ELSEVIER

Soil Biology & Biochemistry 37 (2005) 1093–1104

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Seasonal and land-use induced variations of soil macrofauna composition in the Western Ghats, southern India

Jean-Pierre Rossi[a,*], Eric Blanchart[b]

[a]*UMR 137 Biodiversité et Fonctionnement des Sols IRD/Université Pierre et Marie Curie, 32 Avenue Varagnat, 93143 Bondy, France*
[b]*IRD, Laboratoire MOST, 911 Avenue Agropolis, BP 64501, 34394 Montpellier cedex 5, France*

Received 4 March 2004; received in revised form 12 November 2004; accepted 15 November 2004

Abstract

Soil macrofauna was surveyed in six sites characterised by different vegetation types on five occasions in the Western Ghats, India. Sampling sites included a primary forest, a weakly disturbed forest (slightly logged in the past), a highly disturbed forest (intensively logged), an *Acacia auriculiformis* plantation (8 years old), a pasture with high density of *Phoenix humilis* and a pasture without *P. humilis*. We showed that both land management and temporal variability induced significant changes in the soil macrofauna. Forest sites hosted larger densities of soil macroorganisms. The effect of seasons was apparent as some clear modifications in the fauna composition occurred. Some groups like earthworms mainly exhibited temporal variability whereas others like millipedes were chiefly affected by land management options. The seasonal rhythms of soil macrofauna were poorly expressed in the pasture plots and the *Acacia* plantation, but were particularly clear in the forest sites. This interaction between land management and temporal patterns may be explained by some changes in the species composition associated with certain land-uses. Our approach was based on a between–within classes PCA that proved particularly useful by providing statistical tests and a hierarchy of land management and temporal rhythm effects.

Keywords: *Acacia* plantation; Agricultural systems; Between–within classes PCA; Land-uses; Primary forest; Soil macrofauna; Temporal variability

1. Introduction

Soil organisms comprise a huge number of species (Giller, 1996) that play a central role in various ecosystem functions like soil organic matter turn-over or soil structure dynamics (Dangerfield and Milner, 1996; Lawton et al., 1996; Setälä et al., 1998; Wardle et al., 1998; Wall and Moore, 1999; Barros et al., 2004). Soil management options can have dramatic effects upon soil invertebrate communities (Beare et al., 1997; Fragoso et al., 1997; Giller et al., 1997; Barros et al., 2002, 2003; Decaëns et al., 2004) and may therefore lead to important changes in soil functioning. Species also vary through time as they have seasonal rhythms mainly regulated by temperature and humidity (Dibog et al., 1998; Jiménez et al., 1998). Available data dealing with the changes in soil macrofauna according to various land-uses are often based on one-date sampling campaigns. Consequently, the way seasonal rhythms are affected by land-use and the possible interactions between these factors have rarely been questioned.

This work focused primarily on the effects of land-use options on the macrofauna community. We aimed at identifying the main effects of forest clearance and several subsequent land managements upon soil fauna. Because seasonal rhythms may be important factors of changes in the species assemblage structure, we also assessed its impact on biomass and density of soil macroinvertebrates. As drastic changes in the vegetation cover (forest clearance, tree plantation) deeply change the soil microclimate, we were particularly interested in examining how such changes affected the temporal variability of soil macrofauna.

We designed a survey comprising six sites corresponding to various land-use types common in the Western Ghats,

---

* Corresponding author. Address: INRA, UMR BIOGECO, Domaine de l'Hermitage Pierroton, 69, route d'Arcachon, 33612 Cestas cedex, France. Tel.: +33 5 57 12 28 46; fax: +33 5 56 68 05 46.
E-mail address: rossi@pierroton.inra.fr (J.-P. Rossi).

0038-0717/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2004.11.008

Karnataka State, South India. Sites included a primary forest, a highly and a slightly disturbed forest, a tree plantation (*Acacia auriculiformis*), a pasture without shrubs and a pasture with palm-trees (*Phoenix humilis*). These sites were investigated on five occasions corresponding to various dates and seasons. Soil macrofauna comprises a large number of zoological groups hence leading to a typical multivariate data set. We therefore used a between–within classes PCA (Dolédec and Chessel, 1989, 1991) to properly describe the land-use impact and the season-induced changes in the macrofauna. The aim of the between–within classes analysis is to take into account the experimental objectives; i.e. the time and space effects. It allows determination of what, in a multivariate data set, depends only on space or time and what may be explained by an interaction between these factors.

2. Methods

2.1. Sites

2.1.1. Study area

The study was conducted in the Sagar Forest Range on the western side of the Lingannamaki Reservoir (14°00′N, 74°45′E), Shimoga Division, Karnataka State, India. Average elevation of this region is 600–800 m above sea level. The climate is monsoonal determined primarily by the southwest monsoon (Legris, 1963). This region has six dry months (from November to April) and receives an annual rainfall of around 5000 mm. The monsoon peak is in June and July. Mean annual temperature is ca. 22 °C with maxima in April and October and a minimum in December–January. Minimal temperatures may be less than 10 °C and maximal temperature more than 30 °C. Soils are weakly or moderately desaturated ferrallitic (Bourgeon, 1988; Peterschmitt, 1993). This area consists of mosaics of evergreen, semi-evergreen and moist deciduous forest interspersed with pastures and *Acacia* plantations. The forest vegetation has been broadly described as *Dipterocarpus indicus–Diospyros candollena oocarpa* type (Pascal, 1988). Pastures are continuous layers of grass. Common grasses are *Ischemum indicum* (Houtt.) Merril. and *Arundinella* sp. (Puyravaud, personal communication).

2.1.2. Study sites and sampling occasions

Soil macrofauna was collected in six sites characterised by different vegetation types: a primary forest (PF), a weakly disturbed forest (slightly logged in the past, F1), a highly disturbed forest (recently and intensively logged, F2), an 8-year-old *A. auriculiformis* plantation (A), a pasture with high density of *P. humilis* (PP) and a pasture without *P. humilis* (P).

Sampling was realised in all six plots at five different times over 1 year, i.e. in April, October, December 1991, and February and April 1992.

2.1.3. Macrofauna sampling

Soil macrofauna was sampled by using TSBF (Tropical Soil Biology and Fertility Programme) methodology (Anderson and Ingram, 1993). Sampling points were chosen along random transects. Each transect had 6–10 sampling points spaced 5 m apart. At each sampling point, a metallic frame (25×25 cm^2) was inserted in the soil; the litter was then collected and its soil fauna hand-sorted. A trench was then dug to a depth of 30 cm around the 25×25 cm^2 area to get a soil monolith. Soil monoliths were divided into three layers (0–10, 10–20 and 20–30 cm) and macroinvertebrates were then hand-sorted separately from each layer. Soil fauna from the litter was added with the 0–10 cm soil fauna. All individuals were preserved in 4% formalin. Specimens were later identified in the laboratory, counted and weighed. Soil organisms were separated into 22 broad taxonomical groups (Table 1). Termites and earthworm were identified at the species level and data are reported elsewhere (Basu et al., 1996; Blanchart and Julka, 1997; Julka et al., 2004).

2.2. Data analysis

2.2.1. Between–within classes analysis

The data consisted of an array of values corresponding to p variables (i.e. the macrofauna groups) recorded for n sites at t dates, leading to a data table with p columns (variables) and nt rows (objects). The data were studied using a principal components analysis (PCA). PCA was preferred over a Correspondence Analysis (CA) because of the very high variability in the soil macrofauna numbers that causes stability problems in CA (Cadet and Thioulouse, 1998). Global analysis aimed at extracting the main pattern consisting of a mixture of space–time effects including interactions between these factors. This mixed analysis is supplemented by two subsequent analyses, namely the between classes PCA and the within classes PCA. The basic principle is to examine what is the between or within classes multivariate variability, the classes being defined as groups of either sites or dates. The between classes PCA therefore focuses on between groups differences. A randomisation testing procedure indicates whether the classes are significantly different from what might be expected (under the null hypothesis) from a completely random data set (Manly, 1991). In contrast, the within classes PCA focuses on the remaining variability after the class effect has been removed. Removing the class effect is achieved by placing all centers of classes at the origin of the factorial maps while the sampling units are scattered with the maximal variance around the origin. This operation is simply completed by centring the data by classes (Dolédec and Chessel, 1989, 1991).

