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Relationships between invertebrate communities, litter quality and soil attributes under different cacao agroforestry systems in the south of Bahia, Brazil

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ABSTRACT

This study was undertaken to investigate the relationship between soil and litter attributes to soil and litter fauna, and further to determine which of these attributes would be most significant in explaining the distribution of faunal communities in cacao agroforestry systems in the south of Bahia, Brazil. Soil and litter samples were collected in five cacao agroforestry systems: a cacao system renewed under *Erythrina* sp. (CRE); a cacao system renewed under natural forest (Cabruca—CRF); a cacao system under *Erythrina* sp. (CE); a cacao system under a natural forest system (Cabruca—CNF) and a cacao germplasm collection area (CGC). Soil and litter samples were also collected from natural forest (NF) near the agroforestry systems. The path analysis was used to evaluate the interdependencies among a set of variables including direct and indirect test effects that can be mediated by an intermediary variable. An average of 1367 (±126.5) individuals m^{-2} and 10 (±0.3) taxa per sample were found under these areas. Soil attributes and litter quality under different cacao agroforestry systems affected the diversity of the soil and litter fauna, and these attributes are potential regulators of the fauna functional groups. The chemical components related to acidity, nutrition, and palatability are most decisive for abundant and diverse soil and litter fauna. Attributes which affected soil fauna in cacao agroforestry systems included mainly pH and bulk density in soil and polyphenols and lignin content in the litter. The faunal communities were more sensitive to litter quality than soil quality. Litter management could be a good practice to maintain healthy activities of the faunal community and to maintain improved ecosystem functioning in cacao agroforestry systems.

1. Introduction

Agroforestry is a sustainable alternative to agricultural production systems by providing environmental benefits such as biodiversity conservation, enhanced carbon sequestration and improved water quality control (Nair, 2008; McNeely and Schroth, 2006; Reitsma et al., 2001). The association of perennial crops with shade trees is well known in the humid tropics (Beer et al., 1998), which is the case of cacao-shade tree combination management (Isaac et al., 2007). In agroforestry cacao management systems cacao is grown under thinned natural forest canopy (cabruca) or under introduced legume trees (erythrina, gliricidia, etc.). The use of shade trees in cacao plantations promotes a continuous deposition of plant residues that facilitates the maintenance of high soil organic matter (Smiley and Kroschel, 2008; Oelbermann et al., 2006), which affects the physical (Saha et al., 2007), chemical (Isaac et al., 2007) and biological attributes of the soil (Norgrove et al., 2009; Huerta et al., 2007; Delabie et al., 2007).

In Brazil, successive deforestation cycles, forest burning and continuous land-use with monoculture have resulted in soil degradation and loss of soil biodiversity. In that scenario, cacao agroforestry systems play an important role as land-use systems with diverse and structurally complex shade canopies and also among the agricultural land uses, are most likely to conserve a significant portion of the original forest biodiversity (Schroth and Harvey, 2007). Furthermore, plant diversification in agroforestry and forest systems provide a diversity of microhabitats, contributing to a larger soil biological density and diversity (Laossi et al.,

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2008; Richter et al., 2007; Brown et al., 2006; Wardle et al., 2006; Tapia-Coral et al., 1999). However, the mechanisms responsible for the biological diversity below ground are still not clear. Several studies have documented the effects of different soil and litter attributes and land use practices on the colonization and activity of soil fauna (Yang and Chen, 2009; Aquino et al., 2008; Laossi et al., 2008; Sileshi and Mafongoya, 2006; Rossi and Blanchart, 2005; Reich et al., 2005; Dauber et al., 2003). Remarkably little is known about the general nature of below ground diversity patterns and their relationship to soil and litter quality in cacao agroforestry systems. In tropical soils Geissen and Guzman (2006) reported that organic matter and soil acidity were the soil chemical attributes that most affected soil biota under different land use systems. Salamon and Alphei (2009) suggested that soil pH is an important structuring force for Collembola communities, while the tree species composition appeared to impact Collembola communities moderately (via changes in the amount and quality of food resources) in a Central European forest. Rossi (2003) reported a very strong relationship between soil bulk density and tropical earthworm community structure.

Moço et al. (2009) in these same land-use systems of the present study found that density and richness of total fauna and the density of most functional group were similar between cacao agroforestry systems and natural forest. They concluded that the cacao agroforestry systems adopted in southern of Bahia, Brazil, is a conservative system for soil and litter fauna. These results would bear important implications for conservation of soil biodiversity and ecosystem services. The lack of information about the factors determining the distribution and structure of soil and litter fauna in cacao agroforestry systems, despite the overriding importance of the soil and litter quality as main drivers of soil biota and processes, makes the present study a first approach on this issue that will subsidize future research to better understand the connection between above ground and below ground quality and faunal communities and to develop a model of the influence of different factors on the soil and litter organism trophic assemblage in cacao agroforestry systems. The goal of this study was to link soil and litter fauna communities with soil and litter quality conditions in the surface layer of cacao agroforestry systems and natural forests. The purpose was to see how the soil and litter fauna communities can be influenced by soil and litter quality.

