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ORIGINAL PAPER

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A multi-scale study of soil macrofauna biodiversity in Amazonian pastures

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Abstract The influence of three spatially hierarchical factors upon soil macrofauna biodiversity was studied in four pasture plots in eastern Amazonia. The first factor was the local depth of the soil. The second factor was the ground cover type on the soil samples (bare ground, grass tufts, dead trees lying on the ground). The third factor was the dimensions of the grass tufts sampled (size and shape). The effect of each factor upon the morphospecies richness and density of total soil macrofauna was analysed. Detailed results are given for earthworms, termites, ants, beetles and spiders. All factors significantly affected the morphospecies richness and/or density of the soil macrofauna. The type of ground cover had the strongest influence, affecting the total richness and density of the soil macrofauna and of almost all the groups represented. The soil depth affected only the density of the termites and the global morphospecies richness. Interactions between soil depth and ground cover type affected the total macrofauna morphospecies richness and the density of the earthworms. The dimensions of the grass tuft influenced the global morphospecies richness, the morphospecies richness of the ants and the density of the spiders.

Keywords Soil biodiversity · Scale · Hierarchy · Pasture · Amazonia

Introduction

In Amazonia cattle ranching is very important in terms of land surface (Muchagata and Brown 2003) and is often characterized by a dramatic decrease in pasture productivity after 10 years of exploitation (Costa and Rehman 1999; Muchagata and Brown 2003). This phenomenon is accompanied by a reduction in soil macrofauna biodiversity (Barros et al. 2002; Fragoso et al. 1997).

Soil macrofauna are important in the functioning of ecosystems as they improve nutrient cycling through decomposition processes and modify the physical properties of the soil (de Bruyn and Conacher 1990; Ekschmitt and Griffiths 1998; Lavelle et al. 1997; Wolters 2001). Determining the factors influencing soil macrofauna biodiversity is of prime importance in areas of deforestation in Amazonia.

Biodiversity is shaped by the co-action of numerous factors which determine the maintenance or the extinction of the biota. Because these factors act at different spatial and temporal scales, and may interact, ecological processes are scale dependent and are hierarchically structured (Allen and Starr 1982; Wiens 1989). As a consequence, multi-scale approaches are recommended for the rigorous description of the behaviour of ecological processes (Levin 1992). Soil invertebrate assemblages are good material for testing this set of concepts as they are strongly determined by environmental factors (Lavelle and Spain 2001).

The purpose of this study was to identify spatially hierarchical factors that influence soil macrofauna biodiversity in southeastern Amazonian pastures. The aim was not to describe the entire community fully, but rather to

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describe the multiple-scale relationships between soil macrofauna biodiversity and the environment. A two-level taxonomic approach was adopted to show the effect of changing the taxonomic resolution. The discussion of community aspects, such as species composition, was secondary to the discussion of biodiversity patterns.

Materials and methods

Study site

This study was undertaken at the Benfica Field Station (5° 16′S, 49°50′E), in a 7-year-old community of smallholders of eastern Amazonia, near Marabá, State of Pará, Brazil. The climate is tropical humid with an annual rainfall of 1,800 mm and an average temperature of 26°C. The rainy season generally starts in November or December and ends during May or June. The landscape is fragmented and consists of a network of 50-m-high hillocks mainly covered by forest and pasture. Pasture plots studied were 4–6 years old and dominated by the introduced African grass *Brachiaria bryzanthia* cv. *marandu*.

Clayey Ferralsols (ISSS Working Group R.B. 1998) are the dominant soils. However, from the top of the hillocks to the bottom, the depth of the Ferralsol, i.e. the depth of the permeable horizon, varies from >3 m to <1 m. At the top of the slope the soil is deep, allowing vertical drainage of water. In the middle of the slope the soil depth is intermediate and a change in soil colour from dark brown to yellowish brown shows the poorer drainage conditions. At the bottom of the slope the soil is thinner (Cambisols) and has a lateral, superficial drainage.

In the pastures, grass tufts are clearly separated from one another by bare ground. This produces a kind of clumped vegetation cover, with high spatial heterogeneity.