2.2.2. Decomposition of the variance

In order to determine what part of the variability of any of the original variables can be explained by either space or time, we used projection onto subspaces defined by dates or

Table 1
Soil macrofauna mean density at different sites and dates and code for the variables and sites

Sites	Dates	Earth-worms, Ew	Termites (Isoptera), Te	Ants (formici-dae), An	Coleoptera larvae, CL	Coleoptera adults, Ca	Diptera larvae, Di	Araneae, Ar	Other Arachnida, Ac	Diplopoda, Dp	Chilopoda, Cl	Molluscs, Mo	Apterygota, Ap
P	04/91	13.7	208	32	11.4	8	4.6	13.7	2.3	0	0	0	0
		[11]	[529.3]	[44.3]	[17.8]	[15.3]	[12.1]	[14.4]	[6]	[–]	[–]	[–]	[–]
P	10/91	825.6	1030.4	286.4	57.6	6.4	14.4	0	1.6	0	4.8	0	1.6
		[164.4]	[1915.1]	[481.4]	[60.4]	[8.3]	[20.6]	[–]	[5.1]	[–]	[7.7]	[–]	[5.1]
P	12/91	126.4	1398.4	329.6	20.8	3.2	1.6	4.8	1.6	1.6	8	0	0
		[138.6]	[3739.2]	[394.4]	[23.9]	[6.7]	[5.1]	[7.7]	[5.1]	[5.1]	[15.5]	[–]	[–]
P	02/92	41.6	363.2	1513.6	54.4	4.8	3.2	3.2	0	0	1.6	0	0
		[42.8]	[866.8]	[4201.9]	[97.8]	[10.8]	[10.1]	[6.7]	[–]	[–]	[5.1]	[–]	[–]
P	04/92	14.4	371.2	9.6	20.8	9.6	3.2	1.6	0	0	1.6	0	1.6
		[23.2]	[1118]	[17.2]	[31.1]	[11.2]	[10.1]	[5.1]	[–]	[–]	[5.1]	[–]	[5.1]
PF	04/91	102.4	1625.6	118.4	57.6	28.8	16	41.6	3.2	9.6	48	3.2	12.8
		[62.6]	[2328.4]	[84.4]	[51.3]	[38.2]	[11.3]	[26.8]	[7.2]	[8.8]	[45.3]	[7.2]	[17.5]
PF	10/91	331.6	926.2	92.4	86.2	46.2	30.2	8.9	1.8	40	78.2	0	3.6
		[217.5]	[1030.1]	[136.9]	[32.9]	[47.6]	[27.1]	[11.6]	[5.3]	[53.4]	[53.9]	[–]	[7.1]
PF	12/91	158.4	2700.8	75.2	38.4	17.6	14.4	8	1.6	22.4	46.4	0	0
		[100.2]	[6591.7]	[127.1]	[49]	[20.6]	[29.6]	[11.3]	[5.1]	[30.4]	[36.5]	[–]	[–]
PF	02/92	148.8	4414.4	112	84.8	27.2	6.4	4.8	0	48	65.6	0	6.4
		[105.9]	[9955.2]	[279.9]	[64]	[21.4]	[11.2]	[7.7]	[–]	[43.3]	[26.6]	[–]	[8.3]
PP	04/92	132.8	385.6	344	14.4	11.2	3.2	16	1.6	12.8	27.2	0	0
		[81.6]	[1080.7]	[743.5]	[14]	[13.2]	[6.7]	[13.1]	[5.1]	[10.1]	[21.4]	[–]	[–]
PP	04/91	20.6	205.7	43.4	61.7	2.3	0	0	0	0	0	0	2.3
		[17.8]	[376.6]	[67.7]	[156.3]	[6]	[–]	[–]	[–]	[–]	[–]	[–]	[6]
PP	10/91	290.4	1217.6	356.8	30.4	6.4	1.6	8	1.6	0	4.8	0	0
		[219.8]	[1723.2]	[421.6]	[27.7]	[11.2]	[5.1]	[8.4]	[5.1]	[–]	[7.7]	[–]	[–]
PP	12/91	63.2	2500.8	116.8	22.4	4.8	3.2	1.6	0	0	6.4	0	0
		[33]	[4152.3]	[207.5]	[31.3]	[7.7]	[6.7]	[5.1]	[–]	[–]	[11.2]	[–]	[–]
PP	02/92	51.2	1716.8	123.2	11.2	1.6	0	3.2	0	0	1.6	0	0
		[58.8]	[3455.6]	[206.3]	[10.8]	[5.1]	[–]	[10.1]	[–]	[–]	[5.1]	[–]	[–]
PP	04/92	56	504	12.8	9.6	0	0	4.8	0	0	0	1.6	0
		[39.4]	[1439.3]	[12.6]	[17.2]	[–]	[–]	[10.8]	[–]	[–]	[–]	[5.1]	[–]
A	04/91	37.3	2122.7	130.7	8	13.3	5.3	2.7	0	0	8	0	5.3
		[47.1]	[5199.5]	[147.1]	[13.4]	[18.7]	[8.3]	[6.5]	[–]	[–]	[8.8]	[–]	[8.3]
A	10/91	254.4	446.4	38.4	14.4	8	17.6	1.6	0	4.8	51.2	0	0
		[153.5]	[851.8]	[75.5]	[14]	[8.4]	[25.5]	[5.1]	[–]	[7.7]	[52.7]	[–]	[–]
A	12/91	141.6	142.4	201.6	24	8	9.6	4.8	0	1.6	1.6	0	1.6
		[113.3]	[391.7]	[462.4]	[25.3]	[8.4]	[13.5]	[7.7]	[–]	[5.1]	[5.1]	[–]	[5.1]
A	02/92	121.6	1588.8	195.2	12.8	4.8	8	0	0	6.4	6.4	0	0
		[91.5]	[2978.2]	[402.8]	[14.7]	[7.7]	[11.3]	[–]	[–]	[11.2]	[8.3]	[–]	[–]
A	04/92	35.2	688	131.2	25.6	4.8	20.8	1.6	0	9.6	11.2	0	0
		[55.3]	[2158.8]	[348.7]	[44.7]	[7.7]	[20]	[5.1]	[–]	[13.5]	[13.2]	[–]	[–]
F1	04/91	98.7	3112	170.7	16	40	10.7	34.7	8	29.3	56	0	26.7
		[56.7]	[5516.1]	[180.9]	[20.2]	[29.9]	[8.3]	[42.2]	[8.8]	[21.3]	[16.8]	[–]	[16.5]

(*continued on next page*)

Table 1 (*continued*)

Sites	Dates	Earth-worms, Ew	Termites (Isoptera), Te	Ants (formici-dae), An	Coleoptera larvae, CL	Coleoptera adults, Ca	Diptera larvae, Di	Araneae, Ar	Other Arachnida, Ac	Diplopoda, Dp	Chilopoda, Cl	Molluscs, Mo	Apterygota, Ap
F1	10/91	310.4 [334]	4142.4 [11,957.3]	65.6 [125.2]	36.8 [32.9]	46.4 [58.2]	14.4 [24.4]	12.8 [14.7]	0 [–]	35.2 [28]	78.4 [67.2]	1.6 [5.1]	0 [–]
F1	12/91	44.8 [36.8]	1673.6 [2338.6]	110.4 [135]	36.8 [42.7]	49.6 [81]	9.6 [11.2]	6.4 [11.2]	8 [15.5]	30.4 [27.7]	62.4 [32.4]	3.2 [10.1]	1.6 [5.1]
F1	02/92	68.8 [44]	2740.8 [4008.1]	115.2 [151]	67.2 [129.1]	52.8 [69.1]	6.4 [11.2]	17.6 [15.9]	0 [–]	27.2 [28.3]	115.2 [87.9]	0 [–]	0 [–]
F1	04/92	56 [81]	2892.8 [4308.2]	52.8 [69.6]	33.6 [28.7]	24 [25.3]	17.6 [24.4]	20.8 [15.2]	4.8 [10.8]	19.2 [24.8]	68.8 [42.7]	0 [–]	0 [–]
F2	04/91	53.3 [26.1]	229.3 [323.8]	21.3 [13.1]	24 [29.9]	42.7 [31.5]	5.3 [13.1]	24 [33.2]	5.3 [8.3]	18.7 [18.7]	29.3 [39.7]	2.7 [6.5]	0 [–]
F2	10/91	277.6 [119.2]	1832 [4523.6]	25.6 [17.2]	43.2 [27.2]	24 [25.3]	25.6 [21.6]	6.4 [11.2]	1.6 [5.1]	27.2 [21.4]	44.8 [29]	3.2 [6.7]	3.2 [6.7]
F2	12/91	91.2 [47.6]	1307.2 [3716.4]	46.4 [50.8]	33.6 [19.2]	83.2 [61.6]	19.2 [16.5]	8 [15.5]	4.8 [7.7]	17.6 [23.2]	64 [51.2]	0 [–]	0 [–]
F2	02/92	140.8 [93.5]	1518.4 [2661.9]	281.6 [594.1]	41.6 [28.4]	52.8 [28.3]	1.6 [5.1]	14.4 [20.6]	0 [–]	60.8 [89.8]	33.6 [17.6]	0 [–]	1.6 [5.1]
F2	04/92	36.8 [34.6]	2777.6 [7755.2]	46.4 [59.1]	36.8 [38.5]	16 [13.1]	6.4 [8.3]	6.4 [13.5]	0 [–]	12.8 [14.7]	22.4 [18.8]	0 [–]	0 [–]

