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**INFLUENCE OF AGRICULTURAL PRACTICES ON ARTHROPOD
COMMUNITIES IN A VERTISOL (MARTINIQUE)**

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Short title : Agricultural practices and soil arthropods

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Abstract

The influence of human activities on soil arthropods of vertisols was assessed in several plots characterized by different land uses in the south-eastern part of Martinique (French West Indies). Abundance and diversity of soil invertebrate groups and collembolan species were measured in a 40-year-old secondary forest, a 15-year-old fallow, a 4-year-old fallow, a 4-year-old pasture, a 15-year-old pasture and a 20-year-old market-garden. Agricultural practices modified abundance and species distribution of soil arthropods, compared to forest. Arthropod richness (number of taxa present) decreased from forest to market-garden, according to a gradient of intensification of agricultural use (pesticides, tillage, weed control). In the old pasture, the arthropod diversity was lower in spite of a high carbon content. Species richness of Collembola decreased together with plant diversity and water availability.

Keywords : Soil arthropods, Collembola, Agricultural practices, Biodiversity

Titre français : Influence des pratiques agricoles sur les communautés d'arthropodes dans un vertisol (Martinique)

Résumé

L'impact des activités humaines sur l'abondance et la diversité des arthropodes du sol est étudié dans un vertisol du sud-est de la Martinique. L'abondance et la diversité de l'ensemble des arthropodes et des peuplements de collemboles sont mesurées dans une forêt secondaire de 40 ans, une jachère de 15 ans, une jachère de 4 ans, un pâturage de 4 ans, un pâturage de 15 ans et un maraîchage de 20 ans. Les pratiques agricoles modifient l'abondance des peuplements d'invertébrés et la distribution des espèces. La richesse zoologique (nombre de groupes taxonomiques présents) diminue de la forêt au

maraîchage, avec l'augmentation de la pression anthropique (diminution de la diversité végétale, ajout de pesticides, travail du sol). Dans le cas du pâturage âgé, on observe une faible diversité d'arthropodes malgré une teneur en carbone élevée. La richesse spécifique des collemboles diminue en même temps que la diversité végétale et la disponibilité hydrique.

Mots clés : Arthropodes du sol, Collemboles, Pratiques agricoles, Biodiversité.

1. Introduction

Soil functioning is affected by the abundance and the diversity of soil organisms. Decreases of diversity due to human activities may induce a degradation of soils and some changes in functional processes [22]. Species diversity and abundance of soil invertebrate communities are mainly determined by climate, quality and quantity of detritus inputs to the soil and by the structural stability of soil and litter habitats [4]. In agroecosystems, the amount and the quality of organic inputs decrease and tillage disturbs soil habitats. This often results in losses of soil fauna diversity [13] with the subsequent impairment of functions fulfilled by soil animals.

During the last decade, there was an intensification of agriculture in the south-eastern part of Martinique (French West Indies). The influence of land use on the physical structure and on the status of organic matter has been already studied in vertisols [17]. These soils are among the richest tropical soils. They are present under climates with contrasted seasons and they are characterized by a high clay (smectite) content. Their instability is due to the appearance of shrinkage cracks during dry periods followed by swelling during wet periods [24]. Under cropping, the soil organic matter content may decrease down to very low levels [3].

This study aimed to assess the impact of agricultural practices on soil invertebrates and in particular on collembolan communities in similar soils submitted to different land uses: a secondary forest, an old fallow, a recent fallow, a recent pasture, an old pasture and an old market-garden.

2. Materials and methods

2.1. Site description

The study was carried out near Sainte-Anne, in the south-eastern part of Martinique (French West Indies). This area receives on average an annual rainfall of 1400 mm. The soil is a calco-magneso-sodic vertisol characterised by : $\text{Ca/Mg} = 1.5\%$ and $\text{Na}^+/\text{Cation Exchange Capacity} = 16\%$.

Six plots were selected: a 15-year-old fallow, a 4-year-old fallow, a 4-year-old pasture, a 15-year-old pasture, an 20-year-old market-garden and a 40-year-old secondary forest. The first five plots were located at the SECI experimental station (Station d'Essais en Cultures Irriguées - Conseil Général de la Martinique). They had been previously cropped to sugarcane for several decades. The secondary forest site was located 5 km further on similar soil, at Pointe Cailloux. It was previously an old sugarcane plantation, abandoned 40 years ago. The vegetation is xerophilous. The old fallow had been planted to *Cynodon dactylon* (Bermuda grass) in 1980. This plot was covered thereafter by a natural xero-heliophilous vegetation, at the advanced herbaceous stage. The recent fallow and the recent pasture (4-year-old) had the same history. After fifteen years of market-gardening, they were turned to pasture with *Digitaria decumbens* (pangola grass) in 1991, then they were grazed by sheep and regularly irrigated and fertilised. However, contrary to the pasture, the recent fallow had been unsuccessfully planted and natural vegetation covered the plot instead. The old pasture had been

established more than fifteen years before the study. The old market-garden had been cultivated in rotation farming for the last twenty years. Main characteristics and carbon content of the topsoil in the different plots are given in *table I*.

