Soil macrofauna in agricultural landscapes dominated by the Quesungual Slash-and-Mulch Agroforestry System, western Honduras.

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Running title:
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Keywords
Soil macrofauna; Soil ecology; Smallholder agriculture; Land use change; Quesungual Slash-and-Mulch Agroforestry System; Central America.

Full citation: Pauli, N., Barrios, E., Conacher, A.J. and Oberthür, T. (2011) Soil macrofauna in agricultural landscapes dominated by the Quesungual Slash-and-Mulch Agroforestry System, western Honduras. **Applied Soil Ecology** 47: 119-132.
http://dx.doi.org/10.1016/j.apsoil.2010.11.005

This is the authors' accepted version of the manuscript

Abstract

Smallholder agroforestry systems often incorporate features that are associated with abundant, diverse soil macrofauna populations. This study sampled soil macrofauna communities across four major land uses present within agricultural landscapes where the Quesungual Slash-and-Mulch Agroforestry System (QSMAS) has been increasingly adopted by smallholder farmers in western Honduras. The four land uses were: secondary forest (F), agroforestry plots of less than two years of age (AF<2), agroforestry plots of more than 10 years of age (AF>10), and silvipastoral fields (SP). Transect-based sampling of soil macrofauna using the standard Tropical Soil Biology and Fertility Institute (TSBF) method was employed in both the dry season and wet season. All four land uses sampled in this study harboured diverse, abundant and highly variable soil macrofauna populations. In the dry season, total density of soil macrofauna ranged from 1265±308 individuals m^{-2} in F sites to 1924 ± 436 individuals m^{-2} in AF<2 sites. In the wet season, total density ranged from 907 ± 294 individuals m^{-2} in F, to 1637 ± 358 individuals m^{-2} in AF<2. Biomass values followed a similar pattern, ranging from 4.3 ± 1.1 g m^{-2} to 24.8 ± 8.2 g m^{-2} in the dry season and from 13.1 ± 3.0 g m^{-2} to 41.9 ± 11.1 g m^{-2} in the wet season. In order of decreasing strength of statistical relationship, soil depth, land use and season were all related to some aspects of soil macrofauna density, biomass and community composition. At a broad functional group level, soil macrofauna community composition was very similar across all four land uses. The results suggest that the agricultural practices associated with the 'Quesungual' agroforestry system may promote a relatively abundant, diverse soil macrofauna community. The presence of an abundant soil macrofauna community may have important effects on aspects of soil quality that are particularly important to resource-limited smallholder farmers.

1. Introduction

Land use can exert a strong influence on the overall abundance, biomass, diversity and community composition of soil macrofauna (Lavelle and Pashanasi 1989, Giller et al. 1997, Barros et al. 2002; Barrios et al. 2005). Soil macrofauna have long been recognised for their influence on soil physical, chemical and biological properties and processes (Lobry de Bruyn and Conacher 1990, Lee and Foster 1991, Lavelle et al. 1997, Six et al. 2004, Barrios 2007). The influence of soil macrofauna on soil properties may be particularly important for resource-limited smallholder farmers, who depend on the biological productivity of the soil for their livelihoods (Swift et al. 1994, Giller et al. 1997). However, relatively few of the comparative studies of the effects of different land uses on soil macrofauna abundance have included smallholder or traditional agriculture.

Several agricultural practices that appear to be associated with abundant, diverse soil macrofauna communities, many of which are incorporated within smallholder agricultural systems. These include: the presence of continuous soil cover (Loranger et al. 1998, Vohland and Schroth 1999, Barros et al. 2003); the addition of high quality mulch (Tian et al. 1993, Tian et al. 1997, Wardle et al. 2006); the inclusion of structurally and taxonomically diverse vegetation within fields (Roth et al. 1994, Perfecto and Snelling 1995, Bestelmeyer and Wiens 1996, Birang 2004, Pauli et al. 2010); and the presence of a mosaic of habitat types in the surrounding area (Lavelle and Pashanasi 1989, Dangerfield 1990, Thomas et al. 2004). Conversely, tillage disrupts termites and earthworms, and burning leads to drastic reductions in species density over the short term (Critchley et al. 1979, Bhadauria and Ramakrishnan 1989, Black and Okwakol 1997, Netuzhilin et al. 1999, Rossi et al. 2010).

A number of long-term monitoring and 'chronosequence' studies indicate that the composition and abundance of soil macrofauna in agricultural fields can change considerably with increasing time under cultivation. Following initial disturbance, soil macrofauna density may decline initially and then increase (Decaëns et al. 1994, Netuzhilin et al. 1999, Decaëns et al. 2002, Barros et al. 2004), or exhibit variable patterns, such as peaks and troughs in abundance (Bhadauria and Ramakrishnan 1989, Okwakol 1994, Sileshi and Mafongoya 2006a). Many traditional smallholder agricultural systems are based on rotation of plots between native vegetation, cropping and fallowing, so it is likely that the soil macrofauna communities in these systems are dynamic, responding to changes in management, vegetation and soil organic matter input. Because soil macrofauna communities are likely to be dynamic, it is important to sample across seasons and at different successional stages of agricultural use.

The Quesungual Slash-and-Mulch Agroforestry System (also referred to as QSMAS) from western Honduras (Welchez et al. 2008) was used as the case study in this research because it incorporates many features that should promote abundant, diverse soil macrofauna populations, which should in turn improve soil quality for smallholder farmers. The name 'Quesungual' comes from the name of the village where this agroforestry system was first identified (Hellin et al. 1999). The agroforestry system comprises a suite of land management practices used by resource-poor smallholder farmers. It is notable not only for its heterogeneity and incorporation of high levels of plant diversity, but also for the fact that it represents a transition from traditional slash-and-burn agriculture to a reportedly more sustainable method of slash-and-mulch agroforestry (Welchez et al. 2008). The study area has suffered from land degradation and related issues of food insecurity and poverty in the past (Pender 2001, Ruben and Clercx 2003, Ordoñez Barragan 2004, Ayarza et al. 2005). Today, the apparent success of the new system in improving farmers' standard of living while at the same time increasing vegetation cover and diversity (Hellin et al. 1999, Ayarza et al. 2005) allows for the examination of relationships between above- and below-ground biodiversity in the context of land management practices.

The overall aim of the study was to explore the associations of land use, season and soil depth with soil macrofauna density, biomass and community composition across four land uses found within an agricultural landscape dominated by the Quesungual agroforestry system, including secondary forest, agroforestry plots of two distinct ages, and silvipasture plots. The first objective of the study was to test the assumption that the land uses represent a gradient of change in tree density, vegetation diversity and soil organic carbon content. The second objective was to compare soil macrofauna biomass and abundance among different land uses. The third objective was to characterise seasonal distribution patterns of soil macrofauna abundance and biomass in both the dry and wet season. The fourth objective was to investigate the vertical distribution of soil macrofauna biomass and abundance within the soil pedon. The final objective was to assess changes in soil macrofauna community composition according to land use, season and soil sampling depth. Prior to this study, no systematic information had been collected on the soil macrofauna of the study area.

2. Materials and methods

2.1 Study area and study sites

The study area was located in the zone surrounding the village of Candelaria, in the southern region of Lempira Department in south-western Honduras (Figure 1). The climate of the study area is classified as equatorial winter dry (Aw) according to the Köppen-Geiger classification (Kottek et al., 2006). Annual rainfall, which falls primarily between May and October, averages 1200 to 1400 mm (Cherrett, 1999). Average daily temperatures range between 17 and 25°C (Hellin et al., 1999). The study area falls within the Central American dry tropical forest zone, which has been almost completely converted to agriculture over the last 1000 years (Janzen, 1988; Barrance et al., 2003; Gordon et al., 2003). The soils of the study area are Entisols that are generally shallow, acidic (pH of less than 5.1), with low organic matter content and available phosphorus, and are mostly sandy clay loam and clay loam in texture (Hellin et al., 1999; Ordoñez-Barragan, 2004; Pauli, 2008).

