Earthworm Communities of Tropical Agroecosystems: Origin, Structure and Influence of Management Practices

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Summary

Data of 145 and 69 earthworm communities from managed and natural ecosystems, respectively, of four continents and 15 tropical countries were analysed. The aim of the study was to separate the influence of phylogenetic, environmental and agricultural factors on the structure of earthworm communities in agroecosystems, and to evaluate their relative importance in the whole soil macrofauna community. Earthworms comprise 40–90% of macrofaunal biomass in most ecosystems except for annually cropped systems.

Three major conclusions were drawn from the analysis of community structure (regional analysis): (i) crops were, independently of region, characterized by a loss of native species and by the dominance of exotic endogeics; (ii) pastures were highly heterogenous in terms of native or exotic species dominance; (iii) native species survived better in management ecosystems of India and Africa than in Mexico–Central America.

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Local analysis in selected countries indicated that, as a general rule, the intensity of agricultural practices is negatively correlated with the amount of native species and the total abundance and biomass of earthworms; the only exception was found in the conversion of savannas to pastures, in Colombian llanos.

Introduction

In Chapter 1, a small set of earthworm species that frequently occur in tropical agroecosystems was listed. These species, both natives (widespread and locally distributed) and exotics, were found commonly in a variety of agroecosystems in different countries of the humid tropics. Selection of these species was made on the basis of frequency, without considering other attributes of populations (abundance, biomass or dominance) and communities (number of species, ecological categories). In this chapter, we first discuss the relative importance of earthworms in macrofauna communities, across a wide range of types of land use and sites from four continents. Earthworm communities from four main tropical regions are then described, with emphasis on the effects of different types of land use on structure and diversity. Finally, worldwide comparisons are made in order to discriminate between influences of phylogenetic, environmental and anthropogenic constraints on the structure of these communities.

Determinants of earthworm communities

Earthworm communities are the result of interactions between environmental variables and biological processes occurring over a long time span. The particular species assemblages that we observe in any community reflect selective (predation, competition, mutualism, etc.), stochastic (e.g. sudden unpredictable changes of weather) and historical forces (Ricklefs and Schluter, 1993). In addition, migrations, invasions and extinctions confer a dynamic status on these systems.

Although these communities have not been fully characterized, the following generalizations are observed: (i) a similar number of species in tropical and temperate ecosystems (between 13 and 17 species) (Lavelle, 1983); and (ii) separation of species into a few ecological groups, which represent particular adaptations developed to survive in litter (epigeics), soil (endogeics) or both (anecics). The predominance of one or other ecological group is determined by a hierarchical suite of environmental factors (Lavelle, 1983; Fragoso and Lavelle, 1992). Temperature appears at the higher level of determination, followed by resource availability (soil nutrient richness) and seasonal variation of humidity (Fragoso and Lavelle, 1992). In general, epigeics predominate in colder environments whereas, in the tropics, communities are dominated by endogeics. In tropical regions, where soil temperature generally remains constant, endogeic communities can shift to epigeic communities if soil nutrients and seasonality of rains are low (Fragoso and Lavelle, 1992). Soil organic matter content also influences earthworm communities, by dividing endogeics into groups that feed on rich (polyhumic), medium (mesohumic) or poor (oligohumic) substrates (Lavelle, 1983). More details on the defintion of these ecological groups are given in Lavelle (1988) and Fragoso *et al.* (1997). Phylogenetic constraints could also play a role, because it seems that epigeic communities are more frequent in South American and African soils than in Central American soils.

When natural forests and/or savannas are destroyed and substituted by agroecosystems, the original earthworm communities are modified. Changes can occur at the taxonomical (e.g. substitution of stenoecic natives by exotics and/or euryoecic natives – see Chapter 1), ecological (e.g. increase or decrease in number of species, abundance or number of ecological categories) or both levels.

The main objective of this chapter was to find the patterns and/or rules in the assemblage of earthworm communities in agroecosystems, and to answer the following questions:

1. What is the relative importance of earthworms in macrofaunal communities?
2. What is the importance of phylogenetic constraints for the structure of earthworm communities?
3. How does community structure respond to different types of land-use practices?
4. To what extent do communities retain effects of past disturbances (cropping, application of chemicals, time elapsed)?
5. To what degree does the original natural community determine the structure of the agroecosystem community?

Analysis of Data and Regions

Earthworm community data from a variety of countries and regions throughout the humid tropics were obtained from literature reviews and field sampling. In the first case, data were taken from several localities in Mexico (Fragoso and Lavelle, 1987, 1992; Fragoso, 1989, 1992, 1993; Arteaga, 1992), Costa Rica (Fraile, 1989), Lesser Antilles (Barois *et al.*, 1988), Peru (Lavelle and Pashanasi, 1988, 1989; Rombke and Verhaagh, 1992), Colombia (Decaëns *et al.*, 1995), Ivory Coast (Lavelle, 1978; Tondoh, 1994; Gilot *et al.*, 1995), Congo (Montadert, 1985; M'Boukou, 1997), India (Dash and Patra, 1977; Kale and Krishnamoorthy, 1978; Chaudry and Mitra, 1983; Julka and Mukherjee, 1984; Krishnamoorthy, 1985; Mishra, 1986; Pani, 1986; Julka and Senapati, 1987; Mohanty, 1988; Bhadauria and

Ramakrishnan, 1989; Julka *et al.*, 1989; Ismail *et al.*, 1990; Bano and Kale, 1991; Darlong and Alfred, 1991; Blanchart and Julka, 1997) and Venezuela, Malaysia and Sarawak (Fragoso and Lavelle, 1992). Additional sampling was conducted in Mexico (Ortiz and Fragoso, unpublished), India (Senapati *et al.*, unpublished), Cuba (Martinez, unpublished) and Colombia (Jimenez, unpublished). In total, we analysed 214 sites from 63 localities within 15 tropical countries. Of these numbers, 145 sites were tropical agroecosystems and 69 natural ecosystems. Table 2.1 shows the classification of these sites by country and land-use system; this table also indicates the type of community data. All data were stored in EWDBASE (see Chapter 1).

In order to discriminate between the influence of history (phylogenetic lineages) and environmental–anthropogenic influence (natural and managed ecosystems), communities were separated into four regions and eight major vegetation types. The regions were Asia (India, Sarawak, Malaysia), Africa (Ivory Coast, Congo), Central America (Mexico, Cuba, Lesser Antilles, Costa Rica) and South America (Peru, Colombia, Brazil and Venezuela). The types of vegetation were tropical rainforests (below 1000 m of altitude and annual precipitation over 2000 mm), tropical subdeciduous forests (below 1000 m of altitude and annual precipitation between 900 and 1800 mm), savannas, temperate forests (including cloud, *Eucalyptus*, pine and oak forests over 1000 m of altitude), fallows, crops (including maize, sugar cane, yam, tea, peanuts), pastures, grasslands and tree plantations (including coffee, rubber, banana, mango). Principal component analysis (PCA) was carried out (STATGRAPHICS software) with the following community variables: abundance, biomass and number of species for total, native, exotic, epigeic, endogeic and anecic species.

In order to place earthworm communities correctly in the overall context of soil macrofauna, we used the results obtained by Lavelle *et al.* (1994) for analysis of soil macrofaunal composition, where 73 macroinvertebrate communities from 29 different sites were studied. The importance of each group (Oligochaeta, Formicidae, Isoptera, Aranae, Chilopoda, Diplopoda, Diptera, Aranae, Gasteropoda, Coleoptera) was determined according to their relative contribution to total density and biomasss, for each one of the above-mentioned types of vegetation.

General Patterns of Macroinvertebrate Communities

Tropical soil macrofauna trends

Lavelle *et al.* (1994) identified, by PCA, the major trends in tropical soil macrofaunal composition and the relative effect of vegetation type, biogeography and land-use practices.

Table 2.1. Origin, type of land management and number of earthworm communities analysed in this study.