2. Materials and methods

2.1. Site description and sampling procedure

The study was conducted at the Research Station of MARS Center of Cocoa Science, Itajuípe, situated in the southern region of Bahia, Brazil (14°0′S and 39°2′W). The research farm is located in a humid, tropical region, with an annual mean rainfall of 1500 mm, which is well distributed throughout the year.

Soil and litter samples were taken from five cacao agroforestry systems: renewed cacao (25 years old) under *Erythrina* system (CRE), renewed cacao (25 years old) under natural forest (cabruca system, CRF), a cacao (70 years old) under natural forest system (Cabruca, CNF), a cacao (25 years old) under *Erythrina* system (CE) and cacao germplasm (15 years old) collection area (CGC), where cacao clones resistant to witch broom (*Crinipellis pernicious*) have been planted. Soil samples were also collected from natural forest (NF) next to the agroforestry systems.

Cacao with *Erythrina* spp. represents a cacao plantation under *Erythrina* shade trees (*Erythrina* spp.) and "cabruca" represents a cacao plantation under NF. Renewed cacao systems represent grafting old trees with witch broom (*C. pernicious*) resistant genetic material (5 years old) originated from the cacao germplasm collection of the MARS Center of Cocoa Science. The areas used for NF, CRE, CRF, and CNF were on Oxisols, whereas CE and CGC were established on Inceptsols. The samples were collected during September 2003, February 2004, and August 2004. Four sampling plots in each land-use system were marked out for soil and litter samples. Four soil samples (0–5 cm) and four litter samples were collected at random from each subplot. A quadrate of 0.25 m × 0.25 m was set up for each sample. The discussion about seasonal variations and comparison of faunal communities between cacao agroforestry systems and natural forest was described in Moço et al. (2009).

2.2. Soil and litter fauna extraction

Organisms were extracted over a 15-day period with a Berlese–Tullgren apparatus using 25 W bulbs suspended 10 cm above the top of the samples (Palacios-Vargas et al., 2007; Cassagne et al., 2003, 2006; Chagon et al., 2001). Fauna was collected in 2% acetylsalicylic acid and counted under a binocular microscope (Moço et al., 2005). The invertebrates were then classified into higher taxonomic levels. The values of density and richness used in this research to investigate the relationship between soil and litter attributes and the soil and litter fauna were described in Moço et al. (2009). In this study, we presented the sum of soil + litter (only faunal groups with density equal or greater than 1% of the total number of individuals). Fauna organisms were divided into different functional groups: microbial grazers (included Collembola), social insects, saprophagous, predators, herbivores, and omnivores. Microbial grazers feed on microorganisms and both directly and indirectly influence rates of litter decomposition by comminuting detritus and grazing on fungi (Seastedt, 1984). Social insects were dominated by Formicidae which feed on a variety of plant and animal residue. Saprophagous organisms including Diplopoda, Isopoda, Diptera larvae, Oligochaeta, Pauropoda, etc. feed on decaying organic matter. Predators such as Araneae, Chilopoda and Pseudoscorpionida prey on microbial grazers, saprophagous and herbivores, but also on other predators including individuals of the same or closely related species (Brown et al., 2006). Herbivores (Hemiptera, Lepidoptera larvae and Thysanoptera) feed on above and below ground plant parts. Omnivores such as Coleoptera (larvae and adult) represent more than one feeding habit.

2.3. Analytical procedure

Details on characteristics of soil and litter collected from the studied systems are shown in Table 1. Soil samples were used for determination of soil pH (in water). Mehlich-1 extractable P and K, and exchangeable Ca and Mg were extracted with 1 mol L^{-1} KCl, according to Defelipo and Ribeiro (1981) and Tedesco et al. (1985) and clay content and soil bulk density were determined according to Embrapa (1997). Organic C and total N from soil and litter were measured after oxidation using 0.21 mol L^{-1} $K_2Cr_2O_7$ (Anderson and Ingram, 1996) and regular Kjeldahl method (Bataglia et al., 1983), respectively. Lignin and cellulose contents were measured using the acid detergent fiber method (Van Soest and Wine, 1968), and the concentrations of extracted total polyphenols were determined using the method of Follin Denis, according to Anderson and Ingram (1996).

2.4. Statistical analysis

Co-inertia analysis was used to study relationships between fauna distributions and environmental variables. Co-inertia is a multivariate method that characterizes a global measure of the co-structure of sites in the species and environmental hyperspaces (Dray et al., 2003). This method is based on two data sets (species and environmental variables). Faunal community (total density, richness and functional groups) were used as 'species' and soil attributes (C, N, P and clay content, pH, bulk density and sum of

Table 1
Soil and litter characteristics under cacao agroforestry systems and a natural forest in Bahia, Brazil.

