

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

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24 Soil macrofauna in the 'Quesungual' agroforestry system

25

26 **Abstract**

27 Smallholder agroforestry systems often incorporate features that are associated with abundant,
28 diverse soil macrofauna populations. This study sampled soil macrofauna communities across
29 four major land uses present within agricultural landscapes where the Quesungual Slash-and-
30 Mulch Agroforestry System (QSMAS) has been increasingly adopted by smallholder farmers
31 in western Honduras. The four land uses were: secondary forest (F), agroforestry plots of less
32 than two years of age (AF<2), agroforestry plots of more than 10 years of age (AF>10), and
33 silvipastoral fields (SP). Transect-based sampling of soil macrofauna using the standard
34 Tropical Soil Biology and Fertility Institute (TSBF) method was employed in both the dry
35 season and wet season. All four land uses sampled in this study harboured diverse, abundant
36 and highly variable soil macrofauna populations. In the dry season, total density of soil
37 macrofauna ranged from 1265 ± 308 individuals m^{-2} in F sites to 1924 ± 436 individuals m^{-2} in
38 AF<2 sites. In the wet season, total density ranged from 907 ± 294 individuals m^{-2} in F, to
39 1637 ± 358 individuals m^{-2} in AF<2. Biomass values followed a similar pattern, ranging from
40 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
41 m^{-2} in the wet season. In order of decreasing strength of statistical relationship, soil depth,
42 land use and season were all related to some aspects of soil macrofauna density, biomass and
43 community composition. At a broad functional group level, soil macrofauna community
44 composition was very similar across all four land uses. The results suggest that the
45 agricultural practices associated with the 'Quesungual' agroforestry system may promote a
46 relatively abundant, diverse soil macrofauna community. The presence of an abundant soil
47 macrofauna community may have important effects on aspects of soil quality that are
48 particularly important to resource-limited smallholder farmers.

49

50 **Keywords**

51 Soil macrofauna; Soil ecology; Smallholder agriculture; Land use change; Quesungual Slash-
52 and-Mulch Agroforestry System; Central America.

53

54 **1. Introduction**

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

65
66 Several agricultural practices that appear to be associated with abundant, diverse soil
67 macrofauna communities, many of which are incorporated within smallholder agricultural
68 systems. These include: the presence of continuous soil cover (Loranger et al. 1998, Vohland
69 and Schroth 1999, Barros et al. 2003); the addition of high quality mulch (Tian et al. 1993,
70 Tian et al. 1997, Wardle et al. 2006); the inclusion of structurally and taxonomically diverse
71 vegetation within fields (Roth et al. 1994, Perfecto and Snelling 1995, Bestelmeyer and Wiens
72 1996, Birang 2004, Pauli et al. 2010); and the presence of a mosaic of habitat types in the
73 surrounding area (Lavelle and Pashanasi 1989, Dangerfield 1990, Thomas et al. 2004).
74 Conversely, tillage disrupts termites and earthworms, and burning leads to drastic reductions
75 in species density over the short term (Critchley et al. 1979, Bhadauria and Ramakrishnan
76 1989, Black and Okwakol 1997, Netuzhilin et al. 1999, Rossi et al. 2010).

77

78 A number of long-term monitoring and ‘chronosequence’ studies indicate that the
79 composition and abundance of soil macrofauna in agricultural fields can change considerably
80 with increasing time under cultivation. Following initial disturbance, soil macrofauna density
81 may decline initially and then increase (Decaëns et al. 1994, Netuzhilin et al. 1999, Decaëns
82 et al. 2002, Barros et al. 2004), or exhibit variable patterns, such as peaks and troughs in
83 abundance (Bhadauria and Ramakrishnan 1989, Okwakol 1994, Sileshi and Mafongoya
84 2006a). Many traditional smallholder agricultural systems are based on rotation of plots
85 between native vegetation, cropping and fallowing, so it is likely that the soil macrofauna
86 communities in these systems are dynamic, responding to changes in management, vegetation
87 and soil organic matter input. Because soil macrofauna communities are likely to be dynamic,
88 it is important to sample across seasons and at different successional stages of agricultural use.

89
90 The Quesungual Slash-and-Mulch Agroforestry System (also referred to as QSMAS) from
91 western Honduras (Welchez et al. 2008) was used as the case study in this research because it
92 incorporates many features that should promote abundant, diverse soil macrofauna
93 populations, which should in turn improve soil quality for smallholder farmers. The name
94 ‘Quesungual’ comes from the name of the village where this agroforestry system was first
95 identified (Hellin et al. 1999). The agroforestry system comprises a suite of land management
96 practices used by resource-poor smallholder farmers. It is notable not only for its
97 heterogeneity and incorporation of high levels of plant diversity, but also for the fact that it
98 represents a transition from traditional slash-and-burn agriculture to a reportedly more
99 sustainable method of slash-and-mulch agroforestry (Welchez et al. 2008). The study area has
100 suffered from land degradation and related issues of food insecurity and poverty in the past
101 (Pender 2001, Ruben and Clercx 2003, Ordoñez Barragan 2004, Ayarza et al. 2005). Today,
102 the apparent success of the new system in improving farmers’ standard of living while at the

103 same time increasing vegetation cover and diversity (Hellin et al. 1999, Ayarza et al. 2005)
104 allows for the examination of relationships between above- and below-ground biodiversity in
105 the context of land management practices.

