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Soil macrofauna-mediated impacts of plant species composition on soil functioning in Amazonian pastures

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ABSTRACT

The design of sustainable agroecosystems requires knowledge of plant species impacts on soil functioning. To address this need, we manipulated plant species diversity in pastures of eastern Amazonia. Four plant species (*Arachis pintoi*, *Brachiaria brizantha*, *Leucaena leucocephala* and *Solanum rugosum*) were grown alone and in every possible combination on experimental plots within three replicate farms. After 28 months, soils were sampled to determine impacts on 5 categories of variables: soil macrofauna, aggregate morphology, chemical fertility, water storage and compaction. No clear effects of plant species richness were observed on any of the soil properties measured. However, individual plant species had significant impacts on variables in all 5 categories. Most notably, the herbaceous legume, *A. pintoi*, promoted both earthworm and ant densities and a corresponding 87% increase in biogenic aggregates in plots with vs. without *A. pintoi*. Meanwhile, *B. brizantha* increased the proportion of root-derived aggregates, while negatively impacting ant densities. Significant covariation was observed among many of the 5 data sets (categories), namely soil aggregate morphology and soil macrofauna, as well as aggregate morphology and soil compaction. This research demonstrates that plant species composition can impact soil properties through faunal-mediated effects, and stresses the necessity of considering soil macrofauna in agroecosystem management.

1. Introduction

Deforestation and conversion of Amazonian forests to pasture and croplands can have profound effects on soil biodiversity and functioning, with compaction, erosion, nutrient depletion and overall loss of soil fertility representing very real threats during this transition (Alegre et al., 1996; McGrath et al., 2001; Chauvel et al., 1999; Mathieu et al., 2005). Proper management of these fragile soils is therefore critical for sustaining agroecosystem productivity and avoiding the rapid degradation of soils following forest conversion, yet many questions remain about how exactly this should be done. In relatively intact Amazonian rainforest, high plant diversity and intense soil biological activity contribute significantly to efficient nutrient cycling and productivity (Gentry, 1988; Hofer et al., 2001), in spite of the generally low inherent fertility of these soils. Thus, agroecosystems that replace these forests may benefit greatly from management practices that seek to maintain these key attributes (Ewel, 1999; Lavelle et al., 2001).

Land managers have long sought to regulate soil properties and functions by manipulating plant cover, including efforts to improve soil fertility, increase C sequestration, reduce erosion and nutrient loss, and manage soil pests (Paustian et al., 1997; Snapp et al., 2005; Tonitto et al., 2006). More recently, researchers have begun to examine the influence of plant species composition and diversity in regulating soil processes. For example, Fornara and Tilman (2008) showed increasing functional diversity, specifically combinations of grasses and legumes, to lead to increased soil C and N accumulation in a temperate grassland ecosystem. Others have looked at the impact of plant species mixtures on soil nutrient acquisition (Hooper and Vitousek, 1998; Karanika et al., 2007), and soil physical properties (Niklaus et al., 2007). Despite more recent attention given to the impacts of plant species composition on soil properties, experimental evidence from field studies, particularly from tropical ecosystems, remains scarce and a more complete understanding of plant species identity and diversity impacts on soil physical and chemical properties is needed.

In addition to impacts on chemical and physical soil processes, plant species diversity and composition can have clear effects on

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Abbreviations: BIO, biogenic aggregates; NON, non-macroaggregated soils; PHYS, physical aggregates; RHIZ, rhizosphere aggregates.

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soil biodiversity and biological activity (Wardle, 2006; Chung et al., 2007). Soil macrofauna in particular, have been shown to be sensitive indicators to alterations in plant cover (Lavelle and Pashanasi, 1989; Mathieu et al., 2005; Sileshi et al., 2008; De Deyn et al., 2011) and can, in turn, have considerable impacts on soil processes. Soil ecosystem engineers (e.g., earthworms, ants, and termites) are known to process large quantities of soil and can greatly influence decomposition, soil nutrient availability, aggregation, as well as soil aeration and hydraulic properties (Lavelle et al., 1997). In parts of the humid tropics several hundreds to thousands Mg dry soil per ha may be transformed into biogenic structures annually (Lavelle et al., 1997) and in extreme cases, changes to soil macrofauna communities can generate abrupt alterations to soil structure with important consequences for agroecosystem function (Mando et al., 1996; Chauvel et al., 1999; Evans et al., 2011).

Apart from the sheer quantity of soil processed by macroinvertebrates, biogenic aggregates produced by macrofauna (most notably earthworms) may be particularly important for soil organic matter (SOM) turnover, nutrient cycling and other key soil processes. Such biogenic structures are often enriched in C and nutrients and are highly stable relative to aggregates formed by other mechanisms (Guggenberger et al., 1996; Blanchart et al., 1999), and may contribute greatly to the stabilization of SOM (Martin, 1991; Wolters, 2000; Bossuyt et al., 2005). Additionally, macrofauna structures can influence soil porosity, aeration, hydraulic function (Shipitalo and Le Bayon, 2004), and may have important impacts on decomposer food webs (Loranger et al., 1998; Aira et al., 2008; Briar et al., 2011). Despite these efforts, and research quantifying the role of macrofauna in soil aggregation, macrofauna mediated effects of agroecosystem management (including alterations to plant cover or diversity) on soil structure has received minimal attention.