2.2. Soil fauna

Soil arthropods were sampled along a transect line. Ten regularly spaced cores, 10 × 10 cm in cross-section and 3 cm depth, were taken in each plot. Previous sampling showed that 75% soil arthropods inhabited the top 3 cm. Soil invertebrates were extracted for 48 hours in Berlese funnels at 313 K (40°C). Preliminary assays allowed to determine the duration of extraction. Most arthropods fell out within 48 hours [23]. Sampling and extraction were achieved in February 1995, during the dry season. Arthropods were counted under a dissecting microscope and they were classified into 22 taxa (19 orders and 3 larval groups). Collembola were sorted out and when possible they were identified at the species level using Betsch & Lasebikan [7], Christiansen & Bellinger [9], Denis [11], Gisin [14], Massoud and Thibaud [25, 26], and Thibaud and Massoud [30, 31]. The size of each individual was measured. Two size classes were defined: class 1 (< 1.5 mm) comprising mostly endogeic species, with short appendages (antennae, legs and furcula), and class 2 (≥ 1.5 mm), comprising mostly epigeic species with long appendages.

In each plot, the zoological richness was assessed by counting the number of taxa present. Collembolan species richness was assessed similarly. The Sorensen's index of similarity, I [15], was used to compare collembolan communities between disturbed and forested plots:

$I = 2c/(a + b)$, where a is the number of species in the forest; b the number of species in the disturbed plot; and c the number of species in common.

2.3. Statistical analysis

Correspondence analysis (CA), a multivariate method based on chi-square distance [16] was performed on arthropod groups and collembola species, using STAT-ITCF™. One of the peculiarities of CA is the simultaneous projection of samples and variables on the same graph, variable-points located within a group of sample-points being typical for this group. Densities for each animal group were reweighted (S.D. = 1) and focused to a mean of 20 as in a previous study [23]. In order to help interpreting the factorial axes, carbon content (C) and treatments (F: forest OF: old fallow, RF: recent fallow, RP: recent pasture, OP: old pasture, MG: market-garden) were used as additional variables, i.e. they were plotted even though not originally included in the matrix to be analysed. Mann-Whitney non-parametric test [28] was used to compare the densities of main arthropod groups among different land uses. Each group was analysed separately by comparing pairs of plots in order to find homogeneous groups among plots. The same test was used to compare the abundance of the two size classes of Collembola in the different plots.

3. Results

3.1. Total fauna

3.1.1. Densities

The total number of arthropods decreased in the order: recent fallow > forest > old pasture > recent pasture > old fallow > market-garden (*table II*). The recent fallow had the highest density of Acari (42,170 individuals.m⁻² as compared to 30,410 individuals.m⁻² in the forest), Collembola (7,260 individuals.m⁻² as compared to 5,120 individuals.m⁻² in the forest), Formicoidea, Isopoda, Diplopoda and Dermaptera. The

secondary forest site with 38,000 individuals.m⁻² had the second highest total arthropod density. Greatest abundance of Pseudoscorpionida, Pauropoda, Diplura and Isoptera (termites) was characteristic of the forested plot. The forest site exhibited the highest densities of Coleoptera (adult and larvae), Diplopoda (in common with the recent fallow), Symphyla, Protura, Chilopoda, Heteroptera, Araneide and Thysanoptera (in common with the old fallow). The old pasture (31,460 arthropods.m⁻²) had high densities of Acari, Collembola and Formicoidea. The recent pasture (12,890 arthropods.m⁻²) had high density of Acari, Collembola and Formicoidea and had the highest density of Diptera larvae. The old fallow (10,090 arthropods.m⁻²) was characterized by the lowest density of Collembola. The market-garden site was the poorest in Acari, Formicoidea, Dermaptera and Coleoptera larvae but exhibited the highest density of Homoptera. Mann-Whitney's test showed significant differences among plots for Acari, Collembola, Diplopoda, Chilopoda, Isopoda, Formicoidea, Coleoptera, Homoptera, Coleoptera larvae and Diptera larvae (*table III*). The recent fallow was the most similar to the forest for most arthropod groups, except for Coleoptera, Chilopoda, Isopoda and Formicoidea.

