A Survey of Tropical Earthworms: Taxonomy, Biogeography and Environmental Plasticity

1

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Summary

A worldwide survey of earthworms in the humid tropics revealed that 51 exotics and 151 native species are commonly found in tropical agroecosystems. On the basis of frequency records and climatic and edaphic ranges, 21 exotics and 27 native species have been selected as possible candidates for manipulation. A multivariate analysis separated these species into four groups: (i) native species with wide edaphic and medium climatic tolerances; (ii) exotic species with wide climatic and edaphic tolerances; (iii) native and exotic species with narrow edaphic tolerances but more resistant to climatic variations; and (iv) native species with limited tolerance for climatic and edaphic variations.

Regarding management, species of group (ii) seem to be the most adaptable, both at regional and local levels (multipurpose species); group (i) can be managed for specific climatic conditions whereas group (iii) should be managed in specific soil environments. Species of group (iv) may only be managed at a very local scale.

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Introduction

Earthworms are confined to the soil and, for the majority of tropical farmers and agronomists, their diversity, activities and effects on soils are totally unknown. Even in the field of tropical soil science, the situation is not very different. For example, just a few years ago, there was little concern about earthworm diversity and the possible role of this diversity in the fertility of agroecosystems. During the last 10 years, however, there has been an increasing interest in diversity mainly due to the biodiversity crisis, which could be defined as the dramatic loss of species, habitats and ecological interactions (Wilson, 1985; Wilson and Peter, 1988; McNelly *et al.*, 1990). Although the most diverse tropical biota are insects that spend part of their life cycles in the soil, this environment has been, from a biodiversity viewpoint, one of the least studied.

Earthworms are not very diverse, and our current estimations of the number of existing species are far from complete. The most recent account of earthworm diversity (Reynolds, 1994) comprises 3627 earthworm species described worldwide, with an average annual addition of 68 species. The overall richness is expected to be at least twice this value, with the majority of still unknown species living in the tropics. For most species, the original description is the only information available, and nothing is known about their distribution, ecology, demography, physiology and resistance to disturbance. For example, on the basis of the number of native species found in two moderately well sampled regions, the state of Veracruz, Mexico, 33 species (Fragoso, in press), and Puerto Rico, 18 species (Borges, 1988; Borges and Moreno, 1989, 1990a,b, 1991, 1992), it is possible to predict the possible number of native species to be found in six scarcely sampled countries: three Central American continental countries (Honduras, Nicaragua and Guatemala) and three larger Caribbean islands (Cuba, Hispaniola and Jamaica). In the first group, nearly 50 species per country should be found in the future, whereas in the second group the number of species expected to be discovered is approximately ten (Jamaica), 130 (Hispaniola) and 200 (Cuba). This means that if sampling in these two regions is made with an effort similar to that in Veracruz and Puerto Rico, we should expect to find nearly 500 new native species in the future. Similar conclusions have been reached for Tasmania and Australia, where 150 and 600 species, respectively, are expected to be found once inventories are completed (Kingston and Dyne, 1995).

This chapter is the result of a 6-year project focused on characterizing the identity of earthworms in natural and managed ecosystems of the tropics (outlined in Fragoso *et al.*, 1995). The main objective was to select a group of earthworm species with potential for management in tropical agroecosystems, according to the following criteria: (i) a wide distribution; (ii) with adaptations to a wide range of environmental and edaphic conditions; and (iii) resistance to disturbances induced by agriculture.

Storage and Analysis of Data

The survey was conducted in selected regions of the tropics, and included field sampling and literature data. Most field data were obtained from the experimental sites related to this project (the MACROFAUNA network, see Chapters 4 and 5). Although it was not the principal objective, this survey allowed the discovery and description of approximately 50 new species.

EWDBASE: a database of tropical earthworms

All the information was stored in a database (EWDBASE) that includes information on the taxonomy and distribution of earthworm species, earthworm and other macroinvertebrate communities, climate of localities, edaphic and land-use variables, and socioeconomic aspects of agricultural lands where available.