Sites	Dates	Blattodea, Bl	Orthoptera, Or	Dermaptera, Dm	Lepidoptera, Le	Heteroptera, He	Homoptera, Ho	Isopods, Is	Enchytraeidae, En	Mantoptera, Ma	Other groups, Ot	Total
P	04/91	0 [–]	0 [–]	0 [–]	4.6 [7.8]	2.3 [6]	0 [–]	0 [–]	0 [–]	0 [–]	0 [–]	300.6 [506.3]
P	10/91	0 [–]	3.2 [6.7]	0 [–]	0 [–]	1.6 [5.1]	0 [–]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	139.7 [116.6]
P	12/91	1.6 [5.1]	0 [–]	4.8 [7.7]	0 [–]	4.8 [7.7]	1.6 [5.1]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	119.4 [239.4]
P	02/92	0 [–]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	0 [–]	124.3 [261]
P	04/92	0 [–]	1.6 [5.1]	1.6 [5.1]	0 [–]	0 [–]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	0 [–]	27.4 [70.6]
PF	04/91	16 [22.6]	19.2 [7.2]	76.8 [61.3]	9.6 [14.3]	3.2 [7.2]	6.4 [14.3]	3.2 [7.2]	3.2 [7.2]	6.4 [8.8]	6.4 [8.8]	138.6 [155.8]
PF	10/91	7.1 [11.6]	1.8 [5.3]	17.8 [18.7]	0 [–]	0 [–]	7.1 [11.6]	12.4 [19.2]	7.1 [11.6]	0 [–]	1.8 [5.3]	106.3 [68]
PF	12/91	1.6 [5.1]	1.6 [5.1]	16 [20]	0 [–]	0 [–]	1.6 [5.1]	14.4 [15.9]	11.2 [23.9]	0 [–]	0 [–]	195.6 [423.4]
PF	02/92	1.6 [5.1]	6.4 [8.3]	22.4 [24.1]	1.6 [5.1]	3.2 [6.7]	4.8 [7.7]	8 [13.6]	1.6 [5.1]	0 [–]	0 [–]	310.5 [625.3]
PP	04/92	6.4 [11.2]	0 [–]	16 [20]	0 [–]	3.2 [6.7]	3.2 [6.7]	3.2 [6.7]	3.2 [6.7]	0 [–]	0 [–]	61.5 [86.2]
PP	04/91	0 [–]	0 [–]	0 [–]	0 [–]	0 [–]	2.3 [6]	0 [–]	0 [–]	0 [–]	0 [–]	21.1 [25.8]
PP	10/91	0 [–]	1.6 [5.1]	0 [–]	0 [–]	3.2 [6.7]	0 [–]	3.2 [10.1]	6.4 [15.5]	0 [–]	0 [–]	120.8 [115.8]
PP	12/91	0 [–]	0 [–]	6.4 [13.5]	4.8 [10.8]	3.2 [6.7]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	0 [–]	171 [258.4]
PP	02/92	0 [–]	0 [–]	0 [–]	0 [–]	3.2 [6.7]	0 [–]	0 [–]	0 [–]	0 [–]	0 [–]	119.5 [214.5]
PP	04/92	0 [–]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	0 [–]	8 [25.3]	0 [–]	0 [–]	0 [–]	37.4 [89]
A	04/91	2.7 [6.5]	0 [–]	2.7 [6.5]	0 [–]	0 [–]	0 [–]	0 [–]	0 [–]	0 [–]	8 [19.6]	146.7 [320.7]
A	10/91	0 [–]	0 [–]	0 [–]	1.6 [5.1]	1.6 [5.1]	4.8 [7.7]	16 [16.9]	0 [–]	0 [–]	0 [–]	53.8 [62]
A	12/91	0 [–]	0 [–]	6.4 [11.2]	0 [–]	3.2 [6.7]	8 [11.3]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	34.8 [33.4]
A	02/92	0 [–]	0 [–]	0 [–]	0 [–]	1.6 [5.1]	3.2 [6.7]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	121.9 [178.7]
A	04/92	8 [11.3]	1.6 [5.1]	0 [–]	0 [–]	0 [–]	4.8 [10.8]	0 [–]	0 [–]	0 [–]	0 [–]	58.9 [135.3]
F1	04/91	10.7 [19.4]	2.7 [6.5]	29.3 [47.9]	0 [–]	2.7 [6.5]	0 [–]	5.3 [13.1]	2.7 [6.5]	0 [–]	8 [8.8]	229 [341.7]
F1	10/91	1.6 [5.1]	3.2 [6.7]	14.4 [15.9]	0 [–]	1.6 [5.1]	1.6 [5.1]	9.6 [13.5]	12.8 [30.9]	0 [–]	11.2 [15.2]	300 [768.3]
F1	12/91	0 [–]	3.2 [10.1]	16 [21.3]	0 [–]	0 [–]	3.2 [6.7]	9.6 [11.2]	3.2 [6.7]	0 [–]	0 [–]	129.5 [145.5]
F1	02/92	1.6 [5.1]	8 [11.3]	8 [11.3]	3.2 [6.7]	4.8 [10.8]	9.6 [8.3]	3.2 [6.7]	8 [13.6]	0 [–]	0 [–]	203.6 [270.3]

F1	04/92	4.8 [7.7]	1.6 [5.1]	6.4 [13.5]	1.6 [5.1]	8 [8.4]	8 [15.5]	6.4 [11.2]	0 [–]	0 [–]	0 [–]	201.7 [272.5]
F2	04/91	5.3 [8.3]	10.7 [13.1]	13.3 [25.6]	21.3 [24.1]	16 [10.1]	5.3 [8.3]	0 [–]	2.7 [6.5]	2.7 [6.5]	0 [–]	33.3 [27.5]
F2	10/91	1.6 [5.1]	3.2 [6.7]	24 [40.1]	0 [–]	3.2 [6.7]	4.8 [7.7]	16 [20]	20.8 [29.3]	0 [–]	9.6 [17.2]	149.9 [282.8]
F2	12/91	3.2 [6.7]	1.6 [5.1]	19.2 [25.9]	3.2 [6.7]	6.4 [8.3]	3.2 [6.7]	16 [22.6]	1.6 [5.1]	0 [–]	1.6 [5.1]	108.2 [229.8]
F2	02/92	1.6 [5.1]	6.4 [11.2]	6.4 [8.3]	3.2 [6.7]	3.2 [6.7]	6.4 [15.5]	1.6 [5.1]	0 [–]	1.6 [5.1]	0 [–]	136.1 [166.3]
F2	04/92	0 [–]	1.6 [5.1]	8 [11.3]	0 [–]	3.2 [10.1]	4.8 [7.7]	0 [–]	1.6 [5.1]	0 [–]	1.6 [5.1]	186.4 [490.4]

With the abbreviations: A, 8-year-old *A. auriculiformis* plantation; F1, weakly disturbed forest (slightly logged in the past); F2, highly disturbed forest (recently and intensively logged); P, pasture; PF, primary forest; PP, pasture with high density of *P. humilis*. Mean density is given in individuals per square metre. Standard error is indicated between parentheses.

sites. This approach is described in detail by Dolédec and Chessel (1987).

