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Spatial patterns of grasses influence soil macrofauna biodiversity in Amazonian pastures

Jérôme Mathieu [a,*], Michel Grimaldi [b], Pascal Jouquet [c], Corinne Rouland [a], Patrick Lavelle [a], Thierry Desjardins [a], Jean-Pierre Rossi [d]

[a] Laboratoire d'Écologie des Sols Tropicaux, UMR 137 – BioSol, univ Paris 06 UPMC-IRD, 32 avenue H. Varagnat, 93143 Bondy Cedex, France
[b] UMR137 – Biosol, UFRA ICA, CP917, 66077-530 Belém (PA), Brazil
[c] IRD – IMWI, UMR137 Biosol, SFRI, Dong Ngac, Tu Liem, Hanoï, Viet Nam
[d] INRA – UMR BIOGECO, Domaine de l' Hermitage Pierroton 69, route d'Arcachon, 33 612 Cestas, France

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ABSTRACT

Grasslands are often characterized by small-scale spatial heterogeneity due to the juxtaposition of grass tufts and bare ground. Although the mechanisms generating plant spatial patterns have been widely studied, few studies concentrated on the consequences of these patterns on belowground macrofauna. Our objective was to analyze the impact of grass tuft (*Brachiaria bryzantha* cv. *marandu*) spatial distribution on soil macrofauna diversity in Amazonian pastures, at a small scale (less than 9 m^2). Soil macrofauna was sampled among *B. bryzantha* tufts, which showed a variable spatial distribution ranging from dense to loose vegetation cover. The vegetation configuration explained 69% of the variation in total soil macrofauna density and 68% of the variation in total species richness. Soil macrofauna was mainly found in the upper 10 cm of soil and biodiversity decreased with increasing distances to the nearest grass tuft and increased with increasing vegetation cover. The size of the largest grass tuft and the microlandscape connectivity also had a significant effect on biodiversity. The density and species richness of the three principal soil ecological engineers (earthworms, ants and termites) showed the best correlations with vegetation configuration. In addition, soil temperature significantly decreased near the plants, while soil water content was not influenced by the grass tufts. We conclude that soil macrofauna diversity is low in pastures except close to the grass tufts, which can thus be considered as biodiversity hotspots. The spatial arrangement of *B. bryzantha* tussocks influences soil macrofauna biodiversity by modifying soil properties in their vicinity. The possible mechanisms by which these plants could affect soil macrofauna are discussed.

1. Introduction

Large-scale determinants of soil macrofauna diversity are relatively well known: climate, soil type, land-use management practices and landscape structure are among the most influential factors (Dauber et al., 2003, 2005). At smaller scales, however, there is much less agreement about the environmental factors that drive soil macrofauna diversity and distribution (Lavelle and Spain, 2001). It has been suggested that in general, grassland invertebrates are less likely to be limited by the quantity of food available, but rather by microclimate and food quality (Curry, 1994). Microclimate is very important since the body temperature of soil macrofauna varies with external conditions (thermoconformers) and the range tolerated by many species is quite narrow (Precht et al., 1973; Geiger and Aron, 2003). In addition, soil macrofauna must maintain body water content within fairly narrow limits, which creates a dependence on water. Soil macrofauna organisms are also sensitive to the nutrient content of their food because they need to maintain their internal chemical concentrations and the balance between the different nutrients of their body within a strict range (Sterner and Elser, 2002; Martinson et al., 2008). Thus elements of food quality, such as phosphorus (Kay et al., 2006; McGlynn and Salinas, 2007), nitrogen (Warren and Zou, 2002) or Ca^{2+} (Reich et al., 2005) content, can become a limiting factor. As autogenic ecosystem engineers, plants modify food quality, quantity, and the microclimate of soil macrofauna. With their associated microflora they affect the physical and chemical properties of their environment by producing and taking up organic and mineral substances, creating biopores, and producing litter (Lavelle and Spain, 2001). Plants modify the microclimate in their vicinity by cooling down the soil and air in the shade of their leaves. They also modify

* Corresponding author. Tel.: +33 1 48 02 59 65.
E-mail address: jerome.mathieu@snv.jussieu.fr (J. Mathieu).

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humidity by intercepting wind and rain, and by absorbing water in the ground. As a consequence, they create specific living conditions (i.e. physical habitats and available food for e.g., Jackson and Caldwell, 1993). A wealth of literature deals with the consequence of these engineering effects on microbial communities (Spetch, 1958; Northup et al., 1999) but much less is known about the relationships between vegetation cover and soil macrofauna diversity and distribution.