	CRE	CRF	CE	CNF	CGC	NF
Soil						
N ($g\,kg^{-1}$)	3	3	3	3	2	4
C ($g\,kg^{-1}$)	40	40	17	40	29	41
P ($mg\,dm^{-3}$)	8	7	17	7	73	4
Clay ($g\,kg^{-1}$)	440	398	235	374	205	519
pH	5	5	6	5	6	4
Bulk density ($g\,cm^{-3}$)	1	1	1	1	1	1
Sum of bases ($cmol_c\,dm^{-3}$)	6	8	15	9	19	3
Litter						
N ($g\,kg^{-1}$)	17	16	18	15	16	15
C ($g\,kg^{-1}$)	422	398	373	356	395	405
P ($g\,kg^{-1}$)	1	1	1	1	1	0.4
Lignin ($g\,kg^{-1}$)	347	368	264	313	336	348
Polyphenols ($g\,kg^{-1}$)	5	7	3	7	6	7
Cellulose ($g\,kg^{-1}$)	209	207	163	199	217	195
C:N ratio	25	26	20	24	25	27
Lignin:N ratio	20	24	14	21	21	23
Polyphenols:N ratio	0.3	0.4	0.1	0.4	0.4	0.5

CRE—renewed cacao under *Erythrina* system; CRF—renewed cacao under forest system; CE—cacao under *Erythrina* system; CNF—cacao under forest system; CGC—cacao germoplasm collection; NF—natural forest. N—nitrogen; C—carbon; P—phosphorous.

bases) and litter attributes (C, N, P, lignin, polyphenols and cellulose content) as 'environmental variables'. The faunal community data were transformed to log ($x+1$). The soil and litter data were analyzed separately. The statistical significance of the co-inertia was evaluated with a Monte Carlo test with 10,000 permutations (Thioulouse et al., 1997). The analyses were made with the statistical package R 2.11.1 (R Development Core Team, 2007) and analyzed using the ADE-4 package (Chessel et al., 2004).

Regardless of the similarity or dissimilarity between land use systems, assessed by the co-inertia analysis, our interest was to evaluate how soil and litter quality (attributes) may influence the distribution of fauna functional groups. Thus, we decided to use path analysis that allows distinguishing direct and indirect effects and measuring the relative importance of the potential causal factors involved (Wright, 1921).

Path coefficient analysis between soil and litter attributes and fauna functional groups were performed with SAEG 9.1 (SAEG Inst. Inc.). This technique permits the partitioning of simple correlation coefficients between dependent variables and independent variables into direct and indirect effects (Krishnasamy and Mathan, 2001). While the direct effect represents the direct contribution of an independent variable to the dependent variable, the indirect effect represents the contribution of an independent variable to the dependent variable through the influence of another independent variable (Ige et al., 2007). The soil and litter data were analyzed separately. Both direct and indirect effects of soil attributes (N, C, P content, pH, bulk density, sum of bases and clay content) and litter attributes (C, N, P, lignin, polyphenols and cellulose content) on total density, richness and each functional groups were derived by using path analysis.

3. Results

3.1. Soil faunal communities in different land-use systems

An average of 1367 (±126.5) individuals m^{-2} and 10 (±0.3) taxa per sample were found under various agroforestry systems evaluated (Table 2). Collembola (41%) and Formicidae (32%) were the most abundant taxa; Coleoptera accounted for 6% of the total density (4% adults and 2% larvae) and Diptera larvae represented 3% of the total observed density. Pauropoda, Pseudoscorpionida, Isopoda and Symphyla each accounted for 2% of the total density. Protura, adult Diptera, Formicidae larvae, Gastropoda, Hymenoptera, Diplura, Blattodea, Lepidoptera larvae, Orthoptera, Isoptera, Dermaptera, Thysanura and Embioptera were the less abundant groups and their density was less than 1% of the total and therefore, they were all grouped as "other invertebrates" (Table 2).

3.2. Co-inertia analysis of faunal functional groups and soil and litter attributes

The results of co-inertia (COI) analysis of faunal functional groups and soil and litter attributes showed a low RV coefficient (0.65, $p = 0.09$ and 0.15, $p = 0.99$ for soil and litter, respectively) reflecting the lack of joint structure in these datasets (Figs. 1 and 2).

3.3. Path analysis

3.3.1. Soils

The relationship between soil attributes and soil faunal communities was explored by path analysis that showed no significant

Table 2
Mean number of individual m^{-2} and number of taxa of fauna (±SE) under cacao agroforestry systems and a natural forest in Bahia, Brazil.