Sampling design and factors studied

Four pasture plots of 6 ha on average were studied. Within each plot the influence of soil depth (i.e. the depth of the permeable horizon) was investigated by sampling the soil macrofauna in three depth classes (soil deeper than 1.20 m, soil between 1.20 m and 0.60 m deep and soil shallower than 0.6 m). Within each soil depth class the influence of the ground cover type was studied. Soil samples were taken beneath one of the following types of cover: bare ground (no cover), grass tufts, and dead tree trunks lying on the ground. Samples taken below grass tufts or dead trees are referred to as “covered ground” hereafter. The influence of the dimensions of the grass tuft sampled was studied in deep and shallow soils. The dimensions of the grass tufts sampled comprised basal area (the ground surface area), perimeter and roundness (surface area/perimeter). These features are considered to be among the most important for describing a mapped habitat (Giles and Trani 1999).

All combinations of soil depth and ground cover type were sampled in order to allow the study of each factor separately, as well as the eventual interactions between factors (Winer 1971). In each plot 15 sampling points were distributed regularly along three 50-m-long transects separated by >20 m. Each transect was located along a particular soil depth. In addition to these 60 regular samples, 24 supplementary sampling points were added along the transects in order to complete all combinations of soil depth and cover type. Overall, 42 samples were taken under bare ground, 42 under covered ground. The effects of the grass tuft dimensions were studied using the same samples as used for the other factors. The dimensions of the sampled grass tuft were determined by mapping at 1/200 scale the ground cover under the soil samples.

Soil macrofauna sampling

The soil macrofauna (i.e. animals with body length >2 mm) were sampled using the tropical soil biology and fertility method (Anderson and Ingram 1993) at the end of the 2002 rainy season. Samples consisted of a single block of soil, 25×25×30 cm^3 deep, dug out quickly. A quadrat was fixed on the ground prior to taking the soil samples and the litter macrofauna were collected by hand. The soil macrofauna were sorted and the animals were stored in 75% alcohol except for earthworms which were preserved in 4% formaldehyde.

Statistical analysis

The effects of the factors on soil macrofauna morphospecies richness and density were evaluated by separated two-way factorial ANOVA for each group. Subsequently Scheffé post hoc tests were used for multiple comparisons (Sokal and Rohlf 1995). The analyses of the density were performed using log(x+1)-transformed data sets in order to reduce the skewness and homogenize the variance (Winer 1971; Webster 2001). The relationships between soil macrofauna and microhabitat features were investigated separately using simple linear regression.

Results and discussion

The density of the soil macrofauna was low compared with other studies of Amazonian pastures. We found an average of 520 individuals (ind.) m^{-2} whereas others have found from 840 up to 2,347 ind. m^{-2} in pastures sampled all over South America (Barros et al. 2002; Decaëns et al. 1994; Decaëns et al. 1999; Lavelle and Pashanasi 1989). However, we found far more morphospecies than previously found in Brazilian pastures, with 99 adult morphotypes, as opposed to 48 found by Barros et al. (2001) for example. Termites, ants and earthworms were the most abundant groups as has already been reported by