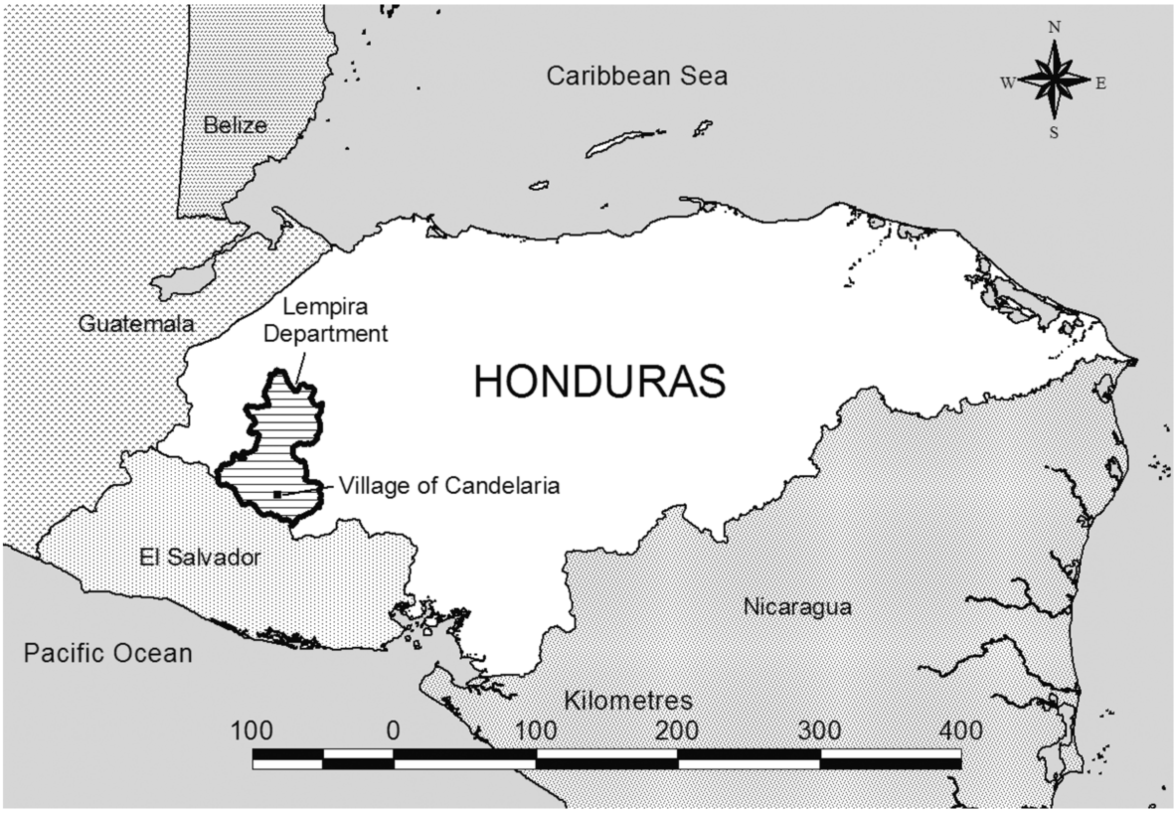

Figure 1: Location of study area. Study sites were selected from the region surrounding the village of Candelaria in Lempira Department, Honduras.

Farmers rotate fallow, crop and pasture areas according to need, soil fertility status and potential for capital investment in livestock. Four 'land uses' found within smallholder farms were sampled, namely: i) secondary forest; ii) agroforestry plots with annual crops cultivated for less than two years since selective slashing and coppicing of secondary forest; iii) agroforestry plots with annual crops cultivated for more than 10 years; and iv) silvipastoral fields. The agroforestry plots that represent the Quesungual Slash-and-Mulch Agroforestry system as defined by Welchez et al. (2008) are generally referred to by local farmers as '*milpa*'. *Milpa* is a generic term that refers to parcels of land where maize is grown and is commonly used in other parts of Central America; here, the term 'agroforestry' will be used. In the study area, annual crops are typically a rotation of maize (*Zea mays* L.) with sorghum (*Sorghum bicolor* (L.) Moench) and/or common bean (*Phaseoulus vulgaris* L.) grown amongst trees and shrubs, which are dispersed throughout the field. Silvipasture plots are typically converted agroforestry plots planted with grasses for grazing cattle, which retain some of the dispersed trees and shrubs. The maximum length of continuous annual cropping is estimated at 12 years within the study area. Farmers may choose to convert their agroforestry plots to pasture at any point in the cropping cycle, although this may reduce the suitability of that field for annual crops in the future (Pauli, 2008). Figure 2 illustrates some of the key changes in vegetation diversity and density that occur as fields pass through each of the land uses.

The agroforestry, secondary forest and silvipastoral sites that were sampled in this research were all actively farmed. The study sites were selected from a larger pool of farms that had previously been studied by staff from Centro Internacional de Agricultura Tropical (CIAT) and the Lempira Extension Service (SEL), based on the degree of similarity of soil, vegetation and topography. The altitude of the chosen sites ranged between 490 and 830 m asl.

<u>*2.2 Field and laboratory methods*</u>

Three fields of each of the four land uses were sampled for soil macrofauna, vegetation density and diversity, and selected soil properties. The field sampling for soil macrofauna was carried out at the end of the dry season, in April 2004, and in the middle of the wet season, in August 2004. In the dry season, three land uses were sampled: secondary forest (F), agroforestry plots less than two years old (AF<2), and agroforestry plots more than 10 years old (AF>10). In the wet season, three silvipastoral sites (SP) were added to the study. One of the secondary forest sites was cleared by the farmer between sampling dates, and had to be replaced with another site. Data from these two secondary forest sites were excluded from between-season analyses.

Macrofauna samples were extracted from a 90 metre transect within each site, with 10 sample points set 10 metres apart. The transects were placed along a diagonal line traversing the plot from one randomly selected upslope corner to the opposing downslope corner. The origin of the transect was located randomly along this line, providing that the entire transect could fit onto the diagonal.

At each sample point, one soil block of 25 cm by 25 cm to 30 cm depth was collected and sorted according to the standard method used by the Tropical Soil Biology and Fertility (TSBF) Institute (referred to as the 'TSBF soil monolith method') (Anderson and Ingram 1993; Moreira et al. 2008). Litter was collected from within a quadrat of 25 cm by 25 cm, and a trench excavated to 30 cm depth around the quadrat. The soil block was removed from the ground, divided into three layers of 10 cm depth (i.e., 0-9.9 cm, 10-19.9 cm and 20-30 cm), and hand-sorted for soil macrofauna. Invertebrates were preserved in 70% ethanol, with earthworms and larvae preserved in 4% formol. Invertebrates were identified to Order level, counted and weighed. Standard correction factors for preserved invertebrates were applied to dry weights (Decaëns et al. 1994).

Vegetation properties were measured from within circular plots of five metre radius at each soil macrofauna sampling point. Common name and diameter at breast height (DBH) were recorded, as well as whether trees were coppiced or free-growing. A local field assistant identified all trees by common name, and a botanist identified specimens to family, genus and species level. At each soil macrofauna sample location, a soil sample was collected to 10 cm depth, air-dried in the shade and passed through a 2 mm sieve. Soil texture was assessed using the standard hydrometer method (Gee and Bauder 1986). Soil organic carbon was determined using the standard loss on ignition (LOI) method (Schulte and Hopkins 1996).

2.3 Data analysis

The differences in vegetation and soil variables among the different land use types were assessed using one-way analysis of variance (ANOVA) for sites that were sampled during the wet season of 2004. The individual properties chosen were: tree density; total tree species richness for each site; tree basal area (in cm^2 m^{-2}, calculated using DBH); soil organic carbon; and % sand (as an indicator of soil texture). Post-hoc pairwise testing was undertaken using the least significant difference (LSD).

The soil macrofauna data did not follow a normal distribution, even after applying standard transformations. Therefore, the non-parametric Kruskal-Wallis test (Kruskal and Wallis 1952) was performed using Genstat 13.2 (VSNi 2010) to compare the effects of land use on a range of response variables, including total soil macrofauna density (individuals m^{-2}), total soil macrofauna biomass (g m^{-2}), and total density of ants, termites, earthworms, adult beetles, beetle larvae, millipedes, centipedes and spiders. The values for all variables were assessed using the entire soil block at each sample point (i.e., litter to 30 cm) rather than individual depths. Separate tests were carried out for wet season and dry season data. Post-hoc pairwise testing was undertaken using the least significant difference (LSD) among mean ranks.

Multivariate analyses of the density of all 23 taxonomic groups sampled were performed with PRIMER (Carr 1996). For each taxonomic group, average density values were calculated using the 10 samples taken at each study site in both sampling seasons. Data were fourth root transformed to down-weigh the most abundant taxa. A similarity matrix comparing samples was constructed based on the Bray-Curtis coefficient (Bray and Curtis 1957). This similarity matrix was used as the basis for multivariate analyses using non-metric multidimensional scaling (nMDS) (Kruskal and Wish 1978) and analysis of similarities (ANOSIM) (Clarke and Green 1988). nMDS was used for graphical representation of the degree of similarity of taxonomic composition among samples. nMDS is a visualisation technique that constructs a 'map' of samples in a specified number of dimensions based on the similarity matrix, so that samples plotted relatively close together on the nMDS map are more similar than samples that are separated by a relatively greater distance.