106

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

120

121 **2. Materials and methods**

122 2.1 Study area and study sites

123 The study area was located in the zone surrounding the village of Candelaria, in the southern
124 region of Lempira Department in south-western Honduras (Figure 1). The climate of the study
125 area is classified as equatorial winter dry (Aw) according to the Köppen-Geiger classification
126 (Kottek et al., 2006). Annual rainfall, which falls primarily between May and October,
127 averages 1200 to 1400 mm (Cherrett, 1999). Average daily temperatures range between 17

128 and 25°C (Hellin et al., 1999). The study area falls within the Central American dry tropical
129 forest zone, which has been almost completely converted to agriculture over the last 1000
130 years (Janzen, 1988; Barrance et al., 2003; Gordon et al., 2003). The soils of the study area
131 are Entisols that are generally shallow, acidic (pH of less than 5.1), with low organic matter
132 content and available phosphorus, and are mostly sandy clay loam and clay loam in texture
133 (Hellin et al., 1999; Ordoñez-Barragan, 2004; Pauli, 2008).

134

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

152 the key changes in vegetation diversity and density that occur as fields pass through each of
153 the land uses.

154

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

160

161 2.2 Field and laboratory methods

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

171

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

177

178 At each sample point, one soil block of 25 cm by 25 cm to 30 cm depth was collected and
179 sorted according to the standard method used by the Tropical Soil Biology and Fertility
180 (TSBF) Institute (referred to as the ‘TSBF soil monolith method’) (Anderson and Ingram
181 1993; Moreira et al. 2008). Litter was collected from within a quadrat of 25 cm by 25 cm, and
182 a trench excavated to 30 cm depth around the quadrat. The soil block was removed from the
183 ground, divided into three layers of 10 cm depth (i.e., 0-9.9 cm, 10-19.9 cm and 20-30 cm),
184 and hand-sorted for soil macrofauna. Invertebrates were preserved in 70% ethanol, with
185 earthworms and larvae preserved in 4% formol. Invertebrates were identified to Order level,
186 counted and weighed. Standard correction factors for preserved invertebrates were applied to
187 dry weights (Decaëns et al. 1994).

188

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

197

198 2.3 Data analysis

199 The differences in vegetation and soil variables among the different land use types were
200 assessed using one-way analysis of variance (ANOVA) for sites that were sampled during the
201 wet season of 2004. The individual properties chosen were: tree density; total tree species

202 richness for each site; tree basal area (in $\text{cm}^2 \text{m}^{-2}$, calculated using DBH); soil organic carbon;
203 and % sand (as an indicator of soil texture). Post-hoc pairwise testing was undertaken using
204 the least significant difference (LSD).

205

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

215

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

226 samples plotted relatively close together on the nMDS map are more similar than samples that
227 are separated by a relatively greater distance.

228

229 Two-way ANOSIM was performed to assess whether season, land use and soil sampling
230 depth had a significant effect on taxonomic composition. ANOSIM is a non-parametric
231 permutational procedure that involves the computation of a test statistic (Global 'R') that
232 compares differences between treatments. R is then recalculated under a specified number of
233 random permutations of the sample labels, and the permutation distribution of R compared
234 with Global R. Three separate two-way ANOSIM analyses were performed with the data,
235 each involving 999 permutations. The first compared the effects of season and land use, using
236 the data from sites that were sampled in both seasons. The second analysis compared the
237 effects of land use and soil sampling depth in the dry season, and the third compared the same
238 factors in the wet season. Pairwise testing based on permutations was applied where
239 significant differences were noted. One hundred permutations were performed for the first
240 ANOSIM comparison of season and land use (the maximum possible number based on the
241 number of samples) and 999 permutations were calculated for the other two ANOSIM
242 comparisons.

243

244 **3. Results**

245 3.1 Summary data

246 Average soil macrofauna density across all land uses sampled was 1614 ± 213 (S.E.)
247 individuals m^{-2} in the dry season and 1289 ± 154 individuals m^{-2} in the wet season. Average
248 total biomass values across all land uses were 12.4 ± 1.9 g m^{-2} in the dry season, and
249 22.3 ± 3.4 g m^{-2} in the wet season.