	Natural ecosystems					Agroecosystems			
Country	No. of localities	Tropical forests	Cloud forests	Temperate forests	Savannas	Pastures	Tree plantations	Fallows	Crops
America									
Brazil	1	1[a]	—	—	—	3[a]	1[a]	—	—
Colombia	2	3[a,b]	1	—	1[a,b]	3[a,b]	2[a,b]	3[a,b]	2[a,b]
Costa Rica	3	2[a]	—	—	—	4[a,b]	—	—	—
Cuba	1	1[a]	—	—	—	1[a,b]	1[a,b]	—	—
Dominica	1	—	—	—	—	1[a]	1[a]	—	—
Guadaloupe	1	—	—	—	—	2[a]	—	—	3[a]
Martinique	1	—	—	—	—	3[a,b]	1[a,b]	—	—
Mexico	23	12[a,b]	2[a,b]	1[a,b]	—	18[a,b]	3[a,b]	2[a,b]	10[a,b]
Peru	2	3[a,b]	—	—	—	3[a,b]	1[a,b]	2[a,b]	3[a,b]
Venezuela	1	3[a,b]	—	—	—	—	—	—	—
Africa									
Congo	1	4[a,b]	—	—	—	1[a,b]	1[a,b]	—	—
Ivory Coast	3	3[a,b]	—	—	6[a,b]	2[a,b]	5[a,b]	3[a,b]	11[a,b]
Asia									
India	21	19[a,b]	—	—	—	26[a,b]	9[a,b]	3[a,b]	11[a,b]
Malaysia	1	3[a]	—	—	—	—	—	—	—
Sarawak	1	4[a]	—	—	—	—	—	—	—
Total	63	58	3	1	7	67	25	13	40

[a] Density and/or biomass data available; [b] ecological categories identified.

The major outcome of this analysis was the identification of three major groups characterized respectively by the dominance of either termites, earthworms or litter arthropods. The groups tend to react separately within ecosystem types and land-use practices. Termites and/or earthworms tend to be dominant in most cases, while termite communities vary widely, depending on biogeographical patterns. They are important components of many African and Australian soils. In America, ants are more important whereas termites often are of little or no importance. This is due, in part, to their lower functional diversity; in South America for example, fungus-growing termites do not occur. Another important characteristic of termites is that they have adapted to a wide range of semi-arid systems where earthworms are not found. Earthworms are best represented in grasslands in humid areas; their abundance decreases towards both forested and dry areas. At a finer level of resolution, they are sensitive to the nutrient status and organic content of soil (Fragoso and Lavelle, 1992). Litter arthropods seem to be predominant in ecosystems where sufficient litter is available as a consequence of low termite and earthworm activities. They are represented mainly by millipedes or coleopterans, which in some areas account for the larger part of the biomass, as in the case of millipedes in the miombo woodlands of southern Africa (Dangerfield, 1990). In such ecosystems, mesofaunal communities may also have higher densities than in systems dominated by earthworms and termites, where their abundance is very low (Adis, 1988).

Effect of land-use practices

Annual crops on land recently cleared of natural vegetation always have highly depleted macro-invertebrate communities (Fig. 2.1). They have the lowest biomass (5.1 g of fresh weight m^{-2} on average) and a very low diversity. Earthworm and litter arthropod populations soon disappear, as native species seldom withstand major disturbances, provided they are not replaced by adaptable exotic species. Some groups of termites (mainly humivorous) tend to be more persistent and comprise a significant proportion of the overall biomass.

Pastures are functionally similar to savannas. They are highly favourable for earthworm development when they have been established in forest areas with high annual rainfall, provided adaptable species are present. This is actually the case in many sites where peregrine species with pantropical distributions (mainly *Pontoscolex corethrurus* and *Polypheretima elongata*) establish biomasses from several hundreds to 4000 kg of fresh weight per hectare (see, e.g. Barois *et al.*, 1988; Lavelle and Pashanasi, 1989). However, in some cases (India and Mexico), native species can survive, reaching similar abundance values. Interestingly, sugar cane plantations show similar patterns, with earthworm biomasses of 33 and 53 g m^{-2} in two sites in tropical Mexico and Guadeloupe, respectively (Barois *et al.*, 1988; Patrón, 1993). In terms of

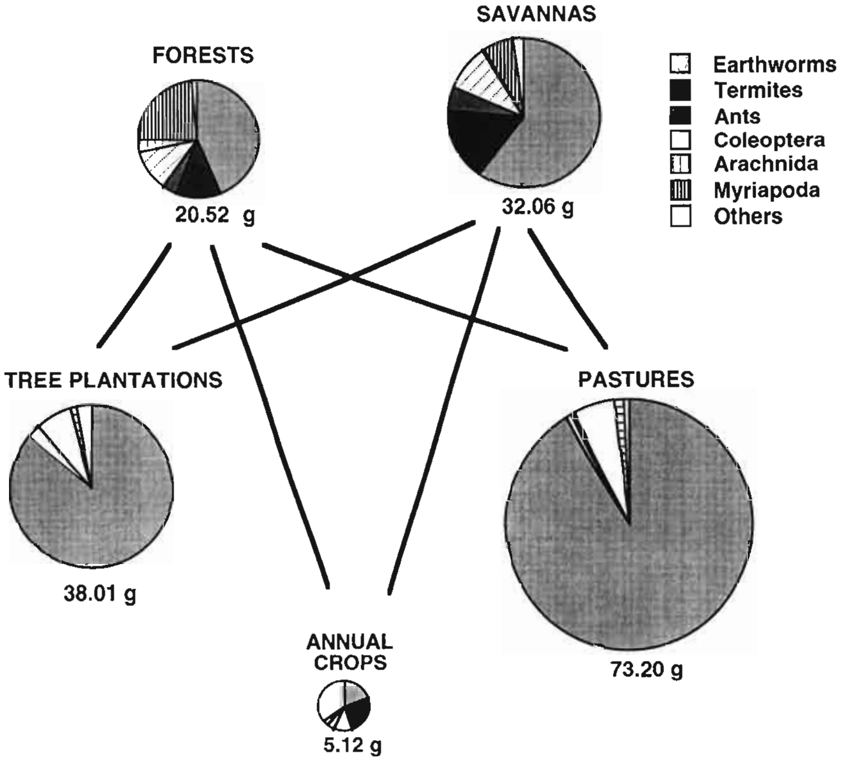


Fig. 2.1. Composition of soil macrofaunal communities in tropical grasslands, fallows + tree plantations, annual crops and forests. The area of circles is proportional to the overall biomass.

soil–fauna relationships, this indicates that these plantations are comparable with humid grasslands.

Tree plantations such as palm tree plantations with herbaceous legume cover, or cocoa with a litter layer at the soil surface and a stratum of high trees, usually have diverse communities. They retain components of the original fauna because some of the original species are still present as the overall structure is close to that of a secondary forest. Nonetheless, the disturbance and/or the establishment of a herbaceous stratum provides niches that allow some exotic species to colonize.

Species richness and diversity

Although no really comprehensive information is available so far, disturbances linked to land-use practices seem to severely affect the species richness of soil arthropod communities. The conversion of forests to annual crops eliminates the vast majority of species which rely on woody or leaf litter material and those which need buffered microclimatic conditions. Conversely, perennial systems, especially those which maintain a multistrata structure, may conserve species from the original ecosystem and provide niches for exotic colonizers. The nature of the original ecosystem greatly influences the effect of land-use practices. In Colombia, conversion of savannas into pastures generally maintains a large part of the original community (54% of species in common), with some changes induced by grazing. In contrast, in a pasture established at Manaus after clearing the forest, species richness of macroinvertebrate communities had decreased from 151 to 48 species, and only 22 from the original communities had resisted the change (22.5% of species in common).

Earthworm Communities of Tropical Agroecosystems

Regional analysis

Here we present the patterns of earthworm communities from several tropical countries. These countries are grouped according to their biogeographic and phylogenetic affinities into four regions: (i) Central America–Caribbean; (ii) South America; (iii)Africa; and (iv) Asia.

Central America and the Caribbean

This region is characterized by the presence of primitive Megascolecidae (Acanthodrilinae and Dichogastrini), Ocnerodrilidae and some derived Glossoscolecidae distributed in the major part of Mexico, Central America (north of Panama) and the Lesser and Greater Antilles. It includes more than 130 species and 25 genera (Fragoso *et al.*, 1995). Only in Mexico, Cuba, some Lesser Antilles and Costa Rica have natural and/or agroecosystem earthworm communities been characterized.

MEXICO

We will restrict case studies to southeastern Mexico, currently considered as the most humid region of the country and very rich in native species (Fragoso and Rojas, 1994). In this region, 48 earthworm communities (15 in natural ecosystems and 33 in agroecosystems) from 23 localities were characterized. Most of the following results are from Fragoso *et al.* (1997.)

