Soil fauna abundance and diversity in a secondary semi-evergreen forest in Guadeloupe (Lesser Antilles): influence of soil type and dominant tree species

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Abstract The importance of secondary tropical forests regarding the maintenance of soil fauna abundance and diversity is poorly known. The aims of this study were (1) to describe soil fauna abundance and diversity and (2) to assess the determinants of soil fauna abundance and diversity in two stands of a tropical semi-evergreen secondary forest. Soil macrofauna and microarthropod abundance and soil macrofauna diversity were described at two sites developed on different soils and with different site histories: (1) a natural secondary stand (natural forest) under two dominant tree species, *Pisonia subcordata* and *Bursera simaruba*, and (2) a planted secondary forest (planted forest) under three tree species, *B. simaruba*, *Swietenia macrophylla*, and *Tabebuia heterophylla*. The effects of both soil and main tree species' litter quality were assessed to explain soil fauna abundance and

diversity. The abundance of soil macrofauna was significantly higher in the soil under the planted forest, and soil fauna communities were contrasted between the two sites. In the planted forest, a soil-dwelling macrofauna community developed (mainly consisting of the anecic earthworm *Polypheretima elongata*). In the natural forest, soil macrofauna and microarthropod communities were located at the soil surface. The effect of plant litter quality varied according to each dominant tree species and was superimposed to soil effect. The lowest macrofauna abundance was associated with *B. simaruba* in the natural forest. *T. heterophylla* supported a much greater macrofauna community than the two other tree species studied at the same soil, and it appears likely that this is due to the palatability of its leaves compared with the other trees (low lignin, tannins, soluble phenols).

Keywords Biodiversity · Litter quality · Macrofauna · Microarthropods · Semi-evergreen forests

Introduction

Secondary forests provide goods and ecosystems services to local populations. Brown and Lugo (1990) pointed out that an increasing proportion (40%) of tropical woodlands were secondary forests, i.e., forests that have been, or are still, influenced by human activities. These authors emphasized the need for a sound, sustainable management of such forested areas, in terms of both biodiversity conservation and human welfare. As in primary forests, soil fauna is essential in secondary forests to efficient nutrient cycling, organic matter dynamics, and maintenance of soil physical structure. Such processes are key determinants for primary production and ecosystem C storage (Petersen and Luxton 1982; Lavelle 1997).

Tropical semi-evergreen dry forests can be regarded as one of the most endangered major tropical ecosystem (Janzen 1988; Lerdau et al. 1991; Gillespie 1999). During the last four centuries, they have been extensively converted to pastures or farmlands, and the remaining secondary woodlands have been exploited for timber, fuel wood, or charcoal production (Murphy and Lugo 1986; Lerdau et al. 1991). In the Caribbean islands, forest decline in dry areas proceeded at an especially high rate due to the small size of landmasses and to the high density of populations (Lugo et al. 1981). At the present time, patches of semi-evergreen, dry secondary natural forests remain on the steepest slopes of these islands. Secondary woodlands issued from forest plantations and intended for timber production may be found on more suitable locations. Soil fauna diversity and its linkage with the whole ecosystem structure and functioning is still poorly known in such forests, as for the

other types of tropical secondary forests (Bernhard-Reversat et al. 2001; Höfer et al. 2001; Warren and Zou 2002).

Soil macrofauna and microarthropod abundance and soil macrofauna diversity were described in two stands of a secondary semi-evergreen dry forest in the island of Grande-Terre, Guadeloupe (Lesser Antilles). These stands had both different soil types and site histories and exhibited various main canopy tree species. The aims of the present work were (1) to measure soil fauna abundance and diversity at the two contrasting sites and (2) to assess the influence of soil physicochemical characteristics and of main tree species on soil fauna abundance and diversity.

