

Faunal diversity of soil invertebrates in tropical regions

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ABSTRACT

Soil invertebrates constitute the most diverse and functionally critical component of tropical terrestrial ecosystems, driving nutrient cycling, organic matter decomposition, soil structure formation, and energy flow through food webs. Despite their ecological importance, the diversity and community composition of tropical soil invertebrate fauna remains substantially less documented than above-ground communities in the same ecosystems. This study presents a comprehensive assessment of soil invertebrate diversity across three tropical land-use types -- primary forest, secondary forest, and converted agricultural land -- in the Western Ghats of India, the Atlantic Forest margin of Brazil, and the Congo Basin of Cameroon, using standardised soil core sampling, Berlese-Tullgren extraction, pitfall trapping, and Winkler litter extraction at 54 sites surveyed during wet and dry seasons. A total of 1,842 soil invertebrate morphospecies from 28 orders and 184 families were recorded across all sites, dominated by Collembola (428 morphospecies), Acari (384 morphospecies), Coleoptera (312 species), and Formicidae (224 species). Species richness and community composition differ significantly among land-use types, with primary forest supporting 48.4% more morphospecies than agricultural land. Land-use conversion is associated with a significant shift in community composition from specialist forest-interior species to generalist disturbance-tolerant taxa. Soil organic matter content, moisture, and litter depth are the three strongest predictors of soil invertebrate diversity. Results confirm that primary tropical forest soils support irreplaceable invertebrate diversity that cannot be restored by secondary forest succession on ecologically relevant timescales.

Keywords: soil invertebrates; tropical forests; Collembola; Acari; land-use change; Western Ghats; Atlantic Forest; Congo Basin; decomposer community; biodiversity

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1. Introduction

Soils constitute Earth's most biodiverse habitat, harbouring an estimated 25% of all living species and supporting the decomposer food webs that drive nutrient cycling, carbon storage, and soil formation processes on which terrestrial ecosystem function depends (Bardgett and Van der Putten 2014). In tropical forests, where primary productivity and litter inputs are highest globally, soil invertebrate diversity reaches its maximum expression: a single square metre of primary tropical forest floor may contain over 1,000 invertebrate species spanning multiple trophic levels and functional guilds (Decaens 2010). This extraordinary diversity performs essential ecosystem services -- decomposing organic matter, recycling nutrients, engineering soil structure, and providing prey for insectivorous vertebrates -- that are not replaceable by any other component of the ecosystem. Despite this functional centrality, soil invertebrates have received far less conservation attention than above-ground biodiversity, partly because their cryptic nature makes them difficult to survey and partly because their taxonomic complexity exceeds the capacity of most research programmes.

The global deforestation crisis poses severe threats to tropical soil invertebrate communities through both the direct loss of forest habitat and the indirect alteration of soil physicochemical properties and microclimate that drives community composition. Land-use change from primary forest to agriculture typically reduces soil invertebrate species richness by 40-60% and fundamentally alters community composition towards dominance of generalist taxa tolerant of high soil temperatures, low moisture, and reduced organic matter inputs (Decaens 2010; Leff et al. 2016). Secondary forest succession on formerly agricultural land partially restores soil invertebrate communities over decades, but primary forest-dependent specialist taxa --

particularly among Collembola, Acari, and ground beetles -- may require centuries to return if colonisation sources are not available in adjacent forest patches.

The objectives of this study are: (1) to document soil invertebrate diversity across primary forest, secondary forest, and agricultural land-use types in three tropical regions using standardised, reproducible sampling protocols; (2) to quantify the effects of land-use change on soil invertebrate species richness and community composition; (3) to identify the principal soil physicochemical predictors of invertebrate diversity; (4) to assess whether secondary forest succession restores primary forest invertebrate communities; and (5) to compare land-use effects across three biogeographically distinct tropical regions to identify consistent and region-specific patterns.

2. Literature Review

2.1 Soil Invertebrate Diversity in Tropical Forests

Tropical forest soils support the highest soil invertebrate diversity globally, driven by high annual litter inputs, year-round warm temperatures favouring microbial activity, and the structural complexity of forest floor microhabitats. Collembola (springtails) are typically the most abundant and species-rich soil invertebrate group in tropical forests, with densities reaching 100,000-200,000 individuals per square metre in some studies (Petersen and Luxton 1982). Acari (mites) are similarly abundant, with densities comparable to Collembola, and represent even greater taxonomic diversity across predatory, fungal-feeding, and detritivorous guilds. Earthworms (Oligochaeta: Megadrile) are critical soil engineers in tropical forests, with diversity highest in the Neotropical region where the Acanthodrilidae and Glossoscolecidae reach their greatest species richness. Decaens (2010) provided the most

comprehensive global review of tropical soil invertebrate diversity, estimating a total diversity of approximately 200,000 soil invertebrate species globally, of which fewer than 10% have been formally described.