With a surface of nearly 488,000 km^2, more than half of the original vegetation of this region has been replaced by agroecosystems; the remaining natural vegetation (tropical rainforests, deciduous and subdeciduous forests) is sparsely distributed over the entire region. Pastures and cultivated lands are the predominant agroecosystems, occupying more than 30% of the total surface of the region (Fragoso, 1993).

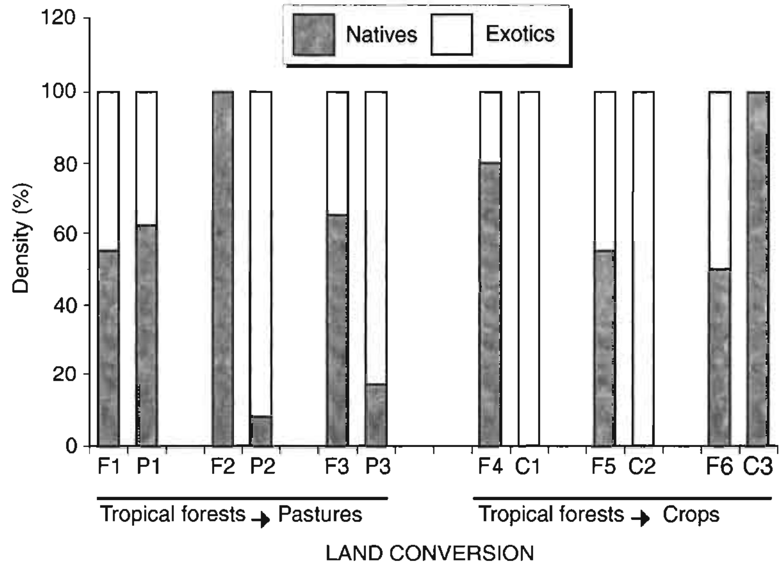


Fig. 2.2. Change of earthworm community composition in different land-use systems of southeastern Mexico. F = forests, P = pastures, C = annual crops. See text for the meaning of numbers. (Modified from Fragoso *et al.*, 1997.)

The current number of species in this region is 95, of which 26 are exotics (Fragoso, 1993). Regional richness (i.e. the total number of species living in a certain type of ecosystem from different geographical localities) is higher in tropical forests (40 species) than in pastures (22 species) and maize crops (15 species); conversely, the area of pastures is almost twice that of tropical forests. From a regional point of view, this means that: (i) with the destruction of natural forests, many native species disappear at the local scale, and (ii) 50% of disturbed below-ground areas of southeastern Mexico are inhabited by a small number of earthworm species (mainly exotics).

The general pattern in this region is that earthworm communities of natural and disturbed ecosystems are composed, to some extent, of a mixture of native and exotic species. The structure of these communities varies greatly with the nature of soil management. In general, communities from natural ecosystems show lower abundances and biomasses than those from disturbed sites; the exception are crops (mainly maize) which present lower values of density, biomass and number of species (average values 42 ind m^{-2}, 1 g m^{-2} and 2 species m^{-2}, respectively). In both natural and disturbed ecosystems, endogeics dominate, indicating that epigeic species are not an important component in Mexican natural earthworm communities, and thus perturbation has a smaller effect on functional diversity. It was also demonstrated that when the community includes the exotics *P. corethrurus* or *P. elongata* (these species seldom coexist in the same site), they are generally dominant. Other common assemblages found in this region include the exotics *P. corethrurus*, *Dichogaster* *bolaui* and *D. saliens* and the euryoecic natives *Balanteodrilus pearsei*, *Lavellodrilus parvus* and *Diplotrema murchiei*.

After comparing the structure of earthworm communities in several agroecosystems, Fragoso (1993) found that the two more important determinants of these communities were the time of disturbance (which measures time elapsed since first perturbation) and the kind of agricultural practices (amount and intensity of soil destructive agricultural practices, e.g. use of tillage, pesticides, fertilizers). Figure 2.2, for example, shows that in recently disturbed pastures (P1, Chajul; Fragoso, 1992) and crops with low-input agricultural practices (C3, Pánuco; Arteaga, 1992), natives remain as an important component; the use of high-input agricultural practices (tillage, pesticides) in combination with a longer time elapsed since perturbation increased the amount of exotics both in pastures (P2, Los Tuxtlas; Fragoso, 1993; P3, Laguna Verde; Lavelle *et al.*, 1981) and in crops (C1, Gómez Farías; C2, La Mancha; Fragoso, 1993).

CUBA

The largest of the Caribbean islands, Cuba harbours a very diverse earthworm fauna. However, there has only been one study in which earthworm communities of agroecosystems have been analysed in relation to natural vegetation (Martínez, unpublished data). Comparisons made at La Habana between tropical subdeciduous secondary forests, pastures and tree plantations indicated that: (i) endogeics dominated (100% of total abundance and biomass) in the tree sites; (ii) higher values of density and biomass were found in forests (413 ind m^{-2} and 170 g m^{-2}) followed by pastures (338 ind m^{-2} and 174 g m^{-2}); (iii) species richness was higher in pastures (seven species) followed by forests (five species); (iv) the most important species in the three systems was the widespread native *Onychochaeta elegans*; and (v) in the two agroecosystems, the second most important species was the exotic *P. elongata*.

LESSER ANTILLES

Barois *et al.* (1988) studied the soil macrofauna and earthworm fauna of different land-use systems from Guadaloupe, Dominica and Martinique. In the first two islands, the exotic *P. corethrurus* was relatively abundant in several kinds of agroecosystems, with some native species scarcely represented; in vertisols of Martinique, on the other hand, the exotic *P. elongata* totally dominated the communities of pastures and other agroecosystems.

COSTA RICA

Fraile (1989), in the only study so far in Costa Rican tropical agroecosystems, analysed earthworm communities in pastures with different treatments of fertilizers and agroforestry techniques. This author found the highest values of abundance, biomass and species richness in a non-grazed pasture (226 ind m^{-2}, 67 g m^{-2} and nine species) and, for all the treatments, an overwhelming dominance of the exotic *P. corethrurus*. In general, epigeics were scarce, the higher values (2% of total biomass) being found in pastures with *E. poeppigiana* trees (mainly the exotic *Metaphire californica*). Only one native species survived (*Glossodrilus nemoralis*) and with very low values of abundance. Thus, intensive management, as in the case of Mexico, affected abundance and species composition.

South America

Although the families Ocnerodrilidae and Megascolecidae also occur in this region, the distinctive feature in this continent is the dominance of family Glossoscolecidae. With 36 genera recognized (Righi, 1996) and hundreds of species distributed both in tropical and temperate ecosystems (except the southern region of Chile and Argentina; Righi, 1971), members of this family often dominate the earthworm communities so far studied in Peru, Brazil and Colombia.

PERU

Lavelle and Pashanasi (1988, 1989) compared earthworm communities from two tropical rainforests with three groups of derived agroecosystems. Their results showed that earthworm communities were modified both at the functional and taxonomic level (Fig. 2.3). Functionally there were changes in the amount and kind of ecological groups; in the majority of the sampled agroecosystems, for example, the community structure was greatly simplified, often to only one ecological category. Structural changes were clear in pastures, fallows and high-input cropping systems, where the forest earthworm communities shifted from an epigeic- to an endogeic-dominated composition; taxonomically, the four original native forest earthworm species were almost totally replaced by the exotic *P. corethrurus*.

Interestingly, as occurred in southeastern Mexico, epigeic and anecic native species remained in palm tree plantations (Pijuayo-kudzu) and in traditional and low-input cropping systems.

In another set of experiments, Pashanasi *et al.* (1994) followed changes in the composition of earthworm communities, from recently burned forest to shifting cultivation and improved agriculture. After the first harvest in both systems, they found that the native epigeic species *Martiodrilus pano* completely disappeared, while populations of the native anecic *Rhinodrilus lavellei* and the endogeic *Rhinodrilus pashanasi* species were maintained and increased, respectively.