This research, conducted in pastures that were recently converted from forest in eastern Amazonia, sought to explore the role of plant diversity and individual plant species contributions to soil quality, via effects on soil structure, SOM, chemical fertility, physical properties and soil macrofauna communities. Additionally, we sought to elucidate the role of macrofauna in mediating the effects of plant composition on soil properties, particularly aggregation. We hypothesized that increasing plant species richness would enhance soil quality via additions of diverse organic matter resources and subsequent increases the populations of beneficial soil macrofauna.

2. Materials and methods

2.1. Study site and experimental design

The research was conducted in eastern Amazonia near the Benfica settlement (5°16′S; 49°50′W), in the Brazilian state of Pará. At roughly 200 m in elevation, this region has a humid tropical climate with an average temperature of 26 °C and a mean annual rainfall of 1800 mm, with precipitation occurring primarily between November and June. The landscape is a mosaic of forest patches, pastures (predominantly planted to *Brachiaria brizantha*), rice cultures and fallows of different ages. Ferralsols dominate the area, with cambisols (much thinner soils) present on the steep footslopes and gleysols in the low-lands (Reis et al., 2007). The upper 10 cm layer has a sandy clay or sandy clay loam texture (data not presented), with an average pH of 5.3 and organic C content of 1.4% in the upper 10 cm of soil (details below).

The experiment was installed in December of 2002 on three replicate pastures with similar site (relief and soil depth) conditions and management history. These pastures were all located within 2.4 km of each other on middle-slope ledges, where soils (ferralsols) were roughly 2 in depth. All plots were converted from forest by slash-and-burn clearance in 1996 or 1997 and cultivated with upland rice for 1 year prior to establishment of *B. brizantha*. Within each pasture, 16 10 m × 10 m plots (separated by 2 m wide bands) were demarcated and seeded to monocultures as well as all possible combinations of: (1) *B. brizantha* – a tall grass frequently planted in tropical pastures (B), (2) *Arachis pintoi* – a low-growing herbaceous legume (A), (3) *Leucaena leucocephala* – a leguminous tree that is common in agroforestry systems (L), and (4) *Solanum rugosum* – a locally invasive shrub (S). An unweeded control treatment was also included containing *B. brizantha* and some weeds (C). Treatment implementation within all plots (except for the control) was achieved via intensive weeding at the start of the experiment and during the first few months after seedling establishment. Plant biomass was controlled as needed (by mowing for *B. brizantha* and pruning for *L. leucocephala*; no action was required for *A. pintoi* or *S. rugosum*) and residues were left on the soil surface. All plots were protected from grazing. Additional details on experimental design, establishment, and biomass production in the plots are reported by Laossi et al. (2008).

2.2. Soil macrofauna assessment

In April of 2005 soil macrofauna were sampled by excavation and hand-sorting of two soil monoliths (25 cm × 25 cm wide, 30 cm deep) according to the TSBF method (Anderson and Ingram, 1993). Invertebrates, visible without magnification, were collected from successive strata: litter, 0–10, 10–20 and 20–30 cm and separated into the broad taxonomic groups: Formicidae, Isoptera, Oligocheata, Isopoda, Coleoptera (adults and larvae), Arachnida, Diplopoda, Gastropoda, Chilopoda, Hemiptera, and others. This paper only reports on macrofauna in the top 10 cm of soil (and the litter layer), due to low macrofauna densities below 10 cm.

2.3. Origins of soil aggregates

Soil morphology was assessed by visual separation of soil macroaggregates based on Velásquez et al. (2007b). A soil sample (5 cm × 5 cm × 5 cm) was removed adjacent to each macrofauna monolith and aggregates (and other morphological items) were separated by gently breaking the soil along natural planes of fracture. We note that most of the macrofauna-generated soil structures occurred in the top 5 cm and we thus expected high correlation between macrofauna collected from deeper layers and the structures formed near the surface. Large macroaggregates (>5 mm) were separated into groups of three different origins: biogenic aggregates (BIO) – produced by soil ecosystem engineers such earthworms, termites, ants and a few Coleoptera and Diplopoda, rhizosphere aggregates (RHIZ) – formed around and clinging to plant roots, and physical aggregates (PHYS) – mainly produced by other factors (wet–dry cycles and mineral interactions). Given that smaller soil aggregates are difficult to identify without magnification, the soil particles and unidentified aggregates <5 mm in size were collected separately and referred to as the non-macroaggregated fraction (NON). All morphological fractions were air-dried and weighed in the lab. Other soil components such as leaves, roots and woody pieces, seeds and small rocks were also quantified.