Taxa (individual m^{-2})	CRE	CRF	CE	CNF	CGC	NF	Mean	%
Collembola	689 ± 178	829 ± 206	488 ± 121	366 ± 110	775 ± 322	199 ± 97	557 ± 78	41
Formicidae	432 ± 118	439 ± 129	358 ± 100	689 ± 299	191 ± 50	504 ± 142	436 ± 65	32
Diplopoda	22 ± 5	21 ± 6	11 ± 4	14 ± 4	17 ± 6	31 ± 10	19 ± 2	1
Isopoda	35 ± 11	57 ± 32	4 ± 2	22 ± 12	1 ± 1	17 ± 9	23 ± 6	2
Diptera (larvae)	35 ± 9	20 ± 5	69 ± 14	13 ± 4	65 ± 42	17 ± 5	36 ± 8	3
Pauropoda	15 ± 4	16 ± 3	13 ± 4	18 ± 4	8 ± 3	13 ± 3	14 ± 2	2
Oligochaeta	50 ± 30	44 ± 22	9 ± 7	66 ± 21	5 ± 3	1 ± 1	29 ± 7	1
Psocoptera	13 ± 5	13 ± 4	17 ± 6	10 ± 4	19 ± 6	23 ± 8	16 ± 2	1
Symphyla	21 ± 9	69 ± 18	5 ± 2	17 ± 5	6 ± 2	13 ± 4	22 ± 4	2
Araneae	13 ± 4	20 ± 5	27 ± 14	15 ± 3	10 ± 4	17 ± 4	17 ± 3	1
Chilopoda	16 ± 6	33 ± 6	15 ± 3	9 ± 2	6 ± 2	11 ± 3	15 ± 2	1
Pseudoscorpionida	35 ± 11	52 ± 11	4 ± 2	23 ± 9	2 ± 1	36 ± 8	25 ± 4	2
Coleoptera (adult)	49 ± 11	73 ± 17	75 ± 26	28 ± 8	27 ± 6	83 ± 16	56 ± 6	4
Coleoptera (larvae)	19 ± 5	43 ± 9	27 ± 6	14 ± 5	19 ± 7	26 ± 5	25 ± 3	2
Hemiptera	9 ± 3	32 ± 16	15 ± 5	10 ± 4	23 ± 7	13 ± 4	17 ± 3	1
Thysanoptera	7 ± 3	16 ± 6	29 ± 14	21 ± 13	14 ± 7	7 ± 4	16 ± 4	1
Other invertebrates	63 ± 19	52 ± 11	39 ± 11	25 ± 9	51 ± 14	42 ± 15	45 ± 5	3
Total density (Ind. m^{-2})	1521 ± 290	1829 ± 307	1205 ± 227	1359 ± 394	1239 ± 365	1051 ± 248	1367 ± 127	100
Richness	11 ± 1	12 ± 1	10 ± 1	9 ± 1	8 ± 1	10 ± 1	10 ± 0.3	

CRE—renewed cacao under *Erythrina* system; CRF—renewed cacao under forest system; CE—cacao under *Erythrina* system; CNF—cacao under forest system; CGC—cacao germoplasm collection; NF—natural forest.

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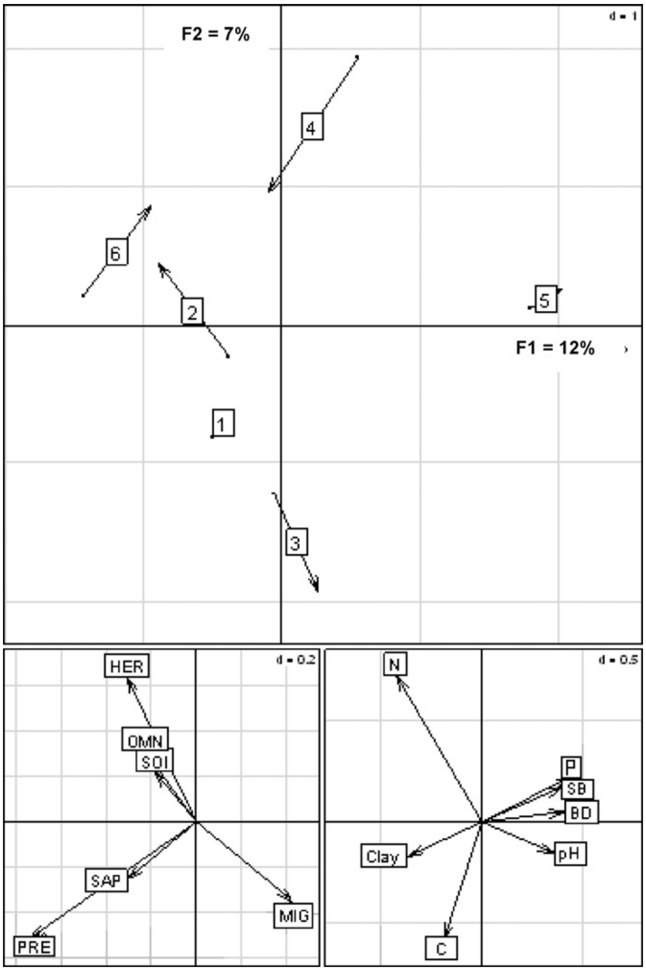