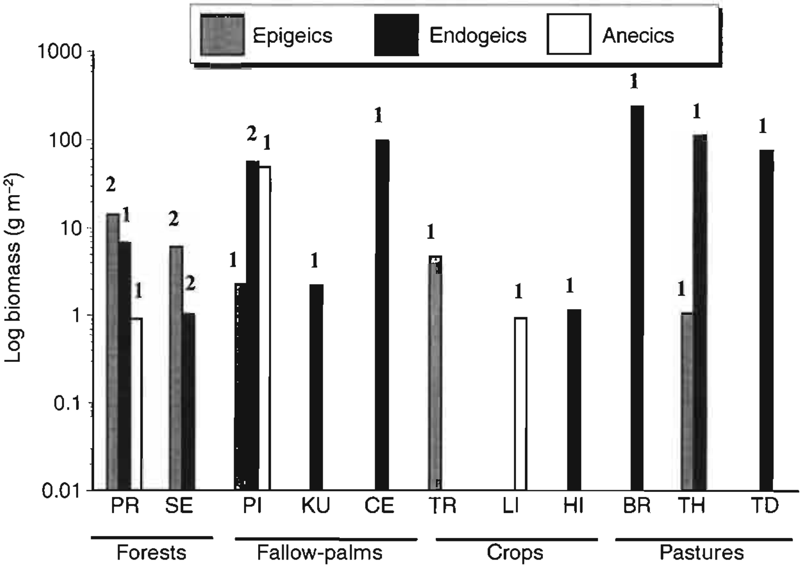


Fig. 2.3. Functional (ecological categories) and taxonomical (number of species) changes of earthworm communities in different land-use systems in Peruvian Amazonia. Values above the bars indicate the number of species in each category (from Fragoso *et al.*, 1997). BR = *Brachiaria*, CE = *Centrosema*, HI = high input, KU = Kudzu, LI = low input, PI = Pijuayo, PR = primary, SE = secondary, TD = traditional dry, TH = traditional humid, TR = traditional.

BRAZIL

At Manaus, Lavelle *et al.* (unpublished data) found pastures and forests with similar values of biomass (approx. 44 g m^{-2}). Density, on the other hand, showed higher values in pastures (602 ind m^{-2} versus 202 ind m^{-2} in forests). The main difference between these systems was the disappearance of native earthworms and the colonization of presumably empty niches and building up of large populations by the exotic species *P. corethrurus*. Dominance of this species and a drastic reduction in other invertebrates resulted in a decompacting effect on soil, which in turn produced a significant degradation of soil physical structure (see Chapter 5).

COLOMBIA

At Carimagua, conversion of savannas into improved pastures with African grasses and herbaceous legumes increased the abundance and biomass of earthworm communities and maintained a large proportion of native species.

Of the eight earthworm species recorded in the original savanna, seven were maintained in improved pastures and the overall earthworm biomass was increased five- to 12-fold (from 4.78 g m^{-2} in the original savanna to 51 g m^{-2} in the improved pasture; Decaëns *et al.*, 1994). Exotic species present in the area did not invade the pastures. The positive effect of improved pastures on native earthworms was reflected in the anecic glossoscolecid *Martiodrilus* sp.nov. In the native savanna, this large species comprised up to 15.1% of total earthworm biomass, whereas in the improved pasture this value increased to 85.1% (Jimenez *et al.*, 1998).

Africa

The earthworm fauna of this continent is represented by ancestral taxa of Megascolecidae and derived Eudrilidae and Microchaetidae. Particularly abundant in Central Africa is the family Eudrilidae, which actually includes 38 genera and more than 274 species (Sims, 1987). In general, earthworm communities contain a mixture of megascolecid [mainly *Dichogaster* or related species with calciferous glands in the region 14–17, grouped by Csuzdi (1996) in the distinctive subfamily Benhamiinae] and eudrilid species. Community studies have been made up to now only in Ivory Coast and Congo.

IVORY COAST

Lavelle (1978) studied several earthworm communities from different types of savannas and gallery forests at Lamto. Their studies revealed rich (up to 13 species) and ecologically diverse communities (in particular the endogeics) flourishing in very poor sandy soils. Interestingly, when these natural systems were shifted to some kind of agroecosystem, none of the exotic species invaded these communities. Tondoh (1994) characterized earthworm populations from several land-use systems that included natural unburned forests, burned forests, savannas and a variety of cultures with different intensities of agricultural practices and ages of disturbance (Fig. 2.4). Their results showed the polyhumic eudrilids *Chuniodrilus* spp. and the megascolecid endogeic *Millsonia anomala* and *Dichogaster agilis* as the only species capable of survival in these systems. The persistence of original earthworms varied with the kind of culture, soil moisture and age of cultures. Very humid agroecosystems (e.g. rice, banana plantation) showed higher total abundances and biomasses than adjacent gallery forests, whereas in maize crops the community changed with age from mesohumic (maize for 1 year, dominated by *M. anomala*) to epigeic-dominated communities (maize for 3 years, dominated by *Dichogaster* spp.). Finally, in a pasture established in a former natural forest, the number of species remained the same although biomass never reached the values found in natural savanna communities (Fig. 2.4). In summary, this study showed that: (i) endogeic earthworms dominate both in natural and managed systems; (ii) exotics never invaded derived communities; and (iii) agroecosystem communities changed their functional structure with time.

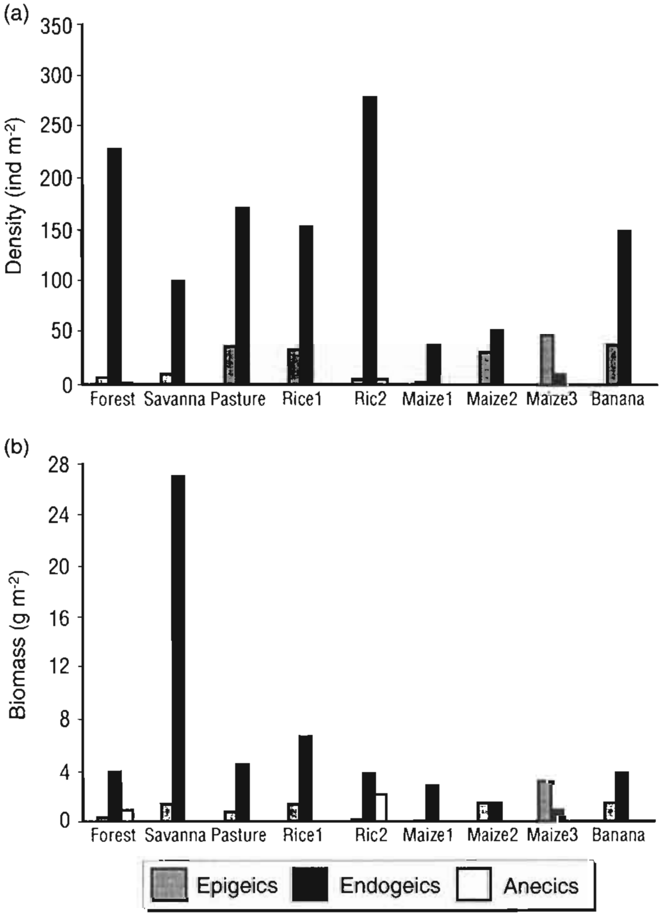


Fig. 2.4. Abundance (a) and biomass (b) of earthworm ecological groups in different land-use systems from central Ivory Coast (Tondoh, 1994). Numbers on the *x*-axis indicate number of years

CONGO

Montadert (1985), working in forests and derived agroecosystems of Dimonika, found that both pastures and cacao plantations showed higher abundance and biomass values than natural forests. The situation in pastures, however, was similar to that found in other American sites: an almost total domination of *P. corethrurus*.

The Maala system investigated in the Niari Valley (M'Boukou, 1997), on the other hand, is an interesting exception to the general patterns observed elsewhere. It is actually the only annual cropping system that enhances earthworm communities. Annual crops are grown on mounds in which grass

Table 2.2. Earthworm density (D) (ind m^{-2}) and biomass (B) (g m^{-2}) in different land-use systems of the Niari region (Congo).

	Savanna D (B)	Slash-and-burn D (B)	Maala 1st year D (B)	Maala 2nd year D (B)	Maala 3rd year D (B)
Epigeics	18 (6)	5 (0.42)	31 (9)	37 (17)	16 (5.3)
Anecics	0	0	33 (12)	11 (4.3)	0
Endogeics	61 (19)	13 (2)	363 (139)	146 (30)	138 (4)
Total m^{-2}	79 (25)	18 (2.42)	427 (160)	194 (51.3)	154 (9.3)

previously had been buried and slowly burned. This practice keeps ashes and a significant proportion of carbon in the soil, with positive effects on earthworm abundance. As shown in Table 2.2, earthworm density decreased from 79 to 18 ind m^{-2} in the slash-and-burn system, whereas in the Maalas earthworm density increased more than fivefold and biomass reached 160 g m^{-2} during the first year. Endogeics and anecics were stimulated more than epigeics. Earthworm abundance and biomass decreased during the second and third year, but the former still remained higher than in the savanna. Functionally, the Maala system enhanced the invasion of anecics, which were not present in the savannas.