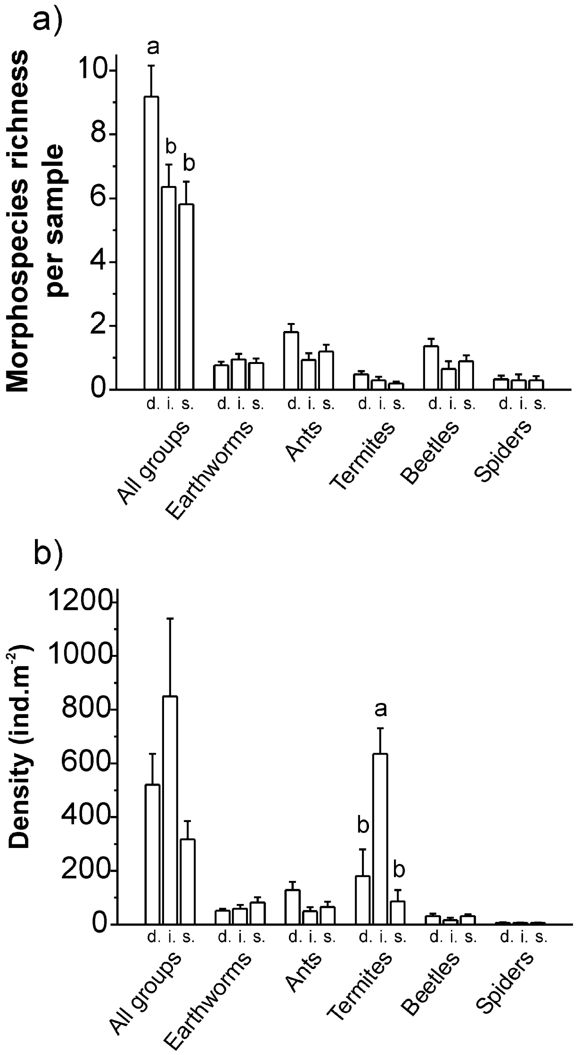

Fig. 1 Average morphospecies richness (**a**) and density (**b**) for the different fauna groups for each soil depth: deep soil (*d.*: >1 m); intermediate soil (*i.*: 1 m>soil>0.6 m); shallow soil (*s.*: <0.6 m). For each group, *different letters* indicate significant differences (Scheffé test, $P<0.05$). *ind.* Individuals

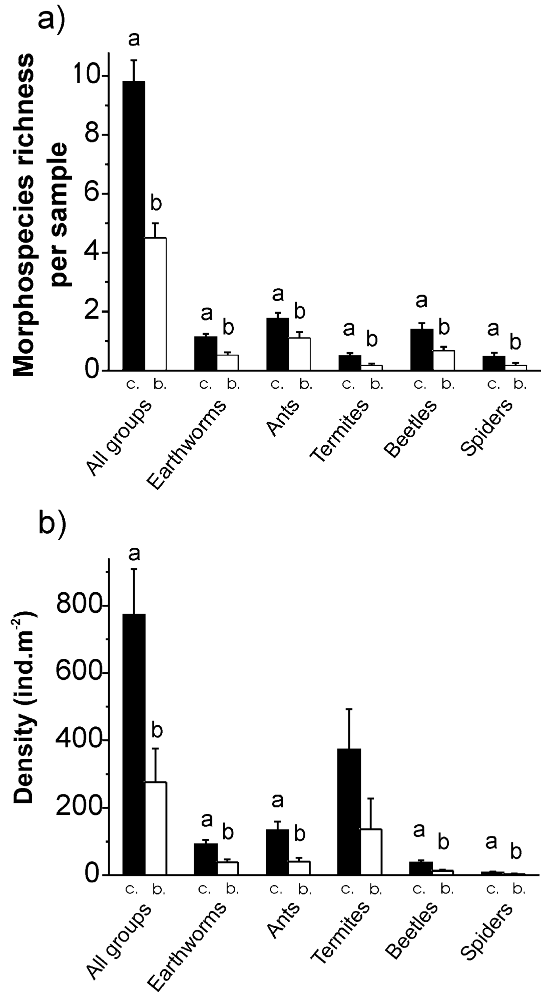

Fig. 2 Average morphospecies richness (**a**) and density (**b**) for the different fauna groups according to the ground cover above the sample [covered soil (*c.*), bare ground (*b.*)]. For each group, *different letters* indicate significant differences (Scheffé test,$P<0.05$)

other studies in tropical areas including Amazonian pastures (e.g. Barros et al. 2002; Barros et al. 2003; Decaëns et al. 1994). Termites were dominated by the *Heterotermes* and *Cornitermes* genera, which are soil feeders. Ants were dominated by the genus *Hypoponera*, and earthworms were dominated by an *Andiorrhinus* species.

Overall morphospecies richness and density of termites were affected by soil depth (Table 1), but in different ways. Overall morphospecies richness was greater in deep soils (nine morphospecies per sample) than in shallow soils (five to six morphospecies per sample, Fig. 1a). Density of termites was dramatically higher in intermedi-

