

Section: Ecology, Behavior and Bionomics Effects of improved *Mimosa caesalpinifolia* fallows and nutrient management on soil arthropod communities in subsequent upland rice cultivation in eastern Amazonia

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Abstract

Frequent slash-and-burns and shortening fallow periods reduce soil fertility and agricultural productivity and threaten the sustainability of shifting cultivation agroecosystems. Improved fallows established with fast-growing N₂-fixing tree legumes have been proposed as a strategy to restore declining soil fertility. Here, we evaluate the legacy effects of improved *Mimosa caesalpiniiifolia* Benth. fallows on soil surface macrofauna and topsoil mesofauna communities during the subsequent upland rice cultivation cycle, and we assess the additional effects of nutrient management. The study was conducted in Pirapemas county, eastern Amazonia. We compare four pairs of rice fields following six-year-old *M.caesalpiniiifolia* fallows vs. same-aged spontaneous secondary forests, and further compare three nutrient management treatments (control, slash-and-burn, and NPK fertilization). We captured soil surface macrofauna with pitfall traps, and extracted topsoil (0-5 cm + litter layer) mesofauna using the Berlese–Tullgren method. Legacy of preceding fallow vegetation significantly affected soil arthropod communities, as indicated by NMDS and PCA analyses. Soil surface Hymenoptera and Araneae were significantly less abundant following *M.caesalpiniiifolia* fallows than after spontaneous secondary vegetation, suggesting vegetation legacy effects on higher trophic levels. In contrast, nutrient management (fertilizer/ash sub-treatments) in the rice fields only had weak effects, limited to increases in Hymenoptera and Hemiptera abundance under NPK fertilization and we also find only weak associations between topsoil mesofauna and soil chemistry. In order to be ecologically sustainable, improved fallow management in shifting cultivation agroecosystems needs to limit potential negative impacts on invertebrate communities, more research on fallow legacies is warranted.

1. Introduction

Slash-and-burn shifting cultivation is a millenary land-use system and continues to sustain approximately 200–500 million people (ca. 7% of the world's population), mainly in the humid tropics. However, increasing fire frequency and shortening fallow cycles have driven a vicious cycle of ecological degradation, declining land productivity, and ultimately rural poverty (Styger et al. 2009; Jacovac et al. 2016, Abrell et al. 2024). Improved fallows incorporating fast-growing nitrogen-fixing legume trees represent a promising strategy to address this socioecological crisis by accelerating the accumulation of organic matter and nutrients during the fallow period (Sugiyama et al. 2024), thereby potentially increasing crop yields in the subsequent cultivation cycle. In the eastern periphery of Amazonia, the multifunctional native tree legume *Mimosa caesalpiniiifolia* ("sabiá", "sanção de campo") provides a promising alternative to commonly used exotic enrichment species such as *Leucaena leucocephala* or *Gliricidia sepium*. Besides improving soil fertility, *M.caesalpiniiifolia* fallows generate additional income through the production of high-protein forage for goats (Alves et al. 2011), abundant nectar and pollen for beekeeping (Aleixo et al. 2014), and high-quality wood and charcoal after the fallow period (Paes et al. 2007). In a previous study, we demonstrated increased soil fertility, particularly higher nitrogen availability, in 3–8-year-old *M.caesalpiniiifolia* fallows than in similarly-aged spontaneous secondary forest fallows in central Maranhão State, Brazil (Gehring & Detert 2018). However, whether these

improvements in soil fertility also translate into changes in soil arthropod communities remains largely unknown.

The effects of improved fallows on crop yields in the subsequent cultivation cycle have been frequently postulated, although their effects may vary depending on local environmental conditions and management practices. This is likely due to both the long time-line required (from enrichment plantings to the following cultivation cycle) and methodological difficulties in distinguishing fallow legacy effects from the wide range of interacting ecological factors. Even less is known about the legacy effects of improved fallows on other components of shifting cultivation agroecosystems, particularly soil biodiversity and belowground ecological processes, although recent studies have begun to demonstrate persistent legacy effects on tropical soil microbial communities (Dhungana et al. 2025). The present study aims to evaluate the legacy effects of six-year-old improved *M.caesalpinifolia* fallows - relative to traditional spontaneous secondary forest fallows - on soil surface and topsoil invertebrate communities in a shifting cultivation system in eastern Amazonia. To disentangle nutrient-mediated effects from true fallow legacy effects, we compared three nutrient sub-treatments in rice fields (control without ash or fertilizer input, ash addition through slash-and-burn, and application of synthetic NPK fertilizer). We also examined relationships between soil physicochemical properties and mesofauna communities.

2. Methods

2.1 Study Region

The field experiment was conducted in Pirapemas county, central Maranhão state, eastern periphery of Amazonia (latitude: 3°43'40" S, longitude: 44°13'24" W, elevation: 24–43 m a.s.l.). Climate according to the Köppen–Geiger classification is tropical subhumid (*Aw*). Mean annual precipitation in the study area ranges from 1580 to 1848 mm (based on 15-year climatological records from Chapadinha meteorological station at 80–100 km distance from the study sites; INMET/BDMEP, 2024).

Soils in the study region are highly weathered and classified as Ultisols according to the USDA Soil Taxonomy. The topsoil had a mean texture composed of 29.1% (mainly fine) sand, 50.1% silt and 20.7% clay. Soils were strongly acidic (mean pH in $\text{CaCl}_2 = 4.24$), with low available phosphorus (2.39 mg dm^{-3}), low exchangeable potassium ($4.51 \text{ mmolc dm}^{-3}$), moderate exchangeable calcium ($96.9 \text{ mmolc dm}^{-3}$) and magnesium ($96.5 \text{ mmolc dm}^{-3}$), high potential acidity ($\text{H} + \text{Al} = 61.6 \text{ mmolc dm}^{-3}$), mean cation exchange capacity (CEC) of $267 \text{ mmolc dm}^{-3}$ and mean base saturation (V) of 76.9%. Mean soil organic matter content was 15.3 g kg^{-1} .

