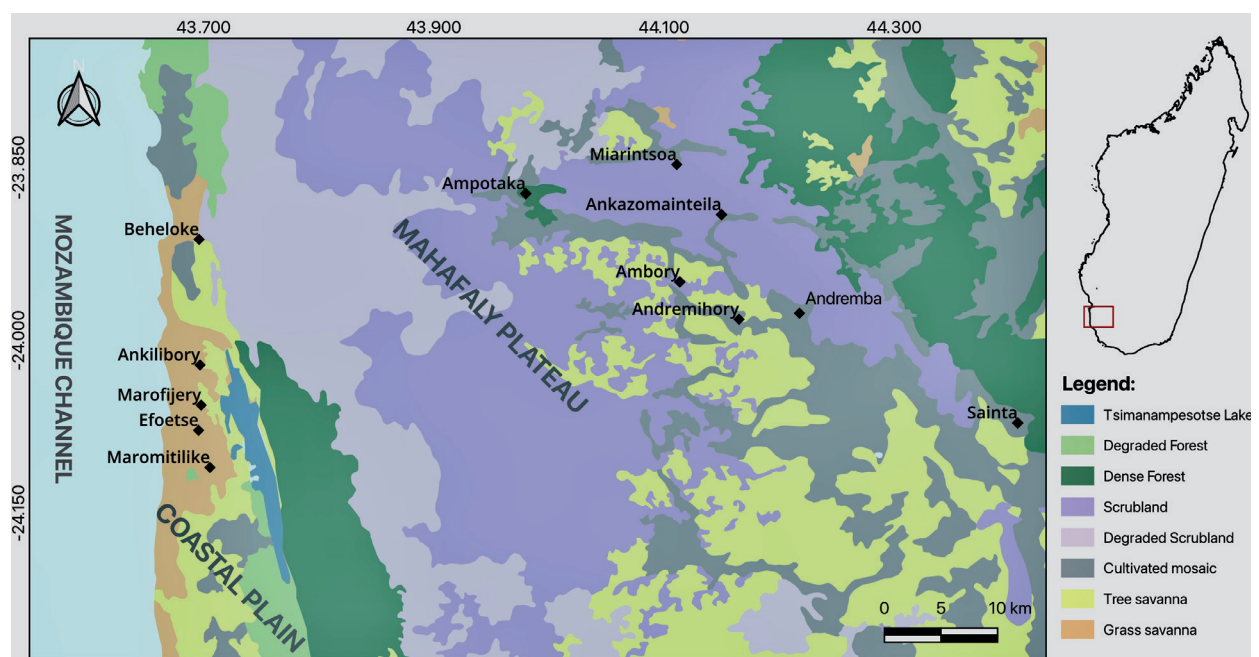
Soil fauna feeding activity (bait-lamina strips) was analyzed using a generalized linear mixed-effects model (GLMM) with a binomial error distribution and logit link function of the lme4 package (Bates et al., 2015). The response variable was binary, coded as 1 when an individual hole in a bait lamina strip was perforated (indicating feeding) and 0 when it remained intact. Bait lamina strips ( $n = 15$  per sampling location with four sampling locations per land use) contained 20 holes each, representing soil depths down to 10 cm. Fixed effects included Region, Land-use type, Season, and Soil depth, as well as all their interactions, to capture potential context-dependent effects on feeding activity. To account for the hierarchical sampling design, random intercepts were included for: Village, nested within Region, Land-use type within each Village, Sampling location within each Land-use type, and Strip number within each Sampling location. Sampling was fully realized wherever a given land-use type was present; when a strip was deployed, it always contained the full complement of 20 holes, and no exclusion criteria were applied. On the Coastal Plain, all villages included all land-use types except: (i) new crop field in Ankilibory during the dry season, and (ii) tamarind tree in Efoetse during the dry season. On the Plateau, the village of Ambory was sampled only for the land-use type field hedge in the dry season, and in Ampotaka and Santa no land-use types were sampled in the wet season. Given these absences, the realized sample comprised 9,660 strips (i.e., 193,200 holes), which is 81.3 % of the 11,880 strips planned (shortfall: 2,220 strips, equivalent to 44,400 holes).

Litter decomposition was quantified as the proportion of mass loss per litterbag (values between 0 and 1). Because the response variable followed a beta distribution, we fitted a generalized linear mixed-effects model (GLMM) with a logit link using the glmmTMB function (Brooks et al., 2017) in R version 4.3. Fixed effects included Region, Land-use type, and Mesh size, as well as their interactions, to test how decomposition responded to



**Table 1.** Geographic and edaphic characteristics of the study villages located in the Coastal Plain and Plateau regions of southwestern Madagascar. The table lists village names, coordinates (DMS, WGS84), altitude, dominant soil types and textures, and indicates which sites were used for bait lamina and litterbag experiments.