All computations and drawings were made using the software ADE-4 (Thioulouse et al., 1997).

The analyses were performed both on the density and on the biomass data. We present here the results we obtained using the density data, however, we got very similar trends in the analyses and identical significance levels in statistical testing using the biomass data.

3. Results

The mean macrofauna density varied distinctly according to dates and sites (Table 1). In terms of density, three groups were dominant: termites, earthworms and ants. The density of these groups was clearly affected both by dates and sites (Table 1). The mean density of termites and ants was maximum in February 1992 (during the dry season) whereas the earthworm group reached its maximum density in October 1991 at the end of the rainy season. Other groups varied according to dates, but the mean density was always low (Table 1). Sites also had a clear effect upon the three main groups. F1, F2 and PF hosted the highest densities of termites. The earthworm and ant density were maximum in P and PF. However, in order to reach a detailed understanding of the macrofauna variability as affected by sites and dates, a specific time–space analysis was necessary.

3.1. General PCA

A PCA on correlation matrix was performed on the data consisting of 22 variables (i.e. fauna groups) and $6\times5=30$ objects (i.e. a given site at a given date). Fig. 1 presents the correlation circle of the first two axes. All the variables, but the ant density were positively correlated to the first axis; ergo the samples ordination along the first axis was mainly explained by a ‘size effect’, i.e. this axis separates sites depending on the fauna density. The position of the variable ant density along axis 1 can be explained by the fact that it was particularly high in one site (Pasture) at one date (Feb. 92). The second axis showed clear differences in macrofauna composition since the variables are either positively or negatively correlated with it (Fig. 1). The first two axes accounted for 48.5% of the total inertia while other axes were associated with low eigenvalues and were therefore discarded from further analyses.

Site and date ordination by the general PCA is shown in Fig. 2. Axis 1 mainly separated objects as a function of the land-uses (Fig. 2A), whereas axis 2 separated objects as a function of the dates (Fig. 2B). Therefore, it revealed that land management chiefly affected the global density (axis 1) while date effect corresponded to changes in the structure of the group assemblage (axis 2). Dates mainly affected groups such as Diptera larvae, Enchytraeidae, Coleoptera larvae and Isopods (positive correlation with axis 2, Fig. 1)

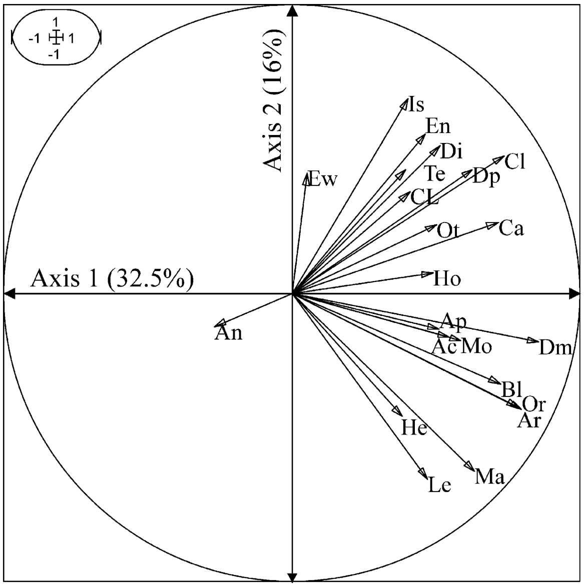

Fig. 1. Simple PCA on macrofauna density. Correlation circle for the axes 1 and 2, respectively, accounting for 32.5 and 16% of the total inertia. See Table 1 for abbreviations.

and Hemiptera, Molluscs, Mantoptera and Lepidoptera (negative correlation with axis 2, Fig. 1). Axis 2 opposed dates corresponding to the beginning of the dry season (October and December 1991) to the dates corresponding to the end of the dry season (April 1991 and 1992). Dates affected soil fauna in two ways. Groups like termites and ants reached their maximum density during the dry season (Figs. 1 and 2 and Table 1) whereas the densities of groups like Lepidoptera declined to very low values at the end of the dry season (Figs. 1 and 2 and Table 1).

The land-use effect concerned almost all groups as shown by the size effect upon axis 1 (Fig. 1). Fig. 2A shows an opposition between forest plots (PF, F1 and F2) versus tree plantation and pastures (A, P and PP) along axis 1. The overall macrofauna density was higher in those woody sites as shown in Table 1 and in Fig. 1. These differences were mainly explained by a higher density of termites (Table 1).

3.2. Between sites analysis

A Monte Carlo test was performed on the object partition by sites in order to test for land-use effect upon soil fauna density. Of the 10,000 random simulations realised, none led to an inertia higher or equal to that of the original data hence indicating that the land-use effect was significant at the probability level $p < 1/10{,}000$. This justified the use of the between–within sites procedure to further analyse the site differences. The between sites PCA yielded a correlation circle (Fig. 3) very similar to the simple PCA (Fig. 1). The distribution of the inertia indicated that axes 1 and 2 accounted for 73.1 and 9.8% of the total variance, respectively. The correlations between the group densities and the axes were particularly close to those obtained with the simple PCA which confirmed that the between sites variability represented the main source of data variability.

The between sites inertia was 7.4 (Table 2), representing 33.5% of the total inertia. Given that the correlation circles are very similar and that the between sites inertia is high (roughly one-third of the total information) it is likely that the first axis of the simple PCA mainly corresponds to a land-use effect upon soil macroorganisms density. Fig. 4 presents the projections of the objects upon the axes 1 and 2 either separated by sites (Fig. 4A) or dates (Fig. 4B). Axis 1 obviously separated the different sites, and the observed pattern was similar to the one yielded by the simple PCA (Fig. 2A). On the other hand, the dates (Fig. 4B) were poorly separated by the between sites PCA. This result reinforces previous conclusions.

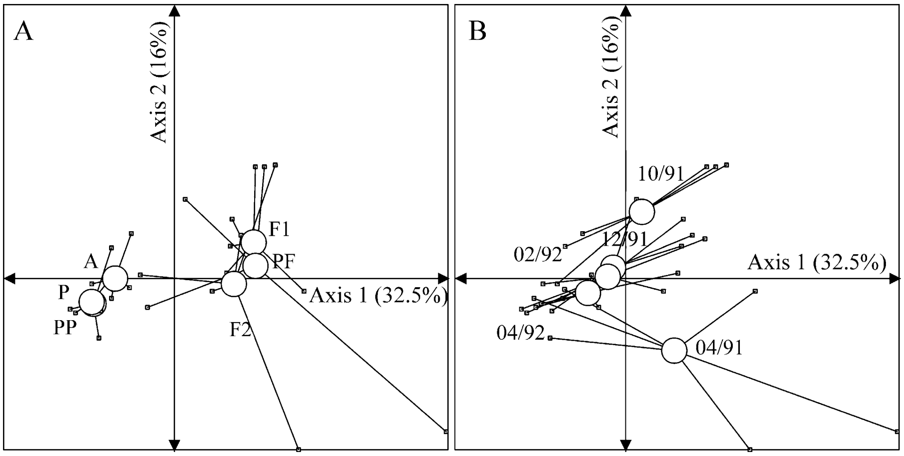

Fig. 2. Simple PCA on macrofauna density. Projection of the sampling units upon the factorial plane 1–2. (A) Variability of scores among sites. (B) Variability of scores among dates. Open circles are placed at the centre of gravity of each site (A) or each date (B). Lines link samples to the corresponding sites or dates. See Table 1 for abbreviations.