2.4. Soil physical and chemical properties

Soils samples for measurement of chemical fertility and bulk density were collected to a depth of 10 cm using metal cylinders (7 cm dia.). Fertility characteristics were determined according to Pansu and Gautheyrou (2006). Total soil organic C and N concentrations were measured with a Fisons NA 1500 CHNS autoanalyzer. Extractable P (Mehlich ‘double acid’ extraction method in 0.05 M

HCl and 0.0125 M H_2SO_4 solutions) was measured by colorimetry and pH was determined in a 1:2.5 soil water suspension. Cation exchange capacity (CEC) at soil pH 7 was calculated as the sum of acidity (H^+ and exchangeable Al) extracted with 0.5 M $(CH_3COO)_2Ca$ solution and base cations (Ca^{2+}, Mg^{2+}, K^+ and Na^+), extracted with 1 M KCl solution. Meanwhile, soil compaction was assessed through estimations of bulk density (core method), calculation of total porosity from bulk and solid density, shear strength and resistance to penetration at the 5 cm depth with torcometer and cone penetrometer, respectively. The water retention characteristics of the soils (0–5 cm depth) included gravimetric water contents at saturation, field capacity (FC; pF = 1.8), permanent wilting point (PWP; pF = 4.2) and plant available water (FC-PWP) measured on undisturbed soil samples (Grimaldi et al., 2002).

2.5. Soil quality and calculation of GISQ

In order to examine the effects of the different plant treatments on soil health and functioning, all soil data were summarized in a general indicator of soil quality (GISQ) according to the methods of Velásquez et al. (2007a). Briefly, this indicator is calculated by first applying principal components analysis (PCA) to groupings of soil properties (macrofauna, aggregate morphology, chemical fertility, soil compaction, and water storage) in order to identify the soil variables that best differentiate the treatments according to soil quality. These variables are then used to generate sub-indicators (with values ranging from 0.1 to 1.0) for each of the five groupings and then combined into one overall indicator of soil quality.

2.6. Statistical analyses

The influence of plant species richness was evaluated by examining simple correlations between the number of species in each treatment (1–4) and the physical, biological and chemical soil variables measured. However, due to a lack of plant diversity effects on any of the examined soil properties, subsequent analyses focused on the influence of plant treatments and plant species identity on soil properties. Impacts of the 16 plant treatments on soil physical and chemical properties, aggregate morphology, macrofauna abundance and indicators were evaluated using ANOVA, with the replicate pastures considered blocks and treated as a random variable. Given that relatively few significant differences between treatments were observed, comparisons focused on plant species identity effects by using orthogonal contrasts. Contrasts compared plots containing a particular plant species to those where that species was absent. These tests of plant species identity impacts were carried out for each of the four plant species and using all 16 treatments. Natural log transformations were applied as needed to meet the assumptions of ANOVA and regression. Sub-replicates within each plot were averaged for use in all analyses.

In addition to the univariate tests, multivariate analyses were used to explore the relationships between the 5 data sets (or categories) of soil variables (soil macrofauna, aggregate morphology, chemical fertility, water storage and compaction). Co-inertia analyses tested for covariation (and similarity in the data structure) among the 5 data tables, by using the same PCA data used in the calculation of the GISQ. All univariate statistics were conducted using JMP 8.0 software (SAS Institute, 2008), while PCA and coinertia analyses were conducted using the ade4 package within R (Thioulouse et al., 1997; Dray et al., 2003).

3. Results

3.1. Soil macrofauna

There were no significant differences among the 16 plant treatments for soil macrofauna groups (Table 1); however, orthogonal contrasts suggest strong individual plant species effects

Table 1
Soil macrofauna density within 16 plant combination treatments in Benfica settlement, Pará State, Brazil, collected in April 2005. Numbers in parentheses to the right of each average represent the standard error of each treatment mean. Effects of plant species identity (as determined by orthogonal contrasts) are reported at the bottom of the table.