| Villages        | Region        | Bait lamina | Litterbags | coordinates (DMS, WGS84)     | Altitude (m) | Soil type           | Soil texture                                                        |
|-----------------|---------------|-------------|------------|------------------------------|--------------|---------------------|---------------------------------------------------------------------|
| Ankilibory      | Coastal Plain | x           | x          | 23°56'24.91"S, 43°40'46.89"E | 15           | Calcareous Regosols | Sandy-silty texture, with variable proportion of pebbles and gravel |
| Beheloke        | Coastal Plain | x           | x          | 23°54'24.04"S, 43°41'19.51"E | 30           | Calcareous Regosols | Sandy-silty texture, with variable proportion of pebbles and gravel |
| Efoetse         | Coastal Plain | x           | x          | 24°04'45.66"S, 43°42'36.32"E | 21           | Calcareous Regosols | Sandy-silty texture, with variable proportion of pebbles and gravel |
| Marofijery      | Coastal Plain | x           | x          | 24°00'42.96"S, 43°42'10.66"E | 21           | Calcareous Regosols | Sandy-silty texture, with variable proportion of pebbles and gravel |
| Maromitilike    | Coastal Plain | x           | x          | 24°06'48.31"S, 43°42'01.66"E | 18           | Calcareous Regosols | Sandy-silty texture, with variable proportion of pebbles and gravel |
| Ambory          | Plateau       | x           | x          | 23°59'09.92"S, 44°05'09.95"E | 218          | Lithosols           | Sandy loam                                                          |
| Ampotaka        | Plateau       | x           | -          | 23°87'25.04"S, 43°97'98.49"E | 126          | Lithosols           | Sandy loam                                                          |
| Andremba        | Plateau       | x           | -          | 23°59'56.85"S, 44°14'00.36"E | 285          | Lithosols           | Sandy loam                                                          |
| Andremihory     | Plateau       | x           | x          | 23°57'58.14"S, 44°08'11.94"E | 241          | Lithosols           | Sandy loam                                                          |
| Ankazomainteila | Plateau       | -           | x          | 23°53'00.63"S, 44°10'00.04"E | 224          | Lithosols           | Sandy loam                                                          |
| Miarintsoa      | Plateau       | x           | x          | 23°50'08.92"S, 44°06'41.24"E | 183          | Chromic Luvisols    | Clay loam                                                           |
| Sainta          | Plateau       | x           | x          | 24°03'35.28"S, 44°25'26.64"E | 358          | Lithosols           | Sandy loam                                                          |



**Figure 1.** Map of the study area.

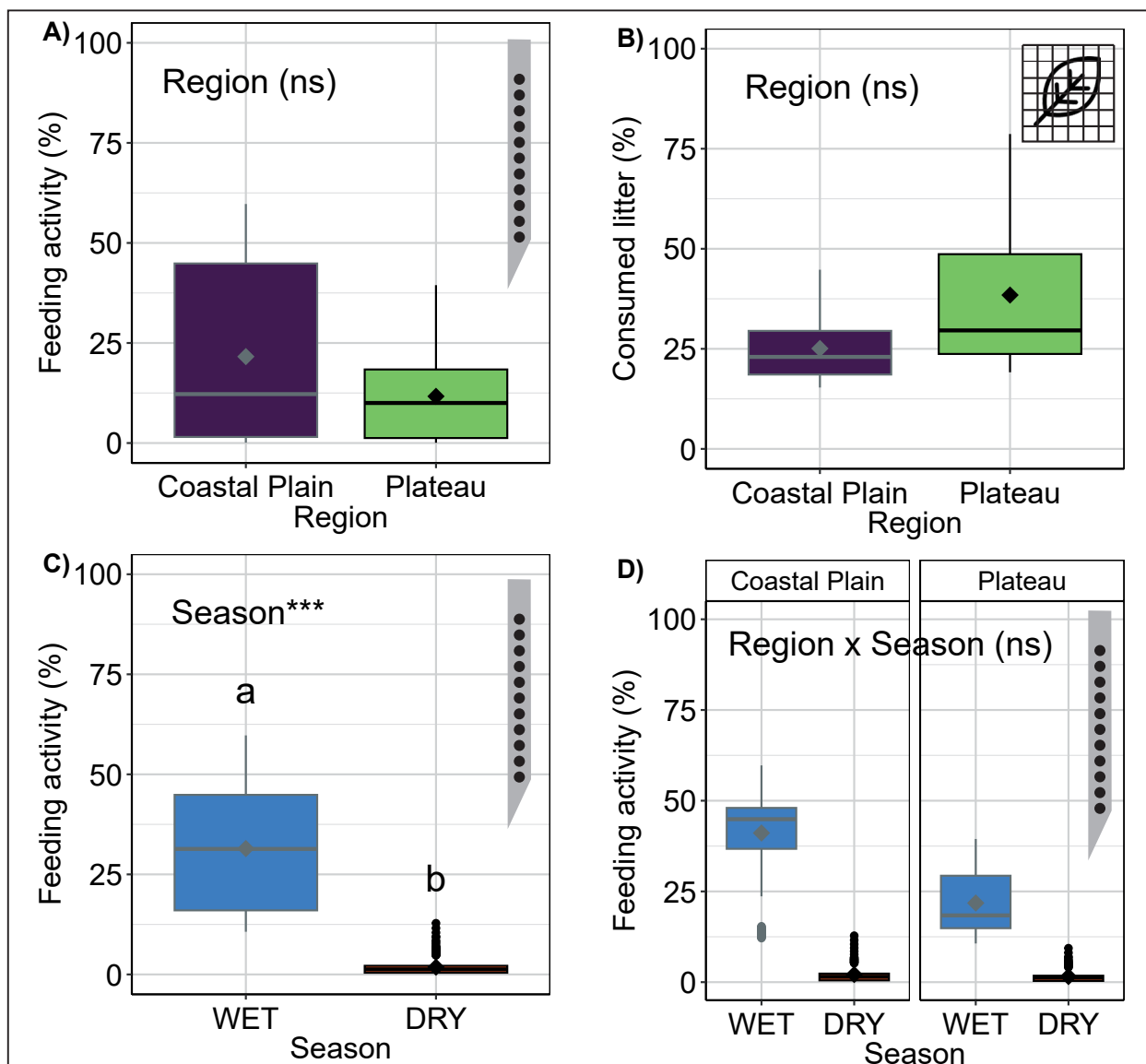
environmental context and faunal access. The two mesh sizes represented different exclusion levels of soil fauna, allowing decomposition driven mainly by microfauna (fine mesh) or by both micro- and mesofauna (coarse mesh). To account for the nested sampling design (two litterbags per mesh size and land use within each site), random intercepts were included for Village (nested within Region), Land-use type (within Village), and Mesh treatment (within Land-use type). The experiment involved 360 litterbags (10 villages  $\times$  9 land-use types  $\times$  2 mesh sizes  $\times$  2 replicates). However, not all bags could be retrieved at harvest (Fig. S2), resulting in a realized sample of 307 litterbags (150 fine- and 157 coarse-mesh), corresponding to 85.3% of the planned total (shortfall: 53 bags). Although replication per treatment was limited,

the large number of treatment combinations constrained further increases in sample size.