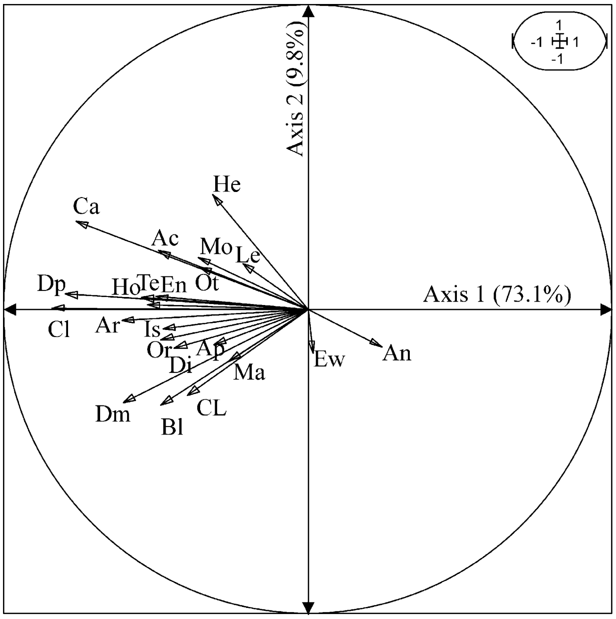

Fig. 3. Between sites PCA of the macrofauna density. Projection of the variables upon PCA axes 1 and 2, respectively, accounting for 73.1 and 9.8% of the between sites inertia. See Table 1 for abbreviations.

3.3. Within sites PCA

The correlation circle showed that the axis 1 of the within sites PCA (Fig. 5A) was close to the axis 2 of the general PCA (Fig. 1). Axes 1 and 2, respectively, accounted for 26.9 and 16.2% of the within sites PCA, a proportion lower than the corresponding values for the between sites analysis. Fig. 5B displays the trajectories of the dates sorted by sites. This graphical representation shows that the temporal typologies were not similar from one site to another. Axis 1 mainly accounts for the differences in the macrofauna composition of one date (04/91), in the forest sites (PF, F1 and F2). These sites at these dates comprised a larger number of the following groups: Araneae, Mantoptera, Orthoptera, Lepidoptera. It should also be noted that the main variability along either axis 1 or 2 is essentially due to the forest sites. There is a noticeable homogeneity of the pasture site and the *Acacia* plantation through time.

Table 2
Total inertia and first eigenvalues of the five PCA composing the between–within sites and dates analysis of the macrofauna density

	Total inertia	First eigenvalue	Inertia ratio (%)
General PCA	22	7.2	
Between site PCA	7.4	5.4	33.5
Within site PCA	14.6	3.9	66.6
Between date PCA	4.6	2.3	20.7
Within date PCA	17.5	6.4	79.3

Inertia ratio indicates the proportion of the variability that is explained either by the between or the within classes effect.

3.4. Between dates PCA

We performed a Monte Carlo randomisation procedure as described above using 10,000 permutations to test for the date effect. Off these random permutations, 207 led to an inertia larger or equal to the observed value thus the date effect was taken as significant ($p=0.0207$) at the 5% confidence level. The between dates PCA represented 20.7% of the total inertia (Table 2). This proportion reflected the prevalence of the land-use impact upon temporal variability. The factorial axis 1 (Fig. 6) was close to the axis 2 of the simple PCA except for the variables ‘earthworm’ and ‘other unidentified groups’ (Figs. 1 and 6). Axis 1 essentially distinguished the dates (not shown) while the different sites were properly segregated along the second factorial axis (not shown). In either case, the objects typology is extremely close to the one resulting from the general PCA (Fig. 2). This analysis also emphasised the importance of the temporal rhythm upon earthworm density.

3.5. Within dates PCA

About 79.3% of the total inertia was not corresponding to any date effect (Table 2). This variability was analysed using a within dates PCA. The first and second PCA axes accounted, respectively, for 36.7 and 13.7% of the within dates inertia. The correlation circle (not shown) is very close to one yielded by the simple PCA with a clear size effect along the first axis (as in Fig. 1). The projection of the objects on the plane defined by the first two factorial axes is given in Fig. 7. The sites were sorted by date to allow a clear examination of the land-use induced macrofauna variability and its own temporal pattern. The general pattern previously noted in Fig. 2 also appears clearly in the within dates PCA. Two groups of sites can be distinguished, the forest sites, and the pastures and *Acacia* plantation (Figs. 2A and 7). The within sites PCA allows examination of extent to which this pattern is stable across time. The latter pattern is expressed in all dates, but to a lesser extent in April 1992 (Fig. 7). The groups are well separated by axis 1 while axis 2 seemingly expresses some important heterogeneities between the forest sites existing in April 1991 (Fig. 7), as well as some more general discrepancies between the two site groups (P, PP and A versus PF, F1 and F2) particularly well expressed in October and December 1991 (Fig. 7). The heterogeneities within the forest sites in April 1991 (axis 2, Fig. 7) are largely explained by termite densities that change sharply from site to site (101, 195 and 14 ind. m^{-2} in PF, F1 and F2, respectively) along with other less marked variations in the macrofauna composition. The difference of the macrofauna hosted by the forest sites in April 1991 has already been emphasised by the within sites PCA (Fig. 5B).

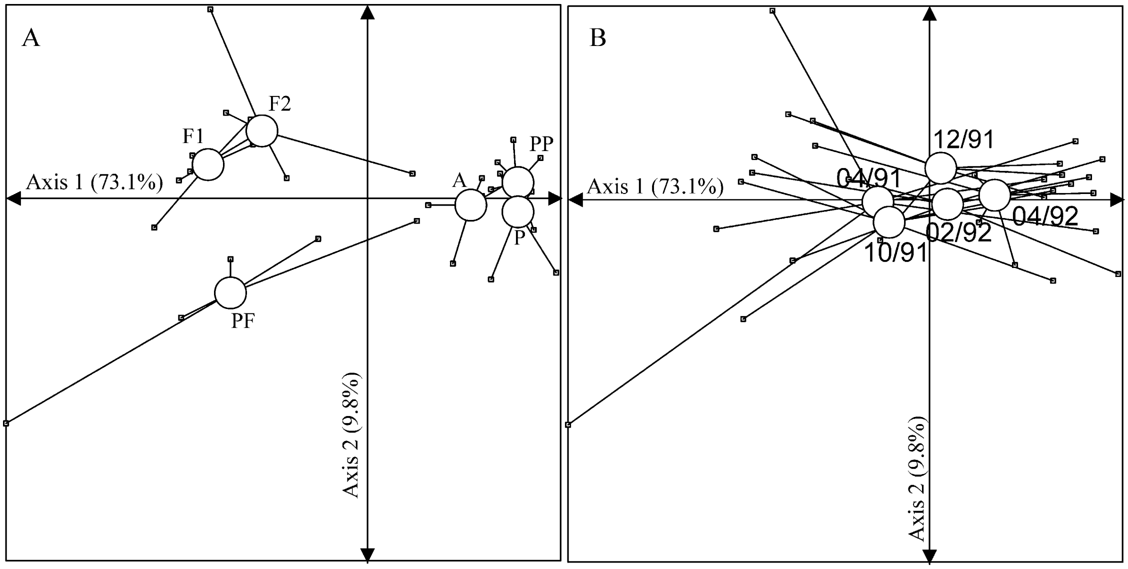

Fig. 4. Between sites PCA of the macrofauna density. Projection of the sampling units onto the factorial plane defined by axes 1 and 2. (A) Variability of scores among sites. (B) Variability of scores among dates. Open circles are placed at the centre of gravity of each sites (A) or each dates (B). Lines link samples to the corresponding sites or dates. See Table 1 for abbreviations.

3.6. Decomposition of the variance: projections onto subspaces

The between–within inertia values allowed quantifying the global effects of time and management upon the whole group assemblage (Table 2). The between sites inertia was larger than the between dates inertia (Table 2), but a substantial part of the variability remained unexplained. These results suggested that a certain part of the within sites variability corresponded to some between dates variance. Ordering the first eigenvalues of each analysis (Table 2) allowed hierarchical arrangement of the factors by order of importance showing the prevalence of the within dates variability, i.e. all the variability that is not explained by the date effect. The between sites analysis led to a first eigenvalue slightly smaller than the one resulting from the within dates analysis thus indicating that a large part of the within dates variance can be ascribed to the land-use effect. Interestingly, the within sites analysis gave a first eigenvalue larger than the one produced by the between dates PCA. This showed which part of the within sites variability could be explained by some temporal patterns of faunal density.