Asia

The Asiatic earthworm fauna is dominated by species of Megascolecidae (Megascolecinae, Dichogastrini and Peryonichini), the primitive Moniligastridae and some Ocnerodrilidae (Edwards and Bohlen, 1996). Within the Megascolecinae, the most diverse and successful group of earthworm species is found: the pheretimoid-related genera (*Pheretima, Polypheretima, Metaphire, Amynthas,* etc.), that include several of the tropical common exotic species (see Chapter 1). From a phylogenetic point of view, this region has strong affinities with Africa and Central America. Notwithstanding their surface and high diversity of species, detailed studies of tropical earthworm communities in this continent have only been carried out in India.

INDIA

India covers only about 2% of the world's total surface, but with 385 species and 64 genera recognized it harbours about 10% of all known earthworm species (Julka, 1999). Earthworm community research in this country has been carried out both at the regional (21 localities) and local level, both in natural (19 sites) and derived agroecosystems (49 sites, Table 2.1).

Changes in earthworm communities are exemplified by the studies carried out in southern Karnataka (Deccan Peninsula) by Bano and Kale (1991) and Blanchart and Julka (1997). In the regional study, Bano and Kale (1991) reported 44 species (36 natives and eight exotics), of which seven and 25 native species were limited to natural forests and managed ecosystems, respectively. Figure 2.5a shows that native species are well adapted to agroecosystems, surviving even in arable lands. That more native species were found in managed ecosystems than in natural forests could be due to: (i) the wide geographical distribution of the majority of natives (widespread natives of Chapter 1), (ii) the prevalence in the region of low-input agricultural practices (Kale, personal communication) and (iii) the fact that most of these earthworms were endogeic species, which are more resistant to changes in land-use practices. In a more local study in the same region, Blanchart and Julka (1997) studied earthworm communities in a gradient of forest disturbance (forest–forest borders–pastures). Their results can be summarized as follows: (i) communities were composed mostly of endogeic species (only one epigeic

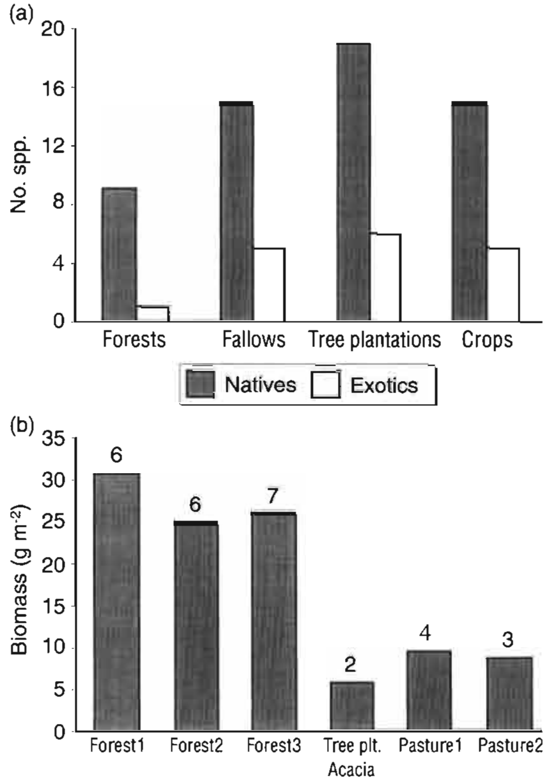


Fig. 2.5. (a) Number of native and exotic species from different land-use systems in southern Karnataka, India (data from Bano and Kale, 1991). (b) Biomass of earthworms found in different land-use systems from the Western Ghats, Karnataka state, India. Values above the bars indicate the number of species (data from Blanchart and Julka, 1997). Numbers of land-use systems are shown only to separate sites.

species from a total of 30 species); (ii) more than 60% of species survived in at least one type of agroecosystem; (iii) no globally distributed exotic species were found; and (iv) lower values of abundance, biomass and species numbers were found in pastures, as opposed to natural forests (Fig. 2.5b).

These examples are representative of the situation currently found in other Indian localities, that can be summarized as follows:

1. In almost all kinds of agroecosystems, earthworm communities are composed mainly of native species which generally dominate in abundance and biomass (e.g. several species of *Drawida*, *Hoplochaetella*, *Eutyphoeus*, *Lennogaster*, etc.; see Chapter 1).
2. The exotics *P. corethrurus* and *P. elongata* are uncommon. In fact, India is the only country in which native species are very common at local and regional levels, not only in pastures but also in tree plantations and crops (Fig. 2.5a). The presumed cause of this pattern is, as in southeastern Mexico, the limited use of mechanized destructive agricultural practices.

A synthesis of regional and worldwide patterns of natural and disturbed tropical earthworm communities

The above case studies show that when natural forests and savannas are converted to agroecosystems, earthworm communities change in abundance, biomass, number of species, ecological categories and species composition. With these data, is it possible to identify a common trend in the direction of change of these communities, and the extent to which phylogenetic–geographic constraints determine specific patterns and trends?

We explored these questions by performing a PCA with data from natural and derived ecosystems in different tropical regions. Thus, we expected to discriminate between the effect of phylogeny, environment and agriculture practices. Because not all sites were fully characterized (e.g. in some cases only abundance data were available), two kinds of PCA were performed. The first (A1) was run considering only density and species number for total, native, exotic, epigeic, endogeic and anecic groups (12 variables) and included 158 sites; the second (A2) was restricted to localities with density, biomass and species richness (18 variables and 129 sites). Standardization of data was carried out in both analyses.

In the case of A1, the first two components explained 50% of total variance (25% each), whereas for A2 the percentage of explained variance was 24 and 20% for components 1 and 2, respectively (44% together). In both analyses, components 1 (C1) and 2 (C2) were similar: they reflected the influence of exotic species, mainly endogeics, on the overall abundance and biomass (C1) and the influence of native species as determinants of community species richness (C2).

The influence of land-use systems

The result of A1 analysis is shown in Fig. 2.6, where sites were separated according to land-use system. In this figure, combinations of C1 and C2 produced four types of communities, represented in Fig. 2.6 by the uppercase letters A, B, C and D. Type A communities are characterized by high numbers of (native) species, a more diverse functional structure (several ecological categories) and low abundance values; they are found in most tropical rainforests and some pastures and savannas. In type B communities, native species richness is still high, but exotic endogeics produce high abundance values; some tropical forests, fallows, crops and several pastures are included in this group. Type C communities represent the most depauperate systems, with low values of abundance, species richness and ecological categories; in these communities, very few natives are represented and even the exotic endogeics are seldom present. Most annual crops and several pastures are included in this group. Finally, type D communities show very few native species but high abundance values due to the dominance of exotic endogeics. All sites with this kind of community correspond to agroecosystems (pastures, tree plantations and crops).

These patterns can be summarized as follows:

1. Considering all sites together, there is some overlap between natural and managed sites, which is simply due to the fact that several agroecosystems maintained their original communities. However, there are clear trends in the composition of communities according to land management. For example, from Fig. 2.6, it is concluded that 56% of natural ecosystems (all savannas and most tropical rainforest sites) are species-rich communities with low abundance values, but with an ecologically diverse native earthworm fauna (e.g. with epigeic, endogeic and anecic species) (quadrant A of central graph in Fig. 2.6). In the case of agroecosystems (fallows, crops, pastures, tree plantations), 44% of the sites are characterized by depauperate earthworm communities with low abundances and number of species (quadrant C), whereas 42% of the sites are characterized by high-abundance communities dominated by exotic endogeics, with low or high native species richness (quadrants B + D).
2. A great deal of crop sites (72%) are characterized by low abundances and low native species richness (quadrant C).
3. Pastures are very heterogeneous in terms of total abundance, dominance of exotics and species richness; in fact, it is the only land-use system which significantly conserved a diversified native fauna (48% of sites, quadrants A + B of Fig. 2.6).

Regional patterns of communities.