In Amazonian pastures, vegetation is typically dominated by large herb tufts of the genus *Brachiaria*, which clearly alternate with bare ground. The vegetation cover is highly variable, from dense to loose, which leads to heterogeneous habitats for soil organisms. Cattle ranching is the dominant activity in Amazonia in terms of land surface (Muchagata and Brown, 2003) and the major motivation for deforestation. Pastures are often characterized by a dramatic decrease in productivity after 10 years of exploitation (Costa and Rehman, 1999; Muchagata and Brown, 2003). This phenomenon is accompanied by a reduction in soil macrofauna biodiversity (Fragoso et al., 1997; Barros et al., 2002). Soil macrofauna biodiversity plays a recognized role in the productivity and soil functioning of these systems (Chauvel et al., 1999; Laossi et al., 2008), but the factors that drive its distribution are still poorly documented. In particular we lack information about the small-scale sources of environmental variability that cause local patterns of soil macrofauna biodiversity (Mathieu et al., 2004).

Our aim was to analyze the effect of vegetation spatial configuration on belowground soil macrofauna density and species richness in Amazonian pastures. We investigated the correlations between the spatial configuration of *Brachiaria bryzantha*, a very common plant in these pastures, and soil macrofauna distribution, and the relations between the spatial configuration of *B. bryzantha* and the soil macrofauna environment. In particular, we discuss the role of soil temperature and water content as factors, which structure the microenvironment, and their possible consequences on soil macrofauna diversity and abundance.

2. Materials and methods

2.1. Site

This study was carried out in a community of smallholders in south-east Amazonia, at the Benfica Field Station (5°16′ S and 49°50′ E, Pará, Brazil). We surveyed three, 6 years old pastures of 20 ha on average, planted with the perennial African grass *B. bryzantha* cv. *Marandu*, the most common species used in this area. Pastures mainly served for cattle ranching. *B. bryzantha* forms massive tufts reaching 0.8 m in diameter that can locally have a fairly even spatial distribution and are separated by bare ground, leading to a heterogeneous vegetation cover (Fig. 1 shows an average configuration). In the pastures under study, grasses were planted individually when the pasture was established. The climate is tropical humid with an annual rainfall of 1800 mm and an average temperature of 26 °C. The rainy season generally starts in November or December and ends during May or June. Clayey Ferralsol soils (Isss, 1998) are dominant with varying thicknesses of aggregated, macroporous and permeable horizons, above compact alterites (subsoil). They are acid (pH = 5.8) and contain 12.7 g kg^{-1} of C, 1.8 cmolc kg^{-1} of Ca^{2+}, 5.0 mg kg^{-1} of P on average in the 10 upper cm.

2.2. Sampling design and procedures

2.2.1. Soil macrofauna

The soil macrofauna was sampled by taking 60 evenly distributed samples along 6 transects in 3 pastures (2 transects per pasture, 10 m between each sample). The sampling design was part of a wider campaign to sample soil macrofauna at the landscape level (Mathieu et al., 2005). Soil macro-organisms were collected following the tropical soil biology and fertility method (Anderson and Ingram, 1993). At each sampling point, an area of 25 × 25 × 30 cm deep was excavated and the surface cover directly above the sample was either classified as "bare ground" or "microsite"(when there was a grass tuft or dead tree trunk on the ground). The corresponding variable is hereafter referred to as "Sample Type" (ST). The litter layer and soil were quickly removed before the macroinvertebrates were hand-sorted and preserved in 4% formalin solution. In the laboratory, adult invertebrates were classified into 7 broad taxonomic groups: earthworms, termites, ants, spiders, coleoptera, centipedes and millipedes and identified at the species level with the help of a number of taxonomists. Individuals of other groups were pooled as a single group called "others". Samples were taken at the end of the rainy season in 2002 when communities were presumed to be at peak abundance and biomass (Anderson and Ingram, 1993). Macrofauna extracted from soil and litter layers was combined in the analyses.

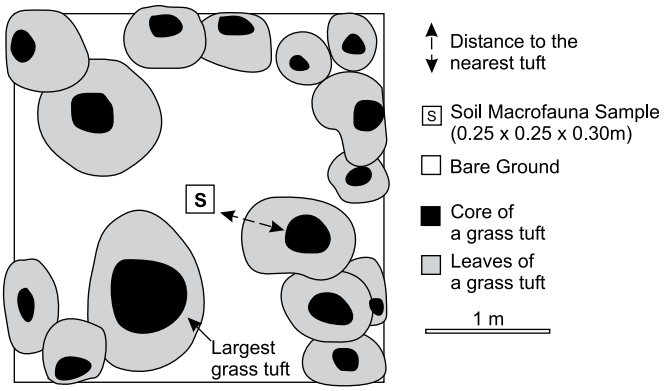

Fig. 1. A typical 9 m^2 map of the vegetation cover illustrating how the configuration of the grass tufts results in a micro-landscape. Grass tufts can be separated into two sections: the core of the tufts (i.e. the basal area), and the area occupied by the leaves (i.e. the canopies. Only the basal areas were used for calculating micro-landscape metrics.