Due to frequent slash-and-burn shifting cultivation cycles and shortened fallow periods, secondary regrowth becomes increasingly dominated by pioneer and ruderal vegetation, especially the babassu palm (*Attalea speciosa* Mart., *Arecaceae*). The productivity of shifting cultivation fields is limited, contributing to the socioeconomic vulnerability of rural communities. This context is reflected by the

relatively low economic indicators of Pirapemas municipality, which had a GDP per capita of R\$ 10,470.22 in 2023 (IBGE, 2025).

2.2 Field Experiment

The field experiment was conducted in 2020 at two locations within Pirapemas county, at 18 km distance from another: in the vicinity of the village of São José da Vitória and within the area of the cooperating NGO 'Education and Environment' – EMA. We selected four pairs of neighboring 6-yr.-old forest sites, one site of spontaneous secondary forest regrowth, the other site improved *M.caesalpiniiifolia* fallow alley plantations. The pairs of sites were in close proximity to each other (< 200 m) and had similar soil texture, all sites were approximately level (< 2° inclination) and were fallows which had developed after a previous slash&burn shifting cultivation phase of two years. Fallow regrowth was cut in November 2019 and cultivated with upland rice during the 2020 agricultural year.

Each study site consisted of a 200 m² (20 × 10 m) experimental plot within a larger rice field, located > 30 m from surrounding secondary forest borders. Fields were subdivided, following a split-plot design, into three subplots (resulting in 18 subplots), with the following three sub-treatments (hereafter termed “nutrient management”): control (aboveground fallow vegetation removed, without fertilization), NPK fertilization after fallow vegetation removal, and slash-and-burn without fertilization. The NPK treatment consisted of the application of a 05–30–15 fertilizer formulation to the upland rice crop. Rice was planted using a manual planter at approximately 25 × 25 cm spacing.

The experiment constitutes a split-plot design, with vegetation type (spontaneous secondary forest regrowth vs. improved sabiá fallow) assigned to whole plots and nutrient management (control, slash-and-burn, and NPK fertilization) assigned to subplots within each plot. We sampled all fauna during the rice anthesis phase (at 65–70 days after planting) in the center of each sub-plot.

2.3 Fauna sampling and taxonomy

We captured land surface arthropods in 11 cm diameter pitfall traps installed for 24 hours at each of the 18 sampling points, following standard procedures described in Brown and Matthews (2016). We taxonomically classified all arthropods to the order/suborder level according to RUGGIERO et al. (2015), using morphological keys from Leite and Sá (2010).

We captured mesofauna in the 0–5 cm layer of topsoil plus litter using three 3 cm diameter soil cores per sampling point (50 cm apart). Mesofauna were extracted using Berlese-Tullgren funnels. The undisturbed contents of the three cores were pooled and placed in a funnel exposed to heat and light from 30 W incandescent lamps, inducing the downward migration of mesofauna into collection flasks containing 70% ethanol. Samples were kept moist throughout the 7-day extraction period. All mesofauna specimens were identified to the order or suborder level following the taxonomic keys provided by Triplehorn and Johnson (2005).

Samples were processed in the Entomology Laboratory of Maranhão State University (UEMA). Arthropod morphology was investigated using a stereoscopic microscope (Stemis 305, Zeiss, Germany). After taxonomic confirmation, vouchers were deposited in the Entomological Collection Iraci Paiva Coelho (CIPC) of UEMA.

2.4 Topsoil physicochemistry

Composite topsoil samples (0–5 cm) were collected from each experimental plot for physicochemical characterization. Soil texture (sand, silt and clay contents) and chemical attributes were determined at the Soil Chemistry Laboratory of Maranhão State University (UEMA) using routine laboratory procedures. Soil pH was measured in CaCl_2 solution. Available P was extracted with synthetic ion-exchange resin, K with the Mehlich-1 method, and Ca and Mg with 2M KCl, potential acidity ($\text{H} + \text{Al}$) was estimated using the SMP buffer method. Soil organic matter was determined by the sulfuric oxidation method.

2.5 Data processing and statistics

For each arthropod order we calculated relative abundances and frequencies, and - as the arithmetic mean of the two - the relative importance index. We also computed order richness, evenness, and diversity indices (Simpson, Shannon–Wiener and Pielou). We defined rare orders as those with overall relative abundances $\leq 2\%$ and pooled rare orders for further analyses. Inferential statistical analyses were conducted using abundance data, as abundance represents a directly measured variable with an appropriate error structure for the split-plot design. Relative importance was used exclusively for descriptive purposes to characterize the ecological relevance of arthropod orders, but was not subjected to inferential testing.

All variables were checked for normality of residuals using the Shapiro–Wilk test, and for homogeneity of variance using the Levene test; logarithmic and Box–Cox transformations were applied when necessary. The effects of vegetation type (secondary forest vs. *M.caesalpiniiifolia* fallow), nutrient management (control, slash-and-burn, and NPK fertilization), and their interaction were evaluated using analysis of variance (ANOVA) for a split-plot design. Differences between the two vegetation types were assessed using F-tests derived from the ANOVA model. For variables significantly affected by nutrient management, means were compared using Tukey's HSD post hoc test.

We explore the relationships between topsoil mesofauna community composition and topsoil physicochemistry with Non-metric Multidimensional Scaling (NMDS), using a Bray–Curtis dissimilarity matrix. In order to obtain a stable solution, we conducted ordination in two dimensions ($k = 2$) with 100 random starts (trymax = 100). We assessed the goodness-of-fit of the ordination using the stress value, which represents the degree of distortion between the original dissimilarities and their representation in the two-dimensional ordination space. Environmental and biological variables were fitted onto the NMDS ordination using the envfit function. The significance of each fitted vector was assessed by permutation tests, and only significant ($P \leq 0.05$) and marginally significant ($P \leq 0.10$) variables are displayed in the ordination plot. We used Permutational Multivariate Analysis of Variance (PERMANOVA) to test for

differences in community composition and soil physicochemical characteristics between vegetation types, management systems, and their interaction.

In order to investigate the relationship between macrofaunal and mesofauna community composition we performed a Principal Component Analysis (PCA). Differences in community composition between vegetation types, management systems, and their interactions were evaluated using Multivariate Analysis of Variance (MANOVA). To assess the similarity between macrofaunal and mesofauna assemblages we used Mantel tests (Pearson correlation, 999 permutations) for comparison of dissimilarity matrices, and performed Procrustes analysis to evaluate the congruence between their ordinations.