### 3 Results

#### Regional differences in soil biological activity (H1)

Soil faunal feeding activity and litter decomposition did not differ significantly between the Plateau and the Coastal plain (Tab. 2, 3; Fig. 2A, B). Both measures showed slightly higher mean values in the Coastal plain, indicating minor regional variation in soil biological activity.



**Figure 2.** Regional and seasonal comparison of soil faunal feeding activity (bait-lamina strips, A, C, D) and litter decomposition (litterbags, B) in southwestern Madagascar. The icons in the right upper corner indicate the method.

### Seasonal variation in soil faunal feeding activity (H2a, H2b)

Feeding activity was strongly affected by season, being significantly higher during the wet season than during the dry season (Tab. 2, 3; Fig. 2C). In the dry season, detritivore feeding activity was nearly absent. Seasonal effects differed slightly between regions but not significantly: while both the Plateau and Coastal plain showed higher feeding activity in the wet season, the difference between dry and season was smaller in the Plateau (Fig. 2D).

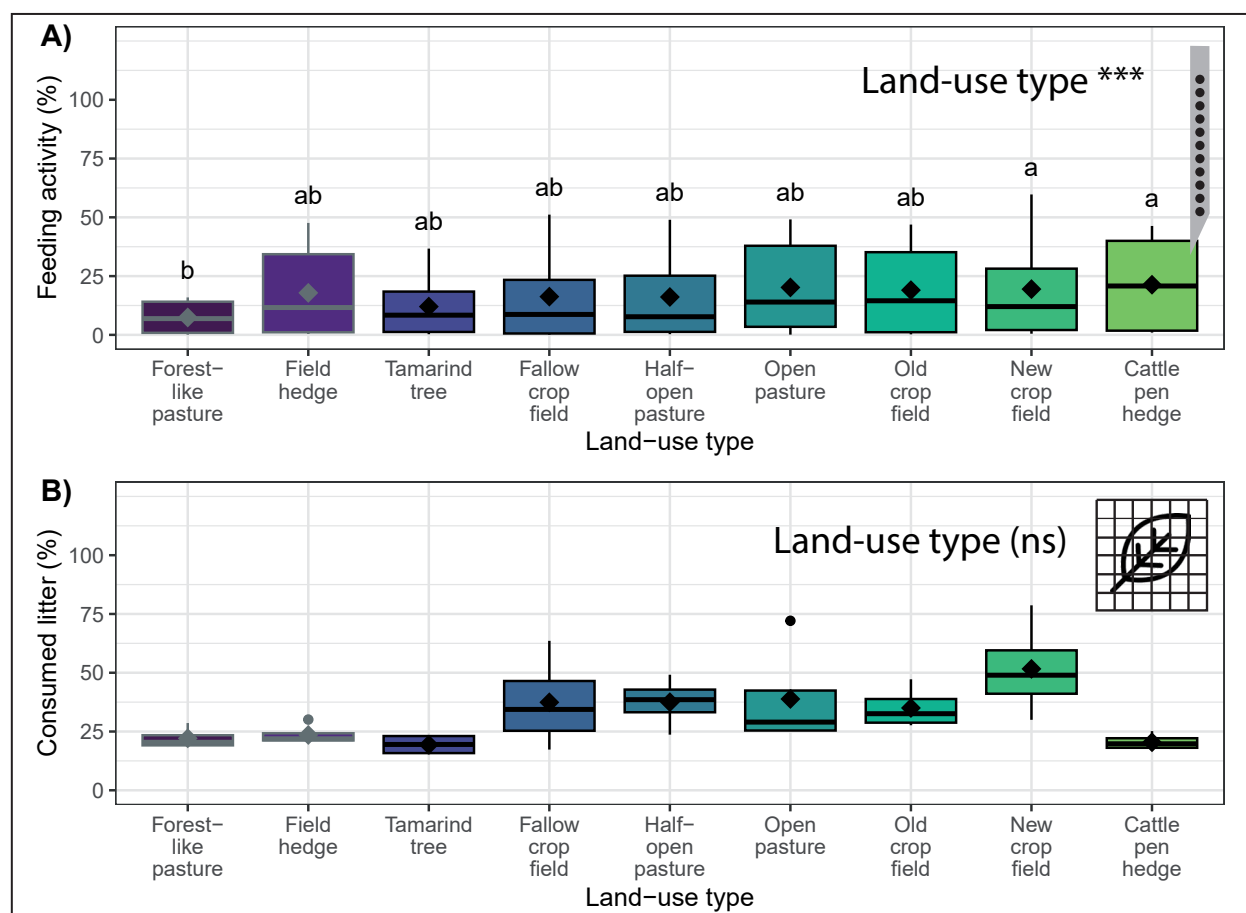
### Effects of land-use intensification on feeding activity and decomposition (H3)

Across land uses ordered from closed, litter-rich systems to open, disturbed systems, bait-lamina feeding activity increased with land-use intensity, whereas no effects were found for litter decomposition (Tab. 2, 3; Fig.