2.2.2. Quantifying the vegetation spatial organization

The vegetation cover around each sample was described within a squared area of 9 m^2 centered on the sample (Fig. 1). Strings were attached to the ground to form a regular grid of 0.3 m × 0.3 m and the soil cover was mapped at a scale of 1:20 to show grass tussocks, grass canopies and the presence of micro-habitats such as dead wood, cattle dung and termite mounds. The maps were then digitalized and rasterized (resolution: 0.1 m × 0.1 m per pixel). This produced simple micro-landscape maps with 2 strata: bare soil (matrix) and grass tufts (patches). The resulting "micro-landscapes" were described by four classical landscape metrics (Giles and Trani, 1999): the percentage of soil occupied by vegetation (PL), the area of the largest grass tuft in the area (LPI, m^2), the Edge Density (ED, m m^{-2} i.e. the length of the vegetation boundary, in meter, per square meter of area) and the Patch Density (PD, ind m^{-2}, i.e. the number of grass tufts per unit area). Only the central part of the tufts (corresponding to the stems, or "basal area", Fig. 1) was considered because these vary considerably less with time compared to the whole leaf system which is grazed by cattle. The distance between the soil macrofauna sample and the nearest grass tuft was also measured. The metrics were calculated using Fragstats (McGarigal and Marks, 1995). In addition we evaluated visually the amount of dead wood on the ground within the area of 9 m^2, and classified it as 0: no wood, 1: some twigs and branches, 2: big branches or trunk. We will refer to this variable as WOOD here in.

2.2.3. Microclimate

Horizontal soil temperature and water content patterns were studied in two quadrats in one of the pastures, with one quadrat of 1 m^2 and another of 9 m^2. Different quadrat sizes were used because it was not possible to determine in advance which size was best suited to assess the soil temperature and water content variability. Measurements were taken in regular grids of 0.1 and 0.3 m mesh, for plots of 1 m^2 and 9 m^2, respectively, giving 100 measurements in each unit. The average temperature of the upper top 15 cm of soil at each point was recorded using a high precision temperature probe. The water content expressed as the volume of water per volume of soil was measured at exactly the same points using time domain reflectometry (TDR: Dalton et al., 1984; Teixeira et al., 2003). In a separate experiment, a vertical profile of soil temperature was also recorded below and around one isolated grass tuft. Measurements were made at regular intervals at 2, 5, 10 and 20 cm depth and every 5 cm horizontally, over 1 m. Measurements started from below the centre of an isolated grass tuft and spread toward bare ground. The radius of the grass tuft's tussock was 15 cm while the canopy reached 35 cm in radius. Measurements were made at midday, when the air temperature was high (37 °C), in May.

2.3. Statistical analyses

2.3.1. Relationship between vegetation cover configuration and soil macrofauna

The relationships between the vegetation spatial organization and macrofauna were explored using backward stepwise multiple regressions. Soil macrofauna density and species richness were $\log(x+1)$ transformed and were entered as the dependent variables, while vegetation metrics ("PL", "ED", "PD", "LPI"), sample type ("ST" in the tables), presence of wood on the ground ("WOOD" in the tables), and distance to the nearest grass tuft ("DIST") were entered as explanatory variables. All variables and their interaction with the sample type (ST) were included in the analysis. All non-significant effects were removed step by step to produce models containing only significant effects (with alpha = 0.05) and minimum AIC (Burnham and Anderson, 2002). Finally, the models were compared with the results of automatic stepwise multiple regression to check for robustness. The Table 2 shows r^2 adjusted by the number of variables. Residuals were analyzed carefully to check for homogeneity of variance, normality and the influence of individual observations. Computations were made using R software (R Development Core Team, 2007).

2.3.2. Spatial pattern of soil temperature and water content

The spatial pattern of soil temperature and water content was assessed by variogram analysis (Rossi et al., 1995; Goovaerts, 1997) and interpolation by point kriging (Isaaks and Srivastava, 1989). Semi-variograms were computed using GSTAT (Pebesma and Wesseling, 1998), with the smallest lag distance equal to the mesh size and the largest lag set to half the maximum distance between sampling points (Isaaks and Srivastava, 1989). The areas where temperature and water content were measured were mapped to calculate the distance to the nearest grass tuft and examine its influence on the measurements using simple regressions.