Finally, as a complementary approach to the NMDS analysis, we explore associations between environmental and biological variables and relationships between mesofauna and macrofaunal variables with Spearman's rank correlations. Given the exploratory nature of correlation matrices and the ecological interdependence between variables we report unadjusted P-values and interpret relationships together with the magnitude of the correlation coefficients and their ecological plausibility.

All statistical analyses were performed using the R statistical software (version 4.4.3) (R Core Team, 2025).

3. Results

3.1 Abundance and composition of soil surface macrofauna and topsoil mesofauna

We captured a total of 618 macrofauna individuals on the soil surface (pitfall traps) and a total of 494 mesofauna individuals from the 0–5 cm topsoil layer (Berlese–Tullgren extraction), distributed across 10 taxonomic orders (macrofauna) and 6 orders (mesofauna). Pitfall traps yielded on average $4.10 \pm SE$ soil surface individuals per sample, while mesofauna extraction yielded $3.98 \pm SE$ individuals per topsoil sample.

Table 1 depicts the absolute and relative composition of soil surface macrofauna orders. Collembola, Hymenoptera, and Hemiptera together accounted for more than 60% of all individuals, with Collembola top-ranking both in abundances and frequencies, followed by Hymenoptera and Araneae. Lower frequencies of Acari and Hemiptera indicate more clustered populations. Six orders (Oribatida, Oligochaeta, Diplura, Blattodea, Diptera, and unidentified taxa) were rare and together combined <4% of total abundance.

Table 1. Composition of soil surface macrofauna orders over all study sites.

Order	Total abundance	Total frequency	Relative abundance (%)	Relative frequency (%)	Importance index
Collembola	209	17	33.82	94.44	64.30
Hymenoptera	101	18	16.34	100.00	58.17
Araneae	64	15	10.36	83.33	46.85
Orthoptera	47	14	7.61	77.78	42.70
Coleoptera	34	14	5.50	77.78	41.64
Acari	56	12	9.06	66.67	37.87
Hemiptera	85	9	13.75	50.00	31.88
Rare*	22	9	3.56	50.00	26.78

*Rare orders were defined as those with relative abundance $\leq 2\%$ of total individuals. The importance index was calculated as the arithmetic mean of relative abundance and relative frequency.

Table 2 shows the absolute and relative composition of topsoil mesofauna orders. Two orders (Collembola and Hymenoptera) were omnipresent and combined >60% of total abundance. Coleoptera were evenly distributed throughout the experiment, whereas Acari and Hemiptera were more clustered. Three rare orders (Oribatida, Araneae, and Blattodea) together combined less than 5% of topsoil mesofauna abundance.

Table 2. Composition of topsoil mesofauna orders over all study sites.

Order	Total abundance	Total frequency	Relative abundance (%)	Relative frequency (%)	Importance index
Collembola	49	17	41.22	94.44	67.63
Hymenoptera	25	18	19.92	100.00	59.96
Coleoptera	224	14	6.71	77.78	42.25
Acari	123	12	11.05	66.67	38.86
Hemiptera	54	9	16.77	50.00	33.39
Rare*	19	9	4.34	50.00	27.17

**Rare orders were defined as those with relative abundance $\leq 2\%$ of total individuals. Orthoptera were not recorded in mesofauna samples due to methodological constraints of the Berlese–Tullgren extraction. The importance index was calculated as the arithmetic mean of relative abundance and relative frequency.

3.2 Impacts of preceding fallow vegetation and nutrient management on soil arthropod orders

Three soil surface macrofauna orders differed significantly between preceding fallow vegetation types (Araneae, Hymenoptera, and Collembola; Fig. 1). Araneae were more abundant in spontaneous secondary vegetation than in *M.caesalpinifolia* fallows ($P = 0.03$; Fig. 1a). Likewise, Hymenoptera showed higher abundances in secondary vegetation ($P = 0.03$; Fig. 1b). In contrast, soil surface Collembola were more abundant in *M.caesalpinifolia* fallows than in spontaneous secondary vegetation ($P = 0.01$; Fig. 1c). Among the topsoil mesofauna, only Collembola differed significantly between vegetation types, with higher abundances in secondary vegetation than in *M.caesalpinifolia* fallows ($P < 0.001$; Fig. 1d).

The effects of nutrient management sub-treatments were limited to only two orders on the soil surface. Hymenoptera abundance was significantly ($P < 0.001$) highest with NPK fertilization, intermediate with slash-and-burn, and lowest in the control treatment (Fig. 2a). Likewise, Hemiptera abundance was significantly higher under NPK fertilization than under both slash-and-burn and control treatments ($P = 0.02$; Fig. 2b).

3.3 Relationships between topsoil physicochemistry and mesofauna community

3.3.1 Nonmetric Multidimensional Scaling

NMDS ordination produced an acceptable two-dimensional solution (stress = 0.15), indicating a reliable representation of multivariate dissimilarities (Clarke, 1993). The ordination showed a partial separation of samples along the first NMDS axis according to vegetation type, whereas samples from different nutrient management treatments largely overlapped (Figure 3). PERMANOVA confirmed a significant effect of vegetation type on community composition (pseudo- $F = 2.654$, $R^2 = 0.14$, $P = 0.038$), whereas nutrient management had no significant effect (pseudo- $F = 0.722$, $R^2 = 0.09$, $P = 0.755$).

Vectors representing mesofauna groups and soil physicochemical variables revealed contrasting associations across the ordination space. Among the environmental variables, exchangeable Ca, Mg, CEC, exchangeable Al, potential acidity (H+Al), clay content and base saturation (V) showed significant associations with the NMDS configuration (envfit, $P < 0.05$), whereas organic matter, potassium and total mesofauna abundance showed marginal associations ($0.05 < P < 0.10$). Base-related soil properties (Ca, Mg, CEC and V) are associated with the negative side of NMDS1, and exchangeable Al, clay content and Coleoptera are associated with the positive side of the same axis. Potential acidity (H+Al) is mainly related to negative values of NMDS2, whereas Collembola are associated with the negative side of NMDS1. Overall, NMDS suggests that topsoil mesofauna community composition is primarily associated with preceding fallow vegetation legacy whereas both the underlying soil physicochemical conditions and nutrient management sub-treatments contribute only little to the observed multivariate variation.