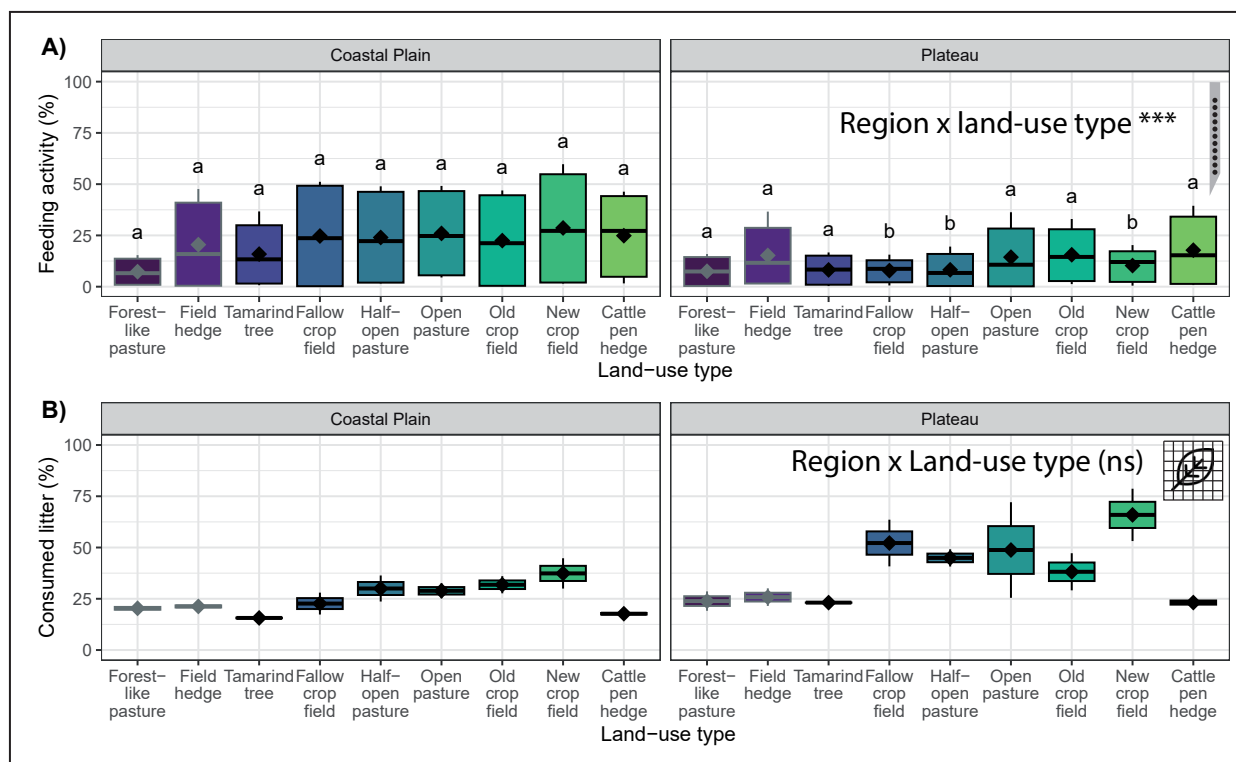
3A, B). Cattle pen hedges and new crop fields showed the highest values, whereas forest-like pastures had the lowest feeding activity. All other land-use types were not different from the others.

### Interaction between region and land use (H4)

Feeding activity across land use types was different in the two regions (Tab. 2, 3; Fig. 4A, B). Feeding activity varied more among land-use types on the Plateau but not in the Coastal Plain, indicating that site-specific conditions enhanced differences in soil faunal activity. On the Plateau, significantly low feeding activity occurred in fallow crop fields, half-open pastures and new crop fields. Although the Tukey post-hoc comparisons identified significant differences from these three land-use types, the overall mean pattern did not show a simple monotonic gradient (i.e., from higher land-use intensity to higher activity).



**Figure 3.** Effects of land-use type on soil faunal feeding activity (A) and litter decomposition (B) across a gradient of decreasing vegetation cover and litter input in southwestern Madagascar. Feeding activity was measured with bait-lamina strips ( $n = 9,660$ ). Distinct letters indicate significant pairwise differences among land-use types (Tukey post hoc tests,  $p < 0.05$ ). Litter decomposition was assessed as the percentage of consumed litter from litterbags ( $n = 307$ ). Boxplots show medians, interquartile ranges, and mean values (diamonds). The icons in the right upper corner indicate the method.



**Figure 4.** Effects of land-use type on soil faunal feeding activity (A) and litter decomposition (B) in the Coastal Plain and Plateau regions of southwestern Madagascar. Feeding activity, measured with bait-lamina strips ( $n = 9,660$ ). Distinct letters indicate significant pairwise differences among land-use types within each region (Tukey post hoc tests,  $p < 0.05$ ). Litter decomposition, expressed as the proportion of consumed litter in litterbags ( $n = 307$ ). Boxplots show medians, interquartile ranges, and mean values (diamonds). The icons in the right upper corner indicate the method.

Litter decomposition, in turn, did not show a significant region  $\times$  land-use interaction, even though mean decomposition rates varied across land-use types. This lack of statistical significance may stem from the limited replication of litterbags per land-use type ( $n = 2$  per mesh size), which reduced statistical power.

#### Effects of soil depth on feeding activity (H5)

Soil feeding activity generally increased unexpectedly with increasing soil depth (Tab. 2, 3; Fig. 5). In the wet season, feeding activity increases with depth in most land-use types. The notable exception were the forest-like pastures (suggested lowest land-use intensity) in both regions, and the tamarind trees on the Plateau, where the wet trend for soil depth was not significant. In the dry season, trends with depth were more flat and less often significant with three out of nine land use-types did not show a significant difference in both regions. Although feeding activity in most land-use types increased with depth or were stable, only in tamarid trees in the Coastal Plain feeding activity decreased significantly with depth, although the magnitude was very low.