Two-way ANOSIM was performed to assess whether season, land use and soil sampling depth had a significant effect on taxonomic composition. ANOSIM is a non-parametric permutational procedure that involves the computation of a test statistic (Global 'R') that compares differences between treatments. R is then recalculated under a specified number of random permutations of the sample labels, and the permutation distribution of R compared with Global R. Three separate two-way

ANOSIM analyses were performed with the data, each involving 999 permutations. The first compared the effects of season and land use, using the data from sites that were sampled in both seasons. The second analysis compared the effects of land use and soil sampling depth in the dry season, and the third compared the same factors in the wet season. Pairwise testing based on permutations was applied where significant differences were noted. One hundred permutations were performed for the first ANOSIM comparison of season and land use (the maximum possible number based on the number of samples) and 999 permutations were calculated for the other two ANOSIM comparisons.

3. Results

3.1 Summary data

Average soil macrofauna density across all land uses sampled was 1614 ± 213 (S.E.) individuals m^{-2} in the dry season and 1289 ± 154 individuals m^{-2} in the wet season. Average total biomass values across all land uses were 12.4 ± 1.9 g m^{-2} in the dry season, and 22.3 ± 3.4 g m^{-2} in the wet season.

A total of 23 soil macrofauna taxa were identified (Table 1), with between 10 and 20 orders found at any one site. Termites were the most abundant taxa, comprising around 50% of individuals sampled in both seasons. Ants comprised 29% of individuals sampled in the dry season and 21% in the wet season. Earthworms made up 6% of organisms sampled in the dry season and 12% in the wet season. Soil macrofauna density was distributed relatively evenly throughout the soil pedon in both seasons, with peak abundance generally occurring in the uppermost 9.9 cm of soil (Figure 3).

Table 1: Proportion of total density and biomass for each taxonomic group encountered. Values given here are average figures across all land uses sampled, for both wet and dry seasons combined.

Taxa	**Common Name**	**Taxonomic Level**	**Density (% of total)**	**Biomass (% of total)**
Insects			***85.4***	***24.0***
Apterygota	Silverfish, wingless insects	Subclass	0.3	0.04
Blattodea	Cockroaches	Order	0.04	0.4
Coleoptera	Beetles (adults)	Order	2.3	6.6
	Beetle grubs (larvae)		2.7	5.8
Dermaptera	Earwigs	Order	1.6	0.3
Diptera	Flies, mosquitoes (larvae)	Order	0.1	0.03
Hemiptera	True bugs	Order	0.3	0.2
Homoptera	Cicadas, leafhoppers, aphids	Order	0.4	0.5
Hymenoptera	Ants [a]	Order	26.1	2.5
Isoptera	Termites	Order	51.1	6.4
Lepidoptera	Butterflies and moths (larvae)	Order	0.3	0.7
Mantodea	Mantises	Order	0.01	< 0.01
Neuroptera	Ant lions	Order	0.02	< 0.01
Orthoptera	Grasshoppers, katydids	Order	0.1	0.6
Pscopotera	Book lice	Order	0.03	< 0.01
Earthworms			***9.2***	***72.7***
Oligochaeta	Earthworms	Subclass	9.2	72.7
Myriapods			***4.0***	***2.3***
Chilopoda	Centipedes	Class	2.5	1.2
Diplopoda	Millipedes	Class	1.4	1.1
Arachnids			***1.1***	***0.6***
Araneae	Spiders	Class	1.0	0.5
Opiliones	Harvestmen	Class	0.04	< 0.01
Pseudoscorpionida	Pseudoscorpions	Class	0.1	0.1
Scorpiones	Scorpions	Order	0.01	< 0.01
Crustaceans			***0.3***	***< 0.01***
Isopoda	Pillbugs, slaters	Order	0.3	< 0.01
Molluscs			***0.03***	***0.01***
Gastropoda	Snails	Class	0.03	0.01

Notes:

[a] The great majority of Hymenoptera sampled in this study were ants, with a few specimens of wingless wasps.

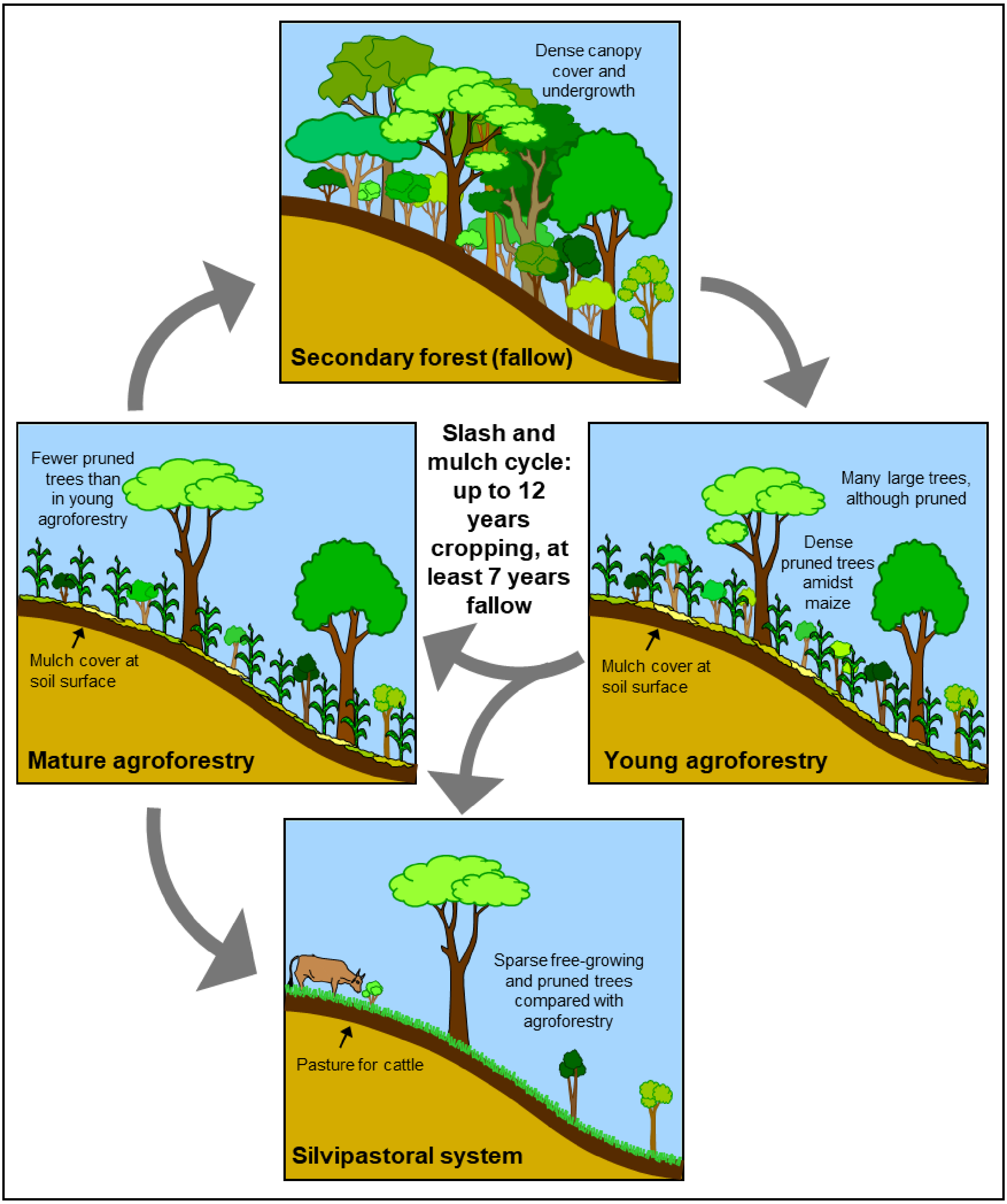

Figure 2: Illustration of key characteristics of land uses of the study area. The four land uses sampled (secondary forest, young agroforestry, mature agroforestry, and silvipastoral) can be seen as successive phases in a continuum of land use change in the study area. Most fields cycle between secondary forest (fallow) and cropping (agroforestry); some fields may be converted to pasture at any point in the cropping cycle.