This approach was supplemented by projecting the initial variables onto subspaces defined by space (sites) and time (dates) (Dolédec and Chessel, 1987). The results of the projections are presented in Table 3. The total inertia associated with the projection onto a given subspace (either space or time) equals the associated between classes inertia (again, space or time). The group that is mainly affected by the temporal rhythms is the earthworms with more than 62% of the variance being explained by the date effect. In contrast, sites have a low effect on this group (ca. 6% of the variance explained). For some groups, the main effect is due to land-use differences rather than temporal variability (e.g. Chilopoda, Isoptera, Coleoptera, Diplopoda, Dermaptera and Homoptera: Table 3). Some fauna groups like the Enchytraeidae or Diptera larvae are equally affected by space and time.

4. Discussion

4.1. Total macrofauna density across land-uses

The macroinvertebrate community clearly responded to the environmental disturbance induced by land-use managements. The general PCA showed two clear site clusters (Fig. 2A) opposing the forest sites (PF, F1 and F2) to the pastures and *Acacia* plantations (P, PP and A), respectively. The first obvious explanation for such a grouping is that the mean density of macrofauna is much higher in the forest sites (ranging from 2416 to 3061 ind. m^{-2}) than in the other sites (pastures and plantation: 1333–1654 ind. m^{-2}) (Table 1). This explanation is supported by the size effect along the first axis of the general PCA. This feature shows that the majority of taxa display larger densities in the forest sites, whatever the degree of disruption. Up to this point, there is no perceivable difference between the primary forest (PF) and the more or less disrupted forest sites (F1 and F2).

It is well known that, tropical forests host higher soil macrofauna densities than cultivated lands. For example, in various tropical forest plots in Mexico, Lavelle and Kohlmann (1984) reported densities ranging from 888 to 3011 ind. m^{-2} whereas in a tropical forest in Côte d'Ivoire, Gilot et al. (1995) reported 5747 ind. m^{-2}. However, the global density of soil macrofauna tends to decrease to low

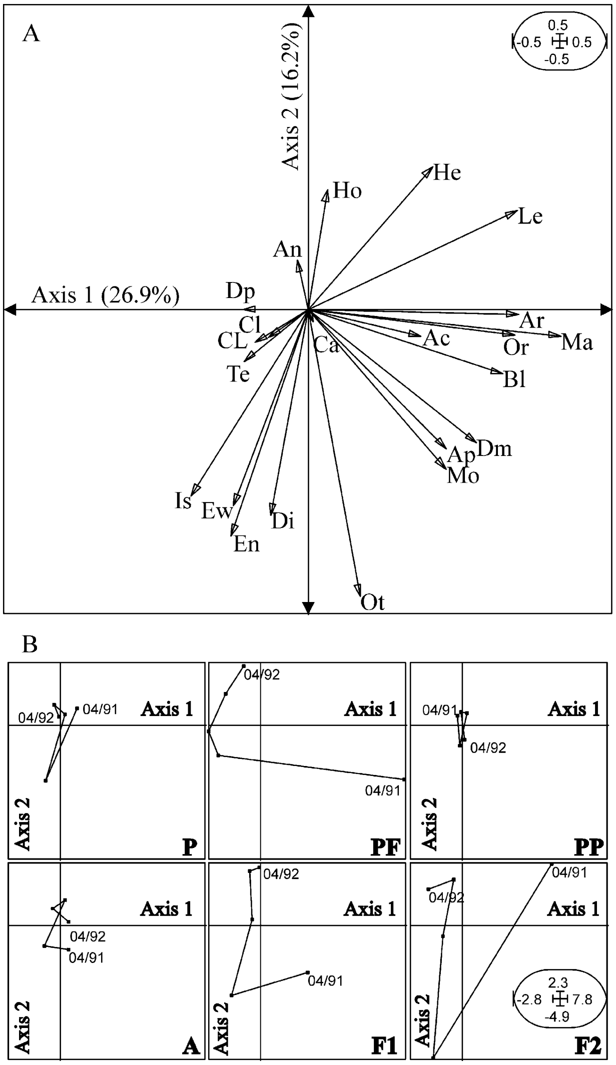

Fig. 5. Within sites PCA of the macrofauna density. (A) Projection of the variables upon PCA axes 1 and 2, respectively, accounting for 26.9 and 16.2% of the within site inertia. (B) Factorial plane (1–2) of date trajectories separated by sites. See Table 1 for abbreviations.

levels in cropped lands; Decaëns et al. (1994) reported densities ranging from 429 to 592 ind. m^{-2} in high input crop in Carimagua (Colombia) and Lavelle and Pashanasi (1989) reported a density of 730 ind. m^{-2} in a similar plot in Peru. In pastures, the mean faunal density is generally higher than in cropped lands and can in some cases be very high, e.g. 1768–2347 ind. m^{-2} in traditional pastures in Peru (Lavelle and Pashanasi, 1989). The results reported here show density data ranging from 1504 to 1654 ind. m^{-2} for the pasture (P) and the pasture with palm trees (PP), respectively. These values are similar to the results reported by several authors (Lavelle and Pashanasi, 1989; Decaëns et al., 1994; Feijoo et al., 1999) for various pasture types. The density reported for 8 years *Acacia* plantations (A, 1332 ind. m^{-2}) is lower than the values reported by Mboukou-Kimbatsa et al. (1998) for 12–13 years *Acacia* plantations in Congo (11,131–2256 ind. m^{-2}).

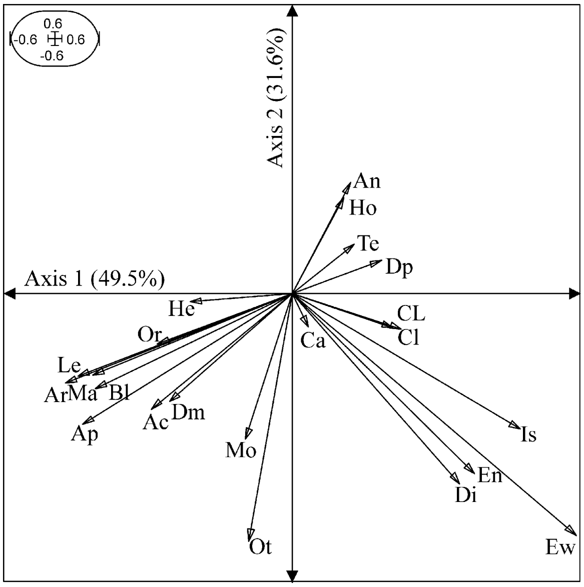

Fig. 6. Between dates PCA of the macrofauna density. Projection of the variables upon PCA axes 1 and 2, respectively, accounting for 49.5 and 31.6% of the between dates inertia. See Table 1 for abbreviations.

The differences are possibly explained by the difference of the plantation age. Caution is needed, however, because comparing sites belonging to very different biogeographic zones may prove meaningless because of huge differences in soil type and properties.

4.2. Site ordination

There is a remarkable similarity between the primary forest (PF) and the disturbed forest plots (F1 and F2) and between the pastures and *Acacia* plot (Table 1, Figs. 2A and 4A). Between and within these groups there are undoubtedly some differences in species composition, but they cannot be assessed with the broad taxonomic categories used in this study. In a study partly based on the earthworms specimen

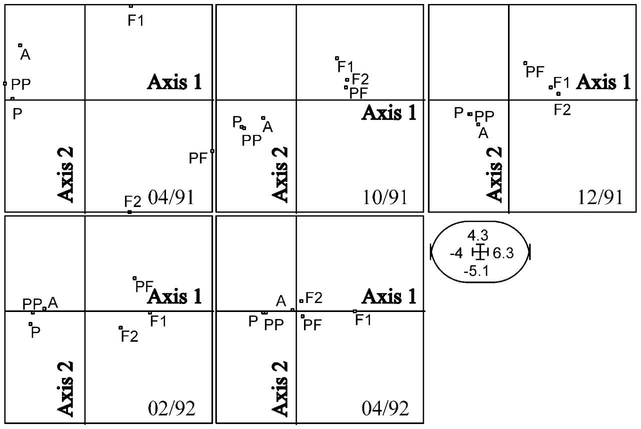

Fig. 7. Within date PCA of the macrofauna density. Projection of sites separated by dates upon the factorial plane defined by axes 1 and 2 accounting for 36.9 and 13.7% of the within date inertia, respectively. See Table 1 for abbreviations.