#### Faunal contribution to litter decomposition (H6)

Litter decomposition showed no effect between region, land use, and mesh size (Tab. 2, 3; Fig. 6). Overall, decomposition was slightly higher in coarse-mesh litterbags than in fine-mesh ones, indicating a higher contribution of meso- and macrofauna to litter breakdown. However, the magnitude and direction of this effect differed among regions and land-use types. On the Plateau, coarse-mesh bags tended to show greater litter loss and higher variation than fine-mesh ones. In the Coastal Plain, the small mesh size had less variability across land types on litter breakdown.

## 4 Discussions

This study aimed to disentangle how climate, land use, and soil fauna jointly shape decomposition processes in the semi-arid ecosystems of southwestern Madagascar. By combining bait-lamina and litterbag approaches across two climatic regions, multiple land-use types, and seasonal and vertical gradients, we provide the first integrative



assessment of soil biological activity in this understudied biodiversity hotspot. Our results show that soil moisture availability is the dominant driver of faunal feeding activity, with pronounced seasonal differences but surprisingly weak regional contrasts. Land-use intensity influenced only feeding activity but not litter decomposition. Faunal activity often peaked in stronger managed systems rather

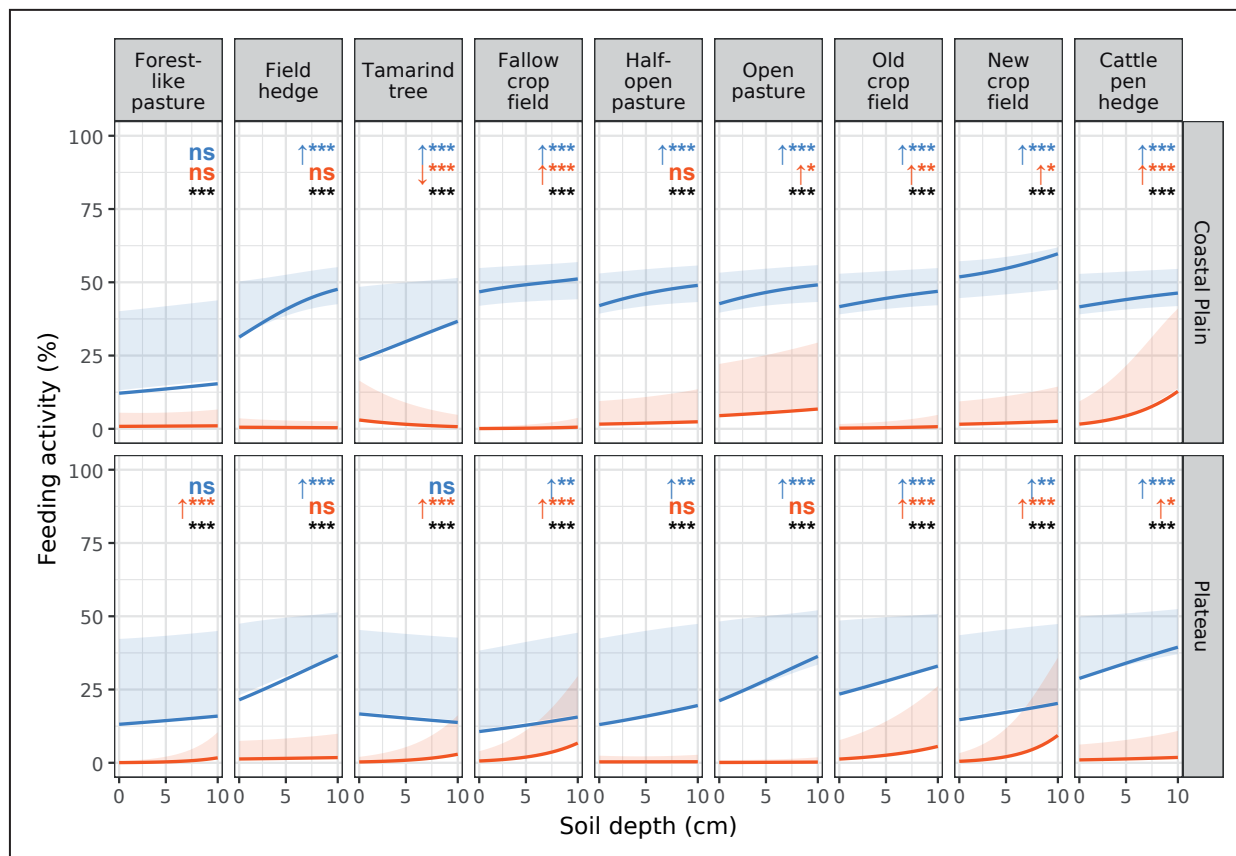
than in the least disturbed habitats. Feeding activity was lowest near the surface and increased with soil depth and strongly reduced during the dry season. Decomposition responses were not modulated by litterbag mesh size, but likely rather due to the low number of replication than no effect of soil organisms and land-use types. Together, these findings highlight that the functioning of decomposer

**Table 2.** Type III Wald  $\chi^2$  tests from the generalized linear mixed-effects model (GLMM) analyzing the effects of Region (Plateau vs Coastal Plain), Land-use type (9 levels), and Mesh size (fine and coarse) on litter decomposition. The model was fitted using the glmmTMB function with a beta error distribution and logit link (family = beta\_family(link = "logit").  $\chi^2$ : chi-square statistics, Df: degrees of freedom, and associated p-values.