3. Results

3.1. Differences of soil macrofauna between bare ground and microsites

Sample location had a major effect on the macrofauna species richness and density (Table 1). The overall species richness was double that in microsites (nine to ten species per sample) than under bare ground (four species per sample). The overall density was treble that in microsites (762 ind m^{-2}) than under bare ground (195 ind m^{-2}). All groups presented the same trend, either in terms of species richness or density. The species composition was also very different between bare ground and microsites: the proportion of shared species was 16% and 17% between bare soil and herb tufts or dead trunks, respectively, whereas it was 28% between herb tufts and dead trunks. Termites were dominated by *Amitermes*, *Heterotermes* and *Cornitermes*, ants were dominated by the genus *Hypoponera*, and earthworms were dominated by a species of *Andiorrhinus*.

3.2. Relationship between soil macrofauna and the spatial organization of the vegetation cover

Stepwise multiple regression analyses for species richness and density are summarized in Table 2. The vegetation configuration explained 69% of the variation in total soil macrofauna density and 68% of the variation in total species richness. In the model, total species richness increased when the vegetation cover (AREA) increased and decreased with increasing distance to the nearest grass tuft (DIST). In bare ground, species richness also decreased with increasing edge density (ED). Total density decreased with increasing distance to the nearest grass tuft (DIST) and increased with the size of the largest grass tuft (LPI). In microsites, density increased with increasing edge density (ED), while in bare ground it decreased with increasing ED.

Considered separately, the diversity and density of all groups of soil macrofauna varied significantly according to the spatial configuration of the vegetation (Table 2). The strongest relationships were obtained for termite density ($r^2 = 0.64$) and earthworm species richness ($r^2 = 0.38$). The weakest relationships were obtained for spiders ($r^2 = 0.07$ for species richness and density). The distance to the nearest grass tuft (DIST) was the most influential micro-landscape variable, affecting all groups except earthworms and centipedes, and was always negatively correlated to the density or the species richness. Edge density (ED) was the second most influential variable. It was generally negatively correlated to density or species richness in bare ground, whereas it was positively correlated in microsites. It had significant influence on ants, termites, and centipedes. The third most important variable was the amount of wood (WOOD), which had always a positive effect on biodiversity. It increased termites and millipedes species richness and density. The size of the largest grass tuft (LPI) was always correlated positively to biodiversity, at the exception of ant density in microsites. It influenced significantly earthworms' species richness, ants' density, and termites' species richness. The vegetation cover (AREA) was positively correlated with ants'

Table 1
Species richness (number of species) and density (ind m^{-2}) per sample (standard error in brackets) of the different groups, below microsites and under bare ground.

	Microsites				Bare ground			
	Species richness		Density		Species richness		Density	
earthworms	1.7	(0.2)	109.3	(21.0)	0.8	(0.1)	30.9	(8.9)
ants	2.0	(0.2)	159.3	(38.0)	1.3	(0.3)	73.1	(24.2)
termites	0.7	(0.1)	326.7	(137.8)	0.2	(0.1)	20.3	(14.5)
coleoptera	1.4	(0.2)	36.7	(6.9)	0.9	(0.2)	24.5	(9.2)
spiders	0.4	(0.1)	7.3	(2.5)	0.1	(0.1)	2.1	(1.0)
centipedes	0.4	(0.1)	14.7	(5.3)	0.1	(0.1)	1.6	(0.9)
millipedes	0.5	(0.2)	16.7	(6.9)	0.1	(0.1)	2.1	(1.0)
Others	4.6	(0.8)	129.3	(29.0)	1.1	(0.3)	44.2	(23.0)
All together	9.5	(0.9)	764.0	(146.3)	4.0	(0.7)	194.7	(54.3)

Table 2
Standardized coefficients of the linear models for species richness and density on environmental variables. Global fit of the model is indicated by the adjusted coefficient of determination (r^2aj). For abbreviations see Material and methods.