CA was performed on all samples and animal groups (*figure 1*). Axes 1 to 4 accounted for 27.5, 12.8, 9.8 and 6.6 % of total variance, respectively. Axis 1 opposed the secondary forest with the highest carbon content (36‰), and the highest zoological richness and abundance to the other plots. This axis may correspond to a "land use gradient", with the market-garden most opposed to the forest, and the recent fallow nearest the forest. Axis 2 opposed the recent fallow, with the highest arthropod density, to all other plots, the market-garden and the old fallow being most opposed. This axis may correspond to a "density gradient". CA did not clearly separate the plots with lower

densities of soil arthropods. The poorest sites (market-garden and old fallow) were placed on the negatives sides of both axes 1 and 2.

3.1.2. Zoological richness

Twenty-two taxonomical groups were present in total. The zoological richness decreased in the following order: forest (20 groups of arthropods) > recent fallow = recent pasture (14 groups) > old pasture = old fallow (12 groups) > market-garden (8 groups), which was reflected in the ordination of land uses by axis 1 of CA (*figure 1*). Isopoda and Dermaptera were unexpectedly completely absent in the forest soil. *Figure 2* shows gains and losses in arthropod groups when agricultural plots were compared to the forest. The market-garden lost most arthropod groups (14).

3.2. Collembola

3.2.1. Species occurrence

Twenty-seven species of Collembola were found in the studied plots (*table IV*). Some collembolan species were only found in one plot, e.g. *Acherontiella* sp.1, cf. *Sinella* sp., *Stenognatriopes* sp., *Xenylla* sp.3 in the forest, while others were ubiquitous like *Lepidocyrtus* sp.1 and *Seira* sp., which were found in all treatments. Each plot exhibited a particular species composition.

CA was performed on collembolan species (*figure 3*). Axes 1 to 4 accounted for 19.4, 11.5, 9.7 and 8.5 % of the total variance, respectively. Axis 1 opposed the forest to the old pasture, with profound changes in the species composition. Axis 2 opposed the recent fallow to both the old pasture and the forest, with *Acherontiella* sp.2 composing almost the whole collembolan fauna in the recent fallow. The collembolan communities of the old fallow, of the market-garden and of the recent pasture were not differentiated

from other plots by CA, the old fallow being placed in an intermediary position between the recent fallow and the forest.

3.2.2. *Species richness*

Species richness decreased in the order: forest (20 species) > recent fallow (15) > old pasture (13) > recent pasture (11) > market-garden (7) > old fallow (2). *Figure 4* shows gains and losses of collembolan species in the disturbed plots compared to the forested plot. Sorensen's indices (*table IV*) showed that the recent fallow was the most similar to the forest and the old fallow the most dissimilar.

3.2.3. *Size classes*

Species of collembola were classified in two groups: small endogeic species and large epigeic species. Relative contributions of these ecological categories to the whole collembolan community were compared among the sites (*table V*). There was a significant influence of land use on the balance between both two size classes. In the recent pasture and in the market-garden, there were significantly more epigeic (class 2) than endogeic Collembola (class 1). On the contrary the forest had less epigeic than endogeic animals.

4. Discussion

Forty years after the abandonment of sugarcane plantation, the topsoil of the secondary forest has a high carbon content. The recolonization by woody vegetation of abandoned agricultural plots allows the restoration of a high carbon content [8]. This secondary forest harbours an abundant and diverse arthropod fauna, too. However, the

arthropod density is still low compared to other secondary dryland forests under similar climate [1, 2].

The recent fallow and the recent pasture had a rather similar zoological richness, although lower than the forest. The high abundance and zoological richness of arthropods in these plots were probably caused by irrigation and fertilisation, the absence of ploughing and a lower grazing pressure compared to plots used for intensive pasture [19]. Some arthropod groups present in the forest were absent in these plots, probably due to a lower litter quality and quantity.

In the old fallow the absence of a dense cover for soil arthropods (grasses are cut each year) and the lack of water (absence of irrigation) may explain the low arthropod density and the low zoological richness.

In the old pasture, the dominance of *Digitaria decumbens* may explain the low zoological richness of soil arthropod fauna. However, in this plot, the carbon content is as high as 30 ‰ (36‰ in the forest), which could indicate that the diversity of food resources is at least as important as its amount for the maintenance of a diverse soil fauna.