Table 3
Decomposition of the variance based on the projection onto subspaces

Variables	Codes	Date (%)	Site (%)
Earthworms	Ew	62.2	5.9
Termites (Isoptera)	Te	6.5	40.4
Ants (formicidae)	An	17.1	19.6
Coleoptera larvae	CL	17.5	31.7
Coleoptera adults	Ca	7.5	67.5
Diptera larvae	Di	30.7	34.2
Araneae	Ar	26.7	40.8
Other Arachnida	Ac	24.7	36.1
Diplopoda	Dp	11.8	64.1
Chilopoda	Cl	7.1	77.3
Molluscs	Mo	10.7	17.4
Apterygota	Ap	28.8	15.1
Blattodea	Bl	23.8	34.3
Orthoptera	Or	16.7	27.8
Dermaptera	Dm	13.1	48.7
Lepidoptera	Le	25	17.6
Heteroptera	He	5.1	30.5
Homoptera	Ho	5.6	40.2
Isopods	Is	34.8	25
Enchytraeidae	En	28.9	27
Mantoptera	Ma	22.1	17.2
Other groups	Ot	29	17.4

The variance of each normalised variable (macrofauna group density) is split up into site or date effects. The results are based on the between–within class PCAs of the macrofauna density.

collected in this study, Blanchart and Julka (1997) showed that some earthworm species were restricted to pastures whereas others were forest specialists and some were found in all milieux. The site ordination along the first axis of the general PCA is very similar to the results yielded by the between sites PCA. This shows that the first source of heterogeneity in the macrofauna pattern is the land-use induced variability in density (size effect: Figs. 1 and 3). However, not all the groups have the same response to land management and using the projection onto the subspace defined by the sites makes it possible to further investigate the proportion of group density variance explained by site differences (Table 3). This variance decomposition allows identification of a group of organisms that mainly respond to site differences. It includes Dermaptera, Coleoptera (both adults and larvae), Diplopoda, Chilopoda and Isoptera. Termite density mainly differed between sites (e.g. 998 ind. m^{-2} in the *Acacia* plantation (A) versus 1816 ind. m^{-2} in the primary forest (PF); Table 1). This is accompanied by a strong modification of the community structure (Basu et al., 1996). Most termite communities are a mosaic of various functional groups including soil feeding humivorous, wood feeding xylophagous, fungus-growers or harvesters (Lavelle, 1997). It is likely that seasonality induces some changes in some termite species foraging activities, but the nests are permanent and the density remains less variable in the soil samples than the density of, for example, earthworms. In tropical forests, both species richness and biomass are higher than in adjacent savannas or open habitats (Eggleton et al., 1995; Lavelle, 1997). The other groups mainly affected by the site effect are clear litter-associated taxa that are dramatically affected by forest clearance and the resulting decrease in available litter. Our results show that the *Acacia* plantation remains closer to the pastures than to the forest, perhaps because these plantations were young (8 years). Moreover, in the *Acacia* plantations the overall vegetation diversity remains low and corresponds to a very low diversification of the organic resources. This can explain a lower density of broad zoological groups, although at the species level, it may be hypothesised that the low resource diversity leads to impoverished species diversity (as it shown for earthworms and termites: Basu et al., 1996; Blanchart and Julka, 1997).

4.3. Date ordination

Many soil organisms display strong seasonality in their life cycles (Fayolle et al., 1997; Dibog et al., 1998), and this has even been shown in the diets of their generalist predators (Measey et al., 2004). Population density and biomass as well as the average depth of an organisms' position in the soil profile is greatly affected by soil temperature and humidity (Lavelle, 1983a,b). The general PCA (Fig. 1) and the between dates PCA (Fig. 5) show that soil macrofauna structure changes through time. The densities of groups like Diptera larvae, Enchytraeidae, Coleoptera larvae, Isopoda, Hemiptera, Mollusca, Mantoptera, Oligocaeta and Lepidoptera changes markedly with time (Fig. 1 and Table 1). The date effect is mainly accounted for by the second axis of the general PCA (Figs. 1 and 2B) and is similarly picked up by the between dates PCA (Fig. 6). Since the date effect is significant, the projection onto subspace allows further investigation of its impact on each macrofaunal group (Table 3). Earthworm variability is mainly driven by a date effect (62% of explained variability) while the land-use effect only explains ca. 6% of the variance. Isopoda and Diptera larvae appear also to be greatly affected by date and to a lesser extent (ca. 25 and 30%, respectively, of explained variability: Table 3) by land-use. Possibly, the low site induced changes in these groups is partly linked to the level of taxonomic resolution used in this study (see above discussion and Blanchart and Julka, 1997).

4.4. Temporal changes of the site typology

An important question related to macrofauna dynamics can be fully examined with the within dates PCA: is the spatial typology common from one date to another? As stated above, the site typology mainly involves differences in the average densities rather than important disparities in the group assemblage. Therefore, the temporal rhythms may or may not be different according to land-uses, irrespective of densities. This aspect of the dynamics is well described by the within dates PCA (Fig. 7). The opposition between forests and pastures is well expressed throughout all the sampling dates, except April 1992 where the typology is less marked (lower site dispersion along the factorial axes 1 and 2).

The similarity between the pastures and the *Acacia* plot remains outstandingly unchanged over the entire course of the study. However, the forest sites are well separated along the second axis of the within dates PCA in April 1991 (Fig. 7). This heterogeneity is mainly due to some difference in the macrofauna abundance (see Fig. 1). F1 displays a larger density of termites (200 ind. m^{-2}) and a low density of Heteroptera, Lepidoptera and Mantoptera. In contrast, F2 shows an unusually low density of termites (15 ind. m^{-2}) along with larger densities of Heteroptera, Lepidoptera and Mantoptera. The high temporal variability of forest site typology and the low variability of non-forest sites may be explained by different hypotheses. First, that we do not perceive non-forest site differences because the density is always very low in these sites and our sampling protocol is not accurate enough to allow for a good description of this pattern. Another hypothesis is that, species inhabiting the non-forest sites do not respond as clearly as forest species to season-induced environmental changes, e.g. drought.

The forest sites make a homogeneous cluster only on certain dates (October 1991, December 1991 and April 1992: Fig. 7). At other sampling occasions, some clear differences in faunal composition appear. Such differences may be explained by environmental variations among habitat types that lead to various effects of season-driven critical parameters like soil water status or soil temperature. The impact on soil fauna may change according to zoological groups and therefore lead to changes in the assemblage structure. Comparing April 1991 and 1992 reveals a noticeable difference between the site ordinations (Fig. 7). This shows the somewhat high inter-annual variability in the macrofauna structure which is probably largely under the influence of some inter-annual climatic variability.

4.5. Land management-induced changes in temporal variability

Since changes in land management imply some severe modification of soil environment (e.g. water dynamics, litter availability and quality), some modifications in the temporal rhythms of soil fauna may be observed. This aspect is fully explored using the within sites PCA and the projection of the temporal trajectories sorted by sites (Fig. 5B). The temporal typologies are not similar from one site to another and two groups can be distinguished: PF, F1, F2 versus P, PP, A (Fig. 5B). The temporal variability is well marked in the forest sites where the densities of groups like Araneae, Mantoptera, Orthoptera and Lepidoptera increased in April 1991 (Fig. 5A). The first axis mainly conveys the specificity of the fauna collected in the forest site in April 1991 whereas axis 2 separates the other dates, especially in the forest sites. Considering both these axes, we conclude that the temporal variability in the macrofauna structure is chiefly expressed in the forest sites.

Acknowledgements

The study was realized while Dr Eric Blanchart worked at the French Institute of Pondicherry (India). We are grateful to Karnataka Forest Department for allowing the study in this area. We are thankful to Arumugam, Balasubramanian, Orukaimani, technicians at the French Institute of Pondicherry and Herbettu villagers for assistance in field work. We thank Drs C. Kerdelhué and J. Measey for their valuable comments on an earlier version of the manuscript and two anonymous reviewers for their very helpful reviews of this article.