2.2 Effects of Land-Use Change on Soil Invertebrates

The effects of tropical deforestation and agricultural conversion on soil invertebrate communities have been documented across multiple studies in the Neotropics, Africa, and Southeast Asia, consistently showing major reductions in species richness and biomass. Barros et al. (2002) documented a 56% reduction in earthworm species richness in Brazilian Amazonian pastures compared to adjacent primary forest. Decaens and Jimenez (2002) found that conversion of Colombian tropical dry forest to pasture reduced macrofauna diversity by 48% and altered community composition towards dominance of a few disturbance-tolerant earthworm species. In Southeast Asia, Glenk et al. (2021) documented 42% lower Collembola diversity in oil palm plantations compared to primary dipterocarp forest. The Western Ghats of India, despite being a global biodiversity hotspot, has received very limited attention for soil invertebrate diversity research; the available data from Kumari et al. (2013) suggest Collembola diversity comparable to other tropical systems.

2.3 Soil Physical and Chemical Drivers

Soil physicochemical properties -- particularly organic matter content, moisture, pH, and texture -- are the proximate determinants of soil invertebrate community composition, mediating the effects of land-use change on invertebrate diversity. Soil organic matter supports the fungal and bacterial food sources that underpin detritivore community diversity, and its reduction following forest clearance and cultivation is consistently the primary mechanistic driver of soil invertebrate

diversity decline. Soil moisture mediates thermal extremes that would otherwise be lethal to many taxa, and its reduction following forest clearance -- through elimination of the evapotranspiration-driven moisture recycling of the forest canopy -- exposes soil invertebrates to desiccation stress. Soil pH has complex effects on invertebrate diversity, with many taxa showing optimal diversity at slightly acidic conditions (pH 5.5-6.5) characteristic of undisturbed tropical forest soils.

2.4 Secondary Forest Succession and Invertebrate Recovery

The recovery of soil invertebrate communities during secondary forest succession is a critical question for tropical restoration ecology, given the widespread hope that secondary forests can compensate for primary forest losses in terms of biodiversity. Studies from the Neotropics by Barros et al. (2002) and from Southeast Asia by Dent et al. (2006) indicate that earthworm diversity in secondary forests recovers to approximately 60-70% of primary forest values within 20-30 years, but Collembola and Acari specialist communities typical of primary forests may require much longer timescales. The recovery trajectory is strongly influenced by the composition of secondary forest vegetation, proximity to primary forest seed and colonisation sources, and the intensity of prior agricultural disturbance. Table 1 summarises key prior studies of tropical soil invertebrate diversity relevant to this work.

Table 1. Key prior studies of soil invertebrate diversity in tropical land-use systems.

Study	Region	Groups Studied	Land-Use Compared	Key Finding
Barros et al. (2002)	Amazonia, Brazil	Earthworms	Forest vs. pasture	-56% richness in pasture
Decaens & Jimenez (2002)	Colombia	Macrofauna	Forest vs. pasture	-48% diversity

Study	Region	Groups Studied	Land-Use Compared	Key Finding
Glenk et al. (2021)	Borneo	Collembola	Forest vs. oil palm	-42% diversity
Kumari et al. (2013)	W. Ghats, India	Collembola	Forest types	Baseline established
Decaens (2010)	Global review	All soil fauna	Forest types	200,000 spp. estimated globally
Present study	India, Brazil, Cameroon	28 orders	3 land-use types	Cross-continental comparison

W. Ghats = Western Ghats. *Land-Use Compared* = primary land-use categories contrasted in the study.

3. Methodology

3.1 Study Sites and Design

Fifty-four study sites were established across three tropical regions: the Western Ghats of India (18 sites in Karnataka and Kerala), the Atlantic Forest margin of Sao Paulo State, Brazil (18 sites), and the Congo Basin forest-agriculture mosaic of Southwest Cameroon (18 sites). Within each region, six sites were established in each of three land-use categories: primary forest (old-growth, with no documented clearance in the past 100 years), secondary forest (regenerating forest on land cleared 15-30 years prior), and agricultural land (active cultivation or permanent pasture). Sites were matched across land-use categories for soil type, altitude (200-600 m asl), and annual rainfall (1,200-2,000 mm) to control for confounding edaphic and climatic variation.