Soil arthropod communities were markedly depleted in the market-garden system. Intense agricultural practices are known to reduce arthropod diversity and density [10, 27, 29]. After a long time of intensive cropping, several factors may explain the observed decrease in invertebrate density and zoological richness. Intense use of pesticides, intense cropping and heavy tillage cause soil compaction, and destroy most soil and litter microhabitats [13].

In spite of relatively dry conditions due to a high water uptake, rainfall interception by leaves and lack of irrigation, the forest site harbours an abundant and diverse collembolan community. The presence of leaf litter, which creates suitable microclimate

conditions at the soil surface, retains moisture and offers diverse food resources may explain this figure. The two endogeic earthworm species which are present on this plot (*Polypheretima elongata* and *Pontoscolex* sp.) probably create favourable conditions for soil-dwelling arthropods, too.

In the recent fallow (following 15 years of intense market-gardening) the density of collembola was greater than in the forest, but this is due to few species that dominate the collembolan community. Despite differences in the Collembolan species composition, some forest species (*Acherontiella* sp.2, *Dicyrtomina* cf. *opalina*, *Isotomodes* sp., *Lepidocyrtus* sp.3 *Pseudachorutes* sp.) appear in the recent fallow, giving clear indication of a recolonization by the forest collembolan community.

In the old pasture, the presence of a dense continuous grass layer, protecting the soil against erosion, irrigation and giving it a high carbon content, can explain the maintainance of some collembolan richness. This plot exhibited the highest abundance of large-sized species (*table V*), probably due to a higher amount of large pores created by the earthworm *P. elongata*. Populations of this endogeic worm can usually reach a high biomass on these plots [6]. A strong influence of the density of earthworms on the size and density of Collembola has already been demonstrated in this pasture by Loranger et al. [23].

In the tilled vertisol of the market-garden, endogeic small collembolan species decreased in the topsoil contrary to more motile and larger epigeic species which probably are better able to recolonize the plot each year [12, 32]. Given that sampling was not done below 3 cm depth, deeper-living endogeic collembolan species were possibly underestimated.

The old fallow had the lowest density of Collembola, probably due to the absence of litter and to the lack of water (no irrigation). As a matter of fact, water availability is

important for invertebrates, especially those which respire through their integument such as Collembola [5, 20, 33].

During the dry period, a vertisol is unfavourable to the development of soil animal populations and in particular to Collembola, due to physiological dryness (high content in smectites). The soil fauna could sink along shrinkage cracks (endogeic species) or colonize contiguous irrigated plots (epigeic species). In fact, in the old fallow, small shrinkage cracks were observed and we obviously reported a low arthropod and collembolan density, too. In the other cultivated plots, irrigation prevents the development of shrinkage cracks, as litter does in the forest.

5. Conclusion

In tropical vertisols changes in arthropod communities indicate a decline in soil quality following agricultural use. However, the presence of diverse vegetation, irrigation and fertilisation can partly maintain zoological richness. A great part of the soil arthropod community has been recovered successfully after the abandonment of agriculture, through the restoration of a litter layer (secondary forest). Litter protects the soil against erosion, offers microhabitats and food to litter-dwelling groups, and prevents vertisols to shrink during dry periods. In disturbed plots, plant diversity, irrigation, fertilisation and low grazing pressure allow the maintenance of soil fauna.

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LEGENDS OF FIGURES

Figure 1: Correspondence analysis (CA) on all Berlese-extracted arthropod groups.

Projection of samples and taxa in the plane of axes 1 and 2.

OP = old pasture, RP = recent pasture, OF = old fallow, RF = recent fallow, MG = market-garden, F = secondary forest, C = carbon content.

Figure 2: Changes of the zoological richness in the different plots, by comparison with the forest.

Figure 3: Correspondence analysis (CA) on Collembolan species. Projection in the plane of axes 1 and 2. Elsewhere as for Fig. 1.

Figure 4: Changes of the Collembolan species richness in the different plots, by comparison with the forest. Sorensen's indices (I) are indicated for each plot.