Inputs to EWDBASE (climatic, edaphic and species distribution data) were taken from the following published literature: Mexico, Central America and the Caribbean islands (Eisen, 1895, 1896, 1900; Michaelsen, 1900, 1908, 1911, 1912, 1923, 1935, 1936; Cognetti, 1904a,b, 1905, 1906, 1907, 1908; Pickford, 1938; Gates, 1954, 1962a,b, 1970a,b, 1971, 1972, 1973, 1977a,b, 1979, 1982; Graff, 1957; Righi, 1972; Righi and Fraile, 1987; Sims, 1987; Borges, 1988, 1994; Borges and Moreno, 1989, 1990a,b, 1991, 1992; Fraile, 1989; James, 1990, 1991, 1993; Csuzdi and Zicsi, 1991; Zicsi and Csuzdi, 1991; Fragoso, 1993, in press; Rodríguez, 1993; Fragoso and Rojas, 1994; Reynolds and Guerra, 1994; Reynolds and Righi, 1994; Fragoso *et al.*, 1995; Reynolds *et al.*, 1995; Rodríguez and Fragoso, 1995), Bolivia (Rombke and Hanagarth, 1994), Ivory Coast (Omodeo, 1958; Lavelle, 1978, 1983; Tondoh, 1994), Congo (Zicsi and Csuzdi, 1986), Ghana (Sims, 1965), Gambia (Sims, 1967), Peru (Yurimaguas; Lavelle and Pashanasi, 1988) and several regions from India (Senapati, 1980; Chaudry and Mitra, 1983; Julka, 1986, 1988; Julka and Paliwal, 1986; Julka and Senapati, 1987; Bhadauria and Ramakrishnan, 1989; Julka *et al.*, 1989; Bano and Kale, 1991; Blanchart and Julka, 1997). EWDBASE was also fed with data obtained from field sampling carried out in Mexico, Panama, Colombia, Ivory Coast, India, Martinique, Guadaloupe, Rwanda, Peru, Congo and Cuba by members of the macrofauna network.

EWDBASE included data relating to 457 species, 745 localities and 836 sites from 28 countries. Distribution and environmental plasticity were analysed by relating species distribution to climate (1310 records), soils (818 records) and types of land use (1755 records).

Data analysis

Data were analysed at three geographic levels, i.e. local, regional and worldwide. At the local level, we intended to characterize the persistence of native earthworm species in different land-use systems (e.g. conversion of tropical deciduous forests to maize or pastures in Panuco, Mexico; maize plantations in native savannas of Lamto, Ivory Coast or the eastern llanos of Colombia; tea plantations in cloud forests of India, etc.). At the regional level, the analysis was extended to geographic areas such as southern Mexico, northern Rwanda or the Baoule region around Lamto (Ivory Coast), with the aim of identifying widespread native species. The worldwide analysis evaluated the distribution of exotic species in different natural and managed tropical ecosystems. The integration of these data in a global analysis produced three main outputs: (i) a list of tropical species of worldwide distribution that can be manipulated in any agroecosystem; (ii) regional lists of species by countries and/or kinds of agroecosystems; and (iii) an evaluation of the environmental and edaphic plasticity of these selected species.

Earthworm species of EWDBASE were classified along three different axes:

1. Biogeography, to divide species depending on this origin into natives and exotics. Native earthworms are those species that evolved in the site or region under study. Exotic species are earthworms that did not originate in the site under study and that were, generally, introduced by human activities; these species have also been called peregrine (Lee, 1987) and anthropochorous (Gates, 1970c).
2. Distribution among land-use systems, to separate species on the basis of their capabilities to adapt to natural (e.g. primary forests or savannas) or managed (e.g. annual crops or pastures) systems.
3. Ecological plasticity, to rank earthworms according to their ecological tolerance to edaphic and environmental variables from stenoecic (narrow range) to euryoecic (wide range) species.

