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Tree Diversity and Microhabitat Structure Drive Harvestmen Assemblages in Amazonian Rainforest

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Abstract

Understanding how vegetation structure influences invertebrate diversity is critical for tropical forest conservation because invertebrates play key roles in ecosystem functioning. This study investigates the role of vegetation and selected microhabitats in shaping harvestmen assemblages across primary and planted forests in the Amazon rainforest. Our findings challenge the traditional view that vegetation quantity alone drives invertebrate distribution, revealing that specific plant species play a key role in shaping harvestmen assemblages. Notably, *Geaya* sp. (Sclerosomatidae) was strongly associated with specific arboreal species, especially *Tetragastris altissima* and *Attalea maripa*, and was identified as a bioindicator of trees. Tree diversity provides critical habitats in primary forests, illustrating how changes in tree composition can disproportionately impact specialist species. Two species of harvestmen were also identified as bioindicators of forest quality. For instance, *Geaya* sp. was exclusively linked to primary forests, while the cosmetid *Gryne* sp. emerged as moderately associated with this type of forest with high structural complexity. By identifying the specific relationships between harvestmen and vegetation, this study demonstrates their potential for monitoring ecosystem health and emphasizes the importance of preserving keystone plant species to maintain ecological integrity in tropical'forests.

Keywords: invertebrates; Opiliones; species interaction; tropical forest; habitat use; indicator species

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1. Introduction

Invertebrates are fundamental components of terrestrial and aquatic food webs. They contribute to ecosystem services through decomposition, nutrient cycling, and the maintenance of soil structure [1–4], as well as through indirect interaction pathways involving plants and soil microbes [5]. Given the nature of these interactions and their relationships with other living organisms and abiotic systems, several invertebrate groups are strongly and rapidly affected by environmental changes. They respond quickly to shifts in forest structure and microclimate, such as soil moisture [6], litter [7], and vegetation cover transformation [8], which are among the most important predictors of community and local species variation across many sites [9–11].

Given their astonishing taxonomic and functional diversity, invertebrates are excellent models for detecting and explaining disturbances in forest systems at both large and small scales [12]. Many invertebrate taxa, including butterflies, ground beetles, spiders, harvestmen, ants, and others, have been used as biological indicators [13–16]. Natural biological indicators are any living organisms used to assess the health of an ecosystem in a specific environment or area [17]. The term bioindicators, however, is used as an aggregate concept referring to any abiotic or biotic response to ecological change [17,18]. These taxa are used not only as tools to measure the levels and extent of natural change but also as sources that indicate and detect positive or negative impacts on natural environments that may affect biodiversity [17] and subsequently influence human society [18]. All these advantages in the use of bioindicators make them very popular tools employed by many national and international organizations for global conservation [18].

Good animal indicators of environmental changes are those that maintain close relationships with their habitat throughout all life stages [19]. These taxa also have great potential to be used as surrogate groups in biological inventories, helping to predict the diversity of other organisms [20]. Harvestmen are good bioindicators of environmental quality [21,22]; they are generalist predators in terrestrial ecosystems, known to be strongly affected by vegetation structure and environmental complexity [21,23,24], as well as by abiotic factors such as temperature and humidity [25,26].

In tropical forests, harvestmen assemblages are closely linked to forest quality and respond to habitat changes [21,25]. Vegetation structure plays a pivotal role in their distribution, with some species using trees as refuges in disturbed environments [27]. Several studies have shown that harvestmen are strongly influenced by microhabitat and habitat complexity [21,25,26,28], and evidence from our previous research suggests that palm tree abundance shapes harvestmen assemblages in upland Amazonian forests [9,21,24]. Larger-diameter trees provide critical microhabitats, supporting more individuals and species [29]. Palms further enhance habitat complexity: stemless palms trap fallen litter at ground level, while arborescent palms offer refuge in their leaf sheaths, both of which are essential for Amazonian harvestmen [9,30,31]. Suspended litter also creates highly moist, protected microhabitats, shielding harvestmen from ground-dwelling predators [24,30,31].

Fallen logs, roots, termite nests, and suspended litter at the base of trees and palm leaves are habitats favored by harvestmen because they provide ideal microclimatic conditions of humidity and temperature for their development [32]. However, how these different types of microhabitats and vegetation structures directly or indirectly influence harvestmen—and many other invertebrate assemblages and species—remains understudied. In addition, at larger scales in the central Amazon, tree and palm species composition changes with topography and edaphic gradients, which are correlated with soil water and nutrient availability at mesoscales [33]. For most plants, the waterlogged soils of bottomlands harbor a more diverse and heterogeneous assemblage compared with the well-drained soils of plateaus [34]. These differences in tree and palm species composition may, in turn, affect harvestman species composition at scales of tens of kilometers.

Despite these advances, there are still significant gaps in understanding the specific relationships between harvestmen and plant composition. While previous studies highlight the influence of vegetation complexity on harvestmen assemblages, we know almost nothing about the interrelationships between particular plant species and harvestmen or how plant species directly shape these communities. This lack of detailed information limits a comprehensive understanding of their ecological roles and their use as precise bioindicators, particularly in diverse and heterogeneous environments such as tropical forests.