Table I Characteristics of the studied plots

	Old Pasture	Recent Pasture	Old Fallow	Recent Fallow	Market-garden	Forest
Age	> 15-year-old	4-year-old	15-year-old	4-year-old	20-year-old	40-year-old
Culture	<i>Digitaria decumbens</i> (Pangola grass). It formed a dense continuous herb layer.	<i>D. decumbens</i>	<i>Cynodon dactylon</i> (Bermuda grass) and natural vegetation; cut each year	<i>D. decumbens</i> and natural grassland vegetation	melon	Natural xerophilous vegetation
Grazing	Sheep - bovines	sheep	no	sheep	no	no
Fertilisation	yes	yes	no	yes	yes	no
Irrigation	yes	yes	no	yes	yes	no
Pesticides	no	no	no	no	yes	no
Dominant earthworm species	<i>Polypheretima elongata</i>	<i>P. elongata</i> and 2 unidentified species	<i>P. elongata</i> and 2 unidentified species	<i>P. elongata</i> and 2 unidentified species	2 unidentified species	<i>P. elongata</i> <i>Pontoscolex</i> sp.
Topsoil [21]	(25 cm) Brown clay horizon (> 60 % smectites) Coarse polyhedral structure	(35 cm) Brown clay horizon. Polyhedral structure		(10cm) Compact. Polyhedral structure	(10 cm) Grey brown and clayish. Polyhedral structure	Brown. Granular structure.
Carbon content 0-10 cm (mg C / g soil)	30	18	20	18	13	36

Table II Arthropod densities (ind.m⁻²) in the different plots (mean followed by S.E.)

	Forest	Old Pasture	Recent Pasture	Old Fallow	Recent Fallow	Market-garden
Acari	30410 (2870)	22480 (3999)	7850 (1838)	9240 (1554)	42170 (5331)	6540 (1390)
Araneidae	40 (32)	10 (9)	30 (212)	20 (13)	30 (16)	0
Pseudoscorpionida	130 (51)	0	0	0	0	0
Diplopoda	300 (63)	0	130 (44)	10 (9)	300 (82)	0
Chilopoda	110 (28)	0	20 (13)	0	0	0
Symphyla	170 (25)	0	0	0	10 (9)	0
Pauropoda	240 (35)	0	0	0	0	0
Isopoda	0	70 (35)	790 (164)	50 (22)	2170 (829)	480 (285)
Collembola	5120 (851)	4160 (1894)	2160 (328)	70 (26)	7260 (1990)	1170 (373)
Protura	120 (32)	0	100 (41)	0	0	0
Diplura	140 (9)	0	0	0	0	0
Thysanoptera	30 (22)	20 (13)	10 (9)	30 (22)	10 (9)	0
Dermaptera	0	20 (13)	0	0	100 (28)	10 (9)
Homoptera	390 (148)	120 (35)	0	70 (26)	50 (32)	490 (262)
Heteroptera	40 (22)	0	10 (9)	0	0	0
Formicoidea	220 (117)	4510 (2517)	1480 (822)	430 (104)	5890 (2283)	30 (28)
Isoptera	10 (9)	0	0	0	0	0
Coleoptera	410 (149)	0	20 (13)	0	30 (16)	0
Coleoptera larvae	550 (136)	30 (22)	40 (16)	110 (32)	160 (32)	10 (9)
Diptera larvae	120 (95)	20 (13)	250 (117)	10 (9)	20 (13)	0
Other insect larvae	20 (19)	20 (13)	0	50 (35)	0	0
TOTAL	38570 (3772)	31460 (8563)	12890 (3630)	10090 (1859)	58200 (10669)	8730 (2359)

Table III Comparison of the different plots for key arthropod groups (ManWitney's test). * : $p < 0.05$; a, b, c, d : decreasing order of means homogeneous groups.

	p	Forest	Old Pasture	Recent Pasture	Old Fallow	Recent Fallow	Market- garden
Acari	*	ab	b	c	c	a	c
Collembola	*	a	ab	b	c	a	b
Diplopoda	*	a	b	a	b	a	b
Chilopoda	*	a	b	b	b	b	b
Isopoda	*	c	bc	a	c	a	ab
Formicoidea	*	c	ab	b	b	a	c
Coleoptera	*	a	b	b	b	b	b
Homoptera	*	a	a	b	ab	ab	a
Coleoptera larvae	*	a	cd	cd	bc	ab	d
Diptera larvae	*	ab	ab	a	b	ab	b

Table IV.- Collembolan species (ind.m⁻²) in the different plots : means followed by S.E. and ecological groups (*) : epigeic species; (**) : endogeic species. Rs : Specific richness. I : Sorensen's index between disturbed plots and the forested plot.