In Fig 2.7, the results of analysis A1 are partitioned according to geographical region. Considering the four types of communities previously recognized (A, B, C and D), the following patterns are observed:

1. In Asia, Africa and South America, more than 50% of natural sites (black bars, Fig. 2.7A) show communities with high numbers of native species and

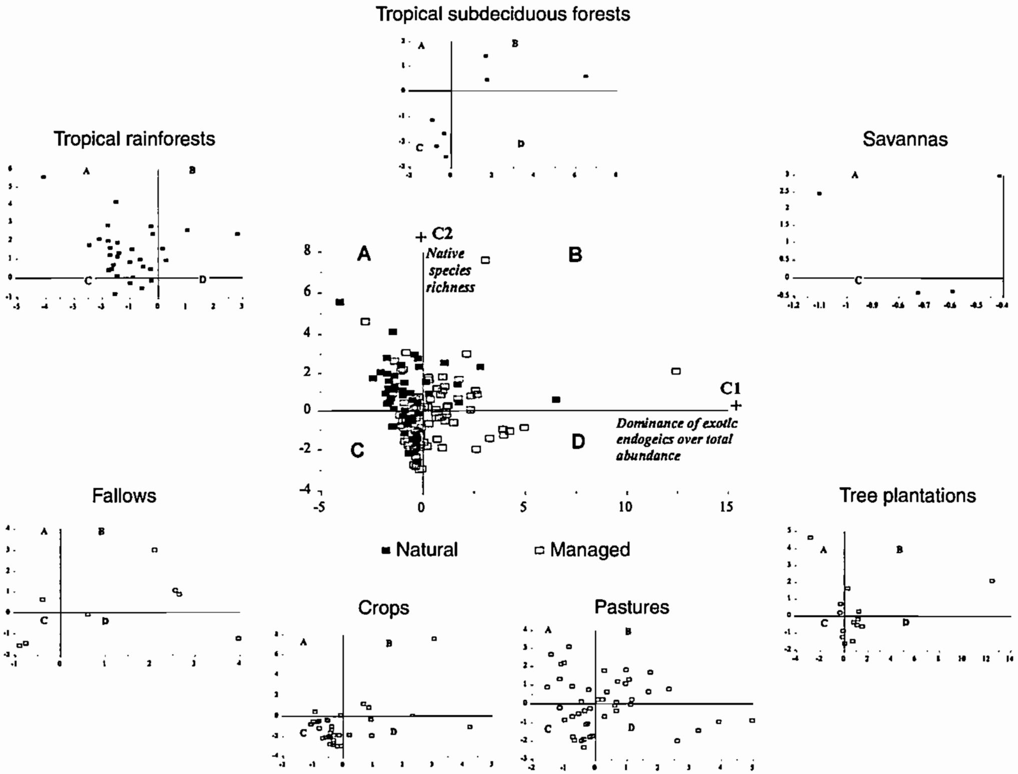


Fig. 2.6. Ordination of 140 earthworm communities from different countries of the humid tropics and separation on the basis of land-use system. Letters for each quadrant are shown only to differentiate the meaning of components and are explained fully in the text.

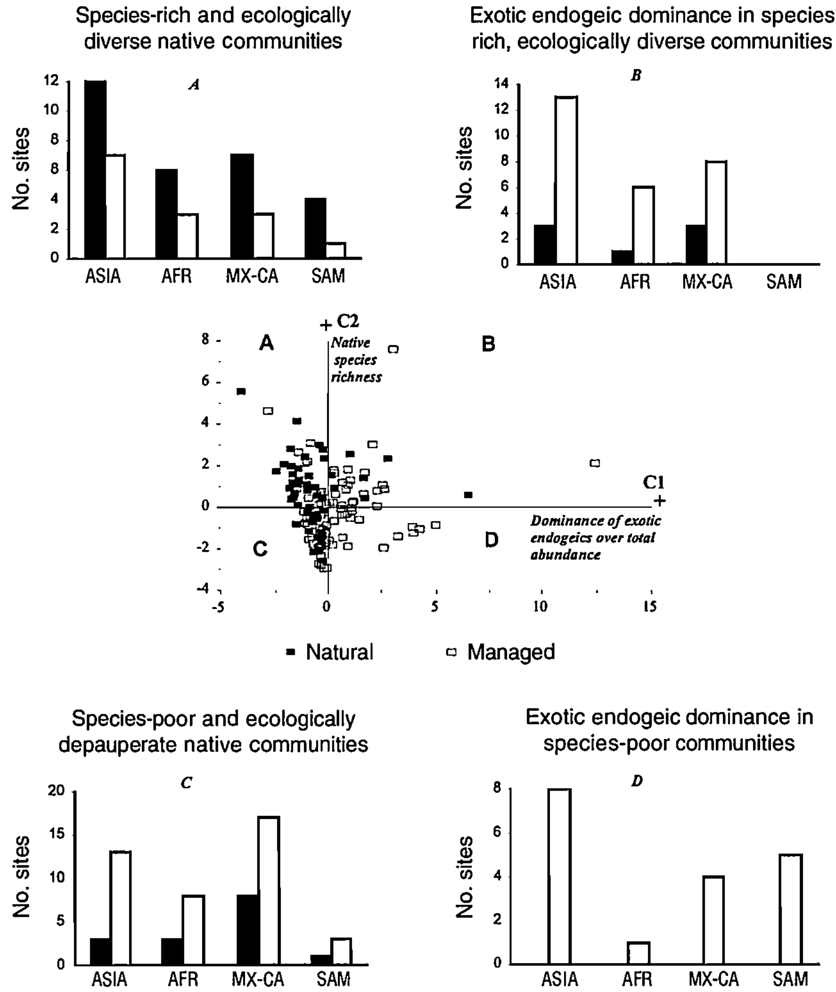
with a diversified functional structure (i.e. several ecological categories); in the Mexico–Central America region, on the other hand, the relatively common low-diversity communities (44% of sites; black bars, Fig. 2.7C) mainly correspond to tropical subdeciduous forests. These forests, found in localities with annual precipitation lower than 900 mm, represent the distributional limit for the majority of tropical native earthworms (Fragoso and Lavelle, 1992), and consequently are inhabited by few native species (mainly endoanecic = large endogeics with deep vertical burrows) and by the more plastic exotic endogeic species (Fig. 2.6B).

2. There is a clear difference between the agroecosystem communities of Asia–Africa and those of Mexico–Central/South America (empty bars, Fig. 2.7). In the first case, nearly 50% of agroecosystems are characterized by rich earthworm communities with several native species (Fig. 2.7 A + B), whereas in the second case this percentage decreases to 35% (Mexico–CA) and 12% (South America). This pattern indicates that in Asia and Africa, managed agroecosystems offer better conditions for the survival of native species and for the conservation of the functional structure of the community.

3. In the recent analysis by Lavelle *et al.* (1994), of 18 agroecosystems from Mexico and Peru, it was found that earthworms were more abundant in pastures than in any other agroecosystem. With more data from other countries and regions, our results indicate that this pattern only holds in tropical America and Africa; in Asia (India), traditional management practices have promoted high densities in tree plantations, equally or slightly higher than those found in pastures (more than half of the managed sites from India in Fig. 2.7D correspond to tree plantations).

The conservation of the richness and functional structure of earthworm communities in agroecosystems is related to the phylogenetic background, the type of agroecosystem (e.g. both in India and Mexico, pastures conserve several native species) and the kind of agricultural practices currently used.

The influence of phylogeny on the functional structure of these communities (measured by the relative importance of ecological categories) can be estimated by comparing natural communities from different regions. After the initial synthesis made by Lavelle (1983) and confirmed by Lavelle *et al.* (1995), it is recognized that tropical savannas and forests are dominated by endogeics, which account for more than 80% of total biomass. Fragoso and Lavelle (1992), in a more detailed analysis of several tropical rainforest communities from Mexico, Central America, Africa and South America, conclude that these communities are rather similar in terms of species richness, the main difference being the predominance of certain ecological categories. They found a predominance of anecic and epigeic species in South American and African communities; in Mexican communities, on the other hand, endogeics dominated. Their main conclusion, however, was that these patterns were the result of environmental determinants (soil nutrient contents and rainfall seasonality), rather than phylogenetic–geographic constraints related to a predominance of


Species-rich and ecologically diverse native communities

Exotic endogeic dominance in species-rich, ecologically diverse communities

Species-poor and ecologically depauperate native communities

Exotic endogeic dominance in species-poor communities

Fig. 2.7. Ordination of 140 earthworm communities from different countries of the humid tropics and separation on the basis of geographical regions (AFR = Africa, MX-CA = Mexico–Central America, SAM = South America). Bars indicate the number of natural (black) and managed (white) sites separated by components and by geographical region (see text).

epigeics and anecics in the families Glossoscolecidae (South America) and Eudrilidae (Africa). Actually, however, discrimination between both hypotheses will rely on the use of appropriate adaptive phylogenetic methods (Harvey and Pagel, 1991).