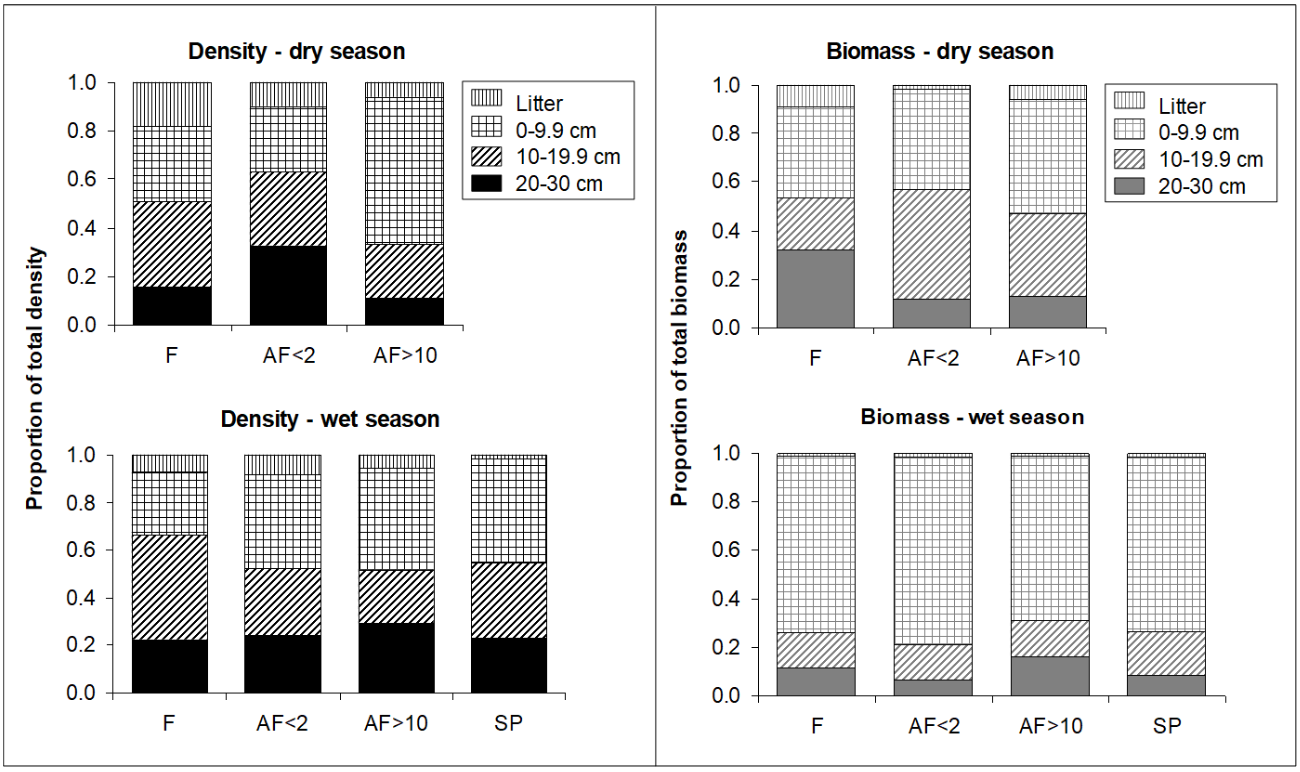

Figure 3: Vertical distribution profiles in the soil of soil macrofauna total density and total biomass in wet and dry seasons, for each land use. Values shown are averages for each of the land uses sampled. F: Secondary forest (*n* = 20). AF<2: Agroforestry <2 years (*n* = 30). M>10: Agroforestry >10 years (*n* = 30). SP: Silvipastoral (*n* = 30). Note that silvipastoral land use was not sampled in the dry season.

Earthworms accounted for over 70% of the total soil macrofauna biomass. Beetle adults and larvae accounted for 12% of the total biomass, and in some land uses they made up over 35% of the biomass. Termites comprised a further 6% of total biomass and ants accounted for 2% of total biomass. Biomass was concentrated in the upper 19.9 cm of soil in the dry season (Figure 3). In the wet season, around 70% of the total soil macrofauna biomass was concentrated in the upper 9.9 cm of soil.

The taxonomic composition of soil macrofauna at each soil depth in each of the seasons and land uses sampled is shown in Figure 4. In secondary forest, overall soil macrofauna density was low, although evenness was relatively high in the litter and upper 9.9 cm of soil due to relatively small ant and termite populations, and the presence of a diverse array of taxa. Ants were the most abundant organisms. For AF<2 sites, termites were abundant at most soil depths in both seasons. Earthworms were present at high density in the upper 9.9 cm of soil during the wet season. In AF>10 sites, the litter layer contained a relatively low density of soil macrofauna. Termite density was high in the 0-9.9 cm soil depth in the dry season, and was more evenly spread within the soil pedon in the wet season. In SP sites, greatest soil macrofauna density occurred between 0 and 9.9 cm, and decreased with depth. Termites and ants were the most abundant taxa.

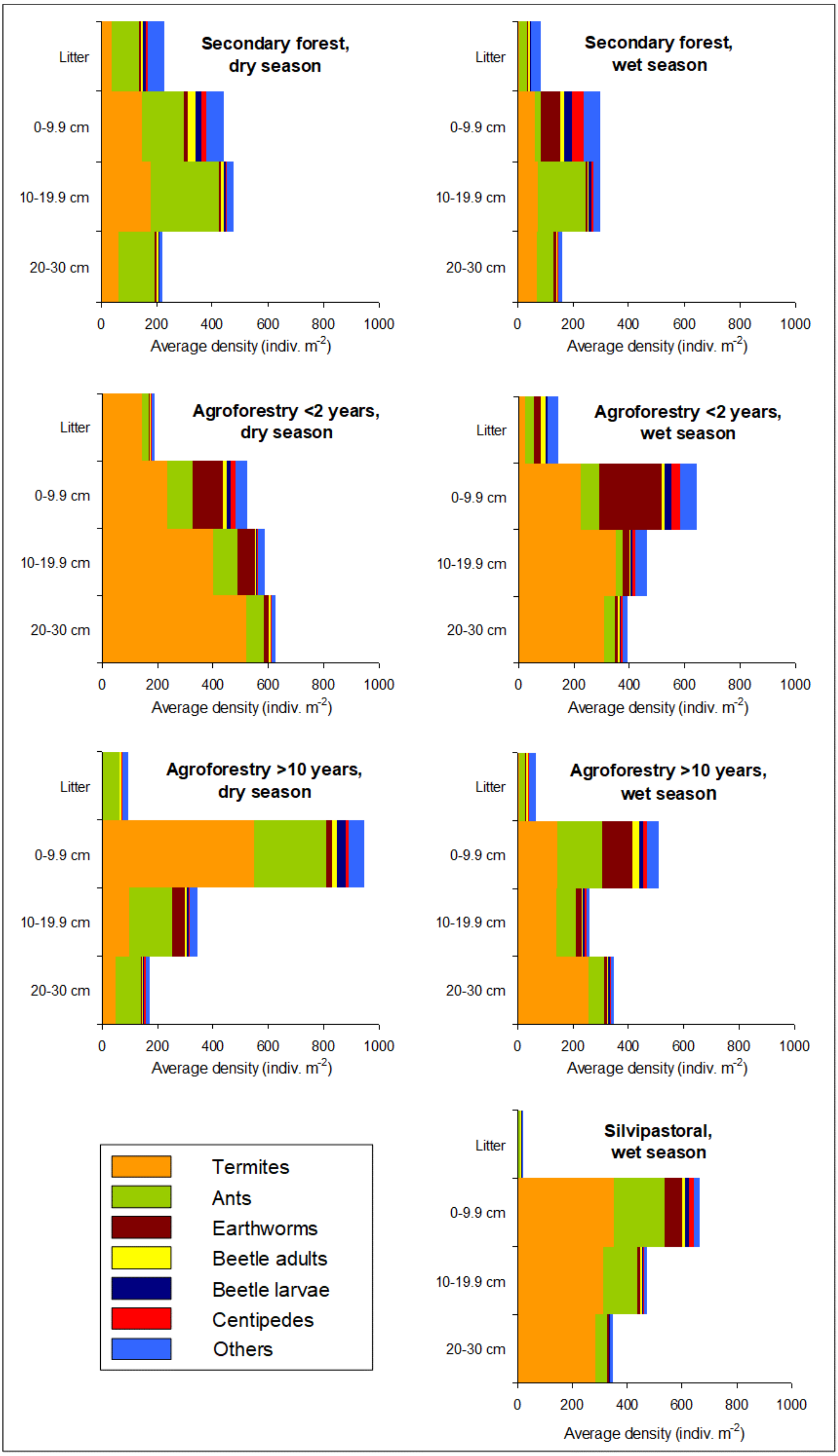

Figure 4: Vertical distribution and taxonomic group composition of soil macrofauna in each soil layer sampled for each land use in both seasons. Values shown are averages across each of the land uses sampled.