Materials and methods

Study sites

The study was carried out in the northern part of the island of Grande-Terre (Guadeloupe, French West Indies) in a tropical semi-evergreen lowland forest (UNESCO classification, Anonymous) that extended more than 2,700 ha. The landscape was characterized by a series of plateaus with frequent outcroppings of the Pleistocene limestone bedrock. The annual rainfall averaged 1,300 mm, February and March being the driest months with less than 60 mm per month on average. The mean annual temperature at the study area was 26°C.

One study site, the natural forest, was located in an old growth, secondary semi-evergreen forest that stretched over a 35-km fault scarp where the steep slope reached 45%. The soil was a shallow calcareous Leptosol (FAO–UNESCO classification, Driessen et al. 2001). Forty-three plant species were present, but *Pisonia subcordata* L. and *Bursera simaruba* (L.) Sarg., two native deciduous tree species, accounted for 40% of the total basal canopy area (Imbert and Portecop 1992).

The other site, the planted forest, was located in a 50-year-old forest plantation grown on a calcareous Vertisol that developed at the edge of a plateau. Despite subsequent silvicultural treatments, natural regeneration of native species has occurred. When the study was conducted, a thick understorey was present, and 46 plant species were present. Among the most abundant tree species were *Swietenia macrophylla* King (planted, exotic), *Tabebuia heterophylla* (DC.) Britton (planted, native), and *B. simaruba* (spontaneous, native), which covered 32, 30, and 7% of the total canopy area, respectively (unpublished data).

Soil physicochemical characteristics

In the natural forest, the upper horizon (A horizon) was 10 cm thick, and the lower horizon (A/C horizon) was found between 10 and 40 cm deep. In the planted forest, the A horizon was 20 cm thick, and the lower horizon (SV horizon) was found between 20 and 60 cm deep. Soil texture was determined at each site, for upper and lower horizons.

Ten soil cores of 40 cm deep were taken randomly at each site, at the beginning of the experiment. These cores were separated in several layers, 0–10, 10–20, 20–30, and 30–40 cm. Samples were sieved to 2 mm and homogenized. Total C and N were performed on subsamples sieved at 200 μm and determined with a CHN Carbo Erba® auto-analyzer.

At each site, three soil samples (10 cm deep) were taken randomly bimonthly during 1 year, and percent moisture was calculated (drying during 72 h at 105°C).

Chemical composition of leaves

Freshly fallen leaves of the chosen plant species were collected from the forest floor. Nitrogen, soluble C, total soluble phenols, tannins, and fibers (cellulose, lignin) were analyzed at the CIRAD laboratory ("Centre de Coopération Internationale en Recherches Agronomiques pour le Développement," Montpellier, France). The leaves were air-dried and milled, and total N content was measured by the Kjeldahl method. Soluble C compounds were extracted by mixing 2 g of the milled leaves in 60-ml cold water during 2 h and determined by the chemical oxygen demand using the HACH method (Jirka and Carter 1975). Total soluble phenolics were extracted with 70% methanol and measured colorimetrically using the Folin–Ciocalteu method (Marigo 1973). Precipitating tannins were measured with the same method after precipitation of bovine serum albumin, washing, and re-dissolution of the precipitate (Hagerman and Butler 1978). Cellulose and lignin were analyzed by sequential digestion of fibers (Van Soest 1963). Samples (0.7 g of the milled leaves) were first extracted with neutral detergent. Lignocellulose ("acid detergent fiber" or ADF) was obtained after extraction with acid detergent. Lignin ("acid detergent lignin" or ADL) was obtained after hydrolysis with 72% H2SO4. Cellulose corresponded to the difference between ADF and ADL.