Group	Dependant variable	Sample type	Coefficients of the linear model
earthworms			
	Species Richness (ln)	Bare Ground	$0.51 + 0.16 \times \text{LPI} - 0.14 \times \text{PD}$
	r^2aj = 0.33	Microsite	$1.02 + 0.01 \times \text{LPI} - 0.14 \times \text{PD}$
	Density (ln)	Bare Ground	$0.78 - 0.22 \times \text{PD}$
	r^2aj = 0.38	Microsite	$1.73 - 0.22 \times \text{PD}$
ants			
	Species Richness (ln)	Bare Ground	$0.8 - 0.25 \times \text{DIST} - 0.19 \times \text{ED}$
	r^2aj = 0.41	Microsite	$0.8 - 0.25 \times \text{DIST} - 0.19 \times \text{ED}$
	Density (ln)	Bare Ground	$1.22 - 0.45 \times \text{DIST} + 0.30 \times \text{AREA} + 0.17 \times \text{LPI}$
	r^2aj = 0.25	Microsite	$1.63 - 0.45 \times \text{DIST} + 2.0 \times \text{AREA} - 1.51 \times \text{LPI}$
termites			
	Species Richness (ln)	Bare Ground	$0.29 - 0.15 \times \text{DIST} + 0.10 \times \text{WOOD}$
	r^2aj = 0.64	Microsite	$0.29 - 0.15 \times \text{DIST} + 0.10 \times \text{WOOD}$
	Density (ln)	Bare Ground	$0.21 + 0.19 \times \text{LPI} + 0.05 \times \text{ED} + 0.24 \times \text{WOOD}$
	r^2aj = 0.27	Microsite	$1.73 + 1.04 \times \text{LPI} + 1.27 \times \text{ED} + 0.24 \times \text{WOOD}$
coleoptera			
	Species Richness (ln)	Bare Ground	$0.62 - 0.23 \times \text{DIST}$
	r^2aj = 0.19	Microsite	$0.62 - 0.23 \times \text{DIST}$
	Density (ln)	Bare Ground	$0.76 - 0.31 \times \text{DIST}$
	r^2aj = 0.17	Microsite	$0.76 - 0.31 \times \text{DIST}$
spiders			
	Species Richness (ln)	Bare Ground	$0.17 - 0.10 \times \text{DIST}$
	r^2aj = 0.07	Microsite	$0.17 - 0.10 \times \text{DIST}$
	Density (ln)	Bare Ground	$0.17 - 0.10 \times \text{DIST}$
	r^2aj = 0.07	Microsite	$0.17 - 0.10 \times \text{DIST}$
centipedes			
	Species Richness (ln)	Bare Ground	$0.06 - 0.11 \times \text{ED}$
	r^2aj = 0.23	Microsite	$0.23 + 0.14 \times \text{ED}$
	Density (ln)	Bare Ground	$0.07 - 0.04 \times \text{AREA} - 0.12 \times \text{ED}$
	r^2aj = 0.24	Microsite	$0.23 + 0.18 \times \text{AREA} + 0.22 \times \text{ED}$
millipedes			
	Species Richness (ln)	Bare Ground	$0.17 + 0.1 \times \text{WOOD}$
	r^2aj = 0.23	Microsite	$0.17 + 0.1 \times \text{WOOD}$
	Density (ln)	Bare Ground	$0.16 - 0.01 \times \text{DIST} + 0.07 \times \text{WOOD}$
	r^2aj = 0.15	Microsite	$0.16 - 0.01 \times \text{DIST} + 0.07 \times \text{WOOD}$
All together			
	Species Richness (ln)	Bare Ground	$1.57 - 0.48 \times \text{DIST} + 0.17 \times \text{AREA} - 0.29 \times \text{ED}$
	r^2aj = 0.68	Microsite	$1.94 - 0.48 \times \text{DIST} + 0.17 \times \text{AREA} + 0.01 \times \text{ED}$
	Density (ln)	Bare Ground	$2.18 - 0.60 \times \text{DIST} + 0.45 \times \text{LPI} - 0.19 \times \text{ED}$
	r^2aj = 0.69	Microsite	$3.15 - 0.60 \times \text{DIST} + 0.45 \times \text{LPI} + 0.33 \times \text{ED}$

density and species richness and to centipedes density in microsites only. Finally, patch density (PD) was the least influential variable, and was negatively correlated to earthworm species richness and density.

3.3. Relationships between soil temperature and water content and vegetation cover

The presence of grass tufts had a significant effect on soil temperature in the upper 15 cm of the soil (Fig. 2a), where soil macrofauna density was also highest (Fig. 2b). There was a difference of 5 °C between the soil, in upper 5 cm, below the centre of the tuft (29 °C) and the hottest location in bare ground (34 °C), Horizontal maps confirmed this result and showed that soil temperature was strongly dependent on the distance to the nearest grass tuft (white points in Fig. 3a). Within the grass tufts, soil temperature increased from the centre to the edge of the tuft, varying from 28 °C to 30 °C (black points in Fig. 3a). However, there was no significant relationship between the water content and the distance to the edge of the nearest grass tuft (Fig. 3b). Table 3 shows the variogram parameter for both soil temperature and water content measured in the different sampling grids. A spherical model satisfactorily fitted the variograms observed in each case. The variogram parameters changed depending on plot size and the minimum inter-sample distance. The range, sill and nugget variance tended to increase with increasing map size (Table 3). There was remarkably little unexplained variation in soil temperature since nugget variance which ranged from 3.4% to 6.4% depending on the plot size (Table 3). However, nugget variance was high for soil water content, ranging from 40% to 37% for plots of 1 and 9 m^2 (Table 3). Both data sets showed that the range was smaller than one third of the plot length.