|                          | Chisq | Df | Pr(>Chisq) |
|--------------------------|-------|----|------------|
| (Intercept)              | 28.2  | 1  | <0.001     |
| Region                   | 0.2   | 1  | 0.683      |
| Land Use                 | 8.1   | 8  | 0.423      |
| Mesh                     | 0.1   | 1  | 0.756      |
| Region : Land Use        | 10.5  | 8  | 0.231      |
| Region : Mesh            | 0.5   | 1  | 0.484      |
| Land Use : Mesh          | 5.6   | 8  | 0.695      |
| Region : Land Use : Mesh | 10.2  | 8  | 0.249      |

**Table 3.** Type III Wald chi-square tests for fixed effects in the generalized linear mixed model (GLMM) of soil faunal feeding activity. Results are based on a binomial GLMM (glmer) with the proportion of perforated bait-lamina holes (0 = not eaten, 1 = eaten) as response variable. Fixed effects included Region (Coastal Plain vs. Plateau), Season (Dry vs. Wet), Land-use type (nine categories), and Soil depth (continuous, 0 – 10 cm), and all interactions.  $\chi^2$ : chi-square statistics, Df: degrees of freedom, and associated p-values. Asterisks indicate significance.

|                                              | $\chi^2$ | Df | p-value |     |
|----------------------------------------------|----------|----|---------|-----|
| (Intercept)                                  | 203.7    | 1  | <0.001  | *** |
| Region                                       | 0.6      | 1  | 0.443   |     |
| Season                                       | 610.6    | 1  | <0.001  | *** |
| Land-use type                                | 46.1     | 8  | <0.001  | *** |
| Soil depth                                   | 120.5    | 1  | <0.001  | *** |
| Region : Season                              | 1.4      | 1  | 0.245   |     |
| Region : Land-use type                       | 64.0     | 8  | <0.001  | *** |
| Region : Soil depth                          | 18.5     | 1  | <0.001  | *** |
| Season : Land-use type                       | 331.5    | 8  | <0.001  | *** |
| Season : Soil depth                          | 62.0     | 1  | <0.001  | *** |
| Land-use type : Soil depth                   | 125.0    | 8  | <0.001  | *** |
| Region : SeasonLand-use type                 | 282.9    | 8  | <0.001  | *** |
| Region : Season : Soil depth                 | 18.5     | 1  | <0.001  | *** |
| Region : Land-use type : Soil depth          | 124.3    | 8  | <0.001  | *** |
| Season : Land-use type : Soil depth          | 132.1    | 8  | <0.001  | *** |
| Land-use type : Region : Season : Soil depth | 135.6    | 8  | <0.001  | *** |



**Figure 5.** Effects of soil depth and season on soil faunal feeding activity across nine land-use types in two regions of southwestern Madagascar (Coastal Plain and Plateau). Model predictions of feeding activity (%) derived from bait-lamina strips are shown for the wet (blue) and dry (red) seasons, with shaded areas representing 95% confidence intervals. Significance annotations indicate (i) differences between seasons (WET vs DRY) and (ii) effects of soil depth within each season (arrows show the direction of change with depth). Significance codes: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ , ns = not significant.

communities in dryland ecosystems is highly context-dependent, driven by interactions among climate, land management, and soil texture.

### H1 – Regional differences in soil biological activity

Contrary to our expectation, feeding activity and litter decomposition did not differ significantly between the Plateau and the Coastal Plain, although mean values were slightly higher in the latter. This suggests that regional differences in soil texture and rainfall (Battistini 1965; Hanisch 2015) were less influential than anticipated, possibly because both systems experience strong moisture limitation during most of the year. Similar findings were reported for other dryland ecosystems, where soil moisture availability rather than mean precipitation governs soil faunal activity (Eggleton et al. 2009; Wall et al. 2012). The low spatial variability in biological activity therefore indicates that both regions are operating near physiological moisture limits for detritivores.

Another explanation for the lack of regional differentiation may be that local heterogeneity within regions, such as differences in vegetation structure, organic matter input, or soil compaction, exceeds the broader regional contrasts. Additionally, long-term land use may have homogenized soil biological conditions, masking climatic or edaphic differences between the Plateau and the Coastal Plain. Because we were unable to measure soil abiotic variables across all land-use types, potential drivers such as soil organic carbon, nutrient availability, or microclimatic buffering (e.g., temperature and humidity fluctuations beneath vegetation cover; Schnabel et al. 2023) remain to be quantified. Future studies combining biotic and abiotic measurements will be essential to disentangle the relative contributions of climate, soil texture, and land use to soil biological functioning in this region.