Soil macroinvertebrates

Macroinvertebrates were sampled during the wet season at both sites under the dominant tree species mentioned above, using the modified Tropical Soil Biology and Fertility method (Anderson and Ingram 1993). Ten or more trees from each species were randomly chosen in the two sites. Four samplings were achieved between 1996 and 1998. During the whole sampling period, 100 samples were taken in the natural forest and 120 in the planted forest. Under the canopy of each tree, soil macroinvertebrates were collected and sorted by hand from a soil block including litter (30×30×30 cm), which was dug out with a spade then sprinkled over a plastic sheet. Soil macroinvertebrates were determined and classified in six groups: Diplopoda, social insects (ants, termites), epigeic earthworms, anecic earthworms, insect larvae, and miscellaneous. The last group contained Coleoptera, Chilopoda, Isopoda, Dermaptera, Blattodea, Araneidae, Heteroptera, Gasteropoda, terrestrial Turbellaria, Homoptera, and Orthoptera. Macroinvertebrates were identified at species level or as morphospecies (i.e., individuals that differed from morphological features).

Soil microarthropods

In November 1996, during the wet season, microarthropods were sampled under the selected tree species in both sites, at the same time than macroinvertebrates. Twenty or more individual trees of each species were randomly chosen in the two sites. Under the canopy of each tree, one core, 100 cm2 in area and 9 cm in depth (including litter layer), was taken. These cores were divided in three layers: 0–3, 3–6, and 6–9 cm, and microarthropods were extracted within a week using the dry funnel method modified from Macfadyen (1957). During the whole sampling period, 55 samples were taken in the natural forest and 60 in the planted forest. The collected animals were classified in three groups: Collembola, Acari, and miscellaneous.

Data processing

The effect of site on soil fauna abundance and diversity was tested with analyses of variance (ANOVA). The within-site effect of plant species on soil fauna abundance and diversity was tested with nested ANOVA, using site as the main factor. The plant species effect was further explored using a posteriori multiple means

comparisons. Fisher's least significant difference (LSD) was used for multiple means comparisons (i.e., LSD comparisons were made only when the main effect of plant species was significant at $p<0.05$). Data were log transformed to normalize the variance across treatments.

Results

Soil physicochemical characteristics

The natural forest soil had a silt loam texture and the planted forest soil had a clayish texture (Table 1). The organic matter content was significantly higher in the Leptosol (natural forest) than in the Vertisol (planted forest), Table 1. Soil moisture (bimonthly measurements) was not significantly different in the two sites (Table 1, $p>0.05$).

Litter analysis

Chemical analyses (Table 2) showed that freshly fallen leaves of *T. heterophylla* had the lowest content in lignin and tannin and were also characterized by the highest cellulose content. Freshly fallen leaves of *S. macrophylla* had a higher phenol content than leaves of *T. heterophylla* and *P. subcordata*. Leaves of *P. subcordata* had a high N content, more than twice that of the other species.

Soil macrofauna

A preliminary analysis of variance showed that there were no significant differences between the four sampling periods, regarding soil fauna collected under the same conditions (i.e., same plant species and site). Thus, the data collected at the four sampling dates were pooled.

Soil macrofauna abundance was significantly higher in the Vertisol of the planted forest than in the Leptosol of the natural forest (Table 3). The effect of tree species on total soil macrofauna density was highly significant ($p<0.001$, Fig. 1, Table 4). *B. simaruba* was associated with the lowest abundance in the natural forest, and *T. heterophylla* was associated with the highest soil macrofauna abundance in the planted forest (Table 4). Diplopoda and epigeic earthworm abundances were the highest under *T. heterophylla* (Table 4).

Tannin content in leaves of the four tree species was weakly negatively correlated with total soil macrofauna abundance ($p=0.09$).

Ninety species and morphospecies were collected over the four sampling dates (Appendix). The two sites had 40 species and morphospecies in common. Three morphospecies and species of earthworms were identified: an epigeic morphospecies *Dichogater sp.* and two anecic species *Amynthas rodericensis* and *Polypheretima elongata*. The anecic species were only found in the planted forest. Seven species of millipedes were identified. There was no significant difference between the two sites regarding soil macrofauna diversity (71 species and morphospecies in the natural forest and 61 in the planted forest). The effect of plant species on soil macrofauna community composition was highly significant ($F=5.4$, $p<0.001$). *B. simaruba* in the natural forest was associated with the lowest soil macrofauna diversity. There was no significant difference between the other tree species regarding soil macrofauna diversity.