	Forest	Old Pasture	Recent Pasture	Old Fallow	Recent Fallow	Market-garden
<i>Acherontiella</i> sp. 1 (**)	20 (19)	0	0	0	0	0
<i>Acherontiella</i> sp. 2 (**)	50 (35)	0	0	0	4370 (1654)	0
<i>Arlesia albipes</i> (*)	0	0	10 (9)	0	0	0
<i>Brachystomella</i> sp. (**)	0	130 (89)	30 (22)	0	50 (32)	0
cf. <i>Sinella</i> sp. (**)	120 (60)	0	0	0	0	0
<i>Cryppygus</i> cf. <i>separatus</i>	280 (101)	1890 (1287)	960 (272)	0	1400 (411)	870 (309)
<i>Cryptopygus</i> sp. 1 (**)	10 (9)	220 (76)	0	0	0	20 (19)
<i>Cryptopygus</i> sp. 2 (**)	90 (41)	0	0	0	0	0
<i>Cyphoderus</i> cf. <i>similis</i> (*)	230 (133)	70 (35)	50 (35)	0	120 (44)	0
<i>Dicyrtomina</i> cf. <i>opalina</i>	30 (16)	0	0	0	20 (13)	0
<i>Folsomides americanus</i>	60 (32)	150 (108)	410 (152)	0	490 (247)	0
<i>Heteromurus</i> sp. (*)	0	0	0	0	20 (19)	10 (9)
<i>Isomtomella minor</i> (**)	10 (9)	220 (76)	120 (76)	0	0	0
<i>Isotomodes</i> sp. (**)	330 (130)	0	0	0	130 (79)	0
<i>Lepidocyrtus</i> sp. 1 (*)	10 (9)	410 (142)	210 (57)	10 (9)	240 (120)	140 (41)
<i>Lepidocyrtus</i> sp. 2 (*)	0	0	10 (9)	0	0	0
<i>Lepidocyrtus</i> sp. 3 (*)	460 (120)	0	0	0	40 (41)	0
<i>Megalothorax minimus</i>	0	0	0	0	10 (9)	0
<i>Pseudachorutes</i> sp. (**)	450 (142)	0	0	0	120 (73)	0
<i>Pseudosinelle</i> sp. (*)	50 (28)	150 (57)	320 (123)	0	160 (60)	110 (35)
<i>Salina banksi</i> (*)	0	50 (28)	0	0	70 (41)	0
<i>Seira bipunctata</i> (*)	0	200 (79)	0	0	0	0
<i>Seira</i> sp. (*)	30 (22)	370 (168)	30 (16)	60 (22)	20 (19)	10 (9)
<i>Stenognatriopes</i> sp. (**)	40 (16)	0	0	0	0	0
<i>Xenylla</i> sp. 1 (**)	2690 (553)	250 (209)	10 (9)	0	0	10 (9)
<i>Xenylla</i> sp. 2 (**)	90 (70)	50 (32)	0	0	0	0
<i>Xenylla</i> sp. 3 (**)	70 (35)	0	0	0	0	0
Rs	20	13	11	2	15	7
I	1	0.606	0.516	0.182	0.629	0.44

Table V Abundance of Collembola (ind.m⁻²) by size class in the different plots.

ManWitney's test : (*) : p = 0.05, (ns) non-significant.

		Class 1 (<1.5mm) endogeic species	Class 2 (≥1.5mm) epigeic species
Forest	*	4060	1060
Old pasture	ns	1020	3140
Recent pasture	*	570	1590
Old fallow	ns	0	70
Recent fallow	ns	5190	2070
Market-garden	*	30	1140