In this study, we sampled two distinct forest landscapes in the southern Brazilian Amazon: primary forest and a fragment of a planted agroforestry system. Our objectives were to investigate the associations between harvestmen assemblages and vegetation structure in different forest types, as well as their potential implications for bioindication. To this end, we tested three main hypotheses: (1) microhabitat structure influences variations in harvestmen diversity (species composition, richness, and abundance) across different forest environments; (2) specific habitats exert the greatest influence on harvestmen diversity, with certain species being more affected by habitat type; and (3) harvestmen species may serve as reliable indicators of forest quality across different forest types. We predicted that higher palm abundance in a given plot would proportionally increase the availability of microhabitats, such as dead leaves, decaying trunks, and litter trapped in acaulescent palms, leading to more palm- and litter-dwelling species. Similarly, we expected that a greater number of trees per plot would increase the availability of associated microhabitats. Consequently, we predicted distinct harvestmen assemblages in primary and planted forests, with harvestmen species serving as indicators for each forest type, potentially influencing conservation practices and area management.

2. Materials and Methods

2.1. Study Area

We conducted our study at São Nicolau Farm (9°48′ S, 58°15′ W; 254 m a.s.l.), located in the municipality of Cotriguaçu, in northern Mato Grosso, Brazil (Figure 1). The farm is a protected area of 10,000 ha, comprising 7000 ha of primary Amazon rainforest, 500 ha of riparian and secondary forest, 300 ha of pasture, and a mosaic of approximately 1700 ha of reforestation areas at different successional stages. Both the reforestation and secondary forests were previously pastures used for cattle grazing before vegetation planting and pasture abandonment, which occurred between 1999 and 2000 [35]. According to the Köppen classification, the climate is tropical humid (Am), with an annual average temperature of 24–26 °C and annual precipitation of around 3000 mm year^{-1} [36]. There are two well-defined seasons: a rainy season between November and April, and a dry season from May to October [37]. The local vegetation is classified as open and dense ombrophilous forest, contrasting with large areas of teak (*Tectona grandis*) plantations and 28 native arboreal tree species [38].

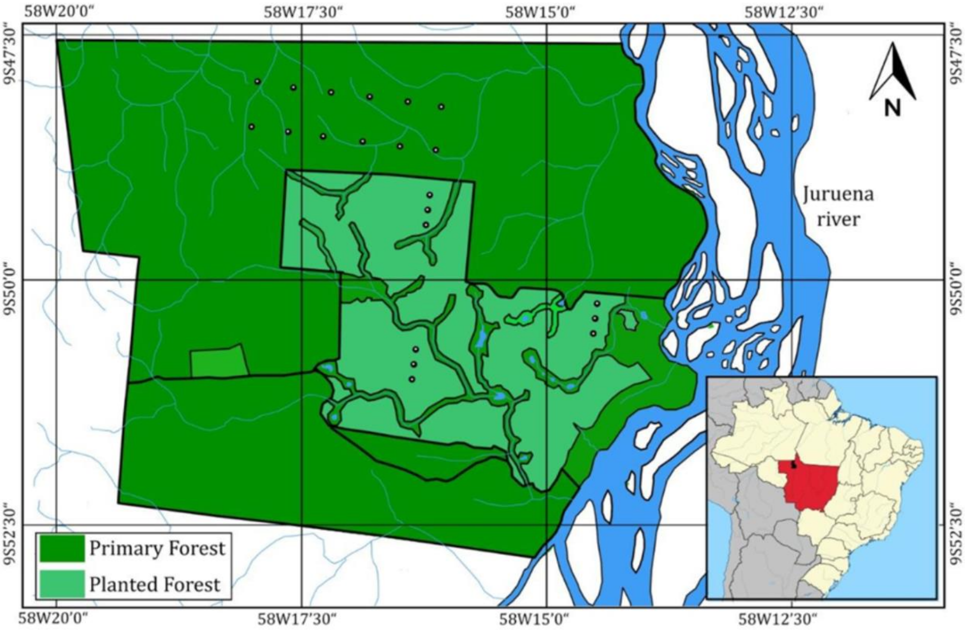

Figure 1. Location of the 21 sampling sites at Fazenda São Nicolau, southern Amazon, Cotriguaçu, Mato Grosso State, Brazil. Primary forests are represented in dark green and planted forests in light green, rivers and lakes are represented in blue.

2.2. Sampling Design

We sampled 21 plots in February 2018 and 2022. Twelve plots are located within a module managed by the Brazilian Research Program in Biodiversity [39] and situated in the undisturbed dense upland rainforest matrix (Figure 1). The module consists of two parallel east–west 5 km trails, 1 km apart, with plots established following the RAPELD protocol [39]. Each plot is a 250 m long transect, regularly spaced at 1 km intervals along the trail system. The central transect in each plot was aligned with the terrain contour to minimize variation in altitude and soil characteristics within plots [39]. We also sampled nine plots in planted forests, installed in three of the farm's agroforestry system (AFS) areas. Among the 50 planted species, including native species, only 10 adapted and developed: *Ficus maxima* (Moraceae), *Astronium* sp. (Anacardiaceae), *Chorysia speciosa* (Malvaceae), *Handroantus* spp. (Bignoniaceae), *Simarouba amara* (Simaroubaceae), *Spondias mombin* (Anacardiaceae), *Schizolobium amazonicum* (Boraginaceae), *Cordia* sp. (Boraginaceae), *Jacaranda copaia* (Bignoniaceae), and *Torresea acreana* (Fabaceae). The teak *Tectona grandis* and *Syzygium* spp., representing the only exotic species planted, exhibited good growth and accounted for less than 20% of the total trees in the AFS.