Soil microarthropods

Acari and Collembola dominated soil microarthropods in the two study sites (from 72 to 83% of total soil microarthropods). The abundance of total soil microarthropods was not significantly different between the two sites (Table 3). However the abundance of Collembola was significantly higher in the planted forest ($p<0.004$, Table 3), and the abundance of Acari was significantly higher in the natural forest ($p<0.004$, Table 3). The effect of plant species on total soil microarthropod abundance was highly significant ($p<0.001$, Table 4). *S. macrophylla* from the planted forest and *B. simaruba* from the planted forest were associated, respectively, to the highest and the lowest soil microarthropod abundance (Table 4). Soil microarthropods was mainly located in the upper 3 cm of soils (Fig. 2). The percentage of soil microarthropods in the 3- to 9-cm layer of the planted forest was significantly higher than in the natural forest ($p<0.001$, Fig. 2).

Discussion

Soil effect

The two sites presented two distinct soil types which were primarily characterized by contrasted texture and organic matter content. Soil depth was also different within the two sites (data not shown): The Leptosol of the

natural forest was shallow (≤55 cm deep), and the Vertisol of the planted forest was deeper (≥80 cm deep). According to the model proposed by Lavelle et al. (1993), soil biological processes are led by a succession of hierarchized factors; parameters which operate at the largest scales (climate and soil properties) constrain parameters operating at smaller scales (soil fauna and microorganisms). Under the same climatic area, the main regulation for organic matter decomposition was probably exerted by soil properties. Our data and observations corroborated this hierarchical model. In fact, under the same tree species (*B. simaruba*), there was a significant difference in soil fauna abundance and diversity between the two soils.

In the Vertisol under the planted forest, we found two macrofauna communities: (1) an epigeic one dominated by millipedes and (2) a soil-dwelling one dominated by the anecic earthworm *P. elongata*. In the Leptosol under the natural forest, we found an epigeic macrofauna community dominated by millipedes but no soil-dwelling macrofauna community. A likely explanation for this is that anecic earthworms such as *P. elongata* do not tolerate dehydratation. During the dry season, these worms usually move to moist, deeper soil horizons to aestivate (Lavelle and Spain 2001). Such behavior was impossible in the shallow Leptosol of the natural forest. Anecic earthworms are known to contribute to the mixing of mineral and organic material and produce solid organo-mineral aggregates that participate to the maintenance of strong macro-porosity (Alegre et al. 1996; Blanchart et al. 1997). In addition, these invertebrates homogenize the upper part of the soil profile and accelerate litter incorporation into the soil, decomposition of fresh soil organic matter, and nutrient turnover (Jabiol et al. 1995). In previous studies comparing organic matter decomposition and humus formation in the two study sites, the high impact of *P. elongata* on soil functioning was demonstrated. In fact, the activity of this keystone species leads to the formation of a Eumull humus form in the planted forest, which is characterized by the rapid incorporation of litter to an organo-mineral horizon with crumb aggregates (Loranger 2001; Loranger et al. 2003). The biological activity of *P. elongata* is also responsible for the much quicker litter disappearance in the planted forest as compared to the natural forest (Loranger et al. 2002).

Soil microarthropods also varied between the two sites. In the natural forest, soil microarthropod community was dominated by Acari. At this site, the high organic matter content of top layers may be favorable to these mainly fungivorous animals. In the planted forest, the microarthropod community was dominated by Collembola; these mainly saprophagous animals may feed on anecic earthworm casts and mucus (Salmon and Ponge 2001). In the natural forest, soil microarthropod activity was located at the soil surface (upper 3 cm), whereas it extended to the upper 10 cm in the soil of the planted forest. The vertical distribution of microarthropod populations is influenced by several factors. Among them, pH, food resources, and pore size

have been highlighted (Ponge 1999). In our study, differences in microarthropod vertical distribution may be attributed to soil structure, in particular pore size (Didden 1987), and to vertical distribution of organic matter (Poursin and Ponge 1984), due to anecic earthworm activities.