3.3.2 Pairwise correlations

Pairwise correlation analyses identified several – but not many - significant relationships between soil physicochemical properties and topsoil mesofauna community attributes. Collembola abundance was positively related with soil cation exchange capacity (CEC) ($\rho = 0.49$, $p = 0.038$) and also with exchangeable Mg ($\rho = 0.62$, $p = 0.006$), whereas Coleoptera abundance was positively correlated with clay content ($\rho = 0.61$, $p = 0.007$). Both total mesofauna abundance ($\rho = 0.54$, $p = 0.021$) and taxonomic richness ($\rho = 0.60$, $p = 0.009$) were positively related with exchangeable Al^{3+} , and exchangeable Mg was positively correlated with Pielou's evenness index ($\rho = 0.69$, $p = 0.001$). Though the reasons for such specific relationships are unknown or speculative, these pairwise correlations do indicate some relationships between topsoil mesofauna and both soil texture and soil chemical attributes.

3.4 Co-structuring of soil surface macrofauna and topsoil mesofauna communities

We observed positive correlations between soil surface macrofauna predators and topsoil mesofauna attributes. Macrofauna Araneae abundance was positively correlated with mesofauna Shannon diversity ($r = 0.51$, $P = 0.029$) and Simpson diversity ($r = 0.47$, $P = 0.048$). In addition, Araneae abundance was positively associated with mesofauna Collembola abundance ($r = 0.51$, $P = 0.031$). Likewise, macrofauna Hymenoptera abundance was positively correlated with mesofauna Collembola abundance ($r = 0.62$, $P = 0.006$). These relationships suggest that greater mesofauna diversity and Collembola abundance may provide increased food resource availability for predatory macrofauna, thereby supporting higher abundances of Araneae and Hymenoptera (Supplementary Fig. S1).

Co-structuring of topsoil mesofauna and soil surface macrofauna communities

Principal component analysis (PCA) summarizes the multivariate relationships between soil surface macrofauna and topsoil mesofauna (Fig. 5). The first two principal components together explain 41.5% of the total variance (PC1 = 23.5% and PC2 = 18.0%). Variables showing the strongest contributions to the ordination ($\cos^2 > 0.5$) include Shannon, Simpson, and Pielou diversity indices, order richness, and the abundances of Hymenoptera and Collembola.

PC1 is primarily associated with topsoil mesofauna diversity indices (Shan_ms, Sim_ms, Pie_ms and Ric_ms), together with Collembola and Araneae abundances, whereas PC2 is mainly related to soil surface macrofauna variables, particularly Pielou evenness (Pie_mc), Hymenoptera abundance (Hym_mc), Simpson diversity (Sim_mc) and Shannon diversity (Shan_mc).

The PCA ordination reveals a clear separation between spontaneous secondary vegetation and *M.caesalpinifolia* fallows, whereas samples from the three nutrient management treatments show substantial overlap. MANOVA confirms this finding, with significant effects of preceding fallow vegetation on multivariate data distribution ($F_{2,11} = 11.869$, $P = 0.002$), as opposed to non-significant effects of nutrient management ($F_{4,22} = 1.496$, $P = 0.238$), nor any interaction between vegetation type and nutrient management ($F_{4,22} = 1.848$, $P = 0.156$).

4. Discussion

4.1 Improved *M.caesalpinifolia* fallows as a sustainable alternative to traditional shifting cultivation

Shifting cultivation remains one of the dominant agricultural systems for millions of smallholder farmers throughout the humid tropics. However, increasing population pressure has progressively shortened traditional fallow periods, resulting in declining soil fertility, biodiversity loss, and reduced ecosystem resilience. Recent evidence from eastern Amazonia has shown that shortened fallow periods and intensified cultivation are associated with declining soil fertility and increasing weed pressure, threatening the long-term sustainability of shifting cultivation systems (Abrell et al. 2024). In this context, improved fallow systems based on native N₂-fixing tree legumes have emerged as a promising strategy to restore soil fertility, reduce dependence on slash-and-burn practices, and promote more sustainable agricultural production. Understanding whether these improved fallows also generate long-lasting legacy effects on soil biodiversity is therefore essential for evaluating their ecological sustainability.

Absolute abundances of soil invertebrates vary considerably among studies due to differences in geographic location, climatic seasonality, sampling methods, and organism mobility (Huvarinen et al., 2006; Sabu et al., 2011; Correa et al., 2021; Lavelle et al., 2021; Auger et al., 2024), making direct quantitative comparisons difficult. Because our sampling was conducted during the middle of the rainy season, we focused primarily on relative differences among vegetation types and nutrient management treatments rather than on absolute abundance values. Soil surface macrofauna and topsoil mesofauna are key components of tropical agroecosystems because they regulate nutrient cycling, organic matter decomposition, soil structure, and multiple trophic interactions that sustain ecosystem functioning (Fitter et al., 2005; Lavelle et al., 2016; Ball et al., 2022; Santos et al., 2022; Wu et al., 2025).

4.2 Legacy effects of preceding fallow vegetation on soil invertebrate communities

Our study demonstrates that preceding fallow vegetation exerted significant effects on soil invertebrate communities, effects were stronger than of short-term nutrient management during cultivation. Both univariate analyses and multivariate ordinations consistently indicated that six-year-old fallow vegetation legacy significantly structured soil arthropod communities. We detected significant differences between spontaneous secondary forest regrowth and improved *M.caesalpinifolia* fallows in the abundance of Araneae, Hymenoptera, and Collembola, fallow vegetation legacy also explained the separation of communities in both NMDS and PCA analyses.

Vegetation legacy effects are expected because plants influence soil communities through multiple ecological pathways. Differences in litter quantity and quality, root biomass, nutrient inputs, canopy structure, soil moisture, temperature, and habitat complexity modify both food availability and microhabitat conditions for soil invertebrates (Lavelle et al., 2016; Moura et al., 2016; Kostenko et al., 2017; Zhou et al., 2023). These indirect effects frequently persist after vegetation removal, generating

ecological legacy effects that continue to influence belowground communities during subsequent cropping cycles.