	Macrofauna groups[b]										
	Isopt	Form	Olig	Chil	Col adult	Col larva	Arac	Dipl	Hemi	Isopo	Gast
	individuals m^{-2}										
Plant treatment[a]											
A	2283 (1194)	1200 (990)	347 (253)	21 (14)	85 (37)	5 (5)	21 (21)	91 (37)	5 (5)	0 (0)	107 (77)
B	5168 (3605)	48 (24)	208 (116)	21 (5)	37 (37)	53 (11)	27 (5)	5 (5)	0 (0)	0 (0)	0 (0)
L	1237 (978)	96 (28)	336 (217)	48 (48)	69 (14)	5 (5)	16 (16)	27 (19)	5 (5)	0 (0)	85 (56)
S	229 (120)	96 (24)	341 (270)	48 (9)	69 (53)	21 (21)	11 (11)	32 (24)	0 (0)	0 (0)	16 (9)
BA	923 (516)	37 (23)	336 (130)	37 (19)	48 (33)	21 (14)	5 (5)	5 (5)	0 (0)	0 (0)	11 (11)
LA	555 (377)	880 (785)	368 (83)	27 (11)	53 (14)	21 (21)	0 (0)	27 (5)	0 (0)	37 (30)	112 (104)
AS	3888 (3760)	560 (225)	411 (115)	27 (19)	32 (16)	16 (0)	5 (5)	69 (37)	0 (0)	0 (0)	27 (5)
BL	357 (235)	309 (254)	128 (40)	27 (11)	128 (0)	21 (11)	16 (9)	21 (14)	11 (11)	5 (5)	27 (27)
BS	533 (494)	11 (11)	117 (56)	0 (0)	16 (9)	11 (5)	11 (11)	48 (48)	0 (0)	0 (0)	0 (0)
LS	7285 (6101)	245 (133)	123 (23)	5 (5)	69 (32)	5 (5)	5 (5)	21 (5)	0 (0)	0 (0)	16 (9)
BLA	2427 (2055)	59 (23)	256 (225)	16 (9)	32 (18)	5 (5)	11 (11)	32 (16)	5 (5)	0 (0)	11 (5)
BAS	10,155 (7349)	128 (120)	325 (116)	16 (16)	21 (11)	123 (83)	11 (5)	16 (9)	117 (117)	0 (0)	27 (14)
LAS	725 (662)	1008 (817)	555 (146)	48 (40)	80 (49)	43 (43)	5 (5)	21 (14)	0 (0)	5 (5)	37 (19)
BLS	3824 (321)	187 (117)	181 (93)	11 (5)	53 (21)	37 (23)	11 (11)	43 (43)	0 (0)	0 (0)	11 (5)
BLAS	1429 (799)	75 (46)	320 (191)	37 (19)	27 (11)	16 (16)	5 (5)	48 (40)	5 (5)	0 (0)	27 (5)
C	10,405 (5088)	48 (32)	304 (33)	27 (27)	43 (11)	27 (27)	11 (5)	21 (5)	0 (0)	5 (5)	16 (9)
Orthogonal contrast results[c]											
A.											
Present	–	–	365	–	–	–	–	–	–	–	–
Absent	–	–	217	–	–	–	–	–	–	–	–
B.											
Present	–	100	–	–	–	–	–	–	–	–	–
Absent	–	583	–	–	–	–	–	–	–	–	–

[a] Plant species: A, *Arachis pintoi*; B, *Brachiaria brizantha*, L, *Leucaena leucocephala*; S, *Solanum rugosum*; C, Control (unweeded *B. brizantha*).

[b] Isopt, Isoptera (termites); Form, Formicidae (ants); Olig, Oligochaeta (earthworms); Chil, Chilopoda; Col, Coleoptera; Arac, Arachnida; Dipl, Diplopoda; Hemi, Hemiptera; Isopo, Isopoda; Gast, Gasteropoda.

[c] Average values for treatments with or without *A. pintoi* and *B. brizantha*. Results shown only for significant ($P < 0.05$) orthogonal contrasts. No significant contrasts were observed for *L. leucocephala* or *S. rugosum*.

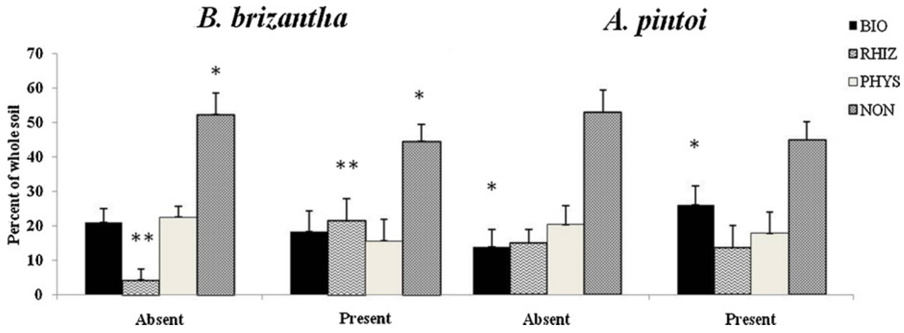

Fig. 1. Effect of individual plant species (*A. Pintoi* and *B. brizantha*) on aggregate morphology in soils collected from 16 plant combination treatments in Benfica settlement, Pará State, Brazil in April 2005. Significant differenced refers to orthogonal contrasts comparing plots with and without *A. pintoi* or *B. brizantha* (*$P < 0.05$; **$P < 0.01$).

on both earthworms and ants. Plots with *A. pintoi* had significantly more earthworms ($P = 0.039$) than those without (365 vs. 217 individuals m^{-2}; respectively). At the same time, the presence of *B. brizantha* appears to reduce ant densities, from 583 to 100 ants m^{-2} in plots with and without *B. brizantha*, respectively ($P = 0.005$). There were no significant treatment or plant species identity effects ($P > 0.05$) on any of the other soil macrofauna groups, nor for total abundance or richness of macrofauna taxa.