250

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

258

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

265

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

275 macrofauna density occurred between 0 and 9.9 cm, and decreased with depth. Termites and
276 ants were the most abundant taxa.

277

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

285

286 3.2 Relationships between land use and environmental variables

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

294

295 3.3 Relationships between soil macrofauna and land use within seasons

296 Results of the Kruskal-Wallis test (Table 4) comparing soil macrofauna variables in different
297 land uses in the dry season showed that total soil macrofauna biomass and density of
298 earthworms, beetle larvae and millipedes were significantly different among land uses. In the

299 wet season, there were significant differences in the total density of soil macrofauna, as well
300 as the density of ants, termites, millipedes and centipedes among different land uses (Table 5) .
301
302 Taxa that were significantly different between land uses responded in different ways across
303 the continuum of land use change. Both termites and earthworms were present in significantly
304 higher densities in AF<2 than in F, while their densities returned to medium values in AF>10.
305 Ants exhibited a different trend, with relatively high densities in F, followed by a sharp drop
306 in AF<2 plots and then intermediate to high values in AF>10 plots. Beetle larvae showed a
307 similar trend in the dry season. Millipede density decreased steadily from secondary forest to
308 agroforestry to pasture. Ant density was highly variable in SP plots, as noted by the disparity
309 between the mean density and mean rank for each of the land uses in the wet season; most SP
310 samples returned relatively low ant densities, with a few recording extremely high densities.
311 The variability within all land uses was very high, as shown by the high standard error values
312 in Tables 4 and 5. It is likely that a large proportion of the variability in the data was not
313 accounted for by the non-parametric statistical tests applied.

314

315 3.4 Changes in community composition according to land use, season and soil sampling

316 depth

317 The ordination analysis using nMDS showed varying degrees of differentiation of the factors
318 season, land use and soil sampling depth (Figure 5). There was a high degree of variation
319 within seasons (Figure 5 (A)). Classification according to land use did not show any visually
320 identifiable separation of the four land use categories (Figure 5 (B)), whereas classification
321 according to soil depth showed strong separation of the four sampling depths (Figure 5 (C)).
322 Of the four soil depths, 0-9.9 cm and 10-19.9 cm were the most similar. The 20-30 cm layer
323 was the most variable, with samples widely dispersed on the nMDS diagram, while the litter

324 layer was the most tightly clustered. The stress value for the nMDS was relatively high
325 (stress = 0.2), indicating a high degree of scatter of the samples around the fitted non-
326 parametric regression line.

327

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

332

333 For the dry season data, ANOSIM did not indicate a significant effect of land use on
334 community composition (Global R = 0.031, p = 0.33), but there was a significant relationship
335 with soil depth (Global R = 0.271, p = 0.001). Pairwise testing indicated that there were
336 significant differences between 20-30 cm and all other soil sampling depths (litter: p = 0.012;
337 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).

338

339 In the wet season, there were significant differences between land uses (Global R = 0.199,
340 p = 0.016) and soil sampling depths (Global R = 0.437, p = 0.001). Pairwise testing showed
341 that there were significant differences between F and SP (R = 0.435, p = 0.009), between
342 AF<2 and SP (R = 0.231, p = 0.048), and between AF>10 and SP (R = 0.222, p = 0.034).

343 Community composition was significantly different between all pairs of soil sampling depths
344 (p = 0.001 or p = 0.002 depending on the comparison), aside from 0-9.9 cm and 10-20 cm.

345

346 **4. Discussion**

347 The areas sampled in this study had a high density of soil macrofauna, relative to other
348 comparable studies from tropical sites (Table 6). Compared with studies from Central

349 America, average soil macrofauna density reported here was more than five times greater than
350 that recorded in the central highlands of Honduras (Ericksen and McSweeney 1999) and
351 nearly twice that from the plains of southeastern Mexico (Brown et al. 2004). Soil macrofauna
352 densities found in this study were similar to those noted by Barros et al. (2002) in the
353 Brazilian Amazon, and by Decaëns et al. (1994) for the eastern plains of Colombia. Studies
354 that recorded substantially higher soil macrofauna densities include those of Feijoo et al.
355 (1999) in the Colombian Andes, Barros et al. (2003, 2004) in the Brazilian Amazon and
356 Mboukou-Kimbatsa et al. (1998) in the Congo basin.

357

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

366

367 4.1 Soil macrofauna community composition

368 The most abundant organisms found in the sites sampled were termites, ants and earthworms,
369 which together made up nearly 90% of all soil macrofauna sampled. Adult and larval beetles
370 comprised 12% of all soil macrofauna biomass. Other studies have also found these groups to
371 be amongst the dominant soil macrofauna taxa (e.g. Lavelle and Pashanasi 1989, Ericksen and
372 McSweeney 1999, Feijoo et al. 1999, Brown et al. 2004, Decaëns et al. 2004, Mathieu et al.
373 2004, Rossi et al. 2006). The high densities of ants and termites are likely to lead to networks

374 of underground tunnels that allow infiltration of water and air and create channels for root
375 growth. The burrowing habits of earthworms are also likely to increase soil macroporosity.
376 Earthworms and beetle larvae feed on soil organic matter, which speeds decomposition and
377 nutrient cycling. The high densities of these organisms found in this study are likely to have
378 an important effect on soil quality and soil macromorphology.