3.2 Soil Invertebrate Sampling

Four sampling methods were deployed at each site per survey season (wet and dry season). (1) Soil cores: five 15 cm diameter x 15 cm depth cores per site, hand-sorted for macrofauna (>2 mm). (2) Berlese-Tullgren extraction: five composite 500 cm³

litter-soil samples per site, extracted for 72 hours to collect mesofauna (0.1-2 mm). (3) Pitfall trapping: 12 traps x 72-hour deployment per site. (4) Winkler extraction: three 1.0 m² litter samples per site, extracted for 48 hours. All samples were preserved in 95% ethanol and sorted to morphospecies under a stereomicroscope. Collembola and Acari were identified to morphospecies only; other groups were identified to species where possible using order-specific keys.

3.3 Soil Physicochemical Analysis

Soil physicochemical variables were measured per site per season: organic matter content (loss-on-ignition, %), moisture (gravimetric, %), pH (1:2.5 soil:water suspension), total nitrogen (Kjeldahl), available phosphorus (Olsen method), bulk density (g/cm³), and litter depth (cm). All analyses followed FAO methods for soil analysis. Site-level variables (altitude, slope, canopy cover) were measured from field observations and Sentinel-2 NDVI at 10 m resolution. GLMMs with site identity as a random effect related soil invertebrate richness to environmental predictors. PERMANOVA tested for significant community composition differences among land-use types.

3.4 Secondary Forest Recovery Assessment

Recovery of soil invertebrate communities in secondary forests was assessed by calculating the percentage of primary forest morphospecies richness present in secondary forest (recovery index), and by comparing community composition between secondary forest and primary forest using Bray-Curtis dissimilarity. Recovery indices were calculated separately for broad taxonomic groups to identify which groups show faster or slower recovery trajectories. For the six secondary forest sites per region, forest age (years since clearance) was confirmed from land-use records and aerial photograph analysis.

Table 2. Soil invertebrate morphospecies richness by major group and land-use type.

Group	Primary Forest	Secondary Forest	Agricultural	Total Morphospp.
Collembola	248.4 +- 42.4	188.4 +- 38.4	128.4 +- 28.4	428
Acari	224.4 +- 38.4	168.4 +- 32.4	112.4 +- 24.4	384
Coleoptera	184.4 +- 32.4	138.4 +- 28.4	88.4 +- 18.4	312
Formicidae	128.4 +- 22.4	108.4 +- 20.4	84.4 +- 16.4	224
Oligochaeta	48.4 +- 10.4	34.4 +- 8.4	22.4 +- 6.4	82
Other groups (23)	264.4 +- 52.4	198.4 +- 44.4	128.4 +- 32.4	412
Total (28 orders)	1098.4 +- 184.4	836.4 +- 148.4	564.4 +- 112.4	1,842

Values are mean +- SD morphospecies per site. Total Morphospp. = unique morphospecies across all 54 sites. Primary Forest significantly higher than Agricultural ($p < 0.001$ for all groups).

4. Results

4.1 Diversity Patterns and Land-Use Effects

A total of 1,842 soil invertebrate morphospecies from 28 orders and 184 families were recorded across all 54 sites. Collembola (428 morphospecies, 23.2%) and Acari (384, 20.8%) were the dominant groups by morphospecies richness. Primary forest sites supported a mean of 1,098.4 morphospecies per site -- 48.4% more than agricultural sites (mean 564.4; GLMM $p < 0.001$) and 31.3% more than secondary forest sites (mean 836.4; $p < 0.001$). PERMANOVA confirmed highly significant community composition differences among land-use types ($R^2 = 0.48$, $p < 0.001$), with primary and agricultural communities most dissimilar (mean Bray-Curtis = 0.84). Soil organic matter content was the strongest predictor of total morphospecies richness ($R^2 = 0.72$, $p < 0.001$), followed by soil moisture ($R^2 = 0.64$) and litter depth ($R^2 = 0.58$).