Soil invertebrate communities shift during Amazonian secondary forest succession (Mathieu et al., 2005; Serra et al., 2021), while tree diversity and forest composition have been shown to regulate arthropod assemblages in restoration systems (Korboulewski et al., 2016; Ugalde et al., 2024). Likewise, exotic vegetation types, including *Eucalyptus* plantations and introduced pastures, substantially modify soil invertebrate communities compared with native vegetation (Juan-Ovejero et al., 2024; Souza et al., 2026). Our results extend these findings by demonstrating that improved *M.caesalpiniiifolia* fallows also generate measurable legacy effects on soil arthropod communities after conversion to upland rice cultivation.

Our findings indicate that the ecological conditions created during the fallow phase may persist well into the subsequent cropping cycle, reinforcing the importance of fallow management for maintaining soil biodiversity in tropical shifting cultivation systems.

4.3 Nutrient management exerted weaker effects than vegetation legacy

Although soil nutrient availability is widely recognized as an important driver of soil biota, nutrient management exerted comparatively weaker effects on arthropod communities than the legacy of preceding fallow vegetation. Only Hymenoptera and Hemiptera responded significantly to nutrient management, whereas most macrofauna and topsoil mesofauna groups showed no detectable response. Likewise, NMDS and PCA revealed substantial overlap among nutrient management treatments, indicating that short-term fertilization contributed relatively little to the overall variation in community composition.

Our results agree with recent evidence indicating that soil arthropod communities are frequently regulated by multiple environmental factors beyond nutrient availability alone. A global meta-analysis demonstrated that fertilization generally increases soil faunal abundance but has inconsistent effects on diversity and community composition, with responses varying according to fertilizer type, taxonomic group and ecosystem characteristics (Zhu et al., 2023). Similarly, recent studies have shown that vegetation structure, litter quality and long-term soil fertility gradients often explain a greater proportion of arthropod community variation than short-term fertilization treatments (Butler et al., 2025).

This pattern is particularly relevant for shifting cultivation systems, where soil ecological conditions are largely determined during the fallow phase. A recent review emphasized that tropical smallholder farmers rely predominantly on the natural recovery of soil fertility during fallow periods, while external fertilizer inputs are generally limited by economic constraints (Mandah et al., 2025). Under such conditions, vegetation history influences litter production, organic matter accumulation, microbial activity and soil structure over several years, generating ecological legacy effects that may persist well beyond vegetation removal and subsequent crop establishment.

The significant legacy impacts of preceding fallow vegetation observed in the present study likely reflects the cumulative ecological effects generated during the six-year fallow period, whereas nutrient management represented only a short-term disturbance. From an ecological perspective, these findings reinforce the importance of designing improved fallows not only to restore land productivity and nutrient availability, but to also maintain (plant) species diversity. Legacy effects apparently are stronger at higher trophic levels, we find significantly reduced abundances of Hymenoptera and Araneae following *M.caesalpiniiifolia* fallows than after spontaneous secondary vegetation.

4.4 Ecological interactions between soil surface macrofauna and topsoil mesofauna

Although most soil surface macrofauna and topsoil mesofauna groups showed limited direct correlations with another, two soil surface predatory groups—Araneae and Hymenoptera—displayed consistent positive relationships with mesofauna. Soil surface Araneae abundance increased with mesofauna diversity (Shannon and Simpson indices) and with Collembola abundance, whereas Hymenoptera abundance was likewise positively associated with Collembola. These relationships indicate that trophic interactions between predators and their potential prey represent an important mechanism structuring soil community.

Spiders are generalist predators whose abundance is frequently regulated by prey availability and habitat complexity. Using spider gut-content metabarcoding, Chen et al. (2025) demonstrated that prey richness and predator–prey network structure are jointly driven by bottom-up effects of plant diversity and top-down effects of spider communities, while Michalko (2025) highlighted that habitat structure and predator diversity interact to determine food-web organization. Our results are consistent with these findings, as higher mesofauna diversity and greater Collembola abundance were associated with increased abundances of predatory macrofauna.

Collembola are among the most abundant components of soil mesofauna and constitute an important food resource for numerous predatory arthropods. A global meta-analysis demonstrated that Collembola represent one of the principal prey groups for actively hunting spiders, particularly in agricultural habitats, emphasizing their key role in sustaining predator populations and trophic interactions (Birkhofer et al., 2021).

The PCA further supports these ecological relationships by grouping Collembola and predatory macrofauna along the same multivariate gradient, suggesting that these taxa respond to common environmental drivers or are linked through trophic interactions. Nevertheless, correlations alone cannot demonstrate direct predator–prey relationships, and part of these associations may also reflect shared responses to litter quality, habitat complexity and soil physicochemical conditions. Additional studies using gut-content analyses or stable isotopes would be valuable to clarify the mechanisms underlying these interactions.

4.5 Ecological role of Collembola in improved fallow systems

Collembola exhibited contrasting responses depending on the sampled habitat. Soil surface Collembola were significantly more abundant in areas previously occupied by *M.caesalpiniifolia* fallows, whereas topsoil Collembola abundance was significantly greater following spontaneous secondary vegetation. This apparently contrasting response highlights the ecological heterogeneity of Collembola communities and suggests that different functional groups responded to distinct environmental conditions created by the preceding fallow vegetation.

Collembola comprise one of the most abundant and functionally important groups of soil mesofauna. Most species are fungivores, detritivores or microbivores, feeding on fungi, microorganisms, algae and decomposing organic matter, thereby contributing directly to litter decomposition, nutrient cycling and soil organic matter formation (Wang et al., 2017; Hänisch et al., 2022). Beyond their contribution to decomposition processes, Collembola also occupy a central position in soil food webs because they constitute an important prey resource for numerous predatory arthropods.