Vegetation quality effect

Because plant species differ both in litter production and quality, individual plant species may have important effects on soil fauna and on the processes they regulate (Wardle et al. 2004). Several other studies report the effect of the chemical composition of decomposing plant material on soil fauna. Soil fauna particularly avoid litter rich in tannin–proteins complexes, polyphenols, and lignin (Satchell 1967; Satchell and Lowe 1967; Tian et al. 1993; Harbone 1997). Those tannin–proteins complexes are degradable only by white rot fungi, and microorganisms found in the guts of earthworm and isopod (Neuhauser et al. 1978). High contents in N and soluble carbohydrates are attractive for soil fauna (Bocock et al. 1960; Satchell and Lowe 1967; Tian et al. 1993).

Therefore, the higher quality of *T. heterophylla* leaves, i.e., their low tannin content (0.3% dry matter), probably explain the development of an abundant macrofauna community under the canopy of this species. On the contrary, soil macrofauna development was limited under *B. simaruba*, *P. subcordata*, and *S. macrophylla* which all have tannin-rich leaves.

Conclusion

Our study shows that, 50 years after tree plantation, soil macrofauna diversity in the planted forest was similar to that of the natural forest. Moreover, soil macrofauna abundance was higher in the planted forest. This is probably due to the fact that these sites were located on two distinct soil types, which were characterized by contrasted features. Moreover, in the planted forest, the activity of the anecic earthworm *P. elongata* may generate food resources (casts, mucus) and microhabitats (burrows, macroaggregates), which favor the development of other soil fauna species. Soil macrofauna abundance and diversity also depended on the tree species effect. The effect of plant litter quality varied according to each dominant tree species and was superimposed to soil effect.

Besides, it has been shown that tree plantations may facilitate secondary succession by reestablishing nutrient cycling, providing habitat for seed dispersers, and improving the microclimate for native species establishment in the understorey (Brown and Lugo 1990). Höfer et al. (2001) also showed that in Amazonian ecosystems, soil fauna in forest plantations was similar to the fauna of the nearby primary forest and, despite structural differences (i.e., in species and dominance spectrum), reached comparable level of functional efficiency (i.e., concerning litter decomposition). Old plantations are known for their high understorey plant species richness, including many native tree species (Lugo 1992). This high plant diversity may, in turn, enhance soil animal diversity.

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Appendix

Soil macrofauna species and morphospecies collected in a natural forest and in a planted forest in North Grande-Terre (Guadeloupe)

1. Diplopoda: 7 species (*Orthomorpha coarctata* Saussure; *Anadenobolus monilicornis* von Porat; *Trigoniulus corallinus* Gervais; *Spirostrophus naresi* Pocock; *Epinannolene pittieri guadeloupensis* Mauriès; *Pseudospirobolellus avernus* Butler; *Siphonophora filiformis* Mauriès)

2. Chilopoda: 3 morphospecies

3. Coleoptera: 4 species (*Phyllophaga patrueloides* Paulian, *Phyllophaga pleei* Blanchard, *Anomala insularis* Castelnau, *Aspisoma ignita* Linnaeus) and 13 morphospecies

4. Formicidae: 4 species (*Acromyrmex octospinosus* Reich, *Ectatomma ruidum* Roger, *Odontomachus chelifer* Latreille, *Azteca delpini antillana* Forel) and 9 morphospecies

5. Isoptera: 1 species (*Nasutitermes costalis* Holmgren) and 2 morphospecies
6. Earthworms: 2 species (*P. elongata* Perrier; *A. rodericensis* Grube) and 1 morphospecies (*Dichogaster sp.*)
7. Insect larvae: 17 morphospecies
8. Isopoda: 3 morphospecies
9. Dermaptera: 1 morphospecies
10. Blattodea: 1 species (*Hemiblabera granulata* Saussure and Zehntner) and 2 morphospecies
11. Araneidae: 13 morphospecies
12. Heteroptera: 2 morphospecies
13. Gasteropoda: 1 morphospecies
14. Turbellaria: 1 morphospecies
15. Homoptera: 1 morphospecies
16. Orthoptera: 2 morphospecies