2.3. Sampling Harvestmen and Environmental Data

We classified habitats into trees, dead trunks, palms, lianas, bushes, herbs, termite nests, and litter. These microhabitats were classified based on previous studies and according to their intrinsic differences in architecture and availability see [9,21,24,27,40]. Harvestmen were sampled using cryptic nocturnal search [25]. Following this method, one experienced collector conducted a one-hour nocturnal search along the entire 250 m length of each plot, sampling a 2 m wide strip, totaling 500 m^2 surveyed per plot. We additionally implemented an integrated protocol developed for this study in which a second person recorded the specific habitats occupied by each harvestmen at the time of capture. Each individual was assigned a unique number, which was also used to record and identify the plant species (habitat) and other associated microhabitats for that individual at the moment of capture. We classified plants according to their developmental stage into adult and juvenile categories.

At the local scale, we measured litter depth, tree abundance, tree richness, palm abundance, palm richness, the number of fallen stems, as well as the richness and abundance of herbs and bushes, and the number of termite nests. These variables were used as proxies for vegetation structure and the availability of habitats for harvestmen [9,21,40]. Within each plot (10 m × 250 m), all trees and palms with a diameter at breast height (DBH) > 10 cm were mapped at 5 m intervals along the long axis of the plot. We also counted the number of juvenile and mature trees and palms. Litter depth was measured using five quadrats (0.5 m × 0.5 m each) per plot. Measurements were taken by inserting a 0.5 cm diameter stick into the litter until it reached the soil and recording the distance in centimeters between the top of the litter and the soil.

2.4. Plant Identification

All plants associated with harvestmen were identified at the time of capture. We also recorded and identified trees, palms, herbs, and bush species within each plot, taking into account their vegetative and reproductive traits according to APG III [41]. The nomenclature of the species was verified using the List of Flora of Brazil [42].

2.5. Harvestmen Identification

Harvestmen species were identified by examining external morphology under a stereomicroscope and comparing it with original descriptions in the literature e.g., [43–46], type material, or images of type specimens. Whenever possible, identifications were made to the species level; otherwise, morphospecie. For groups with highly conserved external morphology and/or poorly understood taxonomy (e.g., *Samoidae*, *Zalmoxidae*), to specific genera (e.g., *Zalmoxidae* sp. 1 and *Samoidae* sp. 1). For these species, confirmation of genus-level classification is only possible after taxonomic revision. (e.g., *Gagrellinae*, genus 1 sp. 1). Material is labeled and deposited in the arachnological collection of the Acervo da Biodiversidade da Amazônia Meridional at the Federal University of Mato Grosso, Sinop campus.

2.6. Data Analysis

We generated two data matrices: one for the local-scale analysis, using the microhabitats recorded at the time of capture (trees, dead trunks, palms, bushes, herbs, termite nests, and litter) as rows and species as columns; and another for the mesoscale analysis, using plots as rows and species as columns.

We standardized species richness among microhabitats using individual-based rarefaction and extrapolation [47]. For each habitat, we estimated extrapolated richness from the observed number of species and the frequencies of singletons and doubletons, projecting the curves to the maximum observed abundance (N** = 221, trees) using the Chao1 estimator. We calculated 95% confidence intervals (CIs) with 600 bootstrap resamplings and compared habitats by evaluating CI overlap and pairwise differences in extrapolated richness, ensuring that richness estimates were comparable despite unequal sample sizes.

To explore differences in harvestmen community composition between native and reforested areas, we first performed a Principal Coordinates Analysis (PCoA), which provides an ordination of plots in a reduced multivariate space, allowing visualization of potential group separation patterns. To formally test whether the observed differences between environments were statistically significant, we then applied ANOSIM (Analysis of Similarities) [48]. The ANOSIM R statistic ranges from –1 to +1, with values close to 1 indicating strong separation between groups, while values near 0 suggest no structural differences. Statistical significance was assessed through 999 random permutations of group labels. We also performed a Permutational Multivariate Analysis of Variance (PERMANOVA) to quantify the proportion of variation in community composition explained by the grouping factor (forest type). PERMANOVA provides an F statistic and p-value based on permutations, offering a direct measure of how forest type influences community composition.

We further used Generalized Linear Models (GLMs) to investigate the relationships between harvestmen species richness, abundance, and composition. Poisson error structures were applied for GLMs of species richness, abundance, and composition, respectively. For all response variables, the global model included all non-collinear environmental variables. Prior to running the GLMs, we performed Pearson correlation tests on all surveyed microhabitat variables to evaluate the level of correlation, excluding variables that were highly correlated ($r \geq 0.50$) from the analyses. This resulted in the following habitat variables being retained in the GLMs: litter depth, palm richness, tree richness, palm abundance, and tree abundance.

Among the correlated variables, we selected those that were previously documented in the literature e.g., [22,26,29] and shown to have a strong influence on harvestmen assemblages, also taking into account the results of the rarefaction curves.

We performed an Indicator Species Analysis considering both abundance [49] and presence–absence [50] to identify species that serve as “indicators” of sample groups and experimental treatments (primary forest and planted forest) within each microhabitat: lianas, trees, palms, litter, and fallen trunks, as well as across each sampled environment: primary forest and planted forest plots. Species–habitat associations were interpreted using thresholds proposed in the indicator value (IndVal) framework [49,50]. IndVal values were classified as strong (≥ 0.70), moderate (0.40–0.69), or weak (0.25–0.39), with values below 0.25 considered absent or negligible. Statistical significance was assessed using permutation tests (999 runs), and only associations with $p < 0.05$ were retained. We conducted all analyses in the R statistical environment [51]. After drafting the manuscript, the authors used ChatGPT-5 [52] to enhance grammar and improve readability.