In this study, and with more data from different land-use systems, we found that the 'phylogenetic' background is important in determining the structural composition of communities, their effect varying as a function of the

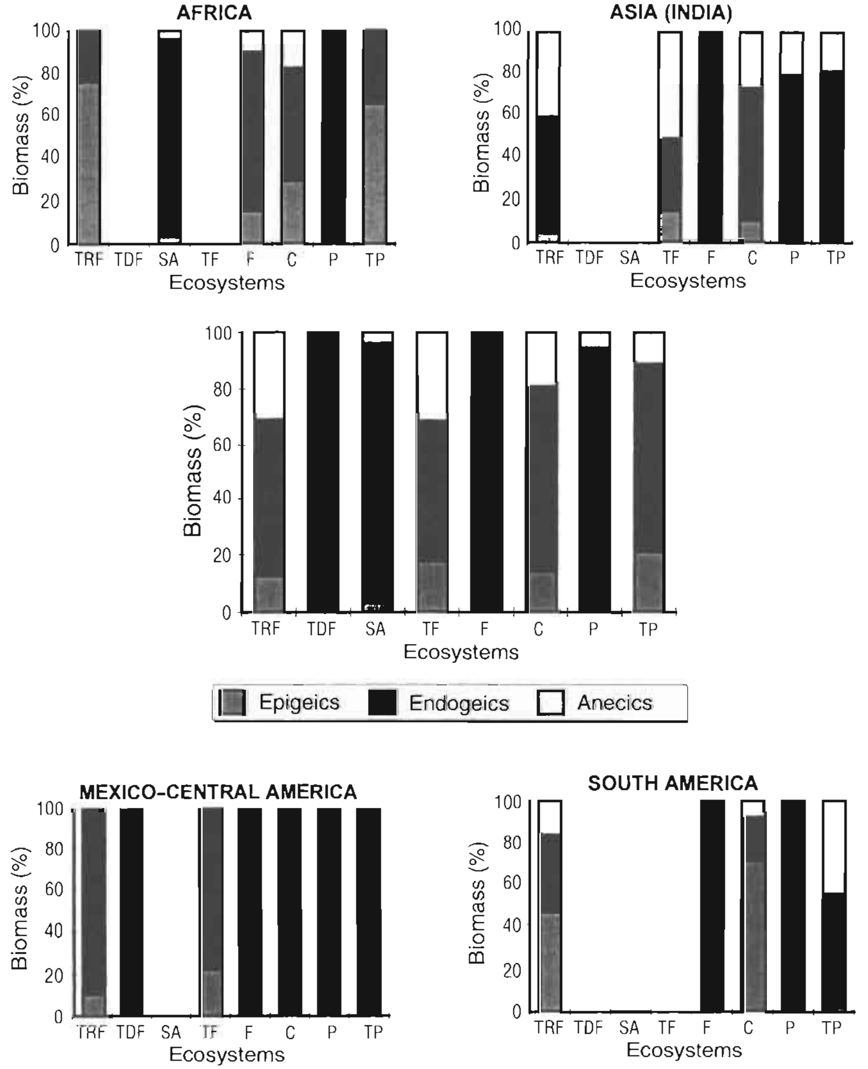


Fig. 2.8. Average functional structure (central graphic) of earthworm communities from natural (TRF, TDF, SA, TF) and managed ecosystems (F, C, P, TP) of the humid tropics. The lateral graphs show average structures according to geographical region (C = crops, F = fallows, P = pastures, SA = savannas, TDF = tropical subdeciduous forests, TF = temperate forests, TRF = tropical rainforests, TP = tree plantations).

kind of agroecosystem. This is clearly illustrated when the percentage of biomass of the main ecological categories is analysed in relation to land-use system and geographical region (Fig. 2.8); accordingly, the following patterns can be recognized:

1. There is a trend towards an endogeic domination in agroecosystems, although this is greatly influenced by the nature of the original community. Thus, in India and South America, anecic species are present in the majority of agroecosystems because they were already common in natural forests; in Mexico–Central America, on the other hand, anecic and epigeic species are totally absent in agroecosystems because these groups are absent or relatively uncommon in the natural forests.
2. If a structurally diverse community exists in natural forests, tree plantations will resemble it more than that in any other land-use system.
3. The structure of pasture communities tends to be dominated by endogeics more than in any other type of land-use system.

Changes in the structure of communities are also produced by the invasion of exotic species, a variable closely linked to the history of parcels and type of agricultural practices. Therefore, one way to make an indirect evaluation of the intensity of disturbance is by comparing the percentage of biomass contributed by native and exotic species in different agroecosystems. From comparisons shown in Fig. 2.9, the following general patterns are observed:

1. In crop and tree plantations, exotic earthworms comprise between 20 and 30% of total biomass; this trend, however, is markedly different between the four regions: in Africa this group is almost non-existent (at least in the cultivated fields of Ivory Coast and Congo), whereas in the other regions their presence is more important, increasingly from Asia (30–50%) to Central America and South America (40–60%).
2. In pastures, exotics are better represented in Mexico–Central America and South America (60–70%) than in Africa (47%) and India (8%). In the first case, the biomass of exotics was far higher than the corresponding value of natives, although recent studies in pastures from Central Veracruz, Mexico, suggest that native species could be more important (Ortiz and Fragoso, unpublished data). This regional difference also applies when we consider absolute values of total density and biomass: in agroecosystems from Africa and India, native earthworms have higher values than in the other two regions.

These results suggest three possibilities: (i) in Mexico, Central America and South America, exotic earthworms have been introduced more often and/or have found fewer restrictions to their dispersal than in African–Indian regions; (ii) agroecosystem practices in Africa and India have been more favourable for survival of native earthworms than in the other regions; and (iii) both (i) and (ii).

The influence of agroecosystem practices

In this section, we will try to determine the extent to which the survival of native species and/or the invasion of exotic species is related to management practices. In this regard, we should try to clarify whether the former African

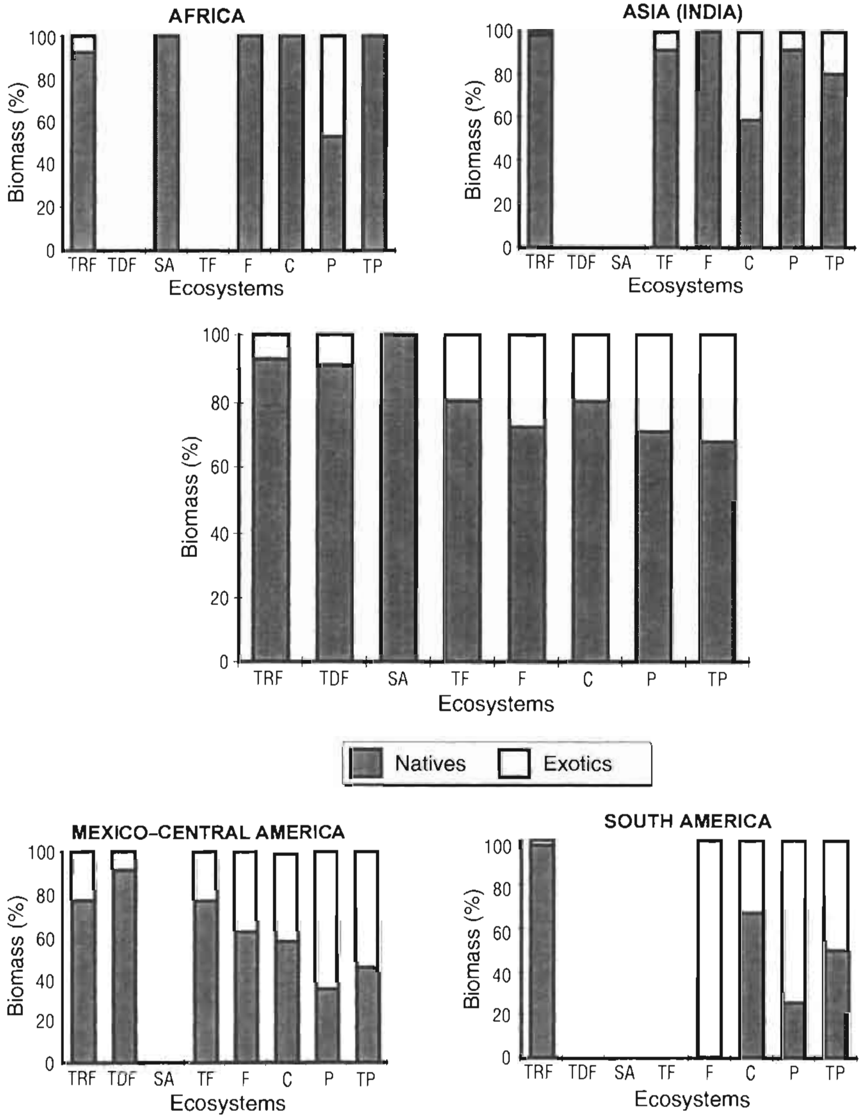


Fig. 2.9. Average relative biomass of exotic and native earthworm species in natural (TRF, TDF, SA, TF) and managed ecosystems (F, C, P, TP) of the humid tropics. The lateral graphs show average values in different geographical regions. (C = crops, F = fallows, P = pastures, SA = savannas, TDF = tropical subdeciduous forests, TF = temperate forests, TRF = tropical rain forests, TP = tree plantations).