3.2. Aggregate morphology

The influence of plant treatments on aggregate morphology was generally more pronounced than for effects on soil macrofauna. For example, ANOVA indicated significant effects of plant treatment on the proportion of whole soil in the BIO ($P = 0.038$), RHYZ ($P = 0.004$) and NON ($P = 0.037$) soil fractions. Orthogonal contrasts revealed clear impacts of plant species on the distribution of aggregates among the different morphological fractions. For example, the presence of *B. brizantha* greatly increased the quantity of rhizosphere aggregates from 4.3% to 21.6% of whole soil when *B. brizantha* was absent vs. present, respectively ($P < 0.001$; Fig. 1). This effect on the RHYZ fraction yielded a corresponding decrease of the NON fraction from 52.2% to 44.5% of the whole soil when *B. brizantha* was absent vs. present ($P = 0.023$). The presence of *A. pintoi* resulted in an 87% increase in the proportion of biogenic aggregates, with 25.3% of the whole soil in the BIO fraction when *A. pintoi* was present (Fig. 1). The presence of *A. pintoi*, also decreased the proportion of whole soil in the NON fraction by roughly 15%, thus suggesting that both *A. pintoi* and *B. brizantha* improve soil macroaggregation. The proportion of whole soil in PHYS was not significantly impacted by any plant species or treatment. Neither *L. leucocephala* nor *S. rugosum* had any significant effects on soil morphological fractions.

Table 2

Selected soil chemical and physical properties for the surface layer (0–10 cm) collected from 16 plant combination treatments in Benfica settlement, Pará State, Brazil in April 2005. Numbers in parentheses to the right of each average represent the standard error of each treatment mean. Effects of plant species identity (as determined by orthogonal contrasts) are reported at the bottom of the table.

	Soil variables[b]						
	pH	Total soil C (g kg^{-1})	C:N	BD (g cm^{-3})	PR (kgf cm^{-2})	SS (kPa)	AW (g kg^{-1})
Plant treatment[a]							
A	5.7 (0.2)	14.2 (1.5)	11.6 (0.3)	1.35 (0.03)	45.2 (5.3)	19.7 (1.6)	83 (9)
B	6.3 (0.4)	14.8 (1.6)	13.4 (0.5)	1.29 (0.04)	70.8 (7.2)	40.2 (6.1)	117 (17)
L	5.1 (0.4)	12.8 (1.1)	11.8 (0.3)	1.32 (0.07)	93.6 (3.6)	32.6 (4.5)	77 (7)
S	5.0 (0.3)	14.7 (1.7)	11.8 (0.2)	1.25 (0.07)	66.9 (2.3)	25.7 (4.9)	90 (10)
BA	5.0 (0.3)	13.1 (1.7)	12.5 (0.2)	1.30 (0.04)	60.0 (6.4)	35.9 (1.8)	87 (3)
LA	5.2 (0.3)	12.9 (0.6)	11.6 (0.5)	1.33 (0.04)	37.9 (9.1)	24.0 (3.4)	70 (0)
AS	5.0 (0.3)	12.2 (1.1)	12.0 (0.6)	1.31 (0.06)	45.4 (4.3)	22.7 (3.0)	77 (3)
BL	5.4 (0.1)	12.6 (0.9)	12.9 (0.6)	1.40 (0.02)	66.2 (14.2)	20.7 (1.0)	90 (0)
BS	5.7 (0.3)	12.7 (2.2)	12.2 (0.2)	1.37 (0.05)	73.7 (9.6)	48.4 (1.8)	87 (12)
LS	4.9 (0.2)	14.3 (2.7)	13.4 (1.2)	1.30 (0.08)	72.2 (5.0)	20.9 (1.8)	77 (9)
BLA	5.3 (0.2)	15.4 (1.2)	12.8 (0.6)	1.27 (0.03)	52.7 (6.2)	30.6 (3.0)	123 (24)
BAS	5.1 (0.3)	13.9 (1.4)	12.3 (0.5)	1.30 (0.05)	73.2 (12.9)	37.7 (3.0)	87 (12)
LAS	5.3 (0.3)	17.3 (3.1)	11.8 (0.5)	1.26 (0.04)	72.3 (10.3)	22.4 (0.6)	80 (6)
BLS	5.3 (0.4)	12.6 (0.3)	12.7 (0.2)	1.32 (0.05)	58.1 (4.5)	35.8 (8.1)	80 (12)
BLAS	5.4 (0.4)	15.7 (2.6)	12.6 (0.7)	1.28 (0.05)	65.2 (3.6)	32.4 (4.2)	90 (10)
C	5.4 (0.5)	14.3 (0.8)	13.9 (0.5)	1.28 (0.06)	58.1 (5.6)	45.8 (8.1)	103 (9)
Orthogonal contrast results[c]							
A.							
Present	–	–	12.1	–	56.5	28.1	–
Absent	–	–	12.8	–	69.9	33.8	–
B.							
Present	5.4	–	12.8	–	–	36.4	95
Absent	5.2	–	12.0	–	–	24.0	79

[a] Plant species: A, *Arachis pintoi*; B, *Brachiaria brizantha*, L, *Leucaena leucocephala*; S, *Solanum rugosum*; C, Control (unweeded B. brizantha).