3. Results

We sampled a total of 509 harvestmen, representing 15 species and 6 families (Table S1). The most species-rich family was Stygnidae, with four species, followed by Zalmoxidae, Manaosbiidae, and Cosmetidae, each with three species. Sclerosomatidae and Samoidae were represented by a single species each. In terms of abundance, Sclerosomatidae was the most abundant family, with 190 individuals, whereas Samoidae was represented by only 2 individuals. In the primary forest, we collected 347 harvestmen, encompassing all 15 species across the 6 families, while in the planted forest, we recorded 159 individuals, 10 species, and only 4 families.

The most species-rich family in both the primary and planted forests was Stygnidae (4 species). In the primary forest, Cosmetidae, Manaosbiidae, and Zalmoxidae each contained three species, whereas in the planted forest, only Stygnidae reached four species. The most abundant species in the primary forest was *Geaya* sp. (n = 190), followed by *Stygnus* sp. (n = 35), while in the planted forest, the most abundant species were *Stygnus* sp. (n = 38), *Eucynortella duapunctata* (n = 28), and *Eucynortella* sp. (n = 48). Zalmoxidae sp. 2 and Zalmoxidae sp. 3 were represented by singletons, and Samoidae sp. by doubletons. Five species were recorded exclusively in the primary forest: *Geaya* sp., Samoidae sp., Zalmoxidae sp. 2, Zalmoxidae sp. 3, and *Manaosbia* sp. 3. No species were found exclusively in planted forest fragments. Trees, litter, and palms were the habitats with the highest harvestmen abundance collectively (Table 1) and when considering primary and planted forests separately.

Rarefaction curves revealed clear differences in species accumulation among microhabitats. In palms, trees, and litter, curves rose steeply at low sampling efforts and continued to increase beyond the observed sampling range, indicating incomplete sampling and the presence of rare species. Fallen trunks and lianas showed mildly asymptotic shapes, suggesting moderately saturated assemblages. In contrast, herbs and shrubs exhibited early stabilization, indicating low richness and rapid saturation under reduced sampling effort (Figure 2). Pairwise comparisons based on bootstrap differences showed no significant difference between trees and palms (CI overlap; $p > 0.05$), indicating functionally equivalent diversity potential. However, trees, palms, and litter were significantly richer than lianas, termite nests, herbs, and shrubs (non-overlapping CIs; $p < 0.01$), revealing a clear dichotomy between high- and low-diversity microhabitats. Extrapolated estimates were consistent with the observed sampling effort. Habitats with higher abundance of sampled individuals (e.g., trees and palms) displayed wider extrapolation ranges, whereas low-sampled habitats (e.g., shrubs) exhibited narrow confidence intervals, confirming genuine low diversity rather than sampling bias.

Table 1. Harvestmen species collected at São Nicolau Farm, Cotriguaçu municipality, Mato Grosso State, Brazil, with the number of records per microhabitat they occupied.

Harvestmen Species	Microhabitat								
	Fallen Trunks	Herb	Liana	Litter	Palm	Termite Nest	Shrub	Tree	Total
Sclerosomatidae									
Geaya sp.	9	5	6	24	18	13	-	115	190
Cosmetidae									
Eucynortella duapunctata Goodnight & Goodnight, 1943	1	3	1	18	17	-	-	14	54
Eucynortella sp.	-	-	3	10	5	-	1	36	55
Gryne sp.	2	-	-	11	6	1	-	8	28
Manaosbiidae									
Manaosbia sp. 1	2	-	-	6	1	-	-	1	10
Manaosbia sp. 2	1	-	-	2	1	1	-	4	9
Manaosbia sp. 3	-	-	-	-	2	-	-	-	2
Samoidae									
Samoidae sp.	-	-	-	1	1	-	-	-	2
Stygnidae									
Protimesius longipalpis (Roewer, 1943)	1	2	-	-	3	-	-	9	15
Sickesia usta (Mello-Leitão, 1941)	-	-	-	8	3	-	-	2	13
Stygnus aff. *Marthae*	-	-	-	4	1	-	-	5	10
Stygnus sp.	11	-	1	23	22	6	-	13	76
Zalmoxidae									
Zalmoxidae sp. 1	12	-	1	11	6	1	-	12	43
Zalmoxidae sp. 2	-	-	-	-	-	-	-	1	1
Zalmoxidae sp. 3	-	-	-	-	-	-	-	1	1
Total	39	10	12	118	86	22	1	221	509