Recent studies have further demonstrated that Collembola do not constitute a functionally uniform group. Soil-dwelling species are frequently associated with fungal-based food webs and relatively stable soil microhabitats, whereas surface-dwelling species are more strongly influenced by vegetation structure, litter quality and fresh plant-derived resources (Brousseau et al., 2024; Potapov et al., 2025). These ecological differences may explain why Collembola responded in opposite directions between the soil surface and the topsoil in the present study.

Although our taxonomic resolution was limited to the order/class level, the contrasting responses observed between soil surface and topsoil Collembola suggests that improved *M.caesalpiniifolia* fallows impact different ecological compartments of the soil environment in distinct ways. Future studies identifying Collembola to family or species level and incorporating functional classifications would help clarify the mechanisms underlying these contrasting responses.

Nutrient availability is generally considered an important driver of soil biological communities, but our results suggest that legacy effects of preceding fallow vegetation outweigh the short-term effects of ashes or mineral fertilization. Sensitivity of arthropod communities to altered preceding fallow vegetation appears to be concentrated especially higher up the food web (Araneae and Hymenoptera). A better understanding of vegetation legacy effects on soil communities is essential for developing more sustainable management strategies for smallholder agriculture throughout the humid tropics. Our results provide a foundation for future studies addressing the functional implications of fallow vegetation legacies on soil ecosystem processes and food-web dynamics.

Declarations

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Ethical Approval:

not applicable

Conflicts of interest/Competing interests:

not applicable

Authors' contributions:

Dayane Valessa Barros Froz and Christoph Gehring were responsible for the experimental layout, execution of the field experiment and sampling campaigns and for data processing and manuscript synthesis, Maria Elisabeth Detert coordinated field support, Marcos da Costa Teixeira helped with the statistical analyses and Ester Azevedo do Amaral gave valuable support in invertebrate taxonomy.

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Figures

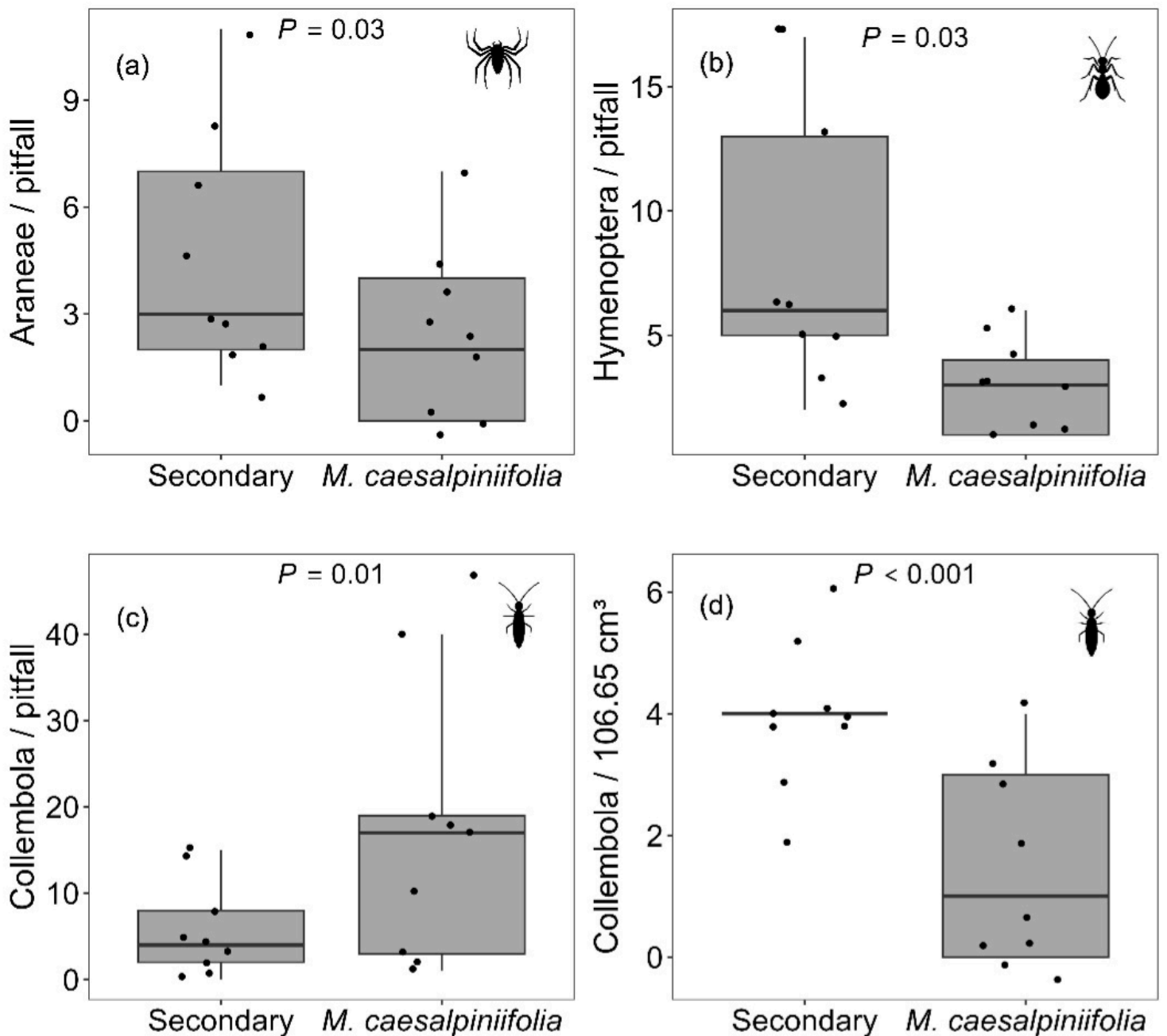


Figure 1

Effects of preceding fallow vegetation (spontaneous secondary vegetation vs. *M. caesalpinifolia* fallows) on the abundance of dominant soil arthropod groups. (a) Soil surface Araneae abundance. (b) Soil surface Hymenoptera abundance. (c) Soil surface Collembola abundance. (d) Topsoil Collembola abundance. Boxes represent the interquartile range (IQR), horizontal lines indicate the median, whiskers extend to the minimum and maximum values, and dots represent individual observations. P-values shown in each panel correspond to F-tests for the effect of vegetation type.