and Indian pattern is due to different management practices. Figure 2.10 shows the relative abundance of exotic and native earthworm species in sites with different types of agricultural practices (low vs. high input) and ages of

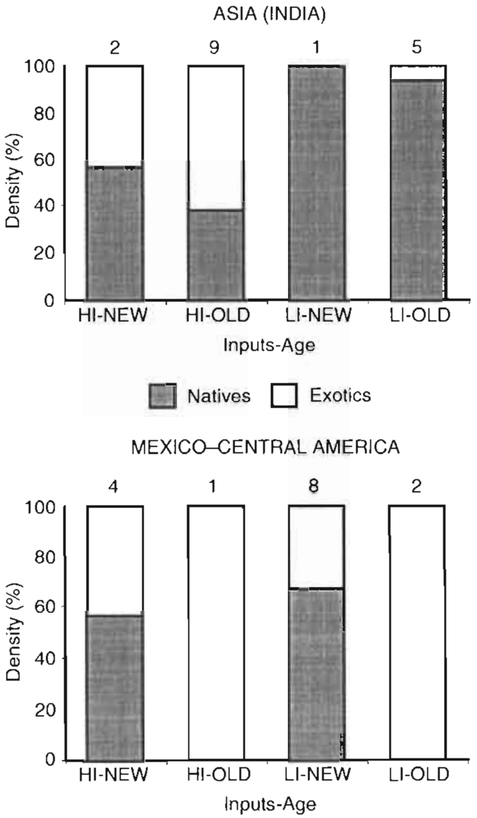


Fig. 2.10. Relative abundance of exotic and native earthworm species in agroecosystems of India and Mexico–Central America, with different intensities of agricultural practices (HI = high input, LI = low input) and ages of disturbance (NEW, OLD). Values above the bars indicate the number of sites.

perturbation (recent vs. old). Due to the small number of sites from which this information was available, Fig. 2.10 only compares the regions of Asia (India) and Mexico–Central America. Notwithstanding that in both regions the abundance of exotics was influenced positively by the intensity of agricultural practices (the average percentage over the two regions for exotic abundance in high- and low-input systems was 62 and 34%, respectively), the main conclusion of this figure is that in India native species are more resistant to disturbance than in Mexico, and/or in Mexico exotic species have been introduced more frequently. Due to the scarce information obtained about the history and management practices in parcels, these conclusions must be drawn with caution.

Conclusions

In this study the fundamental question posed was what are the parameters controlling the structure and composition of earthworm communities in tropical agroecosystems? The results presented in this chapter show that earthworm communities of tropical agroecosystems are modified both at the taxonomical and functional level, due to the action of a suite of three hierarchically related factors.

1. The geographic–phylogenetic component, followed by the influence of soils, is important in determining the functional structure of the community (i.e. ecological categories). For example, the agroecosystem earthworm communities found in Africa and South America and those derived from nutrient-poor and very humid forests found elsewhere, will differ considerably from the original ones (shift from epigeic- to endogeic-dominated communities).
2. Parcel history and local agricultural practices are largely responsible for biodiversity differences (i.e. dominance of native species in India and Africa versus dominance of exotic species in America). Other variables include the available pool of exotic invaders, dispersal rates of invading species, time elapsed since perturbation, etc.
3. Diversity of communities and overall abundance of earthworms is also influenced by the type of agroecosystem. For example, annual crop sites (independently of the geographical region) have the poorest communities, in terms of both abundance and ecological categories.

All the communities analysed in this study were assembled spontaneously, without any human participation. The challenge for the future will be to manipulate these communities in order to assess and optimize the impact of different assemblages on soil fertility and crop production.

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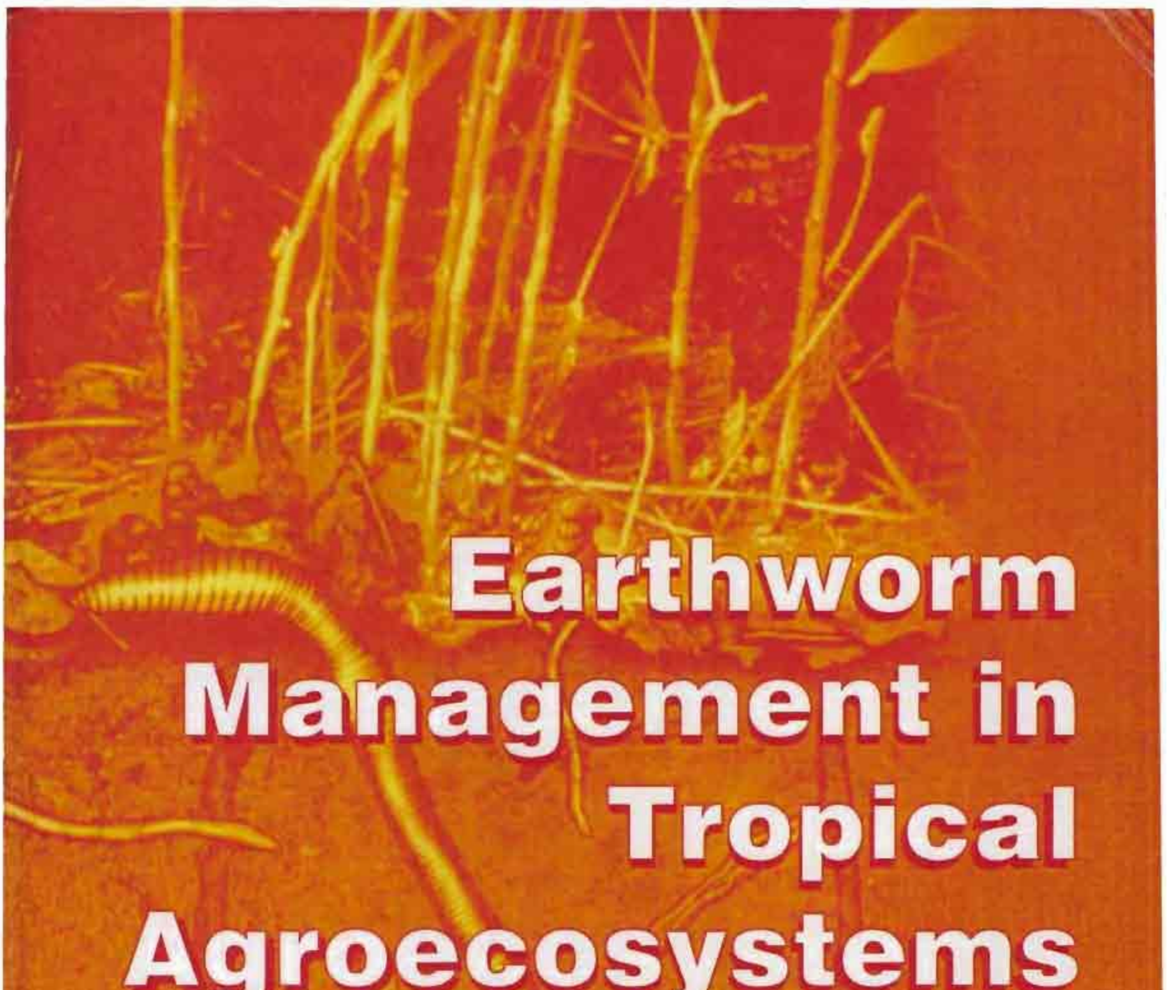

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