Seventy distinct trees and shrubs were identified within the study sites. The 12 most commonly encountered species are set out in Table 2. An average of 23 species were encountered per site, ranging from five species in one of the AF>10 sites, to 46 species in one of the secondary forest sites. An average of 89% of trees were coppiced in AF<2 sites, declining to 46% coppiced in AF>10 sites and 49% in SP sites. Soil organic carbon values ranged between 7.3 and 38.8 g kg^{-1}. The most common soil texture classifications encountered were loam and sandy clay loam.

3.2 Relationships between land use and environmental variables

Mean values for selected environmental variables (tree density, tree species richness, tree basal area, % soil organic carbon, % sand as an indicator of soil texture) are shown in Table 3. Results of one-way ANOVA indicated that all variables were significantly different among land uses ($p<0.001$ for all comparisons except % organic carbon ($p = 0.017$)). Results of pairwise testing are shown in Table 3. Tree species richness, tree density and tree basal area generally decreased from secondary forest through to agroforestry and silvipastoral land use. Soil organic carbon was lowest in the silvipastoral land use.

Table 2: The 12 most commonly encountered tree and shrub species within the study sites. Plant species were sampled along transects within each of the four land uses sampled; figures here are average values across all land uses.

Common Name	Scientific Name	Family	% of Total [a]	Major uses
Laurel	*Cordia alliodora*	Boraginaceae	16.0	Timber
Cangrejillo [b]	*Lonchocarpus* sp.	Papilionaceae	8.4	Firewood, mulch
Pie de venado	*Bauhinia* sp.	Caesalpiniaceae	7.9	Firewood, mulch
Sirin de pava	*Miconia* sp.	Melastomataceae	7.0	Firewood
Guayabo	*Psidium guajava*	Myrtaceae	6.5	Fruit (guava)
Chichipate [b]	*Acosmium panamense*	Papilionaceae	6.3	Firewood, mulch
Chaparro	*Curatella americana*	Dilleniaceae	5.7	Firewood, mulch
Guachipilin [b]	*Diphysa americana*	Papilionaceae	3.8	Timber, mulch
Guacuco	*Casearia* sp.	Flacourtiaceae	3.2	Mulch
Caulote	*Guazuma ulmifolia.*	Sterculiaceae	2.9	Firewood, mulch
Guayabillo	*Psidium hondurensis*	Myrtaceae	2.7	Fruit, firewood
Nance	*Byrsonima crassifolia*	Malphigiaceae	2.3	Fruit

Notes:

[a] The 12 species shown here accounted for 73% of the total number of individual trees and shrubs encountered.

[b] Leguminous that are likely to be nitrogen-fixing.

Table 3: Results of post-hoc testing of statistically significant relationships between land use and environmental variables. Soil and vegetation variables were sampled along transects within four land uses.

	Mean ± standard error				
Response variable	**Secondary Forest** *n*=30 [a]	**Agroforestry <2 years** *n*=30 [a]	**Agroforestry >10 years** *n*=30 [a]	**Silvipastoral** *n*=30 [a]	**LSD** [b]
Tree density (trees ha^{-1})	1120 ± 110 $_{A}$	1162 ± 117 $_{A}$	704 ± 77 $_{B}$	352 ± 43 $_{C}$	241.5
No. of tree spp. per site	35.0 ± 6.4 $_{A}$	25.7 ± 3.4 $_{B}$	13.7 ± 4.5 $_{C}$	14.3 ± 1.8 $_{C}$	5.80
Tree basal area (cm^2 m^{-2})	21.4 ± 3.8 $_{A}$	9.1 ± 1.1 $_{B}$	12.2 ± 2.2 $_{B}$	8.0 ± 1.6 $_{B}$	6.79
Organic carbon (g kg^{-1})	24.9 ± 1.0 $_{A}$	23.4 ± 1.1 $_{A, B}$	25.4 ± 1.3 $_{A}$	20.8 ± 1.0 $_{B}$	3.10
% Sand	47.6 ± 1.2 $_{A, B}$	46.0 ± 1.1 $_{A}$	43.9 ± 1.3 $_{A}$	50.6 ± 1.1 $_{B}$	3.34

Notes:

[a] *n*=3 for number of tree species per site

[b] Multiple comparisons were undertaken for the means in each row (i.e., across the table) using the appropriate LSD (least significant difference). Significant differences ($p<0.05$) were noted for all comparisons using one-way ANOVA. Subscript uppercase letters denote group membership.

3.3 Relationships between soil macrofauna and land use within seasons

Results of the Kruskal-Wallis test (Table 4) comparing soil macrofauna variables in different land uses in the dry season showed that total soil macrofauna biomass and density of earthworms, beetle larvae and millipedes were significantly different among land uses. In the wet season, there were significant differences in the total density of soil macrofauna, as well as the density of ants, termites, millipedes and centipedes among different land uses (Table 5) .

Taxa that were significantly different between land uses responded in different ways across the continuum of land use change. Both termites and earthworms were present in significantly higher densities in AF<2 than in F, while their densities returned to medium values in AF>10. Ants exhibited a different trend, with relatively high densities in F, followed by a sharp drop in AF<2 plots and then intermediate to high values in AF>10 plots. Beetle larvae showed a similar trend in the dry season. Millipede density decreased steadily from secondary forest to agroforestry to pasture. Ant density was highly variable in SP plots, as noted by the disparity between the mean density and mean rank for each of the land uses in the wet season; most SP samples returned relatively low ant densities, with a few recording extremely high densities. The variability within all land uses was very high, as shown by the high standard error values in Tables 4 and 5. It is likely that a large proportion of the variability in the data was not accounted for by the non-parametric statistical tests applied.

Table 4: Comparison of total soil fauna density, total soil fauna biomass, and density of individual taxa among three land uses in the dry season. The table shows the results of one-way Kruskal-Wallis ANOVA for each variable among the three land uses, together with results of post-hoc testing on mean ranks.

	LAND USE [a]		
	F $n = 30$ [b]	**AF<2** $n = 30$ [b]	**AF>10** $n = 30$ [b]
Response variable and p value for Kruskal-Wallis ANOVA [c]	**Mean ± SE (g m^{-2} for biomass and individuals m^{-2} for density)**		
Total soil fauna density (p = 0.912)	1345.1 ± 248.5	1913.1 ± 435.8	1537.6 ± 397.5
Total soil fauna biomass (p = 0.041)	**4.8 ± 1.2**	**24.8 ± 8.2**	**7.6 ± 1.8**
Ant density (p = 0.199)	620.3 ± 206.9	272.5 ± 54.7	569.1 ± 110.5
Termite density (p = 0.135)	451.2 ± 179.8	1298.1 ± 404.1	699.2 ± 354.5
Earthworm density (p = 0.028)	**38.4 ± 13.6**	**189.9 ± 48.9**	**75.7 ± 27.5**
Beetle adult density (p = 0.061)	51.2 ± 11.1	22.4 ± 5.9	34.7 ± 6.7
Beetle larvae density (p = 0.01)	**46.9 ± 6.3**	**24.0 ± 4.7**	**51.2 ± 27.2**
Millipede density (p = 0.005)	**36.8 ± 9.0**	**15.5 ± 6.5**	**13.9 ± 7.0**
Centipede density (p = 0.565)	31.5 ± 5.5	30.9 ± 6.3	22.9 ± 4.2
Spider density (p = 0.711)	15.5 ± 3.5	12.8 ± 2.9	10.7 ± 2.3
Response variable where significant differences among land uses observed	**Mean rank and groups according to Least Significant Difference (LSD) between mean ranks** [d]		
Total soil fauna biomass	37.7 $_{A}$	54.6 $_{B}$	44.3 $_{A, B}$
Earthworm density	37.3 $_{A}$	54.6 $_{B}$	44.7 $_{A, B}$
Beetle larvae density	56.9 $_{A}$	38 $_{B}$	41.6 $_{A, B}$
Millipede density	56.1 $_{A}$	42.5 $_{A, B}$	37.9 $_{B}$

Notes:

[a] F = secondary forest; AF<2 = agroforestry of less than two years of age; AF>10 = agroforestry of more than 10 years of age.