### H2 – Seasonal variation in feeding activity

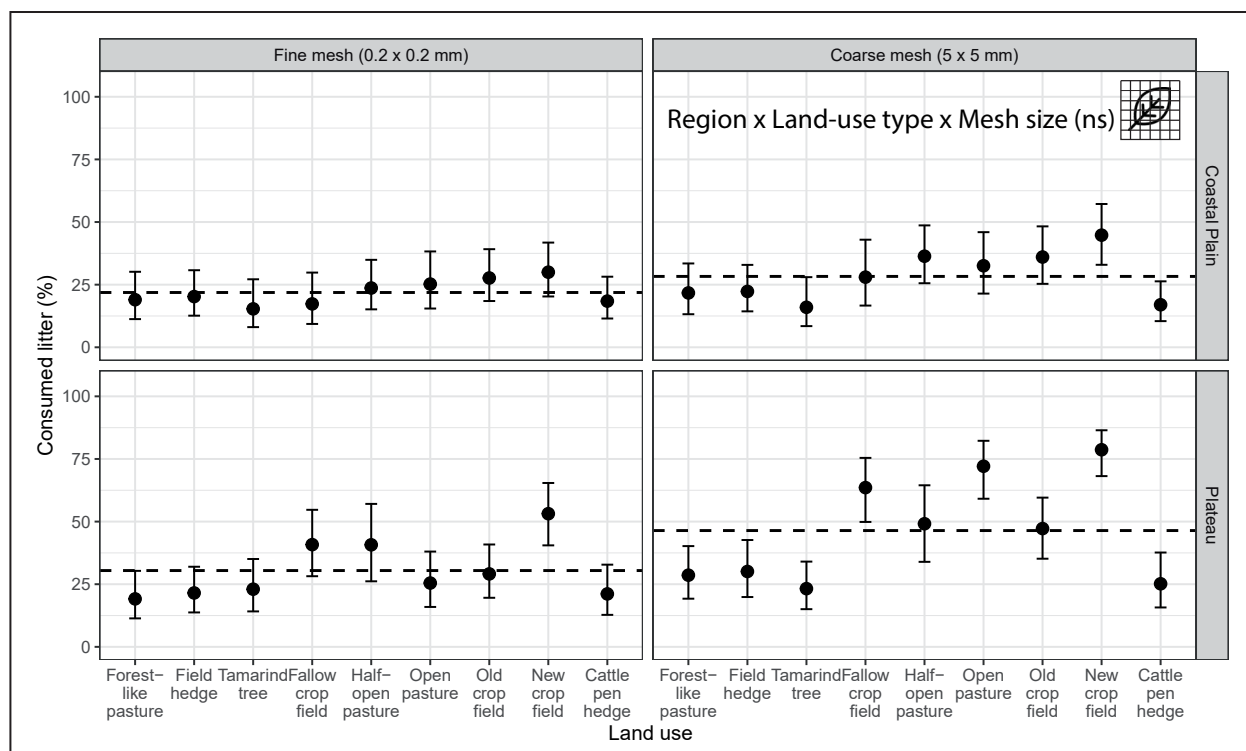
Seasonality exerted the strongest control on soil faunal feeding activity. Feeding activity was nearly absent

during the dry season and peaked during the wet season, confirming the central role of soil moisture in regulating biological processes in semi-arid systems (Larink & Sommer 2002; Reinecke et al. 2008). The slight regional differences (but no significant Region  $\times$  Season interaction) may reflect contrasting soil textures: the sandy soils of the Coastal Plain allow rapid infiltration and drainage, promoting short-term bursts of biological activity after rainfall, whereas the finer Plateau soils retain moisture longer but may limit aeration. However, sandy soils generally contain less organic matter and therefore store less water overall, which could counteract their temporary advantages during rewetting. The balance between rapid infiltration, poor water retention, and oxygen availability may thus create distinct but transient activity patterns across regions.

In semi-arid ecosystems, moisture pulses, i.e., short-lived wetting events following rainfall, are crucial for triggering soil biological activity. These pulses rapidly activate dormant or desiccation-tolerant organisms such as microbes, nematodes, and arthropods, leading to intense but brief periods of respiration and feeding before activity declines again as soils dry (Sponseller 2007; Hastings et al. 2024). The ability to withstand prolonged desiccation varies widely among taxa: many microarthropods and nematodes form resistant

stages (e.g., cysts, dauer larvae, or anhydrobiotic states), allowing survival during dry periods and rapid reactivation after rewetting (Treonis & Wall 2005). Consequently, the composition and functional traits of detritivore communities likely determine how strongly soil faunal activity responds to moisture pulses.

Future studies integrating community composition data, identifying which groups or functional guilds dominate under different land-use and climatic conditions, could therefore provide key mechanistic insight. For instance, communities dominated by taxa with strong drought tolerance or rapid recovery capacity may sustain decomposition even under high climatic variability, whereas sensitive taxa could amplify seasonal contrasts. Linking feeding activity to the trait composition of decomposer communities would thus help clarify the resilience and temporal dynamics of soil functioning in tropical drylands. A limitation of the present study is the lack of time-series data. Feeding activity was assessed only once per season, providing a strong spatial but limited temporal resolution. Previous work from temperate regions has shown pronounced short-term fluctuations in soil faunal activity and decomposition in response to rainfall events (Asato et al. 2025; Thakur et al. 2018; Siebert et al. 2023). Capturing such dynamics would require repeated measurements



**Figure 6.** Effects of land-use type, region, and mesh size on litter decomposition in southwestern Madagascar. Displayed are model-predicted mean percentages of consumed litter ( $\pm$  95% confidence intervals) from fine- ( $0.2 \times 0.2$  mm) and coarse-mesh ( $5 \times 5$  mm) litterbags in the Coastal Plain and Plateau region in southwestern Madagascar. Dashed lines indicate the overall mean within each panel. The icon in the right upper corner indicates the method.

at shorter intervals, ideally spanning pre-rainfall, peak-moisture, and drying phases. However, the extremely large number of strips deployed across seasons, land-use types, and villages (11,860 in total, 9,660 harvested) precluded additional sampling rounds. Future studies could therefore focus on a smaller subset of land-use types or selected locations to enable repeated sampling. Such designs would help quantify the timing, intensity, and duration of faunal responses to rainfall and provide a more detailed understanding of ecosystem resilience and recovery during seasonal transitions.

### **H3 – Land-use effects on feeding activity and decomposition**

Only feeding activity but not litter decomposition varied significantly among land-use types arranged along a gradient of vegetation cover and litter input. Surprisingly, feeding activity increased with land-use intensity, with the highest values in cattle pen hedges and new crop fields and the lowest in forest-like pastures. This pattern contrasts with findings from humid and temperate ecosystems, where dense vegetation cover and high litter input usually enhance decomposition (Römbke et al. 2006; Birkhofer et al. 2011). However, it aligns with results from nutrient-poor or disturbed drylands, where moderate land use and agricultural management can locally increase resource availability for decomposers especially due to fertilizer or manure (Hamel et al. 2007; Faust et al. 2015). In our study, land-use intensity and further attributes like vegetation cover were not directly measured but inferred from field observations of vegetation cover, litter input, and disturbance. Quantitative indices of land-use intensity typically integrate multiple factors such as fertilizer or manure inputs, tillage frequency, grazing pressure, and biomass removal (Blüthgen et al. 2012; Allan et al. 2015). Including such standardized metrics would allow stronger inference about how specific management practices influence soil biological activity. In southwestern Madagascar, cultivated or recently disturbed fields may receive more organic amendments, ash, or occasional watering than tree-dominated or fallow systems, potentially stimulating microbial and faunal activity despite their reduced plant cover.