379
380 Soil macrofauna community composition was similar for all land uses in the study, based on
381 the broad taxonomic groups used. If these groups used are taken as surrogates for functional
382 groups of soil macrofauna, then there was no substantial loss of functional groups or shift in
383 dominance between different land uses. The greatest differences occurred between
384 silvipastoral sites and all other land uses. Substantial changes in the abundance of a number of
385 taxa were also noted between secondary forest and recently converted agroforestry sites. It
386 seems likely that the major changes in vegetation structure, plant diversity, tree cover, organic
387 matter input and litter cover that are associated with conversion of secondary forest to
388 agroforestry are reflected in greatly increased abundance of hardy and opportunist taxa (in this
389 case, termites and earthworms) and reduced abundance of more sensitive taxa (which in this
390 case comprised ants and some litter-dependent arthropods).

391

392 4.2 Differences in environmental variables among land uses

393 Land uses were significantly different in terms of vegetation characteristics and soil organic
394 matter content. However, none of the selected variables was significantly different among all
395 four land uses, and there were important differences in local soil type and soil texture
396 classification among sites that were not included in the analyses. Tree density was the only
397 variable that differed significantly among three of the four land uses. Although tree density
398 decreased as agroforestry fields aged, tree basal area did not. This implies that while some

399 trees die with each successive pruning or are removed for timber or fuel wood, the total area
400 occupied by trees, and by extension, their roots and canopies, remains roughly similar. This is
401 likely to increase the patchiness of organic resource distribution with time under cultivation,
402 which could lead to increased patchiness in the spatial distribution of soil biota (Beare et al.
403 1995, Ettema et al. 1998, Saetre and Bååth 2000, Ettema and Wardle 2002).

404

405 4.3 Differences in soil macrofauna density and biomass among land uses

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

421

422 Soil macrofauna biomass was strongly related to land use change. The observed pattern of a
423 large increase in biomass from secondary forest to young agroforestry sites, followed by a

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

432

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

440

441 4.4 Seasonal differences in soil macrofauna density and biomass

442 Seasonal differences in soil macrofauna densities were less marked than expected, which may
443 indicate that soil organisms are well adapted to seasonal drought. Soil macrofauna may take
444 refuge in moister, more shaded sites and deeper layers over the dry season and disperse and
445 multiply during the wet season, or it may be that different species of each taxa are better
446 adapted to dry or wet conditions. Ants were the only taxa that were more abundant in the dry
447 season. Increased ant abundance in the dry season has been noted in other studies (Höfer et al.
448 2001, Brown et al. 2004, Rossi and Blanchart 2005, Sileshi and Mafongoya 2006b). Biomass

449 was almost twice as great in the wet season than in the dry season. This increase is most likely
450 linked to increased soil moisture in the wet season, which permits the survival of greater
451 numbers of moisture-dependent organisms such as earthworms. Seasonal differences may also
452 be related to higher soil productivity and increased availability of organic matter through litter
453 decomposition and greater root biomass in the wet season.

454

455 4.5 Vertical distribution of soil macrofauna density and biomass

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

464

465 4.6 Conclusions

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

473

474 The relatively high abundance of soil macrofauna noted within the Quesungual Slash-and-
475 Mulch Agroforestry System (QSMAS) may result from the use of certain agricultural
476 practices that have previously been associated with abundant soil fauna populations (such as
477 inclusion of trees within fields and maintenance of soil cover through mulching), and the
478 absence of other practices that have been linked to decline in soil fauna populations (for
479 example, tillage and burning). The agricultural practices associated with the ‘Quesungual’
480 system do not appear to lead to significant imbalances or changes in soil macrofauna
481 functional groups, although there may be changes at a finer level of taxonomic resolution than
482 was applied in this study. The results indicate that the system allows for relatively high soil
483 macrofauna abundance in comparison with what is known from other sub-tropical areas,
484 which could have important effects on aspects of soil quality such as soil structure and
485 nutrient cycling that are particularly important to small-scale farmers.
486

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504

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707

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)
<i>Insects</i>			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
<i>Earthworms</i>			9.2	72.7
Oligochaeta	Earthworms	Subclass	9.2	72.7
<i>Myriapods</i>			4.0	2.3
Chilopoda	Centipedes	Class	2.5	1.2
Diplopoda	Millipedes	Class	1.4	1.1
<i>Arachnids</i>			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
<i>Crustaceans</i>			0.3	< 0.01
Isopoda	Pillbugs, slaters	Order	0.3	< 0.01
<i>Molluscs</i>			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.