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Legends of figures

Fig. 1 Soil macrofauna abundance (indivuals m^{-2}) under five selected plant species in a natural forest and in a planted forest in North Grande-Terre (Guadeloupe)

Fig. 2 Abundance and distribution of soil microarthropods between 0- and 9-cm depth, under five selected plant species in a natural forest and a planted forest in North Grande-Terre (Guadeloupe)

Table 1 Soil physicochemical characteristics of a Leptosol (natural forest) and a Vertisol (planted forest) inNorth Grande-Terre (Guadeloupe)

	Natural forest	Planted forest	*p*
A horizon (upper horizon)			
% Clay	10 (1)	78 (0.1)	<0.001
% Silt	71 (3)	14 (0.1)	<0.001
% Sand	19 (4)	8 (0.2)	ns
A/C or SV horizon (deeper horizon)			
% Clay	49 (3)[a]	76 (1.3)[b]	<0.001
% Silt	28 (3)[a]	14 (0.1)[b]	<0.001
% Sand	23 (5)[a]	10 (0.8)[b]	ns
$C_{0–10\ cm}$ (%)	22 (5)	6 (0.5)	<0.001
$C_{10–20\ cm}$ (%)	13 (5)	5 (0.6)	<0.001
$C_{20–30\ cm}$ (%)	11 (2)	2 (0.2)	<0.001
$C_{30–40\ cm}$ (%)	9 (2)	1.5 (0.1)	<0.001
$N_{0–10\ cm}$ (%)	2 (0.3)	0.5 (0.04)	<0.001
$N_{10–20\ cm}$ (%)	1.2 (0.2)	0.4 (0.02)	<0.001
$N_{20–30\ cm}$ (%)	0.9 (0.2)	0.2 (0.02)	<0.001
$N_{30–40\ cm}$ (%)	0.8 (0.2)	0.1 (0.01)	<0.001
Soil moisture (%)	31 (8)	33 (5)	ns

Standard errors are given in parentheses. *df*=1
ns Non significant
[a] A/C horizon
[b] SV horizon

Table 2 Chemical composition of freshly fallen leaves of five selected tree species, in a natural forest and in a planted forest in North Grande-Terre (Guadeloupe)

	Natural forest		Planted forest			p
	B	P	B	S	T	
Total N (%)	1.1 (0.1) [b]	2.5 (0.1) [a]	1.01 (0.1) [b]	1.1 (0.1) [b]	0.9 (0.1) [b]	<0.001
Soluble C (%)	8.3 (0.3)	2.4 (0.5)	8.3 (0.3)	3.0 (0.3)	5.3 (0.3)	ns
Soluble phenols (%)	10.0 (1.0) [ab]	6.7 (0.6) [bc]	10.0 (1.0) [ab]	12.7 (0.6) [a]	4.5 (2.3) [c]	0.01
Tannins (%)	3.3 (0.7) [a]	1.8 (0.8) [a]	3.3 (0.7) [a]	2.9 (0.6) [a]	0.3 (0.1) [b]	0.03
Cellulose (%)	20.9 (0.4) [b]	19.2 (0.6) [b]	20.9 (0.4) [b]	19.8 (4.1) [b]	32.1 (2.3) [a]	0.01
Lignin (%)	22.8 (9.6) [a]	29.5 (15.1) [a]	22.8 (9.6) [a]	29.1 (10.0) [a]	12.0 (2.1) [b]	0.05