[b] C:N, C to N ratio of soil; BD, bulk density; PR, penetration resistance; SS, shear strength; AW, plant available water holding capacity (field capacity – permanent wilting point).

[c] Average values for treatments with or without *A. pintoi* and *B. brizantha*. Results shown only for significant ($P < 0.05$) orthogonal contrasts. No significant contrasts were observed for *L. leucocephala* or *S. rugosum*.

Table 3
Results of multivariate analyses examining relationships within and among data sets of soil macrofauna, aggregate morphology, soil chemical fertility, compaction and water storage.

Variables	Axis (% variation explained)		Variables	Axis (% variation explained)			P-value[a]
	1	2		1	2	RV	
Principle components analysis			Co-inertia analysis				
Macrofauna	22.0	20.5	Macrofauna – Morphology	39.84	33.25	0.140	0.038
Morphology	38.5	28.7	Macrofauna – Chemical fertility	54.09	30.06	0.108	0.408
Chemical fertility	31.3	26.9	Macrofauna – Soil compaction	60.11	26.95	0.101	0.346
Soil compaction	40.2	28.5	Macrofauna – Water storage	62.9	32.71	0.074	0.372
Water storage	68.3	21.9	Morphology – Chemical fertility	55.78	24.97	0.142	0.019
			Morphology – Soil compaction	69.85	22.51	0.128	0.032
			Morphology – Water storage	73.78	25.35	0.080	0.172
			Chemical fertility – Soil compaction	88.91	7.81	0.276	0.001
			Chemical fertility – Water storage	75.33	24.24	0.264	0.001
			Soil compaction – Water storage	95.54	3.24	0.503	0.001

[a] Based on Monte Carlo Tests (1000 permutations).

3.3. *Physical and chemical properties*

Plant treatments demonstrated important influences on several key soil physical and chemical properties (Table 2). Most notably, shear strength and soil penetration resistance were significantly impacted by treatments ($P < 0.001$ and $P = 0.02$; respectively). Orthogonal contrasts revealed that these measures of soil compaction were generally increased in the presence of *B. brizantha*, but decreased by *A. pintoi*. Planting treatments also impacted soil water storage, such that the presence of *B. brizantha*, was found to increase the storage capacity of plant available water by 21% from 79 to 96 g water kg^{-1} soil ($P < 0.001$; Table 2). For soil chemical fertility, ANOVA results suggest that plant treatment significantly affected soil pH ($P = 0.025$). Contrasts further suggested that the presence of *B. brizantha* was associated with an increase in pH from 5.17 to 5.42 ($P = 0.036$). While, neither total soil C nor N was significantly impacted by plant treatments, ANOVA suggested a significant impact on the C:N ratio ($P = 0.044$). Orthogonal contrasts revealed that *B. brizantha* was related to an increase in the C to N ratio from 12.0 to 12.8 ($P = 0.005$), while the leguminous *A. pintoi* reduced C:N from an average of 12.8 in its absence to 12.1 when it was present ($P = 0.015$; Table 2).

3.4. *Soil quality indicators*

The values for GISQ ranged from 0.33 (for BLS) to 0.73 for (LAS). While ANOVA revealed no significant differences between the 16 treatments, orthogonal contrasts suggested that the presence of *B. brizantha* decreased GISQ by nearly 15% on average from 0.55 in its absence to 0.49 when *B. brizantha* was present. Along with this result for GISQ, several of the sub-indicators were influenced by plant species. For example, orthogonal contrasts showed that *B. brizantha* decreased the indicator for soil morphology ($P < 0.001$), while increasing the indicators for soil compaction ($P < 0.001$) and water dynamics ($P = 0.002$). Additionally, *A. pintoi* was found to significantly decrease the sub-indicator for soil compaction ($P = 0.003$).