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	<i>Cordia alliodora</i>	Boraginaceae	16.0	Timber
	<i>Lonchocarpus</i> sp.	Papilionaceae		Firewood,
Cangrejillo ^b			8.4	mulch
	<i>Bauhinia</i> sp.	Caesalpinaceae		Firewood,
Pie de venado			7.9	mulch
Sirin de pava	<i>Miconia</i> sp.	Melastomataceae	7.0	Firewood
Guayabo	<i>Psidium guajava</i>	Myrtaceae	6.5	Fruit (guava)
	<i>Acosmium</i>	Papilionaceae		Firewood,
Chichipate ^b	<i>panamense</i>		6.3	mulch
	<i>Curatella</i>	Dilleniaceae		Firewood,
Chaparro	<i>americana</i>		5.7	mulch
Guachipilin ^b	<i>Diphysa americana</i>	Papilionaceae	3.8	Timber, mulch
Guacuco	<i>Casearia</i> sp.	Flacourtiaceae	3.2	Mulch
	<i>Guazuma ulmifolia</i> .	Sterculiaceae		Firewood,
Caulote			2.9	mulch
	<i>Psidium</i>	Myrtaceae		
Guayabillo	<i>hondurensis</i>		2.7	Fruit, firewood
	<i>Byrsonima</i>	Malphiaceae		
Nance	<i>crassifolia</i>		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.

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

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 <i>n</i> = 30 ^b	AF<2 <i>n</i> = 30 ^b	AF>10 <i>n</i> = 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 (<i>p</i> = 0.912)	1345.1 ± 248.5	1913.1 ± 435.8	1537.6 ± 397.5
Total soil fauna biomass (<i>p</i> = 0.041)	4.8 ± 1.2	24.8 ± 8.2	7.6 ± 1.8
Ant density (<i>p</i> = 0.199)	620.3 ± 206.9	272.5 ± 54.7	569.1 ± 110.5
Termite density (<i>p</i> = 0.135)	451.2 ± 179.8	1298.1 ± 404.1	699.2 ± 354.5
Earthworm density (<i>p</i> = 0.028)	38.4 ± 13.6	189.9 ± 48.9	75.7 ± 27.5
Beetle adult density (<i>p</i> = 0.061)	51.2 ± 11.1	22.4 ± 5.9	34.7 ± 6.7
Beetle larvae density (<i>p</i> = 0.01)	46.9 ± 6.3	24.0 ± 4.7	51.2 ± 27.2
Millipede density (<i>p</i> = 0.005)	36.8 ± 9.0	15.5 ± 6.5	13.9 ± 7.0
Centipede density (<i>p</i> = 0.565)	31.5 ± 5.5	30.9 ± 6.3	22.9 ± 4.2
Spider density (<i>p</i> = 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 <i>n</i> = 30 ^b	AF<2 <i>n</i> = 30 ^b	AF>10 <i>n</i> = 30 ^b	SP <i>n</i> = 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 $n = 120$, $\alpha = 0.05$, total number of comparisons = 6, group $n = 30$). Subscript uppercase letters denote pairs that were different from each other.

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)
<i>Latin America – Highlands</i>				
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 <i>et al.</i> (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 (<i>Pennisetum clandestinum</i>); pine plantation; <i>Yaragua</i> grass; <i>Brachiaria humidicola</i> pasture	3356	61.6
<i>Latin America - Plains / Savannas</i>				
Brown <i>et al.</i> (2004) ^b	Mexico, Veracruz region	Native pasture; introduced pasture	812	32.1
Blanchart <i>et al.</i> 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 <i>et al.</i> (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 <i>et al.</i> (2002)	Colombia, eastern plains	Native savanna; traditional extensive pasture; two types of intensive pasture	n/a	30.8
Marchão <i>et al.</i> (2009)	Cerrado, central Brazil	Cerrado; continuous crop; crop-pasture rotation; pasture-crop rotation; continuous pasture	2206	n/a
Thomas <i>et al.</i> (2004)	Argentina	Natural grassland; fallows following rice cultivation 2, 4, 7 and 15 years	781	n/a

Table 6 continued

Study	Country/ Region	Agroecosystems sampled	Mean soil fauna density (indiv. m ⁻²)	Mean soil fauna biomass (g m ⁻²)
<i>Latin America - Amazon Basin</i>				
Barros <i>et al.</i> (2002)	Brazil	Disturbed forest; fallow; annual crop; agroforestry; pasture	1393	18.9
Barros <i>et al.</i> (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 <i>et al.</i> (2004)	Brazil	Forest, four year old pasture; abandoned pasture	3664	36.7
Decaëns <i>et al.</i> (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 <i>et al.</i> (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
<i>Africa</i>				
Dangerfield (1990)	Zimbabwe	Natural savannah woodland miombo; maize; fallow; disturbed miombo; mature <i>Eucalyptus grandis</i> plantation	145	12.0
Mboukou-Kimbatsa <i>et al.</i> (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
<i>Asia</i>				
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 <i>et al.</i> (2004)	Sumatra, Indonesia	Primary forest; logged-over forest; <i>Paraserianthes</i> tree plantation; <i>Hevea</i> (rubber) plantation; jungle rubber; degraded <i>Imperata</i> 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