[b] *n* refers to the number of soil blocks sampled from each land use.

[c] Comparisons for which a significant difference was noted are highlighted in **bold**.

[d] LSD among mean ranks was computed as 16.15 (total $n = 90$, $\alpha = 0.05$, total number of comparisons = 3, group $n = 30$). Subscript uppercase letters denote pairs that were different from each other.

Table 5: Comparison of total soil fauna density, total soil fauna biomass, and density of individual taxa among four land uses in the wet season. The table shows the results of one-way Kruskal-Wallis ANOVA for each variable among the four land uses, together with results of post-hoc testing on mean ranks.

	LAND USE [a]			
	F *n* = 30 [b]	**AF<2** *n* = 30 [b]	**AF>10** *n* = 30 [b]	**SP** *n* = 30 [b]
Response variable and p value for Kruskal-Wallis ANOVA [c]	**Mean ± SE (g m^{-2} for biomass and individuals m^{-2} for density)**			
Total soil fauna density (p = 0.03)	**814.4 ± 197.8**	**1612.8 ± 360.0**	**1177.1 ± 232.9**	**1502.4 ± 389.6**
Total soil fauna biomass (p = 0.114)	11.7 ± 2.0	41.3 ± 10.9	20.7 ± 5.6	14.3 ± 3.3
Ant density (p = 0.035)	**278.9 ± 72.9**	**164.8 ± 33.5**	**315.7 ± 65.6**	**360.0 ± 141.1**
Termite density (p = 0.003)	**210.1 ± 170.5**	**910.4 ± 329.5**	**543.5 ± 209.2**	**947.2 ± 317.5**
Earthworm density (p = 0.333)	94.4 ± 26.4	285.3 ± 86.7	146.1 ± 28.0	84.3 ± 15.3
Beetle adult density (p = 0.195)	25.6 ± 4.8	38.4 ± 6.3	38.4 ± 8.2	21.9 ± 4.1
Beetle larvae density (p = 0.138)	43.2 ± 6.0	41.1 ± 8.4	28.8 ± 4.6	30.9 ± 8.5
Millipede density (p<0.001)	**52.3 ± 13.2**	**8.0 ± 2.0**	**13.9 ± 4.9**	**1.6 ± 0.9**
Centipede density (p<0.001)	**57.1 ± 13.7**	**59.7 ± 9.7**	**28.8 ± 5.6**	**19.7 ± 5.8**
Spider density (p = 0.11)	17.1 ± 4.3	20.8 ± 3.9	17.1 ± 4.7	8.5 ± 2.6
Response variable where significant differences observed	**Mean rank and groups according to Least Significant Difference (LSD) between mean ranks** [d]			
Total soil fauna density	48.6 $_{A}$	74.5 $_{B}$	62.9 $_{A, B}$	56.0 $_{A, B}$
Ant density	64.0 $_{A, B}$	58.3 $_{A, B}$	72.7 $_{A}$	47.1 $_{B}$
Termite density	41.1 $_{A}$	68.5 $_{B}$	64.2 $_{A, B}$	68.1 $_{B}$
Millipede density	78.3 $_{A}$	59.4 $_{A, B}$	60.5 $_{A, B}$	43.8 $_{B}$
Centipede density	68.1 $_{A}$	77.3 $_{A}$	54.8 $_{A, B}$	41.8 $_{B}$

Notes:

[a] F = secondary forest; AF<2 = agroforestry of less than two years of age; AF>10 = agroforestry of more than 10 years of age; SP = silvipastoral land use.

[b] *n* refers to the number of soil blocks sampled from each land use.

[c] Comparisons for which a significant difference was noted are highlighted in **bold**.

[d] LSD among mean ranks was computed as 23.70 (total n = 120, α = 0.05, total number of comparisons = 6, group n = 30). Subscript uppercase letters denote pairs that were different from each other.

3.4 Changes in community composition according to land use, season and soil sampling depth

The ordination analysis using nMDS showed varying degrees of differentiation of the factors season, land use and soil sampling depth (Figure 5). There was a high degree of variation within seasons (Figure 5 (A)). Classification according to land use did not show any visually identifiable separation of the four land use categories (Figure 5 (B)), whereas classification according to soil depth showed strong separation of the four sampling depths (Figure 5 (C)). Of the four soil depths, 0-9.9 cm and 10-19.9 cm were the most similar. The 20-30 cm layer was the most variable, with samples widely dispersed on the nMDS diagram, while the litter layer was the most tightly clustered. The stress value for the nMDS was relatively high (stress = 0.2), indicating a high degree of scatter of the samples around the fitted non-parametric regression line.

ANOSIM performed on the data from sites sampled in both seasons indicated significant differences in community composition between seasons (Global R = 0.323, p = 0.03) and land uses (Global R = 0.347, p = 0.015). Pairwise tests between land uses indicated that there was a significant difference between F and AF<2 (R = 0.5, p = 0.03).

For the dry season data, ANOSIM did not indicate a significant effect of land use on community composition (Global R = 0.031, p = 0.33), but there was a significant relationship with soil depth (Global R = 0.271, p = 0.001). Pairwise testing indicated that there were significant differences between 20-30 cm and all other soil sampling depths (litter: p = 0.012; 0-9.9 cm: p = 0.002.; 10-19.9 cm: p = 0.001) and between 10-19.9 cm and litter (p = 0.043).

In the wet season, there were significant differences between land uses (Global R = 0.199, p = 0.016) and soil sampling depths (Global R = 0.437, p = 0.001). Pairwise testing showed that there were significant differences between F and SP (R = 0.435, p = 0.009), between AF<2 and SP (R = 0.231, p = 0.048), and between AF>10 and SP (R = 0.222, p = 0.034). Community composition was significantly different between all pairs of soil sampling depths (p = 0.001 or p = 0.002 depending on the comparison), aside from 0-9.9 cm and 10-20 cm.