Table 1 ANOVA table for morphospecies richness and density of the different fauna groups

	df	All groups		Earthworms		Ants		Termites		Beetles		Spiders	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Morphospecies richness													
Soil type	2	5.4	0.006	0.8	0.451	1.7	0.183	2.0	0.141	2.2	0.123	<0.1	0.957
Soil cover	1	30.3	<0.001	15.9	<0.001	4.0	0.048	7.0	0.01	5.1	0.026	4.7	0.033
Soil type×soil cover	2	4.1	0.02	2.7	0.076	0.7	0.489	0.7	0.518	3.6	0.033	0.6	0.533
Density													
Soil type	2	2.5	0.091	2.9	0.062	2.2	0.114	4.1	0.02	0.9	0.424	<0.1	0.98
Soil cover	1	6.0	0.017	11.6	0.001	7.7	0.007	1.5	0.221	6.4	0.013	5.6	0.021
Soil type×soil cover	2	0.7	0.49	5.2	0.007	1.2	0.308	0.2	0.818	2.1	0.128	1.2	0.32

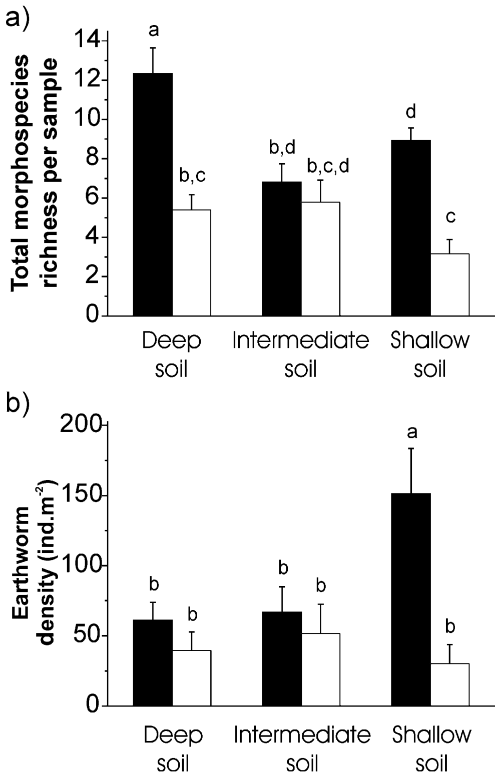

Fig. 3 Details of the interactions between soil depth and ground cover on the overall morphospecies richness and earthworms density. For each soil type, *different letters* indicate significant correlations (P<0.05)

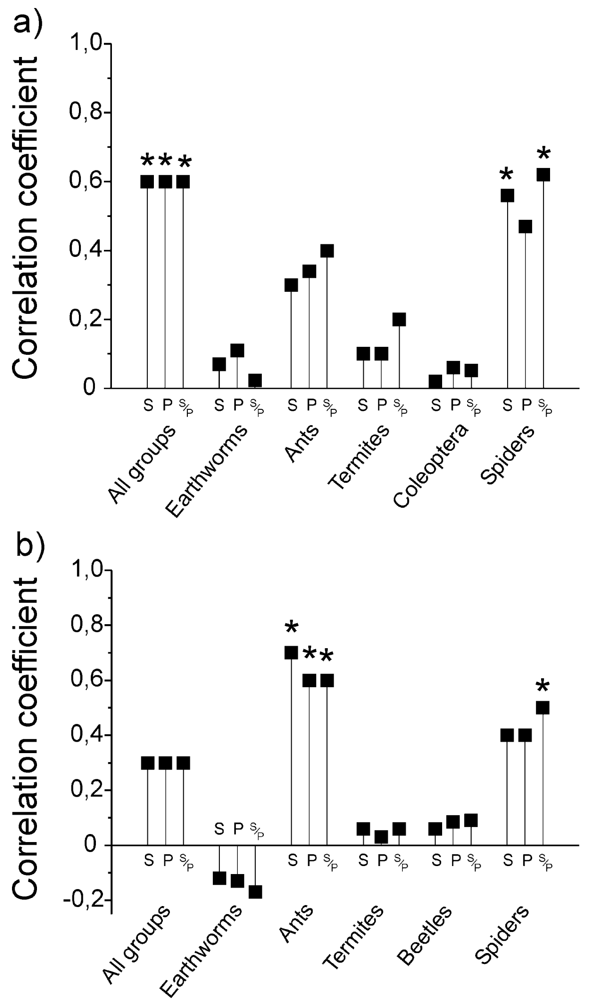

Fig. 4 Regression coefficients between morphospecies richness (**a**) and density (**b**) for the different fauna groups and microhabitat features. *P<0.05 (Scheffé test). *S* Surface area, *P* perimeter, *S/P* surface area/perimeter i.e. roundness