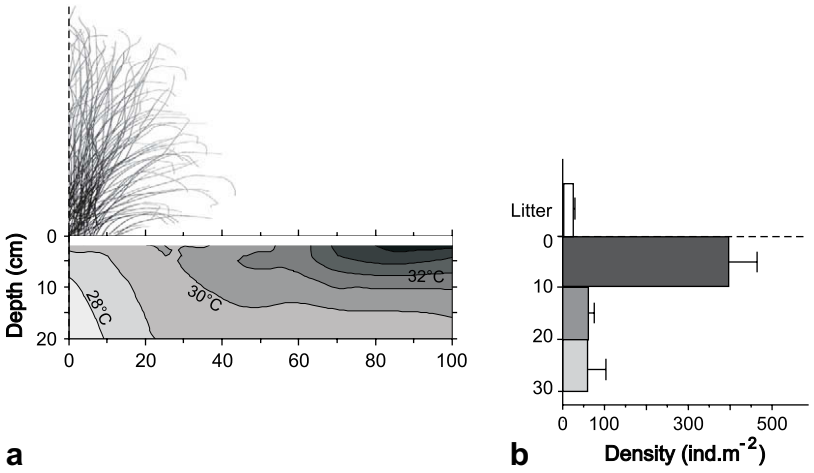

Fig. 2. a) Vertical profile of soil temperature below and near a grass tuft. b) Vertical profile of soil macrofauna density in the upper 30 cm of soil ($n = 60$).

The isarithmic maps for the 9 m^2 plot were obtained by ordinary kriging with the variogram parameters shown in Table 3. Because the variogram range was low, the temperature map showed small patches of high values (Fig. 4a). The high temperature areas were usually located between grass tufts while low temperature areas were located beneath the tufts (Fig. 4a). The map of soil water content showed larger patches of high values compared to soil temperature (the variograms showed larger ranges, Table 3, Fig. 4b) and there was no clear relationship with tuft distribution and temperature.

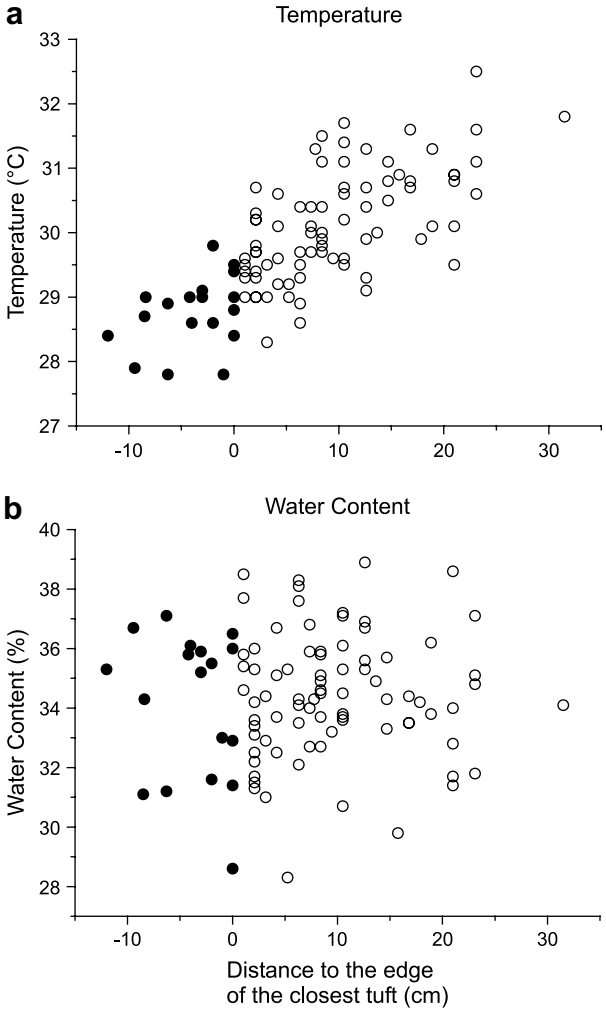

Fig. 3. Relationship between the distance to the edge of the nearest grass tuft and a) the soil temperature, and b) the soil water content, in the 9 m^2 map. Black points represent measures taken inside the grass tufts, white points indicate measures taken outside the grass tufts.

4. Discussion

Our survey showed that the spatial structure of the vegetation cover affected both soil macrofauna density and species richness. This has been well documented for surface invertebrates (Hatley and Macmahon, 1980; Hamazaki, 1996), but data on soil living organisms are less common.