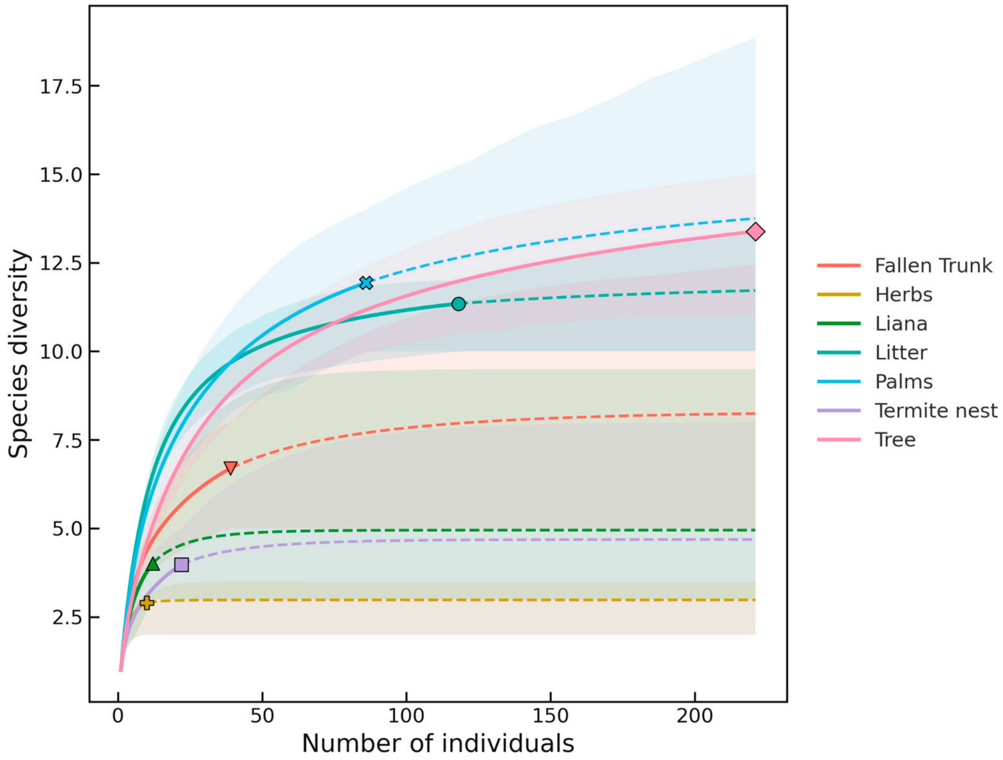

Figure 2. Rarefied and extrapolated species–individual curves for microhabitats occupied by harvestmen species. Differences in the number of individuals sampled result in variation in estimated species richness among microhabitats. All curves were standardized to *N** = 221. Solid lines represent the rarefied (interpolated) portion of the curves, while dashed lines represent the extrapolated portion. Shaded bands indicate geometric 95% confidence intervals for each curve.

Regardless of forest type, the two PCoA axes represent species composition across the 21 sampling sites and together explain 44.2% of the data variation, with the first axis accounting for 28.8% and the second for 15.4% (Figure 3). Harvestmen species composition varied substantially between forest types, with distinct assemblages distributed across the two forest categories (Figure 3), and differences in species distribution at the microhabitat scale between forest types. The ANOSIM test indicated significant differences between environments (R = 0.599; p = 0.001), confirming a consistent divergence in harvestmen community composition between native and planted forests. This pattern was corroborated by PERMANOVA (F = 5.070; R^2 = 0.210; p = 0.001), which showed that forest type accounted for 21% of the total variation in community composition, while the remaining variation was explained by within-forest heterogeneity and microhabitat-scale factors.

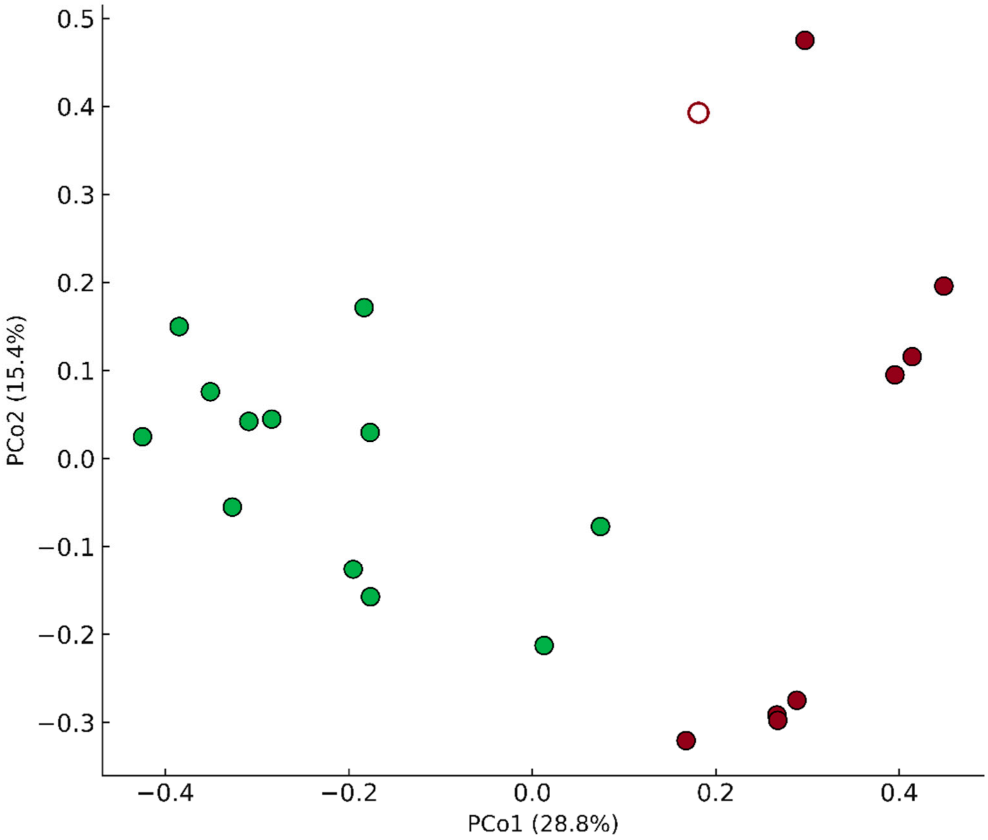

Figure 3. Variation in harvestmen species composition between primary (green) and planted forests (brown) in the southern Amazon, Cotriguaçu, Mato Grosso State, Brazil. White site in planted forest meaning no harvestmen individuals were collected.