The observed divergence between bait-lamina and litterbag responses for the different land-use types also suggests that only the bait-lamina strips capture aspects of decomposition. Bait-lamina primarily reflects the feeding potential of surface-dwelling fauna responding rapidly to transient inputs, whereas litterbags integrate microbial and faunal decomposition processes over time.

The high variability in litter bag data suggests specific activities of the decomposer activity. A higher replication of litter bags is therefore key to better assess litter decomposition. In managed systems with low organic matter and high disturbance, short-term faunal feeding may be high due to fresh inputs or increased aeration, while long-term litter decomposition remains limited by low moisture or substrate quality. Together, these findings underscore that in semi-arid agricultural landscapes, soil biological activity does not necessarily decline with land-use intensity, but instead depends on the type, timing, and distribution of organic and moisture inputs.

### **H4 – Interaction between region and land use**

A significant interaction between region and land use was found for feeding activity but not for decomposition. Feeding activity differed more strongly among land-use types on the Plateau, suggesting that regional conditions (e.g., soil moisture retention, litter quality) modulate the impact of land use on fauna. However, the lack of a consistent gradient across land uses implies that local factors such as vegetation composition and microclimate override general trends. The absence of a significant interaction for decomposition may result from the limited replication of litterbags, but also indicates that microbial-driven processes are less sensitive to land-use contrasts than faunal feeding.

### **H5 – Depth-dependent feeding activity**

Feeding activity unexpectedly increased with soil depth, particularly during the wet season. This pattern contrasts with findings from temperate regions, where activity usually declines with depth due to reduced organic matter and oxygen availability (Von Törne 1990; Römbke et al. 2006). In the semi-arid soils of southwestern Madagascar, however, surface layers dry rapidly and experience large temperature fluctuations, while deeper horizons retain moisture and maintain more stable thermal conditions. These microclimatic refuges may allow soil fauna to remain active longer and feed more continuously during the wet season (Reinecke et al. 2008). During the dry season, activity declined across all depths, indicating that prolonged drought suppresses even these deeper faunal communities.

Differences among land-use types, with stronger depth responses in croplands and hedges, may reflect variation in rooting depth, organic matter infiltration, and shading effects on soil microclimate. Agricultural management

practices such as ploughing, irrigation, or manure application can also promote organic matter transport and biopore formation in deeper layers, supporting higher faunal activity below the surface (Teramage et al. 2023; Kautz 2015). Conversely, compacted or bare soils in degraded pastures may limit oxygen diffusion and root penetration, reducing deep-soil habitat quality. From a management perspective, maintaining or enhancing deeper soil biological activity could be achieved through measures that stabilize soil moisture and promote organic matter transfer to depth. Practices such as mulching, the use of deep-rooted perennial vegetation, reduced tillage, and regular organic amendments (e.g., compost or manure) can improve soil structure and water infiltration, creating more favorable conditions for detritivores in sub-surface layers (Demo & Asafe Bogale 2024). Such approaches not only sustain soil faunal communities but also enhance carbon sequestration and nutrient cycling in semi-arid agroecosystems.

## H6 – Mesh-size effects on litter decomposition

Litter decomposition showed no significant effects of Region, Land-use type, or Mesh size (Fig. 6), indicating that the relative contribution of meso- and macrofauna to litter breakdown did not differ substantially across sites or environmental contexts. The absence of strong mesh-size effects suggests that microbial and microfaunal processes dominated litter decomposition under the prevailing dry conditions, while larger decomposers contributed little to overall mass loss. This aligns with findings from other semi-arid systems, where soil fauna activity is often constrained by low and highly variable moisture availability (Torsekar et al. 2024).

Although mean decomposition rates were slightly higher in coarse-mesh than in fine-mesh litterbags, this difference was small and inconsistent among regions. On the Plateau, coarse-mesh bags tended to show somewhat greater litter loss and higher variability, whereas decomposition in the Coastal Plain was more uniform across land-use types. Such patterns may reflect localized variation in faunal abundance or microclimatic conditions rather than systematic differences among treatments.

As mentioned previously, the low replication limits the statistical power to detect subtle effects, particularly given the large spatial and land-use heterogeneity of the study design. Increasing replication within a reduced set of land-use types or focusing on selected microhabitats could improve future assessments of faunal contributions. Additionally, combining litterbag approaches with direct

assessments of decomposer community composition or activity (e.g., through fauna extraction or enzyme assays) would help disentangle microbial versus faunal pathways of litter decomposition in tropical drylands.

## 5 Conclusions

The combined use of bait-lamina and litterbag assays revealed that soil faunal activity but not decomposition are tightly linked to water availability and land management. While bait-lamina tests capture short-term feeding responses to moisture, litterbags can theoretically integrate longer-term breakdown processes including microbial activity. The weak correspondence between the two suggests that distinct components of the decomposer community respond differently to environmental stress. Maintaining vegetation cover, organic matter input, and soil structure is therefore essential to sustain soil biotic functions in dryland agroecosystems. Future studies should include continuous soil moisture monitoring and faunal community analyses to better link functional activity with biodiversity patterns.

## Supplementary Material

Supplementary material, including Appendix, Figures S1–S2, and Tables S1–S2, is available online.

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