4.1. Defining mechanisms scale

In pastures, the factors affecting soil macrofaunal communities can be considered at two scales: (i) the micro-site scale, where the only factor of interest is the nature of the sample (bare ground, or microsite) and (ii) the "micro-landscape" scale, where the environment surrounding the sample is also taken into account to explain the soil macrofauna biodiversity

4.2. Micro-site scale effects

Micro-site scale effects were straightforward: samples taken below herb tufts or branches hosted a much higher abundance and diversity of soil macrofauna than the bare ground, showing a striking local limitation by habitat and/or food availability. For instance, a dead trunk on the ground was seen to be a specific resource that favored diplopod and termite activity, especially the soil and wood feeding genus *Amitermes* (Termitinae), that was dominant in our study (data not shown). *B. bryzantha* tussocks offer both specific environmental and feeding resources for soil macrofauna and thus their size and shape influence soil macrofauna biodiversity (Mathieu

Table 3
Parameters for the models fitted to the soil temperature and soil water content semi-variograms, in the 1 m^2 and 9 m^2 maps. The range indicates the distance at which the sill was reached.

Variable	Grid extent (m)	Mesh size (m)	Model	Nugget (C_0)	Sill (C)	Range (m)
Temperature	1×1	0.1×0.1	spheric	0.02	0.57	0.34
Temperature	3×3	0.3×0.3	spheric	0.07	1.02	0.60
Water content	1×1	0.1×0.1	spheric	2.25	3.32	0.40
Water content	3×3	0.3×0.3	spheric	2.7	4.64	1.00

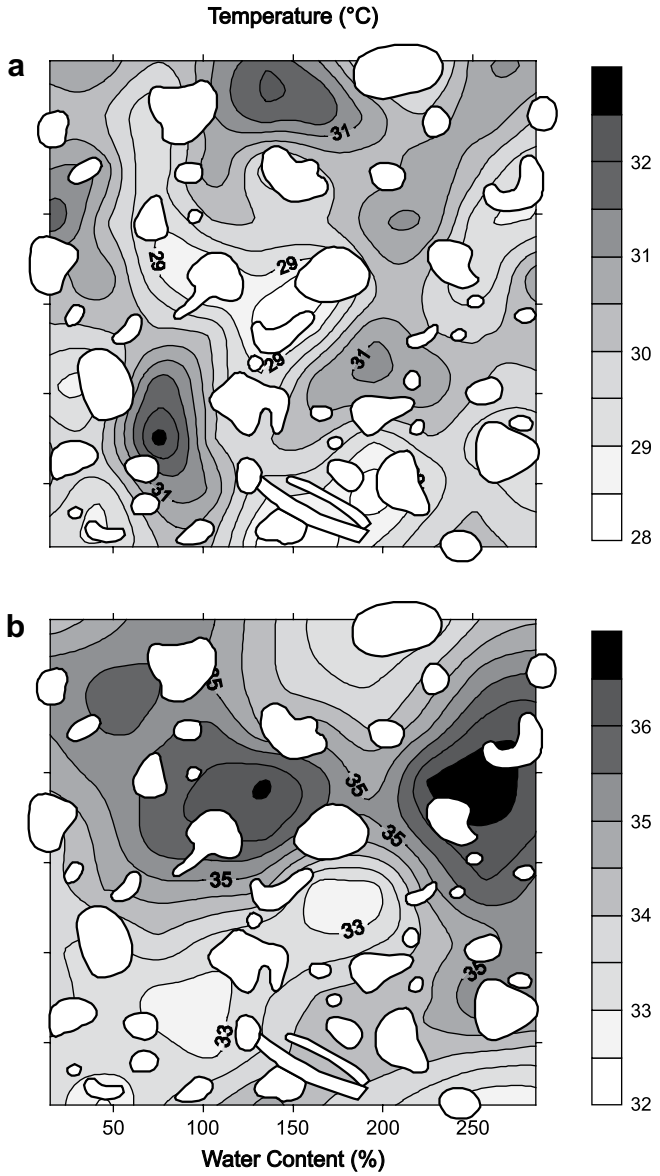

Fig. 4. Interpolated maps of the soil temperature a), and the soil water content b), on a 9 m^2 surface. Parameters from the semi-variograms (Table 3) were used for kriging. Grass tufts are shown as white surfaces delimited by a black line.

et al., 2004). Grass tussocks are therefore biodiversity hotspots for soil macrofauna in Amazonian pastures.