At the taxonomic scale, harvestmen distribution is also structured by tree and palm families and species (Table 2). Across the 21 sampling plots, we recorded 176 arboreal species. Although harvestmen prefer trees and palms, they were only found in 20 families, encompassing 46 species—42 tree species and 4 palm species—with a preference for Arecaceae (13 spp.), Burseraceae (8 spp.), Moraceae (7 spp.), and Myrtaceae (6 spp.) (Table 2). One palm species, *Attalea maripa* (13 spp.), and three tree species harbored the highest number of harvestmen species: *Tetragastris altissima* (7 spp.), *Eugenia* sp. (6 spp.), and *Moraceae* sp. (6 spp.). *Attalea maripa* (70 individuals), *Tetragastris altissima* (62 individuals), and *Eugenia* sp. (21 individuals) were also the three arboreal species with the highest harvestmen abundances (Table 2).

Table 2. Occurrence of harvestmen species on plant species in the southern Amazon, Cotriguaçu, Mato Grosso State, Brazil. 1 = *Eucynortella duapunctata*; 2 = *Eucynortella* sp.; 3 = *Geaya* sp.; 4 = *Gryne* sp.; 5 = *Manaosbia* sp. 1; 6 = 5 = *Manaosbia* sp. 2; 7 = 5 = *Manaosbia* sp. 3; 8 = *Protimesius longipalpis*; 9 = *Sickesia usta*; 10 = Samoidae sp.; 11 = *Stygnus* aff. *marthae*; 12 = *Stygnus* sp.; 13 = Zalmoxidae sp. 1; 14 = Zalmoxidae sp. 2; 15 = Zalmoxidae sp. 3.

Plant Species	**Harvestmen Species**															**Total**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	
Anacardiaceae																
Thyrsodium sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Annonaceae																
Anaxagorea sp.	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Xylopia benthamii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Xylopia cf. *brasiliensis*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Xylopia sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Arecaceae																
Astrocaryum aculeatum	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Attalea maripa	17	5	12	6	1	1	2	3	1	1	1	22	5	-	-	77
Attalea speciosa	-	1	5	-	-	-	-	-	2	-	-	-	1	-	-	9
Iriartella sp.	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Burseraceae																
Protium sp.	-	-	1	1	-	-	-	-	-	-	1	-	-	-	-	3
Protium cf. *heptaphyllum*	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Protium heptaphyllum	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	5
Protium spruceanum	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Protium unifoliatum	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Tetragastris altissima	4	-	50	3	-	-	-	-	-	-	3	5	3	-	1	69
Trattinnickia glaziovii	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Chrysobalanaceae																
Hirtella gracilipes	-	-	4	-	-	-	-	1	-	-	-	-	-	-	-	5
Elaeocarpaceae																
Sloanea sp.	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	4
Erythroxylaceae																
Erythroxylon sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Fabaceae																
Fabaceae sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Hymenolobium isp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Inga cf. *macrophylla*	-	-	2	-	-	-	-	-	-	-	-	-	2	-	-	4
Inga cf. *marginata*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Inga cordoalata	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Inga macrophylla	-	-	6	2	-	-	-	-	-	-	-	-	-	-	-	8
Sclerobium sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Hypericaceae																
Vismia sp.	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	2
Lacistemataceae																
Lacistema aggregatum	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Lamiaceae																
Tectona grandis	2	24	-	-	1	1	-	-	-	-	-	6	3	-	-	37
Vitex triflora	-	-	-	-	-	-	-	6	-	-	-	-	1	-	-	7
Lauraceae																
Aniba sp.	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	4
Ocotea cf. *longifolia*	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Ocotea longifolia	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Malvaceae																
Pseudobombax sp.	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	3
Theobroma speciosum	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Moraceae																
Brosimum guianensis	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-	3
Ficus sp.	1	3	-	-	-	1	-	-	-	-	-	-	-	-	-	5
Moraceae																
Moraceae sp.	-	1	1	-	-	1	-	-	1	-	-	1	1	-	-	6
Myristicaceae																
Virola sebifera	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2
Myrtaceae																
Eugenia sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Syzygium sp.	6	7	-	-	-	1	-	-	-	-	1	1	-	-	-	16
Quinaceae																
Quinaceae sp.	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Rubiaceae																
Faramea capillipes	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	2
Psychotria erecta	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2
Salicaceae																
Casearia sp.	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Sapindaceae																
Toulicia guianensis	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1

GLMs showed that palm richness, palm abundance, tree richness, and litter, as well as their combinations, were all significant predictors of harvestmen abundance and community composition (Table 3). In contrast, none of the selected microhabitat variables were significant predictors of species richness in any of the models (Table 3).

Table 3. Results of the generalized linear models showing the effects of tree richness and abundance, palm richness and abundance, litter, and their combinations on harvestman diversity. Significative *p*-values are given in bold.