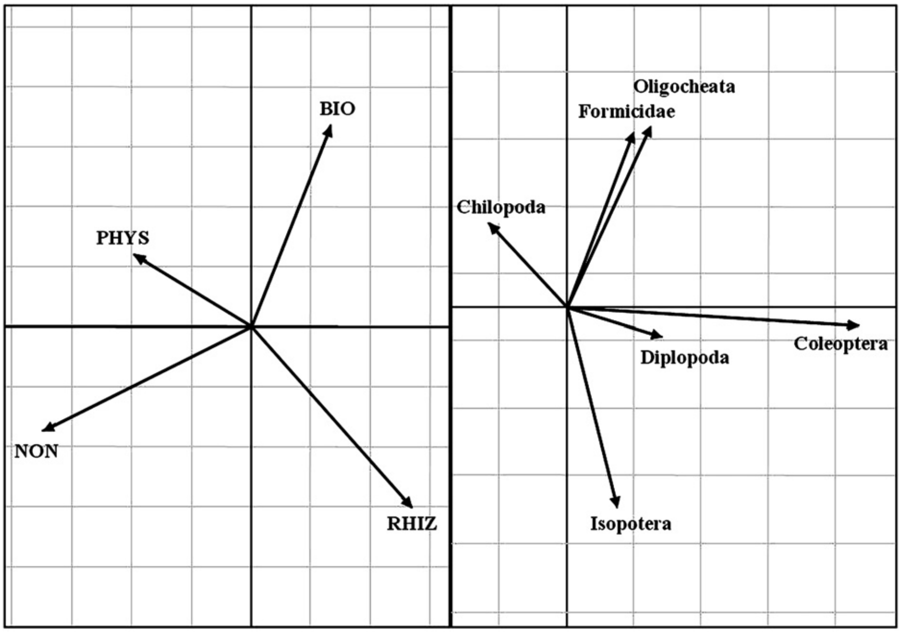

Fig. 2. Projection in factorial plane F1/F2 of a co inertia analysis of soil macrofauna variables (left) and aggregate morphology variables (right) measured in 16 plant combination treatments in Benfica settlement, Pará State, Brazil in April 2005 (BIO, biogenic aggregates; RHIZ, rhizosphere aggregates; PHYS, physical aggregates; NON, non-aggregated soil).

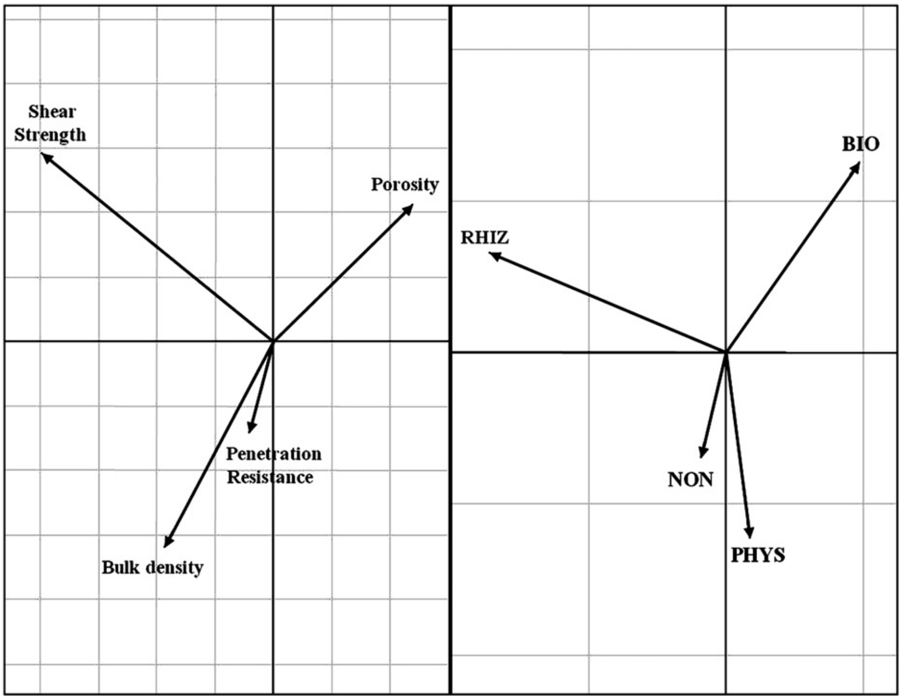

Fig. 3. Projection in factorial plane F1/F2 of a co inertia analysis of soil compaction variables (left) and aggregate morphology variables (right) measured in 16 plant combination treatments in Benfica settlement, Pará State, Brazil in April 2005 (BIO, biogenic aggregates; RHIZ, rhizosphere aggregates; PHYS, physical aggregates; NON, non-aggregated soil).

3.5. Covariation between data tables

Co-inertia analyses revealed significant covariation between several of the soil data sets (see Table 3). For example, soil macrofauna were found to be significantly associated with aggregate morphology ($P = 0.038$), where BIO aggregates are shown to be positively associated with earthworms and ants, but negatively associated with termite abundance along axis 2 (see Fig. 2). Aggregate morphology also demonstrated significant covariation with soil compaction variables ($P = 0.032$) and chemical fertility ($P = 0.019$), such that shear strength and root influence were associated along axis 1, non-aggregated soil was aligned with bulk density and penetration resistance along axis 2, and earthworms were positively associated with soil porosity (Fig. 3). Strong covariation ($P < 0.005$) was also observed among chemical fertility, soil compaction, and water storage (Table 3).

4. Discussion

The development of agroecosystems that sustain productivity, while promoting biodiversity and critical ecosystem services, remains a fundamental challenge for improving rural livelihoods and achieving conservation goals in tropical Latin America. To address this issue, this study examined the potential of enhanced plant diversity to improve soil functioning in tropical pasture systems of Amazonia.