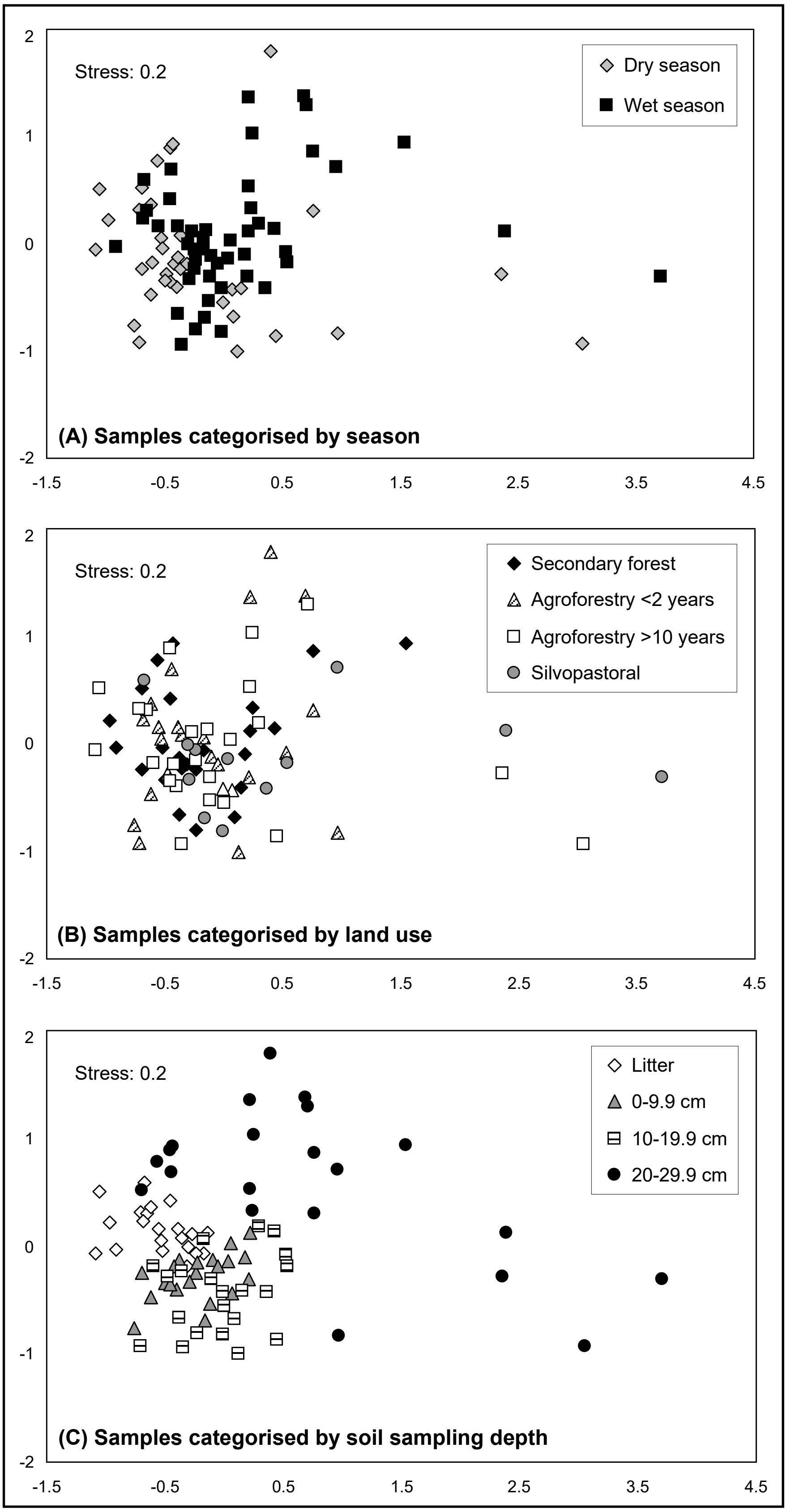

Figure 5: Ordination analysis (nMDS) of the taxonomic composition of soil macrofauna communities at sample points. Each point in the diagrams corresponds to the average of the 10 samples taken from within each study site during each sampling period (dry and wet seasons).Diagrams A, B and C are identical to one another, aside from the symbols used. Each point can be labelled according to (A) season, (B) land use and (C) soil sampling depth. Points that are closer together on the nMDS diagram are more similar in their taxonomic composition than those that are further apart.

4. Discussion

The areas sampled in this study had a high density of soil macrofauna, relative to other comparable studies from tropical sites (Table 6). Compared with studies from Central America, average soil macrofauna density reported here was more than five times greater than that recorded in the central highlands of Honduras (Ericksen and McSweeney 1999) and nearly twice that from the plains of southeastern Mexico (Brown et al. 2004). Soil macrofauna densities found in this study were similar to those noted by Barros et al. (2002) in the Brazilian Amazon, and by Decaëns et al. (1994) for the eastern plains of Colombia. Studies that recorded substantially higher soil macrofauna densities include those of Feijoo et al. (1999) in the Colombian Andes, Barros et al. (2003, 2004) in the Brazilian Amazon and Mboukou-Kimbatsa et al. (1998) in the Congo basin.

Overall biomass values were low to moderate in comparison with biomass values recorded from other tropical studies (Table 6). The highest biomass values were typically recorded from sites located in rainforest regions. Sites from savannas and plains often recorded relatively high biomass values, largely due to the presence of abundant earthworms, while sites on hillsides tended to record similar biomass values to those presented here. The steep slopes and shallow, sandy soils of the study area may mean that water is drained rapidly from agricultural areas on sloping land, with few areas retaining enough soil moisture throughout the long, hot dry season to support larger-bodied soil organisms.

4.1 Soil macrofauna community composition

The most abundant organisms found in the sites sampled were termites, ants and earthworms, which together made up nearly 90% of all soil macrofauna sampled. Adult and larval beetles comprised 12% of all soil macrofauna biomass. Other studies have also found these groups to be amongst the dominant soil macrofauna taxa (e.g. Lavelle and Pashanasi 1989, Ericksen and McSweeney 1999, Feijoo et al. 1999, Brown et al. 2004, Decaëns et al. 2004, Mathieu et al. 2004, Rossi et al. 2006). The high densities of ants and termites are likely to lead to networks of underground tunnels that allow infiltration of water and air and create channels for root growth. The burrowing habits of earthworms are also likely to increase soil macroporosity. Earthworms and beetle larvae feed on soil organic matter, which speeds decomposition and nutrient cycling. The high densities of these organisms found in this study are likely to have an important effect on soil quality and soil macromorphology.

Table 6: Comparison of total soil fauna biomass and density in studies using Tropical Soil Biology and Fertility Institute (TSBF) sampling method [a] in tropical regions. The table lists average figures for mean soil fauna density and biomass across all land uses and seasons sampled.

Study	Country/ Region	Agroecosystems sampled	Mean soil fauna density (indiv. m^{-2})	Mean soil fauna biomass (g m^{-2})
Latin America – Highlands				
This study	Honduras, sub-humid tropical southern highlands	Secondary forest; young maize agroforestry; mature maize agroforestry; silvipastoral	1426	18.2
Ericksen and McSweeney (1999)	Honduras, sub-humid tropical central highlands	Pasture; forest; irrigated agriculture; temporal agriculture; flooded area; fallow; shaded coffee	271	n/a
Feijoo *et al.* (1999)	Colombia, Andean slopes from 1450 to 2200 m asl	Secondary forest; 40 year old forest; old growth forest; traditional coffee; fallow; cassava with beans and maize; kikuyu grass (*Pennisetum clandestinum*); pine plantation; *Yaragua* grass; *Brachiaria humidicola* pasture	3356	61.6
Latin America - Plains / Savannas				
Brown *et al.* (2004) [b]	Mexico, Veracruz region	Native pasture; introduced pasture	812	32.1
Blanchart *et al.* 2007	Cerrado, central Brazil	Mulch-based cropping of soybean in rotation with millet, maize or sorghum of 1, 5, 7, 11 and 13 years; conventional tillage (soybean); savanna vegetation (cerrado)	1652	14.0
Decaëns *et al.* (1994)	Colombia, eastern Plains	Native gallery forest; native savanna, protected from fire and grazing; native savanna burned, grazed, at low, medium and high stocking rates at various post-fire intervals; two types of pasture; high input rice crop; high input cassava crop	1814	17.1
Decaëns *et al.* (2002)	Colombia, eastern plains	Native savanna; traditional extensive pasture; two types of intensive pasture	n/a	30.8
Marchão *et al.* (2009)	Cerrado, central Brazil	Cerrado; continuous crop; crop-pasture rotation; pasture-crop rotation; continuous pasture	2206	n/a
Thomas *et al.* (2004)	Argentina	Natural grassland; fallows following rice cultivation 2, 4, 7 and 15 years	781	n/a

Study	Country/ Region	Agroecosystems sampled	Mean soil fauna density (indiv. m^{-2})	Mean soil fauna biomass (g m^{-2})
Latin America - Amazon Basin				
Barros *et al.* (2002)	Brazil	Disturbed forest; fallow; annual crop; agroforestry; pasture	1393	18.9

Study	Country/ Region	Agroecosystems sampled	Mean soil fauna density (indiv. m^{-2})	Mean soil fauna biomass (g m^{-2})
Barros *et al.* (2003)	Brazil	Palm-based system with crops; fruit tree-based system with crops; high-input system: trees, crops, & fodder; low-input system: trees, crops & fodder; fallow	11 560	44.0
Barros *et al.* (2004)	Brazil	Forest, four year old pasture; abandoned pasture	3664	36.7
Decaëns *et al.* (2004)	Brazil	Primary rainforest; pasture in varying stages of degradation	n/a	44.2
Lavelle and Pashanasi (1989)	Peru	Forest primary and secondary; high input maize; low input rice; traditional cassava; three types of pasture; three types of fallow	2244	61.9
Rossi *et al.* (2010)	French Guiana	Traditional slash and burn with long fallow, including secondary forest, recently burnt forest, and crop fields; slash and burn with short fallow, including woody fallow and crop field	860	n/a
Africa				
Dangerfield (1990)	Zimbabwe	Natural savannah woodland miombo; maize; fallow; disturbed miombo; mature *Eucalyptus grandis* plantation	145	12.0
Mboukou-Kimbatsa *et al.* (1998)	Congo	Savanna; eucalypt plantation 6, 11, 20 and 26 years; forest; acacia plantation 12 and 13 years; pine plantation 27 and 16 years	3511	26.7
Okwakol (1994)	Uganda	Natural forest; cleared and uncultivated; banana plantation 2, 3, 4, 5 and 20 years	614	6.9
Sileshi and Mafongoya (2006b)	Zambia	Coppicing fallow / maize 2, 5 and 10 years; maize monoculture without fertiliser 2, 5 and 10 years; maize monoculture with fertiliser 2, 5 and 10 years; mixed species fallow / maize 2 years; non-coppicing fallow 2 years	243	n/a
Asia				
Rossi and Blanchart (2005)	Southern India, monsoon affected	Primary forest; weakly disturbed forest; highly disturbed forest; acacia plantation 8 years; two types of pasture	136	n/a
Bignell *et al.* (2004)	Sumatra, Indonesia	Primary forest; logged-over forest; *Paraserianthes* tree plantation; *Hevea* (rubber) plantation; jungle rubber; degraded *Imperata* grassland; cassava garden	1144	14.9

Notes:

[a] The table shows studies that used the TSBF soil macrofauna sampling method (Anderson and Ingram 1993) to determine density and/or biomass of soil macrofauna associated with various land uses found in the areas studied.