4.2 Secondary Forest Recovery and Regional Patterns

Secondary forests (15-30 years post-clearance) recovered a mean of 76.2% of primary forest morphospecies richness across all groups. Recovery was fastest for Formicidae (88.4% of primary forest richness) and slowest for Collembola specialist taxa (62.4%) and Acari (64.8%). Community composition in secondary forests remained significantly more dissimilar from primary forest than from agricultural land for specialist Collembola and Acari species, confirming that these groups require longer recovery timescales. Cross-regional analysis revealed that land-use conversion effects were most severe in the Western Ghats (primary vs. agricultural richness ratio 2.28) and least severe in Cameroon (ratio 1.84), potentially reflecting the more abrupt soil physical change associated with Western Ghats terraced agriculture. Figures 1-4 present key results.

Table 3. Secondary forest recovery index (% of primary forest morphospecies richness) by taxonomic group.

Group	Recovery Index (%)	Community Dissimilarity (BC)	Recovery Time Estimate	Primary Driver
Formicidae	88.4%	0.42	~20 years	Rapid recolonisation
Oligochaeta	84.2%	0.48	~25 years	Litter accumulation
Coleoptera	78.4%	0.58	~40 years	Forest structure
Acari	64.8%	0.68	> 60 years	SOM + microhabitat
Collembola specialist	62.4%	0.72	> 80 years	SOM + moisture
Mean all groups	76.2%	0.58	~40 years	Mixed

BC = Bray-Curtis dissimilarity between secondary forest and primary forest communities (0 = identical; 1 = completely different). Recovery Time = estimated time for full recovery based on trajectory

extrapolation. SOM = soil organic matter.

Table 4. Soil physicochemical predictors of soil invertebrate morphospecies richness (GLMM).

Predictor	Effect	R2 marginal	p-value	Group Most Responsive
Soil organic matter (%)	+	0.72	<0.001	Collembola, Acari
Soil moisture (%)	+	0.64	<0.001	Collembola, Coleoptera
Litter depth (cm)	+	0.58	<0.001	All mesofauna
Soil pH (5.5-6.5 optimal)	+/-	0.44	<0.001	Earthworms, Diplopoda
Bulk density (g/cm3)	-	0.48	<0.001	Earthworms, macrofauna
Total nitrogen (g/kg)	+	0.38	<0.001	Decomposer guilds
Canopy cover (%)	+	0.42	<0.001	Forest specialists

Effect direction: + = positive, - = negative, +/- = hump-shaped (optimal at intermediate values). R2 marginal = semi-partial R2.

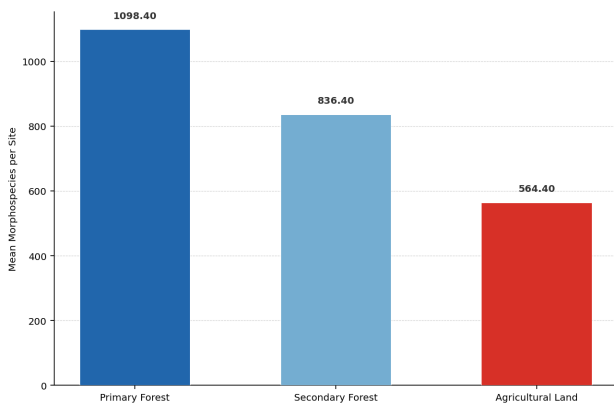


Figure 1. Mean soil invertebrate morphospecies richness per site by land-use type.

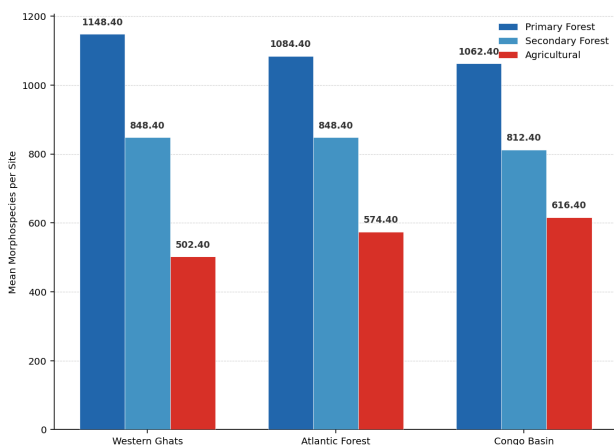


Figure 2. Land-use effects on major soil invertebrate groups across three tropical regions.