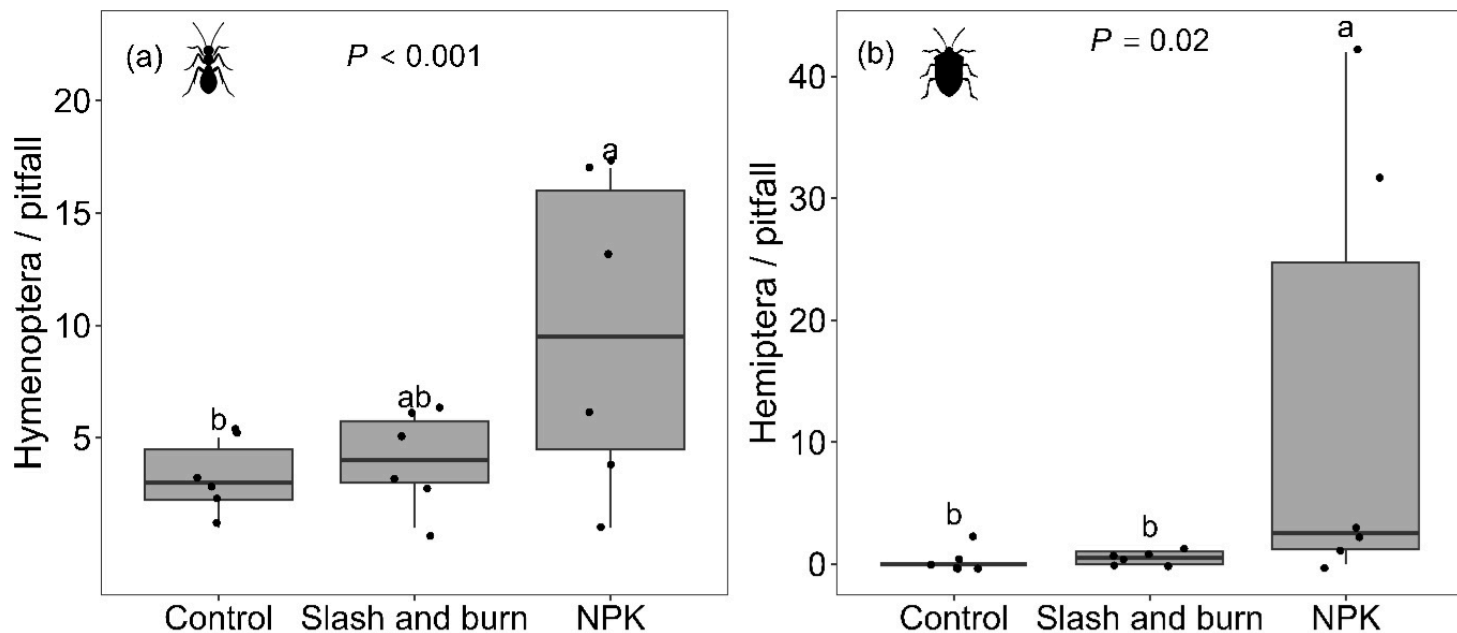


Figure 2

Effects of nutrient management (control, slash-and-burn, and NPK fertilization) on the abundance of dominant soil surface arthropod groups. (a) Hymenoptera abundance. (b) Hemiptera abundance. Different letters indicate significant differences between nutrient management treatments according to Tukey's HSD test ($\alpha = 0.05$). Boxes represent the interquartile range (IQR), horizontal lines indicate the median, whiskers extend to the minimum and maximum values, and dots represent individual observations.