Contrary to our expectations, plant species richness did not yield any detectable influence on the soil factors examined here. The lack of a diversity effect was not entirely unexpected, as research on biodiversity–function relationships has yielded mixed results for impacts on soil functioning, with some studies showing a clear effect on soil processes (Chung et al., 2007; Fornara and Tilman, 2008) and others suggesting little or no apparent influence (Niklaus et al., 2007). Within this same experiment, Laossi et al. (2008) observed no impact of plant species richness on above- or belowground biomass production. Given that many soil processes are driven by organic matter inputs from plants and their rooting activity, we might not expect large impacts of plant diversity on soil properties in the absence of significant concomitant impacts on plant growth. Although we found no effects of diversity per se, there were strong individual species impacts on a number of soil properties. Several authors have suggested that plant species composition and individual species impacts are more relevant for ecosystem functioning (e.g., Tillman, 1997; Hooper and Vitousek, 1998; Spehn et al., 2002). In accordance with previous findings (Fornara and Tilman, 2008), grasses and herbaceous legumes appear to represent the dominant functional groups in impacting soils, at least in the short-term. Further elucidation of these individual species or functional group impacts is critical for understanding and improving agroecosystem function and design.

Of the soil properties studied, plant species effects on aggregate morphology were among the most prominent. Direct impacts of plant species are demonstrated by the increased proportion of root derived aggregates in the presence of *B. brizantha*. Grasses in general are known to have dense rooting systems and have been suggested to have strong impacts on soil aggregation (Oades, 1984). However, past research on plant species impacts on soil structure have yielded mixed results, with some studies suggesting that herbaceous legumes have greater impacts on aggregation than grasses due to N inputs and associated stimulation of soil microbial communities. Perhaps of greater interest is the increase in biogenic aggregates in the presence of *A. pintoi* (Fig. 1), indicating an indirect influence of *A. pintoi* on soil aggregation. While other studies have associated land management with macrofauna communities and the structures they produce (Pulleman et al., 2005; Velásquez et al., 2007b; Fonte et al., 2009; Ayuke et al., 2011), few have been able to demonstrate so clearly the potential for the management of plant cover to alter soils through faunal-mediated processes. The parallel increase in earthworm abundance and decreased soil C:N ratio under *A. pintoi*, suggests that earthworms benefited from improved nutrition in the presence of *A. pintoi*, thus enhancing earthworm activity and their influence on soil structure. This idea is further supported by the strong association between BIO and earthworm abundance, as suggested by co-inertia analysis (Fig. 2). While ants displayed the same general trends as earthworms, they are less likely to be responsible for the observed increases in BIO, as earthworms, but not ants, were found to be correlated with *A. pintoi* biomass (Laossi et al., 2008). We also note that morphological structures formed by ants are generally smaller and a large number of these aggregates may have been included within the NON soil fraction (soil particles and aggregates <5 mm). From these results it appears that earthworms were actively feeding on *A. pintoi* residues, while ants may have been simply benefiting from improved physical habitat associated with this species (Laossi et al., 2008). A number of other studies have shown earthworm growth and reproduction to respond well to legume covers (Garcia and Fragoso, 2003; van Eekeren et al., 2009), thus supporting this idea.

Related to the increase in BIO structures, *A. pintoi* also affected soil compaction, via reductions in both penetration resistance and shear strength. Significant covariation between aggregate morphology and soil compaction variables, along with an apparent association between BIO and porosity (Fig. 3) suggests that the formation of soil structures by macrofauna contributes to the decompaction of these soils under *A. pintoi.* Meanwhile, shear strength was positively associated with RHIZ (Fig. 3), suggesting that increasing rooting under *B. brizantha* (as reported by Laossi et al., 2008) lead to an increase in this component of compaction. We also note that plants affected water storage and that these impacts are difficult to separate from those on soil compaction, since soil moisture likely influences penetration resistance and shear strength. This relationship between soil compaction and water storage is evident from the high degree of covariation between these data sets in Table 3.

In this study we sought to explore the value of the GISQ for evaluating the impact of different plant treatments on soil quality. Rather small differences in the GISQ suggest that the overall impacts of plant composition in this experiment were subtle, but that species effects, particularly *B. brizantha*, can be important. Significant differences in the sub-indicators largely reflected the observed differences for individual properties, suggesting that these sub-indicators provide a valuable means of summarizing treatment effects on various aspects of soil quality. At the same time, the large differences observed by Velásquez et al. (2007a) suggest that the GISQ is perhaps more useful for evaluating soil quality across more divergent land-use types at larger scales, rather than among the small plots used here to test only a single factor of plant cover.

5. Conclusion

This research ultimately sought to clarify the role of plant composition in driving key soil processes and advance our understanding of relationships between soil physical, chemical and biological properties in tropical pasture systems of Amazonia. While species diversity (richness) failed to generate clear impacts on soil properties, the presence or absence of individual plant species (notably *B. brizantha* and *A. pintoi*) was found to yield significant impacts on soil s. Plant species impacted soil properties both directly (via changes in C:N ratio and pH) as well as indirectly, through effects on soil fauna and their activity (and subsequent changes in soil morphology). For the recently deforested Amazonian pastures studied here, our findings suggest a need to include herbaceous legume species, such as *A. pintoi*, that promote soil biological functioning to protect against soil compaction and continued degradation. More generally, this research demonstrates the importance of considering soil fauna in agroecosystem management and restoration, as they can be important mediators of plant community impacts on soil functioning.

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