Values (percent of dry matter) are means of three replicates; standard errors are given in parentheses. For each tree species, means with the same letter are not significantly different based on a LSD test. df=3
ns Nonsignificant; B *Bursera simaruba*; P *Pisonia subcordata*; S *Swietenia macrophylla*; T *Tabebuia heterophylla*

Table 3 Means (individuals per m2), standard errors (in parentheses), F ratio, and p values (ANOVA tests) for the responses of soil fauna abundance to site effects in a natural forest and in a planted forest in North Grande-Terre (Guadeloupe)

	Natural forest	Planted forest	*F*	*p*
Diplopoda	37 (7)	82 (14)	32.7	<0.001
Epigeic earthworms	2 (1)	10 (3)	8.4	0.004
Anecic earthworms	0 (0)	7 (2)	9.8	0.002
Insect larvae	9 (2)	33 (9)	27.6	<0.001
Social insects	20 (6)	31 (11)	0.1	ns
Total soil macrofauna	100 (14)	183 (24)	32.8	<0.001
Collembola	1.104 (3.103)	2.104 (3.103)	8.5	0.004
Acari	3.104 (4.103)	2.104 (2.103)	8.8	0.004
Total soil microarthropods	5.104 (7.103)	6.104 (6.103)	0.4	ns

df=1
ns Nonsignificant

Table 4 Means (individuals per m^2), standard errors (in parentheses), F ratio, and p values (ANOVA tests) for the responses of soil fauna abundance to plant species nested within sites effect [plant species (sites)], in a natural forest and in a planted forest in North Grande-Terre (Guadeloupe)

	Natural forest		Planted forest			*F*	*p*
	B	P	B	S	T		
Diplopoda	16 (3) ^{c}	59 (12) ^{b}	64 (16) ^{b}	67 (10) ^{b}	115 (16) ^{a}	8.9	<0.001
Epigeic earthworms	1 (1) ^{b}	2 (1) ^{b}	5 (2) ^{b}	4 (1) ^{b}	22 (6) ^{a}	8.8	<0.001
Anecic earthworms	0 (0)	0 (0)	2 (1)	10 (3)	9 (3)	1.7	ns
Insect larvae	9 (2)	9 (2)	36 (18)	24 (4)	38 (7)	2.1	ns
Social insects	19 (7)	22 (4)	12 (5)	34 (11)	46 (17)	1.2	ns
Total soil macrofauna	66 (16) ^{c}	132 (26) ^{b}	146 (47) ^{b}	155 (31) ^{b}	248 (51) ^{a}	11.8	<0.001
Collembola	1.104 (3.103) ^{b}	9.103 (4.103) ^{c}	2.103 (3.102) ^{c}	4.104 (7.103) ^{a}	1.104 (3.103) ^{b}	8.7	<0.001
Acari	4.104 (7.103) ^{a}	3.104 (6.103) ^{a}	6.103 (6.102) ^{b}	3.104 (4.103) ^{a}	2.104 (3.103) ^{a}	10.8	<0.001
Total soil microarthropods	5.104 (1.104) ^{b}	4.104 (9.103) ^{b}	1.104 (7.102) ^{c}	9.104 (1.104) ^{a}	5.104 (5.103) ^{b}	15.9	<0.001

For each group, means with the same letter are not significantly different based on LSD. *df*=3
ns Nonsignificant; B *Bursera simaruba*; P *Pisonia subcordata*; S *Swietenia macrophylla*; T *Tabebuia heterophylla*