References

Anderson, J.M., Ingram, J.S.I., 1993. Tropical Soil Biology and Fertility: a Hanbook of Methods. CAB International, Oxford. 221 pp.

Barros, E., Pashanasi, B., Constantino, R., Lavelle, P., 2002. Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biology and Fertility of Soils 35, 338–347.

Barros, E., Neves, A., Blanchart, E., Fernandes, E.C.M., Wandelli, E., Lavelle, P., 2003. Development of the soil macrofauna community under silvopastoral and agrosilvicultural systems in Amazonia. Pedobiologia 47, 273–280.

Barros, E., Grimaldi, M., Sarrazin, M., Chauvel, A., Mitja, D., Desjardins, T., Lavelle, P., 2004. Soil physical degradation and changes in macrofaunal communities in Central Amazon. Applied Soil Ecology 26, 157–168.

Basu, P., Blanchart, E., Lepage, M., 1996. Termite (Isoptera) community in the Western Ghats, South India: influence of anthropogenic disturbance of natural vegetation. European Journal of Soil Biology 32, 113–121.

Beare, M.H., Reddy, M.V., Tian, G., Srivastava, S.C., 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of decomposer biota. Applied Soil Ecology 6, 87–108.

Blanchart, E., Julka, J.M., 1997. Influence of forest disturbance on earthworm (Oligochaeta) communities in the Western Ghats (South India). Soil Biology & Biochemistry 29, 303–306.

Bourgeon, G., 1988. Esquisse sur les grandes zones de sols du Sud de l'Inde. Cahiers ORSTOM, série Pédologie 24, 303–328.

Cadet, P., Thioulouse, J., 1998. Identification of soil factors that relate to plant parasitic nematode communities on tomato and yam in the French West Indies. Applied Soil Ecology 8, 35–49.

Dangerfield, J.M., Milner, A.E., 1996. Millipede fecal pellet production in selected natural and managed habitats of Southern Africa: implications for litter dynamics. Biotropica 28, 113–120.

Decaëns, T., Lavelle, P., Jimenez, J.J., Escobar, G., Rippstein, G., 1994. Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. European Journal of Soil Biology 30, 157–168.

Decaëns, T., Jimenez, J.J., Barros, E., Chauvel, A., Blanchart, E., Fragoso, C., Lavelle, P., 2004. Soil macrofaunal communities in permanent pastures derived from tropical forest or savanna. Agriculture Ecosystems and Environment 103, 301–312.

Dibog, L., Eggleton, P., Forzi, F., 1998. Seasonality of soil termites in a humid tropical forest, Mbalmayo, southern Cameroon. Journal of Tropical Ecology 14, 841–849.

Dolédec, S., Chessel, D., 1987. Rythmes saisonniers et composantes stationnelles en milieu aquatique I. Description d'un plan d'observation complet par projection de variables. Acta Oecologica Œcologia Generalis 8, 403–426.

Dolédec, S., Chessel, D., 1989. Rythmes saisonniers et composantes stationnelles en milieu aquatique II. Prise en compte et élimination d'effets dans un tableau faunistique. Acta Oecologica Œcologia Generalis 10, 207–232.

Dolédec, S., Chessel, D., 1991. Recent developments in linear ordination methods for environmental Sciences. Advances in Ecology India 1, 133–155.

Eggleton, P., Bignell, D.E., Sands, W.A., Waite, B., Wood, T.G., Lawton, J.H., 1995. The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. Journal of Tropical Ecology 11, 85–98.

Fayolle, L., Michaud, H., Cluzeau, D., Stawiecki, J., 1997. Influence of temperature and food source on the life cycle of the earthworm *Dendrobaena veneta* (Oligochaeta). Soil Biology & Biochemistry 29, 747–750.

Feijoo, A., Knapp, E.B., Lavelle, P., Moreno, A.G., 1999. Quantifying soil macrofauna in a Colombian watershed. Pedobiologia 43, 513–517.

Fragoso, C., Brown, G.G., Patron, J.C., Blanchart, E., Lavelle, P., Pashanasi, B., Senapati, B., Kumar, T., 1997. Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. Applied Soil Ecology 6, 17–35.

Giller, P.S., 1996. The diversity of soil communities, the 'poor man's tropical rainforest'. Biodiversity and Conservation 5, 135–168.

Giller, K.E., Beare, M.H., Lavelle, P., Izac, A.M.N., Swift, M.J., 1997. Agricultural intensification, soil biodiversity and agroecosystem function. Applied Soil Ecology 6, 3–16.

Gilot, C., Lavelle, P., Blanchart, E., Keli, J., Kouassi, P., Guillaume, G., 1995. Biological activity of soils in Hevea stands of different ages in Côte d'Ivoire. Acta Zoologica Fennica 196, 186–190.

Jiménez, J.J., Moreno, A.G., Lavelle, P., Decaens, T., 1998. Population dynamics and adaptive strategies of *Martiodrilus carimaguensis* (Oligochaeta, Glossoscolecidae), a native species from the well-drained savannas of Colombia. Applied Soil Ecology 9, 153–160.

Julka, J.M., Blanchart, E., Chapuis-Lardy, L., 2004. New genera and new species of earthworms from the Western Ghats, South India. Zootaxa 486, 1–27.

Lavelle, P., 1983a. The soil fauna of tropical savannas. 1—The community structure. In: Bourlière, F. (Ed.), Tropical Savannas. Elsevier, Amsterdam, pp. 477–484.

Lavelle, P., 1983b. The soil fauna of tropical savannas. 2—The earthworms. In: Bourlière, F. (Ed.), Tropical Savannas. Elsevier, Amsterdam, pp. 485–504.

Lavelle, P., 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. Advances in Ecological Reseach 27, 93–132.

Lavelle, P., Kohlmann, B., 1984. Etude quantitative de la macrofaune du sol dans une forêt tropicale humide du Mexique (Bonampak, Chiapas). Pedobiologia 27, 377–393.

Lavelle, P., Pashanasi, B., 1989. Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). Pedobiologia 33, 283–291.

Lawton, J.H., Bignell, D.E., Bloemers, G.F., Eggleton, P., Hodda, M.E., 1996. Carbon flux and diversity of nematodes and termites in Cameroon forest soils. Biodiversity and Conservation 5, 261–273.

Legris, P., 1963. La végétation de l'Inde: écologie et flore, Institut Français de Pondichéry. Travaux de la Section Scientifique et Technique, vol. 6 1963. 596 pp.

Manly, B.F.J., 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London. 281 pp.

Mboukou-Kimbatsa, I.M.C., Bernhard-Reversat, F., Loumeto, J.J., 1998. Change in soil macrofauna and vegetation when fast-growing trees are planted on savanna soils. Forest Ecology and Management 110, 1–12.

Measey, G.J., Gower, D.J., Oommen, O.V., Wilkinson, M., 2004. A subterranean generalist predator: diet of the soil-dwelling caecilian *Gegeneophis ramaswamii* (Amphibia; Gymnophiona; Caeciliidae) in southern India. Comptes Rendus Biologies 327, 65–76.

Pascal, J.P., 1988. Wet evergreen forests of the Western Ghats, South of India. Institut Français de Pondichéry, Pondichéry. 345 pp.

Peterschmitt, E., 1993. Les couvertures ferrallitiques des Ghats Occidentaux en Inde du Sud, Caractères généraux sur l'escarpement et dégradation par hydromorphie sur le revers. Publications du Département d'Ecologie 32, Institut Français de Pondichéry, 145 pp.

Setälä, H., Laakso, J., Mikola, J., Huhta, V., 1998. Functional diversity of decomposer organisms in relation to primary production. Applied Soil Ecology 9, 25–31.

Thioulouse, J., Chessel, D., Dolédec, S., Olivier, J.M., 1997. ADE-4: a multivariate analysis and graphical display software. Statistics and Computing 7, 75–83.

Wall, D.H., Moore, J.C., 1999. Interactions underground—soil biodiversity, mutualism, and ecosystem processes. Bioscience 49, 109–117.

Wardle, D.A., Verhoef, H.A., Clarholm, M., 1998. Trophic relationships in the soil microfood-web: predicting the responses to a changing global environment. Global Change Biology 4, 713–727.