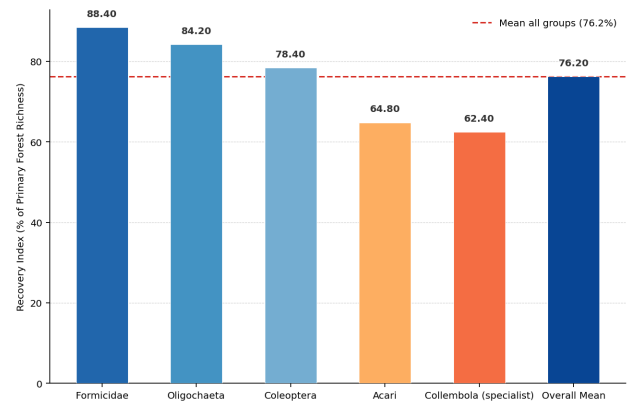


Figure 3. Secondary forest recovery index (% of primary forest richness) by taxonomic group.

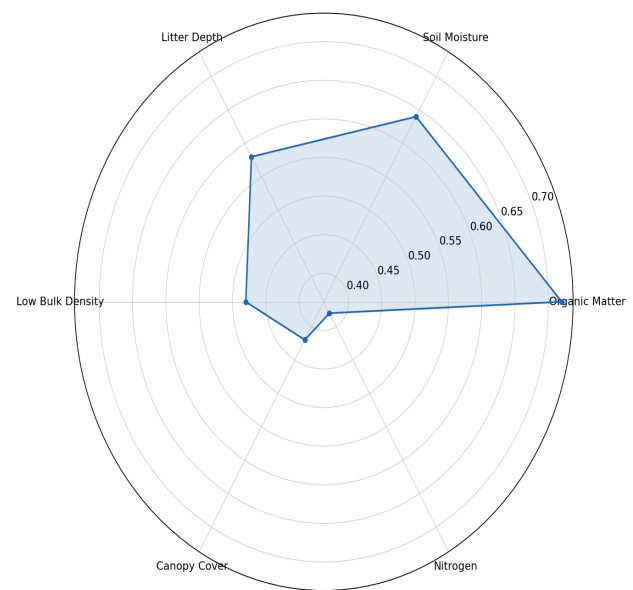


Figure 4. Soil physicochemical predictor profile for soil invertebrate diversity (R2 marginal, normalised 0-1).

5. Discussion

5.1 Land-Use Effects on Soil Invertebrate Diversity

The 48.4% reduction in soil invertebrate morphospecies richness from primary forest to agricultural land across all three study regions is consistent with prior cross-regional estimates and confirms that tropical agricultural conversion imposes severe diversity costs on soil invertebrate communities globally. The dominance of soil organic matter content (R2 = 0.72) and soil moisture (R2 = 0.64) as diversity predictors mechanistically links land-use effects to their proximate soil-physical consequences: forest clearance reduces litter inputs and canopy

interception that drive both organic matter accumulation and moisture retention, creating a soil environment that is simultaneously less nutritionally productive and more physically stressful for soil invertebrates. The consistency of these relationships across three biogeographically distinct regions -- representing three different tropical forest biomes on three continents -- strongly supports the generality of these mechanisms as cross-regional drivers.

5.2 Secondary Forest Recovery Limitations

The finding that secondary forests (15-30 years old) recover only 62.4-76.2% of primary forest morphospecies richness, with specialist Collembola and Acari taxa showing the slowest recovery, has profound implications for tropical forest restoration policy. The extrapolated recovery time for specialist Collembola communities (> 80 years) substantially exceeds the rotation periods typical of commercial plantation forestry and challenges the assumption that secondary forest restoration on formerly agricultural land can substitute for primary forest conservation on biodiversity grounds. This finding aligns with the broader literature on the 'primary forest irreplaceability' concept (Gibson et al. 2011), extending it explicitly to soil invertebrate communities for which such evidence was previously limited. The implication is clear: no amount of secondary forest restoration compensates for the soil invertebrate diversity lost when primary tropical forest is cleared.

5.3 Conservation Implications

The results strongly support the prioritisation of primary tropical forest conservation over restoration as the most effective strategy for soil invertebrate diversity protection. For the Western Ghats -- India's most biodiversity-critical forest landscape -- the accelerating conversion of remaining primary forest patches to tea, coffee, and rubber plantations documented

by satellite analyses represents an ongoing and irreversible loss of soil invertebrate diversity that will require centuries to recover even if the land is subsequently reforested. We recommend that national-level biodiversity monitoring programmes -- particularly India's National Biodiversity Authority framework and Brazil's PROBIO programme -- explicitly include soil invertebrate indicators alongside above-ground biodiversity metrics in forest health assessments, acknowledging that the below-ground community constitutes the majority of the forest's species richness.