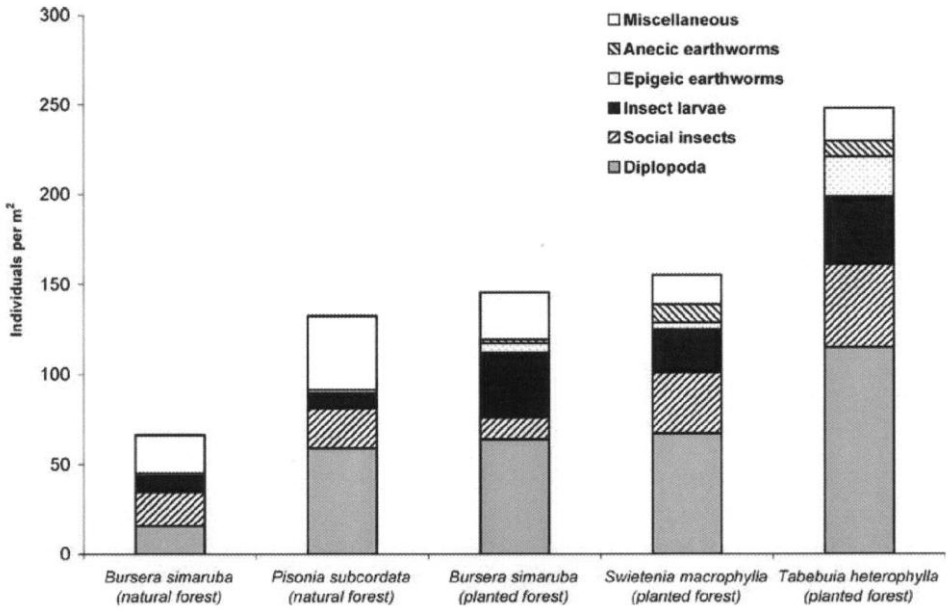
Miscellaneous
Anecic earthworms
Epigeic earthworms
Insect larvae
Social insects
Diplopoda
Individuals per m²
300
250
200
150
100
50
0
Bursera simaruba (natural forest)
Pisonia subcordata (natural forest)
Bursera simaruba (planted forest)
Swietenia macrophylla (planted forest)
Tabebuia heterophylla (planted forest)

Fig. 1

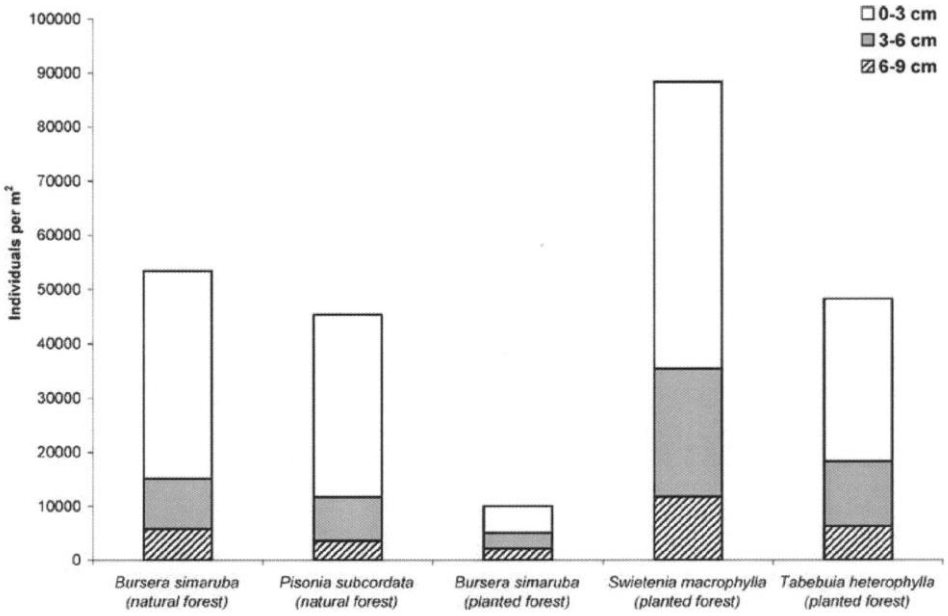
0-3 cm
3-6 cm
6-9 cm
Individuals per m²
100000
90000
80000
70000
60000
50000
40000
30000
20000
10000
0
Bursera simaruba (natural forest)
Pisonia subcordata (natural forest)
Bursera simaruba (planted forest)
Swietenia macrophylla (planted forest)
Tabebuia heterophylla (planted forest)

Fig. 2