Fig. 1. Co-inertia analysis combining soil attributes and fauna functional groups. 1—CRE (renewed cacao under *Erythrina* system); 2—CRF (renewed cacao under forest system); 3—CNF (cacao under forest system); 4—CE (cacao under *Erythrina* system); 5—CGC (cacao germoplasm collection); 6—NF (natural forest). MIG—microbial grazers; SOI—social insects; SAP—saprophagous; PRE—predators; HER—herbivores; OMN—omnivores. N—nitrogen; C—carbon; P—phosphorous; BD—bulk density; SB—sum of bases.

relationship between soil attributes and the faunal total density. However, soil pH had a significant positive direct effect on richness of fauna; and also the sum of bases and bulk density of soil had positive indirect effect that was mediated via soil pH. However organic C, total N and clay content of the soil had negative indirect effects on richness of fauna which was mediated via soil pH (Fig. 3A).

Functional groups were affected by many soil attributes: microbial grazers were positively and directly affected by pH and also negatively and directly affected by C content, bulk density (BD), sum of bases (SB) and clay content. The effect of N content on microbial grazers was indirect and negative mediated via pH and clay content. N also content had indirect positive effect mediated via BD (Fig. 3B). Saprophagous organisms were directly and positively affected by BD and clay content. N and C content had indirect positive or negative effect which was mediated via BD and clay content; P content had indirect effect which was mediated via C (negative) and clay (positive) content while pH had indirect negative effect which was mediated via P and clay content and positively mediated via BD (Fig. 3C). Predators were only directly and positively affected by pH and clay content. The other soil attributes had only indirect effect which were mediated via pH and clay content (Fig. 3D). Herbivores were only directly and positively affected by BD and Omnivores as well as social insects were not affected by any soil attributes (data not shown).

3.3.2. *Litter*

According to path coefficient analysis, polyphenol content was the only litter attribute that had a direct negative effect on density of total fauna. N and P content had indirect positive effects which were mediated via polyphenol content, while lignin and cellulose content had indirect negative effects which were mediated via polyphenol content (Fig. 4A). Richness of fauna was directly and positively affected by lignin and directly and negatively affected by polyphenol content. Richness of fauna was also indirectly and negatively affected by N and P content which was mediated via lignin content and indirectly and positively affected by polyphenol content. C and cellulose content also had indirect positive effects which were mediated via lignin content (Fig. 4B).

Microbial grazers were directly and positively affected by P and lignin content. Polyphenol content had an indirect effect on microbial grazers which was mediated via P content (negative effect) and via lignin content (positive effect) and cellulose content had an indirect and positive effect which was mediated via lignin content (Fig. 4C). P, lignin, polyphenol and cellulose content had signifi-