ate soils than in shallow and deep soils (640 vs. 128 and 86 ind. m^{-2}, Fig. 1b). Soil properties are often cited as one of the dominant factors influencing soil macrofauna, vegetation and soil processes (Curry 1987; Lavelle et al. 1997; Lavelle and Spain 2001; Radford et al. 2001). In the Benfica area, the soil cover was organized in the same way as that in a previous study in French Guiana (Sabatier et al. 1997). In this type of soil cover, the soil depth is related to the local soil hydraulics. When the soil is deep it allows vertical water flow, whereas in shallow soil the drainage of water is almost entirely superficial and lateral. As a consequence, deep soils retain water for longer periods and maintain higher humidity levels than shallow soils. This might explain the observed sensitivity of the termites to the soil depth in this work. The termites found were all soil feeders and thus the soil moisture content might be critical for their soil consumption, especially during the dry season. Surprisingly, earthworms were not influenced by the soil depth. This is surprising because earthworms are known to be sensitive to soil moisture (Edwards and Bohlen 1996).

The ground cover type had a major effect on the overall macrofauna and all the groups (Table 1). The overall morphospecies richness was twice as high under covered soil (nine to ten morphospecies per sample) than under bare ground (four to five morphospecies per sample, Fig. 2a). The overall density was almost 3 times higher under covered ground (768 ind. m^{-2}) than under bare ground (272 ind. m^{-2}, Fig. 2b). The morphospecies richness and density of all groups were higher under covered soil than in the bare ground. The density of ants, beetles and spiders was higher under the grass than under tree trunks or in bare ground (results not shown). The density of termites and earthworms was higher under tree trunks than under grass tufts and under bare ground (results not shown). The soil under grass tufts and tree trunks, therefore, provides an attractive microenvironment for soil macrofauna. The effect of tree trunks suggests that their presence on the surface was detected by the soil macrofauna beneath. It has already been shown that earthworm casts attract soil macrofauna in Colombian pastures (Decaëns et al. 1999) and that subterranean termites use the soil temperature for surface food location (Ettershank et al. 1980). In our case, the tree trunks may affect the macrofauna in the underlying soil by modifying the local soil microclimatic conditions, such as soil temperature and soil humidity, or by nutrients leaching from the wood during rainfall. Gaps between the soil and the tree trunks might also provide shelter for species that

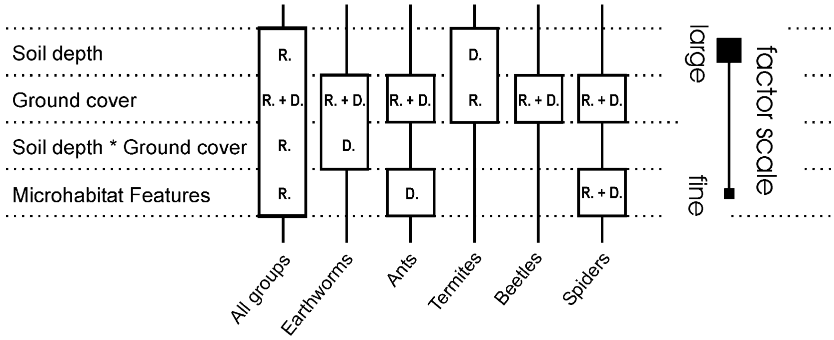

Fig. 5 Summary of the results. Significant effect observed on morphospecies richness (*R.*) and density (*D.*), respectively, for each factor and each fauna group

had surface activity, such as anecic earthworms, diplopods (Hamazaki 1996) and spiders. Grass tufts may also modify the properties of the underlying soil as their leaves act as a protection against solar radiation, which is critical for termites when foraging (Smith and Rust 1994). In our survey, the soil temperature was much cooler under the grass tufts than in bare ground (unpublished data). However, the part of the tufts below the ground, i.e. the roots, also probably had an effect because the rhizosphere is a particular microenvironment for the soil fauna (Lavelle and Spain 2001). The roots of grass tufts may also provide physical support for the nests of ants and termites. It is, however, surprising that the morphospecies richness of ants was higher in the microhabitats as they are very competitive social insects (Hölldobler and Wilson 1990). On the surface of the land, the structures formed by the grass tuft leaves might provide a habitat for cryptic soil arthropods with surface activity, such as spiders (Mrzljak and Wiegleb 2000).