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

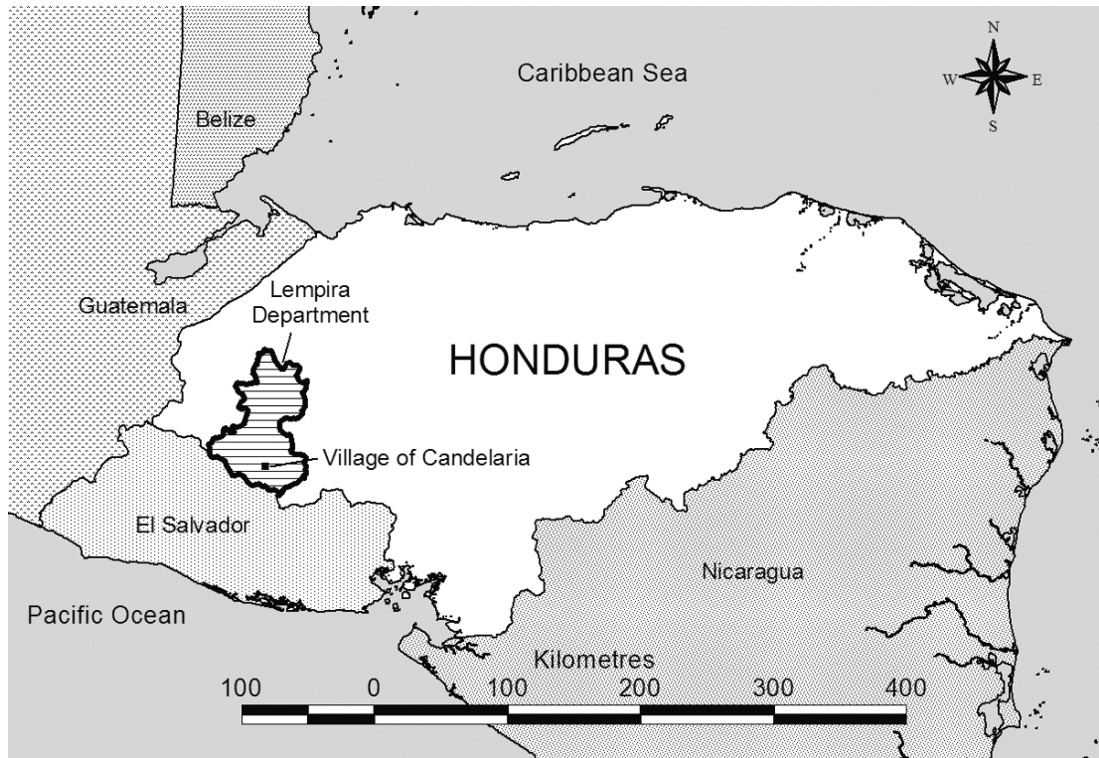


Figure 2: Illustration of key characteristics of land uses of the study area. The four land uses sampled (secondary forest, young agroforestry, mature agroforestry, and silvipastoral) can be seen as successive phases in a continuum of land use change in the study area. Most fields cycle between secondary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