Response Variable	Predictors Variables	AIC	*p*-Value	Std Error
Species richness	NULL	70.48	0.000	0.479
	Tree Richness (RichTree)		0.392	0.006
	Palm Richness (RichPalm)		0.728	0.109
	Tree abundance (TreeAb)		0.813	0.001
	Palm Abundance (PalmAb)		0.789	0.001
	Litter		0.888	0.160
	TreeAb + RichPalm + Litter		0.837	0.163
Species Abundance	NULL	127.65	0.005	4.568
	Palm Richness (RichPalm)		**0.009**	1.679
	Tree abundance (TreeAb)		**0.037**	0.515
	RichTree + RichPalm		**0.007**	0.0342
	TreeAb + PalmAb + RichPalm		**0.023**	0.000
	RichArv + RichPalm + Litter		**0.023**	0.023
Species Composition	NULL	112.08	0.103	10.444
	Tree abundance (TreeAb)		**0.007**	0.034
	Tree Richness (RichTree)		**0.012**	0.142
	Palm Abundance (PalmAb)		**0.024**	2.656

Individually, two harvestmen species were identified as indicators of primary forests: *Geaya* sp. (Sclerosomatidae) and *Gryne* sp. (Cosmetidae). *Geaya* sp. showed a strong association with this environment (IndVal = 0.917; *p* = 0.002); it was the most abundant species recorded at the site and was not found in any of the nine planted forest plots (Table 4), being exclusive to primary forests. *Gryne* sp., on the other hand, showed a moderate association with primary forest (IndVal = 0.669; *p* = 0.010) (Table 4). Regarding specific microhabitats, only *Geaya* sp. was a unique and strong indicator of tree habitats (IndVal = 139.59; *p* = 0.005).

Table 4. Indicator Value analysis showing the positive associations of each harvestman species with lianas, trees, palms, litter, and fallen trunks, as well as within native and planted forest plots, considering both abundance and presence–absence data. * Significant *p*-values are shown in bold.

Harvestmen Species	Forest Type Association	IndVal	* *p*-Value	Number of Plots	Class
Geaya sp.	Primary Forest	0.917	**0.002**	12	Strong
Eucynortella duapunctata	Primary Forest & Planted Forest	0.762	1	16	Strong
Gryne sp.	Primary Forest	0.669	**0.010**	11	Moderate
Stygnus sp.	Primary Forest & Planted Forest	0.667	1	14	Moderate
Zalmoxidae sp. 1	Primary Forest & Planted Forest	0.667	1	14	Moderate
Manaosbia sp. 1	Planted Forest	0.450	0.078	8	Moderate
Sickesia usta	Primary Forest	0.291	0.192	5	Weak
Eucynortella sp.	Primary Forest & Planted Forest	0.286	1	6	Weak
Manaosbia sp. 2	Primary Forest & Planted Forest	0.286	1	6	Weak
Stygnus aff marthae	Primary Forest & Planted Forest	0.286	1	6	Weak
Eucynortella sp.	Primary Forest & Planted Forest	0.238	1	5	Absent
Samoidae sp.	Primary Forest	0.182	0.252	2	Absent
Protimesius longipalpis	Primary Forest & Planted Forest	0.143	1	3	Absent
Zalmoxidae sp. 3	Primary Forest	0.091	0.505	1	Absent
Manaosbia sp. 3	Primary Forest	0.091	0.508	1	Absent
Zalmoxidae sp. 2	Primary Forest	0.091	0.524	1	Absent

4. Discussion

Our study highlights that harvestmen diversity is highly responsive to microhabitat gradients shaped by vegetation in both primary and planted forests of the Southern Amazon. These findings underscore the potential of harvestmen species to serve as bioindicators of forest type, habitat quality, and possibly as surrogate taxa for plant diversity. As anticipated, planted forests supported fewer species than primary forests. Within these forest types, tree, palm richness and abundance significantly influenced harvestmen diversity in terms of species abundance and composition, but not overall species richness. While the selected variables did not directly explain species richness, microhabitats emerged as a critical factor driving harvestmen species distribution and variation. Changes in vegetation consistently altered harvestmen assemblages, e.g., [27,53,54], reflecting their strong associations with specific vegetation components, such as tree and palm richness and abundance, across both planted and primary forests examined in our study.

Notably, one harvestman species demonstrated great potential as a bioindicator, being closely associated with primary native forests and tree microhabitats. Furthermore, highlighting the specificity of these relationships, our results reveal that associations between harvestmen species and plant species occur at a taxonomic scale. Our data suggest, for example, that certain species, such as *Geaya* sp. (Sclerosomatidae), may depend on particular plant species (trees and palms), limiting their ability to colonize disturbed areas. This finding emphasizes the critical role of vegetation structure and microhabitat composition in shaping harvestmen assemblages and their ecological functions.

4.1. Influence of Forest Types and Microhabitat Structure on Harvestmen Diversity

Our results reveal that fine-scale microhabitat structure exerts a major influence on harvestmen diversity, specifically in terms of species abundance and composition, although it does not directly affect species richness. This pattern was observed across both primary and planted forests at the study site. Primary forests consistently exhibited higher species richness and supported a greater abundance of individuals compared to planted forests. Similarly, previous research has demonstrated that vegetation cover and structure are key factors influencing harvestmen assemblage composition in both upland and island areas of the Amazon rainforest, where tree and palm abundance drive assemblage composition at meso-spatial scales [21,28].