The effect of the ground cover type on the overall morphospecies richness and earthworm density interacted with the effect of the soil depth (Table 1). The effect of the ground cover type on morphospecies richness was significant in deep and shallow soil, but not in intermediate soil (Fig. 3a). Its effect on earthworm density was significant only in shallow soil (Fig. 3b). On the other hand, the soil depth effect on total morphospecies richness was significant only in deep soil. The soil depth effect on earthworm density was significant in deep soil but not in intermediate or shallow soil, and not significant when no interaction with ground cover type was taken into account (Table 1, Fig. 1b). This results show that factors of different spatial scale may interact and produce complex responses of the soil biota.

Overall morphospecies richness was positively correlated with all grass tuft dimensions (Fig. 4a). Overall density was not correlated with grass tuft dimensions but the relationship was positive (Fig. 4b). The morphospecies richness of spiders and the density of ants were positively correlated with the dimensions of the grass tufts. The morphospecies richness and density of other groups were not correlated with the grass tuft dimension but the relationship was always positive, with the exception of the density of earthworms. These results suggest that soil macrofauna may be influenced by the size and shape of the microhabitat. The relationship between the area/shape of a patch and biodiversity has already been studied extensively (e.g. Forman and Godron 1986; Buechner 1987) with numerous examples at the scale of islands or forest patches (e.g. in Amazonia: Bierregard et al. 2001), with plants, birds, mammals, arthropods (Jolimakï et al. 1998) or ants (Cole 1983), but there are very few studies of soil macrofauna at the microhabitat scale. Our results confirm those reported by Goldsbrough et al. (2003) who showed a correlation between the diversity of surface arthropods and the size of the rocks used as shelter, and contradict the relationship between the density of diplopods and the surface area/perimeter ratio found by Hamazaki (1996). However, in this case, the correlation between the density and the surface area/perimeter ratio of the habitat was interpreted as a result of the higher probability of diplopods encountering a narrow habitat during movement.

All the factors considered in the present study had an influence on the soil macrofauna biodiversity (Fig. 5), which might serve as a basis for ranking species according to their sensitivity and grain size. By definition (Forman and Godron 1986; Kotliar and Wiens 1990), a coarse-grain species is influenced only by large-scale factors; a fine-scale species is sensitive to small-scale as well as to large-scale factors. In this study we apply this concept to biodiversity although it was initially defined for species. An estimation of the sensitivity may be done according to the number of factors affecting the considered group. A sensitive group would be influenced by most of the factors (in terms of morphospecies richness or density in this study), whereas a less sensitive group would be influenced by fewer factors.

Conclusion

All the factors considered in the present study had an influence on the soil macrofauna, despite their variety of spatial scale. The statistical interactions between soil depth and ground cover demonstrated that these factors may interact in the field, and as a consequence, are not fully independent. In other words, these factors are hierarchically organized. Furthermore, the two-taxonomic-level approach we adopted showed that the trends obtained at a coarse taxonomic resolution are not necessarily found at a finer resolution. This illustrates the importance of choosing the appropriate taxonomic resolution for the questions being studied.

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References

Allen TFH, Starr TB (1982) Hierarchy: perspectives for ecological complexity, 1st edn. University of Chicago Press, Chicago, Ill.

Anderson JM, Ingram JSI (1993) Tropical soil biology and fertility. A handbook of methods, 1st edn. CAB International, Wallingford

Barros E, Curmi P, Hallaire V, Chauvel A, Lavelle P (2001) The role of macrofauna in the transformation and reversibility of soil structure of an oxisol in the process of forest to pasture conversion. Geoderma 100:193–213

Barros E, Pashani B, Constantino R, Lavelle P (2002) Effects of land-use system on the soil macrofauna in western Brazilian Amazonia. Biol Fertil Soils 35:338–347

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

Bierregard RO, Gascon C, Lovejoy TE, Mesquita RCG (2001) Lessons from Amazonia. The ecology and conservation of a fragmented forest. Yale University Press, New Haven, Conn.

de Bruyn LA, Conacher AJ (1990) The role of termites and ants in soil modification: a review. Aust J Soil Res 28:55–93