4.3. Micro-landscape scale effects

Nevertheless, we observed that the difference between bare ground and grass tufts is more subtle than it first appeared. Soil macrofauna biodiversity was seen to (1) decrease with increasing distance to the nearest grass tuft (DIST) (2) increase with increasing vegetation cover (AREA) (3) be influenced by the size of the largest herb tuft in the micro-landscape (LPI). These remote effects appear to be due to *B. bryzantha* gradually inducing modifications to the surrounding environment. Indeed, plants are known to change their micro-environments by intercepting sun rays and rain and absorbing soil water (Geiger and Aron, 2003). In addition, they modify the chemical properties of the soil near their roots by adsorbing mineral nutrients and releasing organic-C exudates, lowering pH, activating microflora, and deposing litter (Jackson and Caldwell, 1993; Amiotti et al., 2000). This process known as "ecological engineering" (Jones et al., 1994) creates a gradient of specific physical and chemical properties which are beneficial to the soil microflora (Zaman and Chang, 2004), and also probably to soil macrofauna, mainly through bottom-up processes such as increasing soil organic matter. *B. bryzantha* grasses also influenced the soil environment by cooling down and reducing soil temperature variations beneath and around them, in the upper 15 cm of soil, where soil macrofauna is the most abundant. Numerous studies have shown that soil macrofauna in tropical areas is limited by high temperatures (earthworms: Uvarov and Scheu, 2004; Opilions: Almeida-Neto et al., 2006; ants: Albrecht and Gotelli, 2001; termites: Smith and Rust, 1994; coleoptera: Horgan, 2002) and that temperature is a strong determinant of many soil macrofauna ecological niches (Bezkorovainaya and Yashikhin, 2003). Thus, the reduction of soil temperature observed here due to the *B. bryzantha* tussocks is likely to have important effects on soil macrofauna, at least during the day.

Nevertheless, we suggest that micro-landscape scale effects not only result from the modification of the environment in the vicinity of the tufts. These also appear to exist because of limitation by habitat and/or resource availability for species with homing range larger than just the size of our samples. For instance, the observed increase in ant density with increasing vegetation cover (AREA), as well as the increase in termite abundance with the size of the largest herb tuft (LPI) may be explained by the fact that the galleries and chambers produced as part of their nest-structures are preferably constructed below herb tufts and are organized in networks with connections to other grasses (Mathieu et al., 2004). As a consequence, a remote increase of habitat availability or suitability can lead to local increases in the density of the colony due to the interconnections between chambers, while loose vegetation cover may lead to habitat and/or resource-limitation.

4.4. Movement patterns

Lastly, micro-landscape effects may occur by modifying movement patterns of individuals. Such effects were previously demonstrated for surface beetles which followed different foraging trajectories depending on the micro-landscape configuration on a 25 m^2 scale (Wiens and Milne, 1989). In our study, connectivity, measured by the edge density (ED), and patch density (PD) (Giles and Trani, 1999) was related to soil macrofauna biodiversity. Theoretically, if assuming that soil fauna movements are random, a longer edge will increase the probability of encountering the habitat. It was shown experimentally that higher numbers of millipedes inhabited patches with long edges than other patches with the same area but shorter edges (Hamazaki, 1996). However, it is doubtful that this phenomenon can be transposed to the whole soil macrofauna community. In particular, soil fauna movements are not necessarily random and information is required on the range of daily movements made by the different groups. With the exception of species that construct nests, there is currently little information available regarding foraging behavior among the groups found and the distances they are able to cover daily. Social insects (ants and termites) create costly perennial nest-structures that require foraging on scales much larger than 9 m^2. Although foraging efficiency may be influenced by habitat connectivity, it is unlikely that it constitutes a limiting factor for social insects. Higher vegetation cover may also favor movement by motile organisms such as millipedes because it provides shelter from predators, sunlight and high temperatures. Therefore in dense vegetation cover, organisms can extend their foraging range at a low cost. To confirm this hypothesis, it would be interesting to study soil macrofauna movement amid different micro-landscape configurations,

using a technique such as individual tagging for example (e.g., Butt and Lowe, 2007).

4.5. Reversing the correlations: feedback loops between plants and soil engineers

Interestingly, the density and species richness of earthworms, termites and ants showed the best correlations with the vegetation pattern. Since all of these animals are soil ecosystem engineers, they are assumed to induce positive feedback loops on vegetation growth (Jouquet et al., 2006). Therefore, the correlation between their abundance and vegetation cover or the area of largest grass tuft could be due to improved plants growth in the presence of soil engineers. Because increased vegetation cover is then also beneficial to soil macrofauna, grass tufts and soil macrofauna appear to be involved in a reciprocal beneficial relationship.

4.6. Conclusions

Our study shows that *B. bryzantha* tufts have a strong influence upon soil macrofauna diversity and abundance within pasture ecosystems at both the micro-site ($\leq$0.016 m^2) and micro-landscape (9 m^2) scales. These environments provide habitats and create complex gradients of soil properties to which soil macrofauna respond. Therefore to fully understand soil macrofauna biodiversity distribution in these systems a careful study of the vegetation cover around the samples is required. We argue that these types of patterns are not unique to Amazonian pastures, but are also likely to occur in many other systems and should be taken into account in soil macrofauna biodiversity studies.

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