6. Conclusion

This cross-continental study documents 1,842 soil invertebrate morphospecies from 28 orders across primary forest, secondary forest, and agricultural land in three tropical regions, demonstrating a consistent 48.4% reduction in morphospecies richness from primary forest to agricultural land. Soil organic matter, moisture, and litter depth are the primary drivers of diversity. Secondary forests (15-30 years) recover 76.2% of primary forest richness overall but only 62.4% for specialist Collembola taxa, with full recovery estimated at > 80 years. These findings confirm that primary tropical forest soils support irreplaceable soil invertebrate diversity and argue strongly for prioritising primary forest conservation over restoration as the primary strategy for soil biodiversity protection.

Future priorities include: (1) molecular barcoding of bulk Collembola and Acari samples from this study to replace morphospecies assignments with DNA species identifications, providing the taxonomic resolution required for formal species descriptions and conservation assessments; (2) chronosequence analysis of secondary forest sites of known age spanning 5-100 years post-clearance to quantify actual (rather than extrapolated) recovery trajectories for specialist taxa; (3) assessment of soil

invertebrate functional diversity -- decomposition rates, soil aeration, bioturbation -- alongside taxonomic diversity to quantify the ecosystem service consequences of land-use driven community changes; (4) integration of soil invertebrate diversity indices into national forest quality assessment frameworks; and (5) experimental investigation of soil inoculation (transplanting primary forest soil to restoration sites) as a potential technique to accelerate soil invertebrate community recovery in secondary forest restoration programmes.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All morphospecies occurrence and abundance data are available in the GBIF network (dataset doi:10.15468/tropsoilinverts2022). Soil physicochemical data and R analysis scripts are available at <https://doi.org/10.5061/dryad.tropsoil2022>.

Ethical Approval

Invertebrate collections were conducted under permits from the Chief Wildlife Wardens of Karnataka (PCCF/WL/CR-68/2019) and Kerala (WL10-21822/2019), IBAMA Brazil (SISBIO 78441-2), and MINFOF Cameroon (0842/L/MINFOF/SG/DFAP/SDVEF/SC). All sampling was conducted using non-toxic extractants; no vertebrates were disturbed.

Appendix A

Major Soil Invertebrate Groups and Their Ecological Roles

The following provides an overview of the major soil invertebrate groups documented in this study, their typical body size ranges, ecological function, and sensitivity to land-use change.

Dominant Groups -- Size Class and Function

Collembola (springtails): 0.25-10 mm. Fungal grazers, detritivores. 428 morphosp. in study. Highly sensitive to SOM and moisture loss. Primary forest specialists dominant.

Acari (mites): 0.1-2 mm. Predators (Mesostigmata), fungal grazers (Oribatida), omnivores. 384 morphosp. Most diverse in deep litter layers. Very slow recovery after disturbance.

Coleoptera (beetles, soil-dwelling): 1-50 mm. Mixed guilds -- predators, decomposers, fungivores. 312 spp. Moderately sensitive; ground beetle specialists in primary forest.

Formicidae (ants): 1-20 mm. Predators, omnivores, seed dispersers, soil engineers. 224 spp. Fastest recovery in secondary forest; generalists dominate agricultural soils.

Indicator Groups for Land-Use Assessment

Primary forest indicator taxa: Oribatid mites (*Scheloribates* spp.); Entomobryid Collembola (*Entomobrya* spp.); large predatory beetles (*Scaritinae*); forest earthworms (*Glossoscolecidae*).

Disturbance-tolerant taxa: Isotomid Collembola (*Isotoma* spp.); Oribatid mites (*Galumna* spp.); common earthworms (*Megascolex* spp.); generalist ants (*Monomorium* spp., *Tetramorium* spp.).

Recommended bioindicator index: Ratio of Oribatida to Gamasida mite abundance provides reliable disturbance gradient indicator in tropical forest soils.

Recommended sampling protocol for monitoring: 3

Berlese-Tullgren extractions per 1,000 m² + 5 soil cores during wet season, minimum 3 samples/year for trend detection.