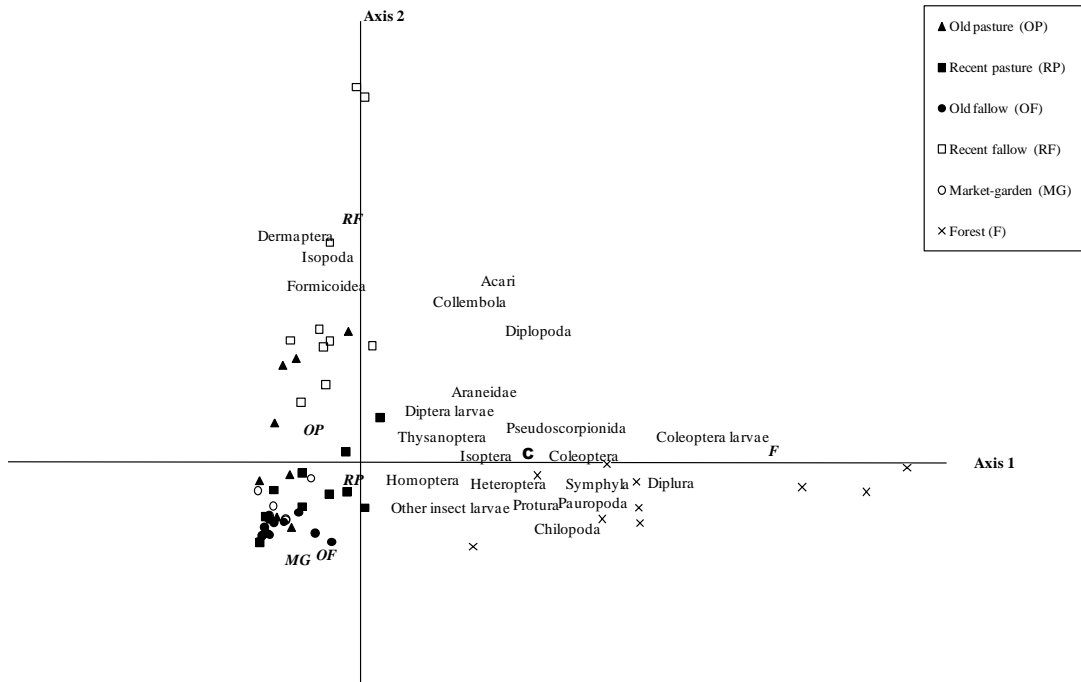


Fig. 1

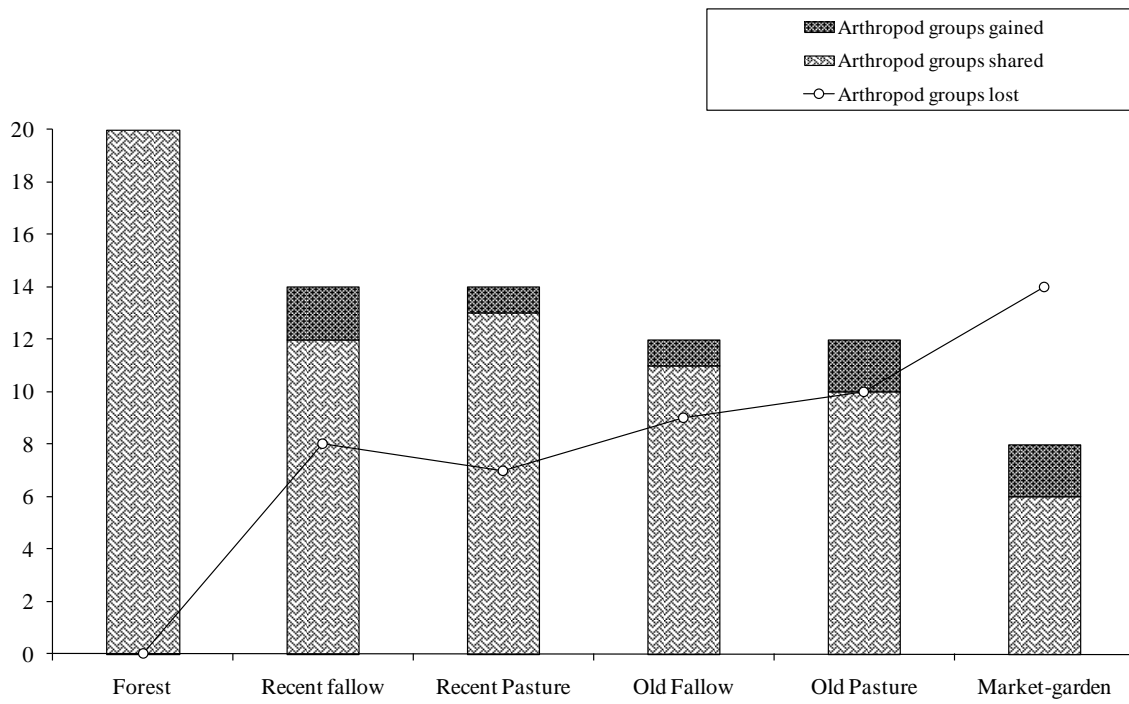


Fig. 2