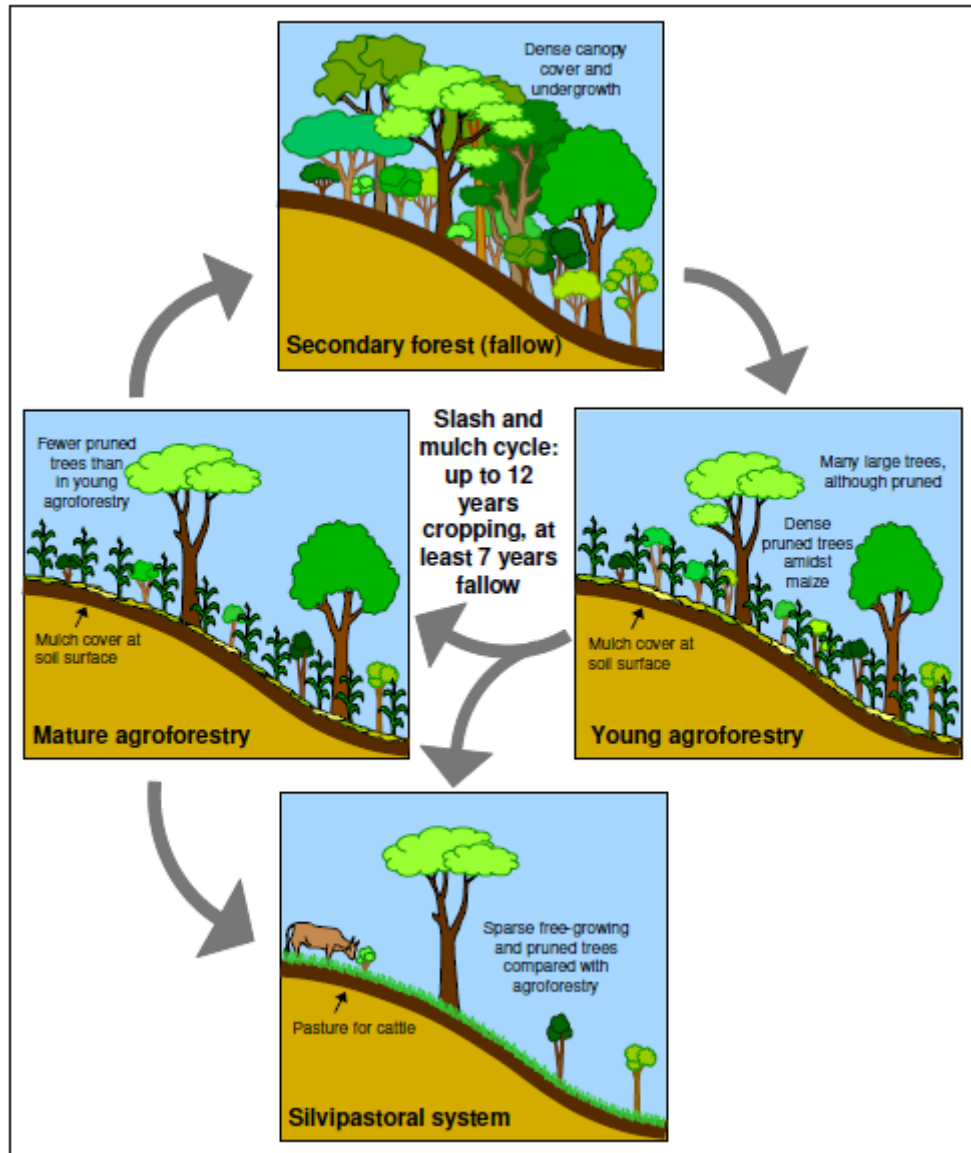


Figure 3: Vertical distribution profiles in the soil of soil macrofauna total density and total biomass in wet and dry seasons, for each land use. Values shown are averages for each of the land uses sampled. F: Secondary forest ($n = 20$). AF<2: Agroforestry <2 years ($n = 30$). M>10: Agroforestry >10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

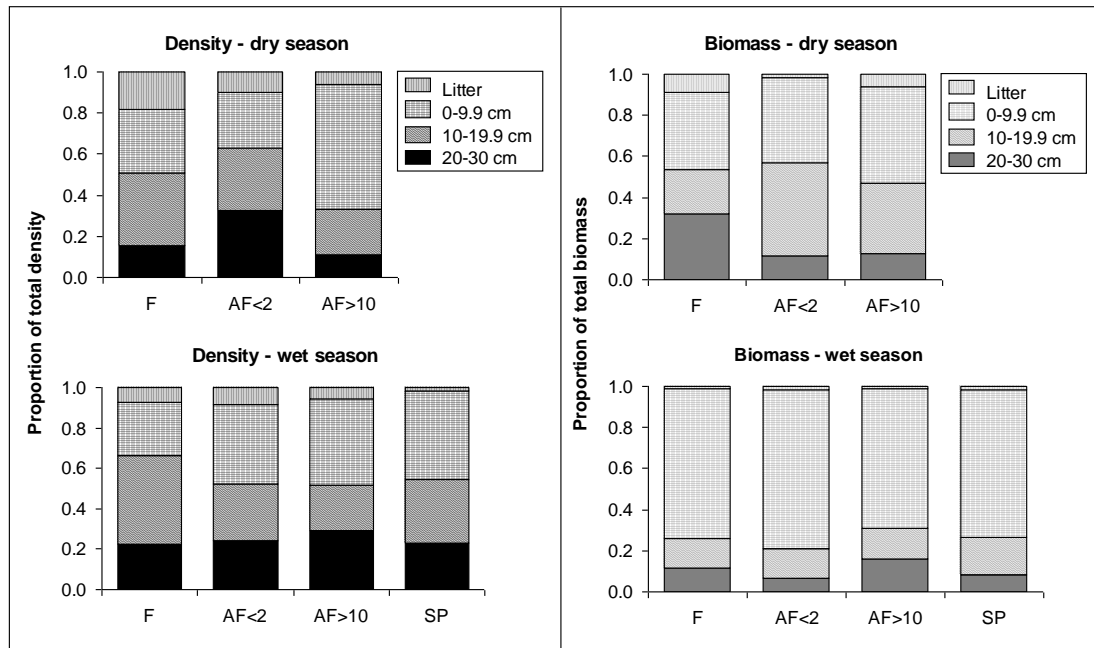


Figure 4: Vertical distribution and taxonomic group composition of soil macrofauna in each soil layer sampled for each land use in both seasons. Values shown are averages across each of the land uses sampled.