Buechner M (1987) Conservation in insular parks: simulation of factors affecting the movements of animal across park boundaries. Biol Conserv 41:57–76

Cole BJ (1983) Assembly of mangrove ant communities: colonization abilities. J Anim Ecol 52:349–355

Costa FP, Rehman T (1999) Exploring the link between farmer's objectives and the phenomenon of pasture degradation in the beef production systems of Central Brazil. Agric Syst 61:135–146

Curry JP (1987) The invertebrate fauna of grassland and its influence on productivity. III. Effects on soil fertility and plant growth. Grass Forage Sci 42:325–341

Decaëns T, Lavelle P, Jiménez JJ, Escobar G, Rippenstein G (1994) Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. Eur J Soil Biol 30:157–168

Decaëns T, Mariani L, Lavelle P (1999) Soil surface macrofauna communities associated with earthworm casts of the Eastern Plains of Colombia. Appl Soil Ecol 13:87–100

Edwards CA, Bohlen PJ (1996) Biology and ecology of earthworms, 3rd edn. Chapman and Hall, London

Ekschmitt K, Griffiths BS (1998) Soil biodiversity and its implications for ecosystem functioning in a heterogeneous and variable environment. Appl Soil Ecol 10:201–215

Ettershank G, Ettershank JA, Withford WG (1980) Location of sources by subterranean termites. Environ Entomol 9:645–648

Forman RTT, Godron M (1986) Landscape ecology, 1st edn. Wiley, New York

Fragoso C, Brown GG, Patron JC, Blanchart E, Lavelle P, Pashanasi B, Senapati B, Klumar T (1997) Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. Appl Soil Ecol 6:17–35

Giles RH Jr, Trani MK (1999) Key elements of landscape pattern measures. Environ Manage 23:477–481

Goldsbrough CL, Hochuli DF, Shine R (2003) Invertebrate biodiversity under hot rocks: habitat use by the fauna of sandstone outcrops in the Sydney region. Biol Conserv 109:85–93

Hamazaki T (1996) Effects of patch shape on the number of organisms. Landsc Ecol 11:299–306

Hölldobler B, Wilson EO (1990) The ants, 1st edn. Harvard University Press, Cambridge, Mass.

ISSS Working Group R.B. (1998) World reference base for soil resources: introduction. In: Deckers JA, Nachtergaele FO, Spaargaren OC (eds) International Society of Soil Science (ISSS), 1st edn. ISRIC, FAO, ISSS, Leuven

Jolimakï J, Huhta E, Itämies J, Rahko P (1998) Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Can J For Res 28:1068–1072

Kotliar NB, Wiens JA (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59:253–260

Lavelle P, Pashanasi B (1989) Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). Pedobiologia 22:283–291

Lavelle P, Spain AV (2001) Soil ecology, 1st edn. Kluwer, Amsterdam

Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillion S (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. Eur J Soil Biol 33:159–193

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Mrzljak J, Wiegleb G (2000) Spider colonization of former brown coal mining areas-time or structure dependent? Landsc Urban Plan 51:131–146

Muchagata M, Brown K (2003) Cows, colonists and trees: rethinking cattle and environmental degradation in Brazilian Amazonia. Agric Syst 76:797–816

Radford BJ, Wilson-Rummenie AC, Simpson GB, Bell KL, Fergusson MA (2001) Compacted soil affects soil macrofauna populations in a semi-arid environment in central Queensland. Soil Biol Biochem 33:1869–1872

Sabatier D, Grimaldi M, Prévost M-F, Guillaume J, Godron M, Dosso M, Curmi P (1997) The influence of soil cover organisation on the floristic and structural heterogeneity of a Guianan rain forest. Plant Ecol 131:81–108

Smith JL, Rust MK (1994) Temperature preference of the western subterranean termite, *Reticulitermes hesperus* Banks. J Arid Environ 28:313–323

Sokal RR, Rohlf FJ (1995) Biometry: the principles and practice of statistics in biological research, 3rd edn. Freeman, New York

Webster R (2001) Statistics to support soil research and their presentation. Eur J Soil Sci 52:331–340

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Winer BJ (1971) Statistical principles in experimental design, 1st edn. McGraw-Hill, New York

Wolters V (2001) Biodiversity of soil animals and its function. Eur J Soil Biol 37:221–227