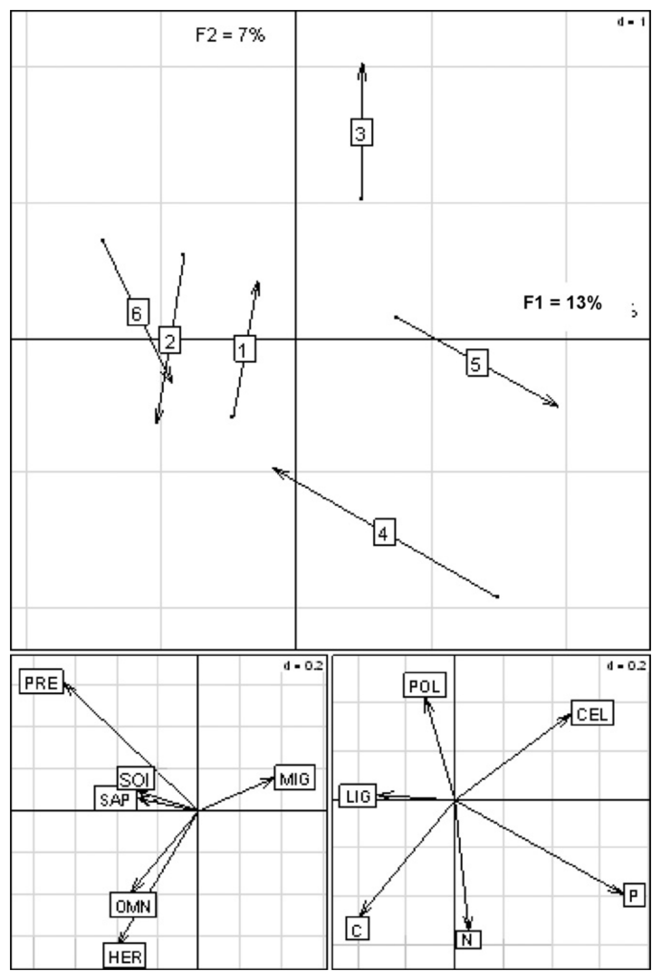

Fig. 2. Co-inertia analysis combining litter attributes and fauna functional groups in cacao agroforestry systems and a natural forest in Bahia, Brazil. 1—CRE (renewed cacao under *Erythrina* system); 2—CRF (renewed cacao under forest system); 3—CNF (cacao under forest system); 4—CE (cacao under *Erythrina* system); 5—CGC (cacao germoplasm collection); 6—NF (natural forest). MIG—microbial grazers; SOI—social insects; SAP—saprophagous; PRE—predators; HER—herbivores; OMN—omnivores. N—nitrogen; C—carbon; P—phosphorous; LIG—lignin; POL—polyphenols; CEL—cellulose.

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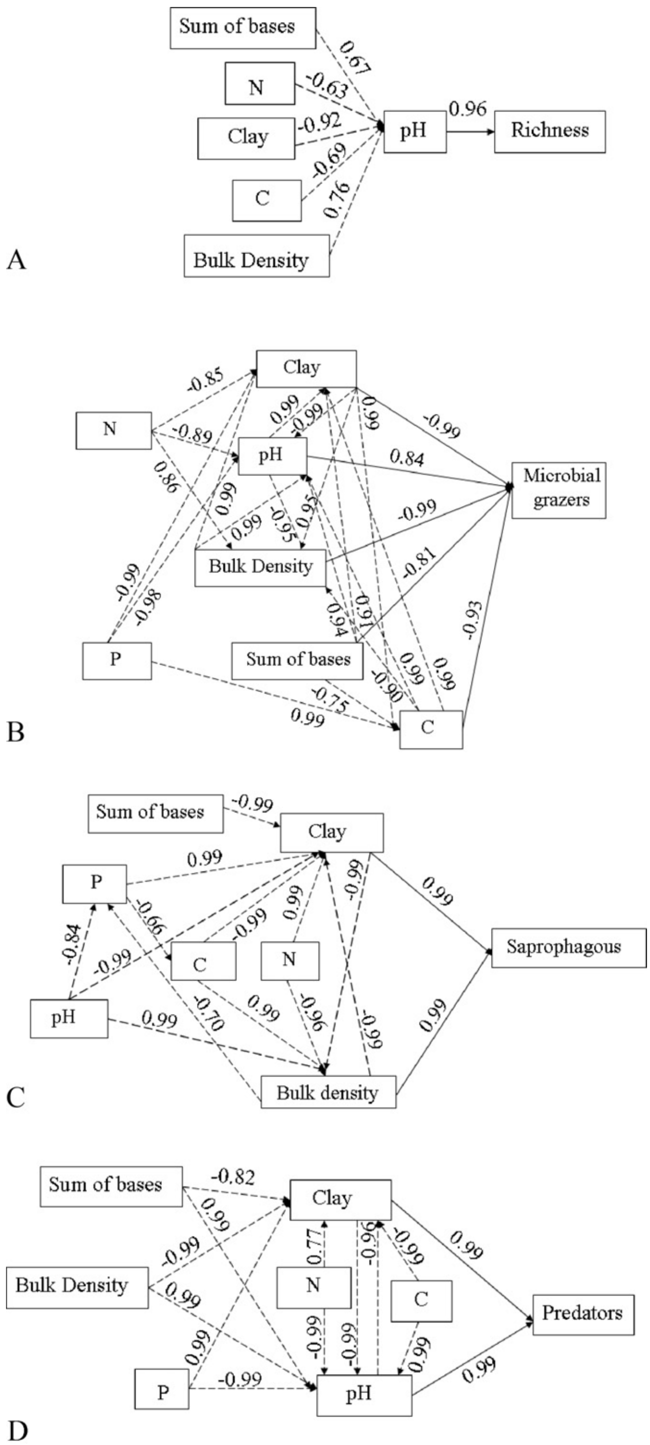

Fig. 3. Path coefficient analysis of the direct and indirect effects of soil attributes on faunal community (significant at $p < 0.05$) in cacao agroforestry systems in Bahia, Brazil. Arrows connecting soil attributes to the fauna (A—richness; B—microbial grazers; C—saprophagous; D—predators) indicate direct effects (solid lines), while soil attributes linked to the fauna via other soil attributes constitute indirect effects (dashed lines). The numbers along the lines connecting the boxes represent the path coefficient.

cant direct effects on social insects; cellulose content was the only one that had positive effect. Social insects were also indirect and negatively affected by N content which was mediated via P content and positively via polyphenol content (Fig. 4D). Saprophagous organisms were directly affected by C, lignin and polyphenol, but lignin content was the only attribute that had a positive effects. In this case, N and P content had indirect and negative effects mediated via lignin content and positive effect via polyphenol content (Fig. 4E). Predators were directly affected only by lignin (positive effect) and cellulose (negative effect) content. N and P content had indirect negative effects and C and polyphenol content had indirect positive effect on predators which were mediated via lignin content (Fig. 4F). Herbivores were not affected by any litter attributes (data not shown). Omnivores groups were directly and positively affected by P and lignin content and negatively affected by cellulose content (Fig. 4G).