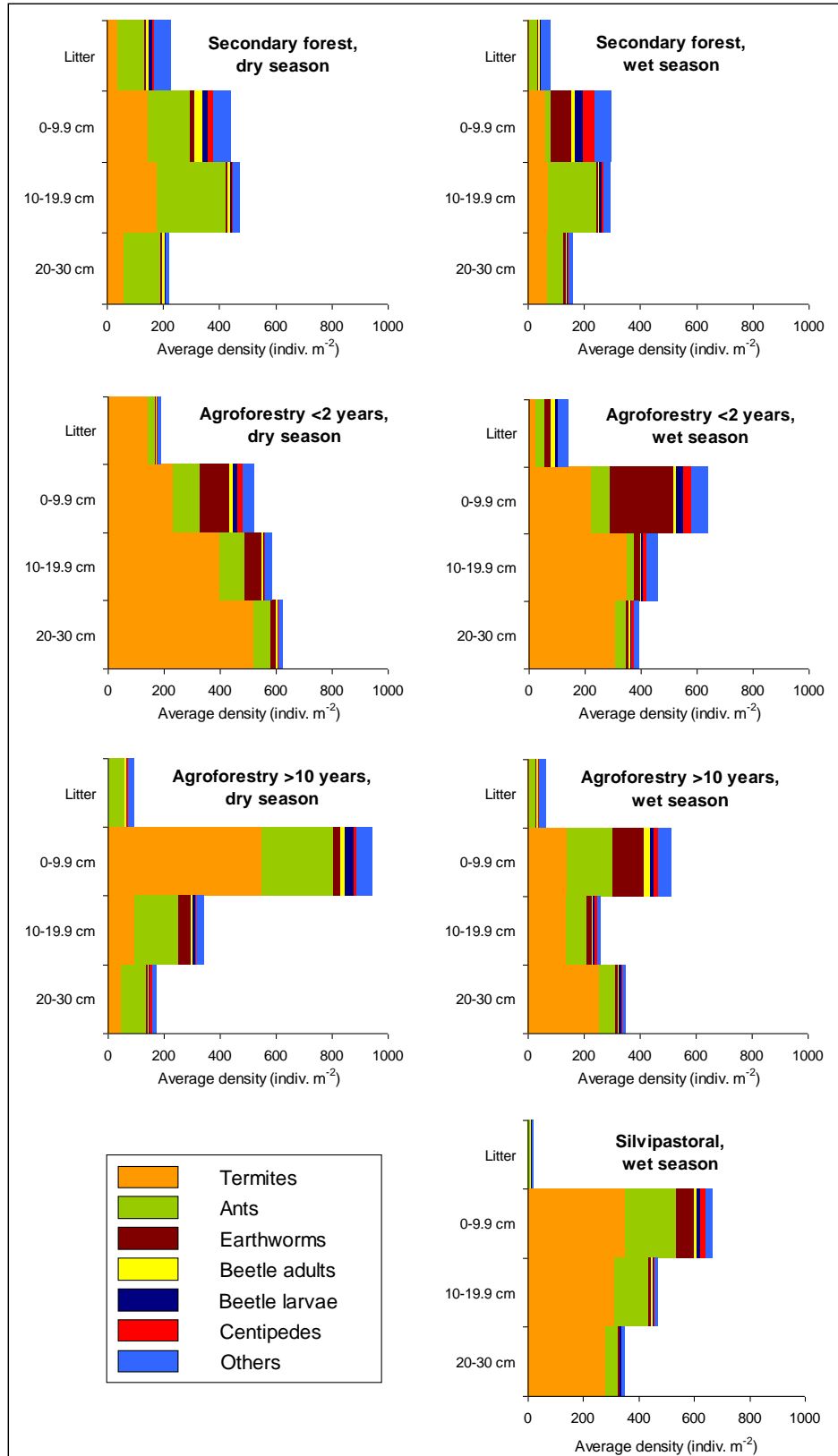


Figure 5: Ordination analysis (nMDS) of the taxonomic composition of soil macrofauna communities at sample points [overleaf]. Each point in the diagrams corresponds to the average of the 10 samples taken from within each study site during each sampling period (dry and wet seasons). Diagrams A, B and 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.