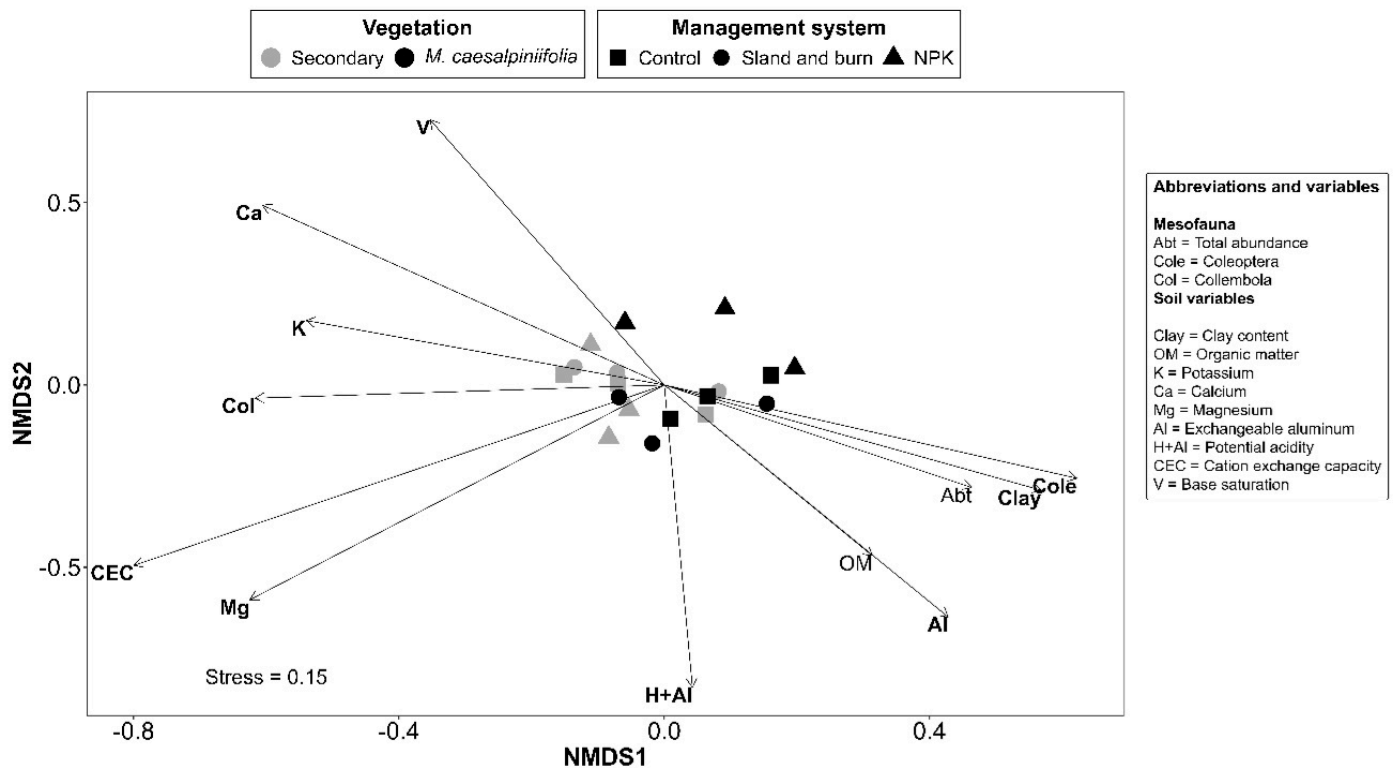


Figure 3

NMDS ordination of treatments/subtreatments, topsoil physicochemical properties, and mesofauna arthropod communities based on Bray–Curtis dissimilarities. Points represent sampling units, with vegetation types distinguished by grayscale shading (secondary forest regrowth in gray and *Mimosa caesalpinifolia* fallow in black) and nutrient management systems distinguished by symbol shape (Control, Slash and burn, and NPK fertilization). Vectors indicate the direction and strength of associations of mesofauna groups and soil physicochemical variables with the ordination configuration. Stress = 0.15.

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Figure 4

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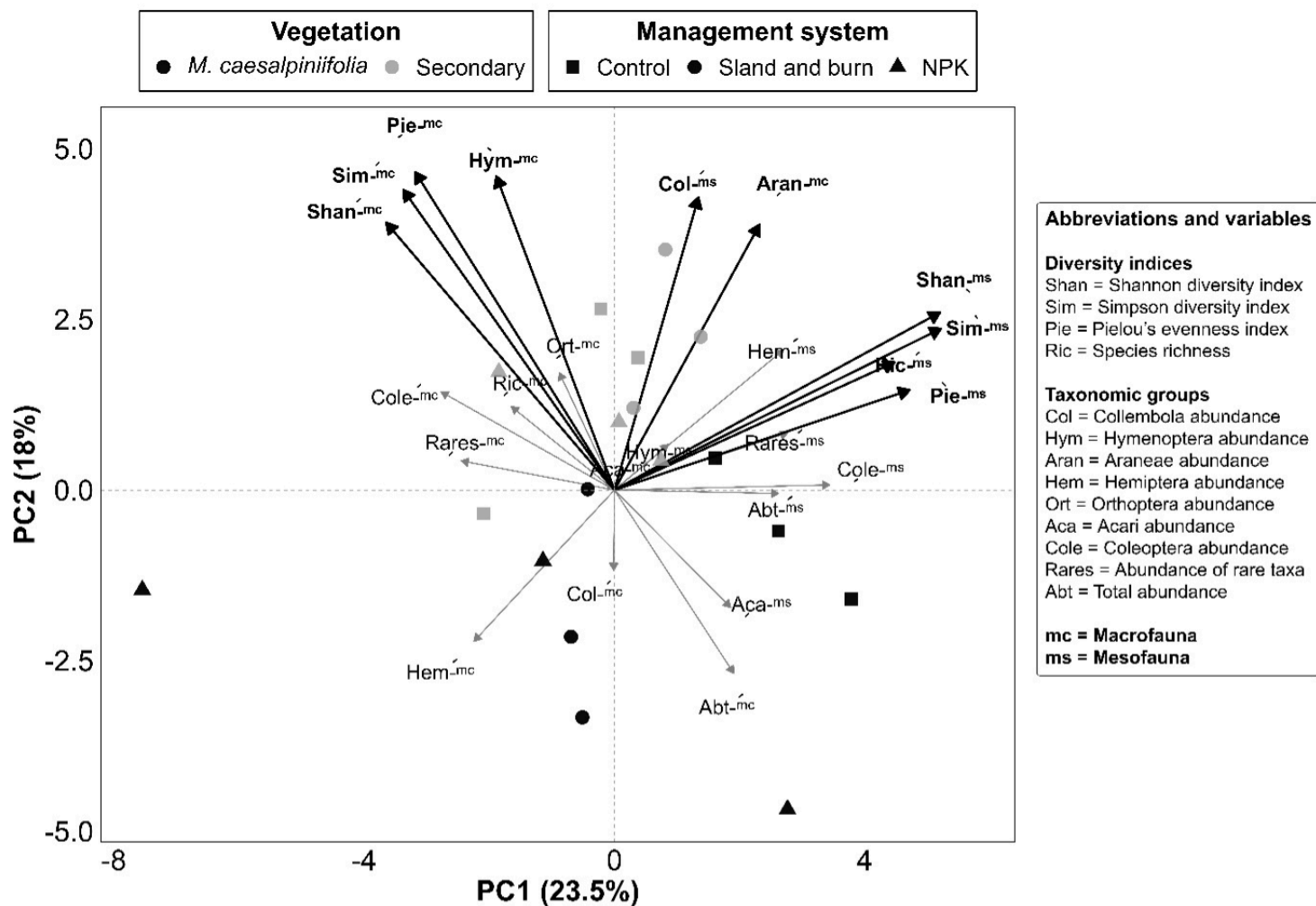


Figure 5

Principal component analysis (PCA) ordination of soil surface macrofauna (–mc) and topsoil mesofauna (–ms) variables under different preceding fallow vegetation types (spontaneous secondary vegetation and *Mimosa caesalpinifolia* fallows) and nutrient management treatments (Control, Slash-and-burn, and NPK fertilization) in upland rice fields. Sampling units are distinguished by grayscale shading according to preceding fallow vegetation (*M. caesalpinifolia* in black and spontaneous secondary vegetation in gray) and by symbol shape according to nutrient management treatment. Black arrows indicate variables with high contributions to the ordination ($\cos^2 > 0.5$), whereas gray arrows indicate variables with lower contributions ($\cos^2 \leq 0.5$). The percentages on the axes indicate the proportion of total variance explained by each principal component (PC1 = 23.5%; PC2 = 18.0%).

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