4. Discussion

The Monte Carlo tests of COI detected no relationships between faunal functional groups and soil and litter attributes. Such findings suggest that these two datasets vary independently. In this case, all cacao agroforestry systems (AFS) were similar to natural forest. These findings reinforce the idea that cacao agroforestry systems may be considered as a conservative land use system (Moço et al., 2009). The constant addition of organic materials via litterfall (Müller and Gama-Rodrigues, 2007) or sloughed-off roots (Gama-Rodrigues and Cadima-Zevallos, 1991) and the presence of leguminous tree roots (Haynes and Beare, 1997), coupled with the absence of tillage and use of machinery (no-till) in cacao AFS, helps maintain the high soil organic carbon stock (to 1 m depth) similar to natural forest (Gama-Rodrigues et al., 2010) creating beneficial effects on soil and litter faunal communities.

The abundance of the soil fauna was not influenced by soil attributes. However, the soil faunal diversity was greatly affected by soil quality components mostly by soil pH that affected directly and positively the richness of soil fauna. N and C content, BD, SB and clay content had indirect effects on richness of soil fauna which were mediated via pH (Fig. 3A). The obtained results indicate that the composition of faunal communities is significantly affected by pH. In general, the soil acidity and low P content reduce the abundance of macrofauna and mesofauna and the activity of decomposer organisms (Geissen et al., 2007; Debeljak et al., 2007; Ke et al., 2004). Clay and acidic soils had high C and N content (Table 1) suggesting that soil acidity is a determinant factor for mineralization and decomposition of organic matter, which can explain the negative effect of C and N content mediated via pH on the richness of soil fauna and also the mostly negative effect of clay content on functional groups (Fig. 3). In general, the functional groups were affected by mostly soil attributes, except where social insects and omnivores that were not affected by any attributes and herbivores that were affected only by BD. In soil, path analysis showed that pH, bulk density and clay content played an important role in most of functional groups. Our results indicated that pH positively affected microbial grazers and predators. In fact, the composition of faunal communities is significantly affected by pH (Lavelle et al., 1995; Debeljak et al., 2007), and microbial grazers, dominated by groups Collembola, have been found to be strongly associated with soil pH, where soil acidification causes serious changes in collembolan community composition (Crommentuijn et al., 1997; Rusek, 1998; Ke et al., 2004).

Another important aspect is related to the BD that negatively affected the microbial grazers (Collembola) (Fig. 3B) which are microarthropods that inhabit pores in the soil (Rusek, 1998). High BD is related to soil compaction and reduction of soil porosity which can influence the mobility and activity of the fauna (Whalley et al., 1995). Larsen et al. (2004) suggested that the effect of compaction on Collembola is most likely due to a decrease in habitable pore spaces in the soil.

Path analysis showed that polyphenols content of litter seems to control directly the abundance and diversity of the faunal community (Fig. 4A and B). Polyphenol and lignin content were the main attributes related to litter functional groups besides P and cellulose content. Polyphenol content had only direct negative effects on functional groups (Fig. 4D and E). Polyphenol may affect the palatability of populations of decomposer organisms (Swift et al., 1979) and consequently cause a negative effect on density and diversity of the fauna. On the other hand, the positive direct effect of lignin on fauna communities on cacao agroforestry systems (Fig. 4C, E, F and G) could be explained by the suppression of decomposition due to the high amounts of this compound that regulate the decomposition of organic matter. It is known that soil fauna is responsible for the breakdown of organic matter and cycling of nutrients, but their activities are extremely dependent of litter quality (Tian et al., 1993). Litter quality refers to the concentration of nutrients, and of recalcitrant components (lignin and cellulose) that require specific groups of organisms for their decomposition and are inhibiting some fauna individuals. Then, litter quality may affect the microclimatic conditions such as moisture, temperature and physical habitat. Small animals have a very large surface area in proportion to their mass; consequently, the conservation of water and the maintenance of a fairly constant internal medium are especially important to them (Cloudsley-Thompson, 1962). Thus, litter with low nutritional quality, which decomposes slowly and has a large effect on the microclimate could offer favorable microenvironmental conditions (Tian et al., 1993).

In cacao agroforestry systems the relationship between environmental quality and faunal communities vary between faunal habitat (soil or litter), so the litter functional groups were more affected by litter quality than soil functional groups by soil attributes of quality.