[b] Brown *et al.* (2004) modified the standard TSBF method by taking samples of up to 40 to 50 cm depth instead of 30 cm. This study was included due to its proximity to Honduras

Soil macrofauna community composition was similar for all land uses in the study, based on the broad taxonomic groups used. If these groups used are taken as surrogates for functional groups of soil macrofauna, then there was no substantial loss of functional groups or shift in dominance between different land uses. The greatest differences occurred between silvipastoral sites and all other land uses. Substantial changes in the abundance of a number of taxa were also noted between secondary forest and recently converted agroforestry sites. It seems likely that the major changes in vegetation structure, plant diversity, tree cover, organic matter input and litter cover that are associated with conversion of secondary forest to agroforestry are reflected in greatly increased abundance of hardy and opportunist taxa (in this case, termites and earthworms) and reduced abundance of more sensitive taxa (which in this case comprised ants and some litter-dependent arthropods).

4.2 Differences in environmental variables among land uses

Land uses were significantly different in terms of vegetation characteristics and soil organic matter content. However, none of the selected variables was significantly different among all four land uses, and there were important differences in local soil type and soil texture classification among sites that were not included in the analyses. Tree density was the only variable that differed significantly among three of the four land uses. Although tree density decreased as agroforestry fields aged, tree basal area did not. This implies that while some trees die with each successive pruning or are removed for timber or fuel wood, the total area occupied by trees, and by extension, their roots and canopies, remains roughly similar. This is likely to increase the patchiness of organic resource distribution with time under cultivation, which could lead to increased patchiness in the spatial distribution of soil biota (Beare et al. 1995, Ettema et al. 1998, Saetre and Bååth 2000, Ettema and Wardle 2002).

4.3 Differences in soil macrofauna density and biomass among land uses

The differences in overall soil macrofauna density among the different land uses were not as pronounced as expected. Many taxa were present in similar densities in all four land uses, including several that depend on the litter layer. Ants and millipedes appeared to be the most sensitive indicators of land use change. Ant species diversity has been used in several studies as a biological indicator of soil health (Perfecto and Snelling 1995, Peck et al. 1998, Netuzhilin et al. 1999). Millipedes can also be sensitive indicators of land use change, disappearing following forest conversion and removal of the litter layer (Barros et al. 2003, Rossi and Blanchart 2005). Termites and earthworms were among the more adaptable organisms in our study, increasing in density in agricultural land uses. While earthworms have been found to be sensitive to disturbance (Lavelle et al. 1994), several studies have noted abundant termite and earthworm populations in agricultural land uses, especially those with limited- or no-tillage management (Lavelle and Pashanasi 1989, Barros et al. 2001, Decaëns et al. 2004). It is possible that the observed increase in density of termites and earthworms in agricultural land is a result of increased availability of soil organic matter following conversion of secondary forest to agriculture.

Soil macrofauna biomass was strongly related to land use change. The observed pattern of a large increase in biomass from secondary forest to young agroforestry sites, followed by a decrease in older agroforestry sites and silvipastoral sites, corresponds to the likely differences in productivity among these four land uses. The pattern also concurs with the likely volume of soil organic matter input in the form of litter fall, mulch and crop residue in the different land uses. Two of the organisms that contributed most to the total soil macrofauna biomass were white grub larvae and earthworms, both of which are associated by local farmers with areas of rich, dark soil with high organic matter content (Pauli, 2008). Fonte et al. (2010) also found a significant increase in earthworm biomass between secondary forest and agroforestry sites.

In this study, we opted for a transect-based approach, with replicate transects located in three examples of each land use. This design has been presented as an option for soil fauna surveys in a number of studies and reports, including Huising et al. (2008). Here, a transect-based approach allowed us to sample a large proportion of the variability present in each sampled plot. Due to the very high variability in soil fauna abundance within plots, the use of more transects in additional replicate plots for each land use may have assisted with identifying clearer trends in soil macrofauna density among land uses.

4.4 Seasonal differences in soil macrofauna density and biomass

Seasonal differences in soil macrofauna densities were less marked than expected, which may indicate that soil organisms are well adapted to seasonal drought. Soil macrofauna may take refuge in moister, more shaded sites and deeper layers over the dry season and disperse and multiply during the wet season, or it may be that different species of each taxa are better adapted to dry or wet conditions. Ants were the only taxa that were more abundant in the dry season. Increased ant abundance in the dry season has been noted in other studies (Höfer et al. 2001, Brown et al. 2004, Rossi and Blanchart 2005, Sileshi and Mafongoya 2006b). Biomass was almost twice as great in the wet season than in the dry season. This increase is most likely linked to increased soil moisture in the wet season, which permits the survival of greater numbers of moisture-dependent organisms such as earthworms. Seasonal differences may also be related to higher soil productivity and increased availability of organic matter through litter decomposition and greater root biomass in the wet season.

4.5 Vertical distribution of soil macrofauna density and biomass

Of the three environmental factors included in the analysis, soil depth was the factor that was most strongly related to soil macrofauna community composition. With increasing depth, the soil macrofauna community tended to include a smaller number of taxonomic groups. Soils were typically shallow; in some cases the depth to parent material was less than 30 cm and in other cases the topsoil was underlain at shallower depths by a hardpan layer. It is likely that the upper soil layer contains the highest concentration of soil organic matter and root biomass. For example, Barros et al. (2003) found gradients of carbon, nitrogen and soil moisture within Amazon basin soils, with the highest concentrations in the uppermost 5 cm of soil.

4.6 Conclusions

All four land uses sampled in this study harboured diverse, abundant and highly variable soil macrofauna populations. While there were some differences between the four land uses sampled, the magnitude of these differences was not as great as expected. Of all the land uses, silvipastoral land use differed most from the others, recording relatively low taxonomic richness, evenness and biomass. Soil depth was more strongly related to patterns of soil macrofauna distribution and community composition than season or land use, indicating that vertical distribution patterns remain largely unchanged among the different land uses.

The relatively high abundance of soil macrofauna noted within the Quesungual Slash-and-Mulch Agroforestry System (QSMAS) may result from the use of certain agricultural practices that have previously been associated with abundant soil fauna populations (such as inclusion of trees within fields and maintenance of soil cover through mulching), and the absence of other practices that have been linked to decline in soil fauna populations (for example, tillage and burning). The agricultural practices associated with the 'Quesungual' system do not appear to lead to significant imbalances or changes in soil macrofauna functional groups, although there may be changes at a finer level of taxonomic resolution than was applied in this study. The results indicate that the system allows for relatively high soil macrofauna abundance in comparison with what is known from other sub-tropical areas, which could have important effects on aspects of soil quality such as soil structure and nutrient cycling that are particularly important to small-scale farmers.

Acknowledgements

The authors wish to thank the farmers of the Candelaria region who allowed their fields to be sampled for this study. The authors are grateful to: Jesús Leonel Martínez, Edwin García, Daniel Vásquez and Odvin Ayala for their contributions as field assistants in Candelaria; José María Bonilla, principal of the Instituto Técnico Comunitario (ITC) in Candelaria and the students of ITC for assisting with the field surveys for soil macrofauna; Marco Tulio Trejo and Jimmy Eguigure of CIAT Honduras for logistical support; Miguel Ayarza for overall coordination of activities through the CIAT Honduras office; Fernando Sevilla Guío for his valuable assistance with counting and weighing soil macrofauna specimens; Edilfonso Melo, Jesús Galvis and Arnulfo Rodríguez of CIAT Cali for assistance with soil analyses; Zoila Avila of the Escuela Nacional de Ciéncias Forestales (ESNACIFOR) for identification of plant specimens; Richard Cookson and Louise Cullen with advice with statistical analysis; and staff at CIAT Cali, CIAT Honduras, FAO Candelaria, FAO Tegucigalpa and the School of Earth and Environment at the University of Western Australia. Financial support was provided by Centro Internacional de Agricultura Tropical (CIAT), the School of Earth and Environment at the University of Western Australia, and an Australian Postgraduate Award to the first author.

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