At both local and mesoscales, however, harvestmen richness remained unaffected by any of the forest structure variables tested. This pattern, observed in our study, aligns with previous research [9,21,22], which also found no correlations between harvestmen richness and variables of forest structure or climate. Collectively, the results of this study and previous ones highlight the complexity of ecological interactions that drive harvestmen distribution and diversity in the Amazon. Tree and palm richness and abundance, along with litter, emerged as important determinants of harvestmen abundance and composition, contributing substantially to variation in species composition between plots. The findings underscore the critical role of habitat complexity, particularly tree and palm diversity, in structuring diverse harvestman assemblages, especially because the patterns observed in our study persisted across both primary and planted forests. This indicates a strong influence of trees, palms, and leaf-litter microhabitats even in human-altered environments [55,56]. These results highlight the necessity of preserving structural complexity in forest habitats to sustain diverse and stable invertebrate communities such as harvestmen.

4.2. Harvestmen Microhabitat Specialization and Bioindication

Harvestmen exhibit a high degree of selectivity and specificity in their associations with vegetation, as demonstrated by their strong preference for certain tree and palm species. As previously reported, trees have been identified as key factors structuring harvestmen assemblages in the Amazon and other tropical forests [40], as well as in temperate regions [57]. However, earlier studies did not investigate species-specific relationships between harvestmen and particular arboreal species. In our study, among the 174 arboreal species recorded in the study area, only 46 species were preferentially used by harvestmen, highlighting the critical role of specific plant species in shaping these assemblages. Notably, the palm species *Attalea maripa* and the tree *Tetragastris altissima* emerged as key species, hosting the highest numbers of both individuals and harvestmen species, including the most abundant species, *Geaya* sp. and *Stygnus* sp. The exotic species *Tectona grandis* also served as an important microhabitat in some planted sites, where it was the sole tree present, supporting six harvestmen species (Table 2).

These results indicate that it is not merely the presence or density of trees and palms, but their species identity, that strongly influences harvestmen assemblages. These specific relationships suggest that certain plant species are fundamental for maintaining the ecological integrity of harvestmen assemblages in Amazonian forests. *Geaya* sp. (family Sclerosomatidae), for example, although occasionally found in other microhabitats (Table 1), was strongly associated with tree microhabitats and specific tree species, indicating its ecological dependence on this habitat (Table 2. As expected for Sclerosomatidae, this species exhibited the highest abundance among the harvestmen sampled, with 190 individuals recorded, of which 115 were found in trees (Table 1). Remarkably, 45 individuals were associated with *Tetragastris altissima* and 8 with *Attalea maripa*, additionally indicating the species' reliance on specific arboreal hosts.

The ecological dependency of *Geaya* sp. on specific plant species is also suggested by its complete absence in the planted forest sites, where *T. altissima* is absent and the other Burseraceae representatives present belong to the genus *Protium*. The potential vulnerability of *Geaya* sp. to changes in forest composition appears closely linked to the presence of key arboreal species. As reported in a study conducted in the Balbina Mega Dam islands, Sclerosomatidae species are highly responsive to forest alteration and fragmentation, being unable to successfully colonize highly fragmented and degraded insular environments, where they remain absent [21]. Similarly, in our study, the limited presence of *Geaya* sp. in altered and fragmented environments appears strongly associated with the availability of specific tree species from certain families, such as Burseraceae. The major role of arboreal diversity in supporting the persistence of Sclerosomatidae species is clearly demonstrated here, suggesting that the loss of key tree species could disproportionately affect Sclerosomatidae populations and their major ecological functions, as they are among the most abundant species across every Amazonian site studied.

The nature of harvestmen–Burseraceae relationships is currently unknown, but certain Burseraceae species, such as *Persea* and *Dacryodes*, exhibit significant interactions with arthropods [58]. The phytotelmata formed by these plants, including leaf cavities and tree holes, provide essential habitats for dipterans, hemipterans, and hymenopterans [59]. Other Burseraceae–arthropod interactions involve beetles and the resin produced by the plant's canals [60]. For example, *Bursera* species employ a "squirt-gun" resin defense, while chrysomelid beetles have developed specialized strategies to neutralize it, reflecting a history of close ecological association [60,61]. Dipterans and other arthropods are also often attracted to plant resins, sometimes becoming trapped [61]. Similarly, resin has been highlighted as a "necrophagous trap," attracting scavenger flies and beetles to decaying matter within the resin, which can lead to their entrapment [62]. These arthropods are drawn to the carcasses of insects and other organisms trapped in the resin, where they feed and sometimes reproduce. Such interactions indicate that Burseraceae play an important role not only in maintaining arthropod diversity but also in shaping ecological interactions [58,63].

Finally, we identified two harvestmen species as bioindicators of forest quality: *Geaya* sp. emerged as a strong indicator of primary forests, reflecting the high structural complexity and ecological stability of these undisturbed habitats, while *Gryne* sp. appeared as a moderate indicator of the same forest type. The adaptability of *Gryne* sp. Indicates its ecological plasticity and further supports its value as an indicator of habitat quality and resilience in altered environments, as the species is linked to highly structured and complex habitats but is also capable of persisting in planted forests. In addition to forest type, *Geaya* sp. is an important bioindicator of tree microhabitats. The associations of these specific harvestmen species with primary forests and trees underline the role of microhabitat availability and diversity in shaping harvestman assemblages and their suitability as ecological indicators. The strong correlations between harvestmen species composition, forest types, and microhabitat characteristics also reinforce their value as bioindicators. As generalist predators sensitive to changes in vegetation structure, harvestmen provide insights into habitat complexity and environmental quality across different forest systems, making them particularly valuable for monitoring forest health, detecting environmental disturbances, and guiding conservation and restoration strategies.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17100737/s1, Table S1: Tourinho et al. 2025_dataset.

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