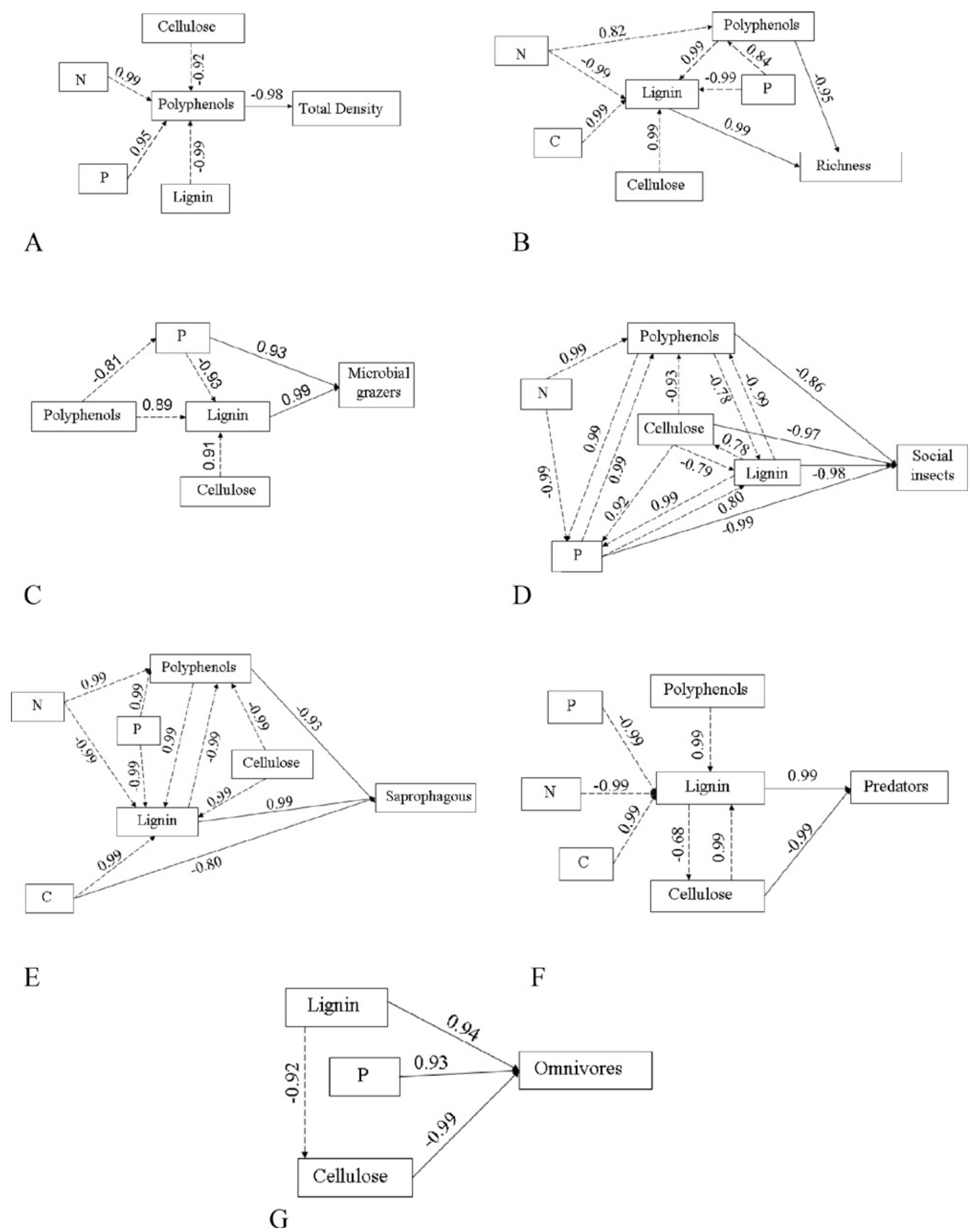

Fig. 4. Path coefficient analysis of the direct and indirect effects of litter attributes on faunal community (significant at $p < 0.05$) in cacao agroforestry systems in Bahia, Brazil. Arrows connecting litter attributes to the fauna (A—richness; B—total density; C—microbial grazers; D—social insects; E—saprophagous; F—Predators; G—omnivores) indicate direct effects (solid lines), while litter attributes linked to the fauna via other litter attributes constitute indirect effects (dashed lines). The numbers along the lines connecting the boxes represent the path coefficient.

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5. Conclusions

Soil attributes and litter quality under different cacao agroforestry systems affect the diversity of the soil and litter fauna, and these attributes are potential regulators of the functional groups. The chemical components related to soil acidity, litter nutrient concentrations and palatability are the most decisive attributes for an abundant and diverse soil and litter fauna. Attributes which affected soil fauna in cacao agroforestry systems included mainly pH, and bulk density in soil and polyphenols and lignin content in the litter. The faunal communities were more sensitive to litter quality than soil quality. Litter management could be a good practice to maintain healthy activities of faunal community to improve ecosystem functioning in cacao agroforestry systems.

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