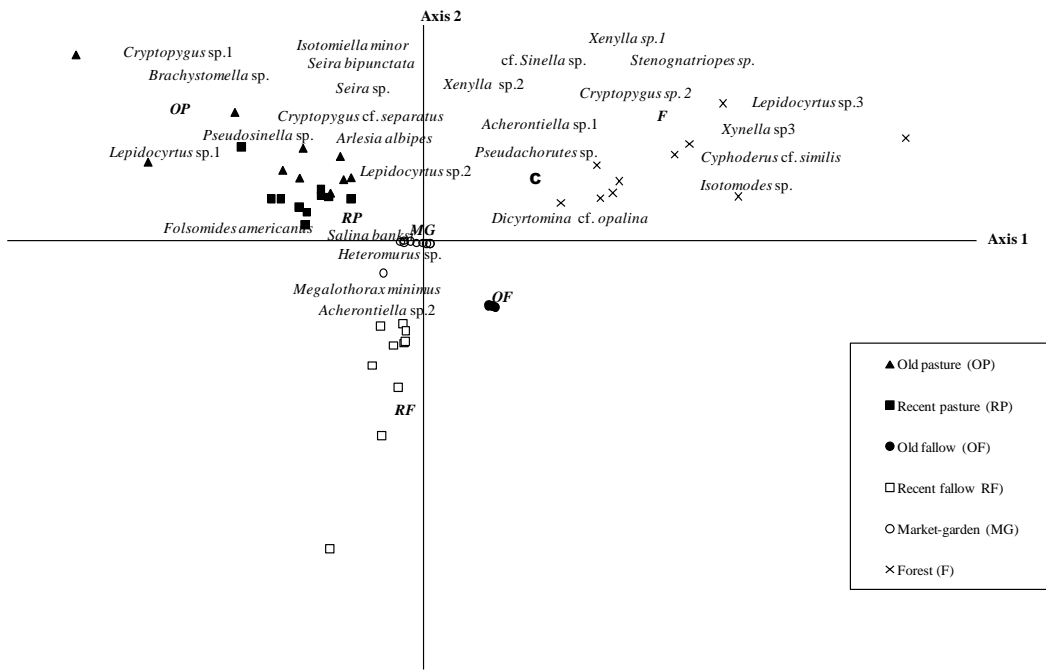


Fig. 3

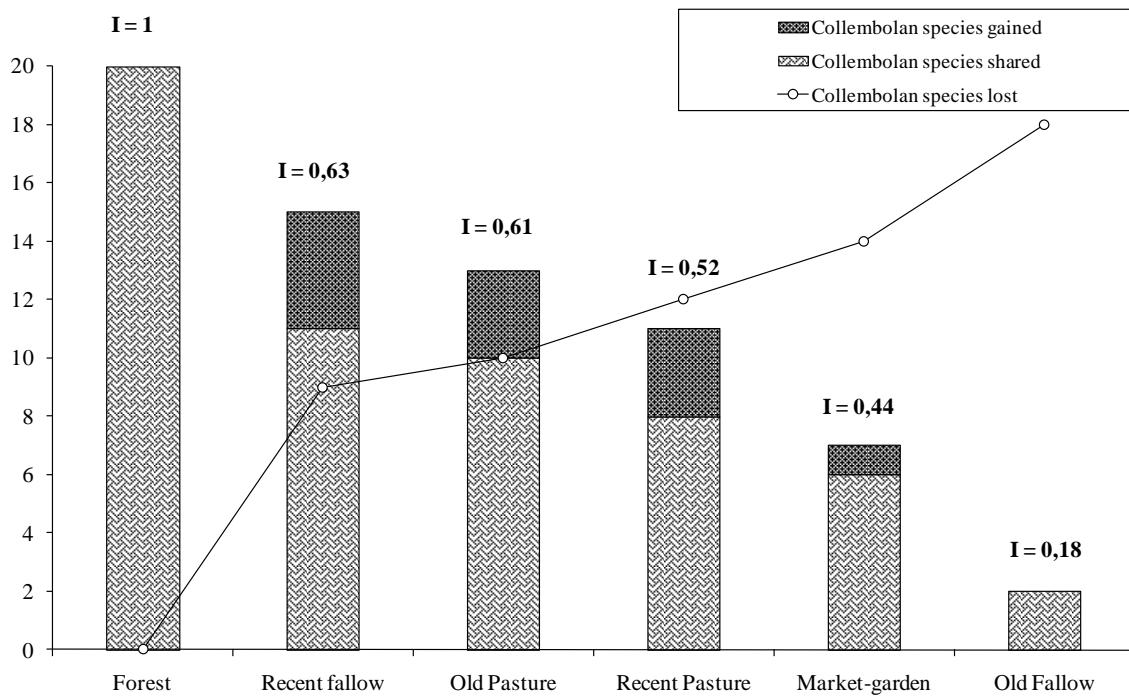


Fig. 4