These three axes were combined with the three geographic scales of analysis (local, regional and global) in order to propose the most appropiate earthworm species for manipulation in a given region and/or country in a specific agricultural situation.

Earthworm Species of Tropical Agroecosystems

The exotic earthworms of the tropics

Since the early studies of Eisen (1900) and Michaelsen (1903, 1935), it has been observed that peregrine worms were very common in tropical disturbed ecosystems. In a paper that analysed the distribution and dispersal of this group of species, Lee (1987) stated that these species '... more than any others, . . . are important in maintaining soil fertility in agricultural and pastoral lands.' Although the author did not present the complete list of species, he mentioned that peregrine species comprise nearly 100 species (approx. 3% of all earthworms). Peregrine earthworms become exotics when the geographic area of occurrence does not correspond to the original area of distribution.

The number of records of tropical exotic species is enormous, and their distribution should be analysed using the three scales mentioned above (worldwide, regional and local), because some species with wide distributions may be restricted to one kind of land-use system or have narrow climatic and edaphic niches that are not represented in a given country or continent.

From EWDBASE and a literature review (Gates, 1972, 1982; Lee, 1987; Mele *et al.*, 1995), we identified 51 exotic species commonly distributed across tropical countries (Table 1.1). Fifteen were temperate Lumbricidae of European origin, restricted to high altitude mountain localities. Their frequent occurrence in natural temperate forests suggests that these species may have replaced natives, as has been observed by Fragoso (in press) in the temperate forests of Veracruz, Mexico. The absence of this group of exotics in low altitude tropical agroecosystems (from EWDBASE queries) eliminates their potential for manipulation and, therefore, this group of species will no longer be considered in this chapter.

From Table 1.1, we selected a group of 20 species distributed worldwide, which are mainly from localities below 1000 m. This group is presented in Table 1.2, ranked according to their frequencies in agroecosystems; Table 1.3 shows, for the above group of species, the ranges of environmental (precipitation and temperature) and edaphic (pH, organic matter, nitrogen, sand and clay) situations in which they occur. From the data in Tables 1.2 and 1.3, it is possible to make a preliminary separation of another group of species adapted to different managed agroecosystems and with wide ranges of environmental and/or edaphic plasticity. These species include *Pontoscolex corethrurus, Polypheretima elongata, Dichogaster bolaui, Ocnerodrilus occidentalis, Amynthas gracilis, A. corticis, Dichogaster affinis* and *D. saliens*, and all of them are tolerant to very low soil concentrations of nutrients, organic matter and nitrogen.

The widespread native earthworms of the tropics

The majority of native species are not very tolerant and are restricted mainly to natural environments. Of the 404 native species stored in EWDBASE, 274 species (67%) were restricted to a single locality, whereas 207 (51%) were found exclusively in natural environments. On the other hand, nearly 40% of native species of EWDBASE were found inhabiting at least one of five types of agricultural land-use systems: pastures, crops, tree plantations, organic wastes and fallows (Table 1.4). Only a small proportion of these native species,

Continued p.16

Table 1.1. The exotic earthworms of the tropics. Continental, country and altitudinal distribution.

Species	Family	Origin	Distribution		Altitude (m) (average)
			Continents	Countries	
Allolobophora chlorotica	Lumbricidae	Europe	3	34	3000
Amynthas corticis	Megascolecidae	Asia	5	40	0–2500 (1243)
Amynthas gracilis	Megascolecidae	Asia	5	31	0–2000 (962)
Amynthas morrisi	Megascolecidae	Asia	4	23	610
Amynthas rodericensis	Megascolecidae	Asia	3	26	0–1200 (420)
Aporrectodea caliginosa	Lumbricidae	Europe	4	15	1150–3850 (3168)
Aporrectodea longa	Lumbricidae	Europe	5	27	2240–2400
Aporrectodea rosea	Lumbricidae	Europe	5	52	500–4650 (2972)
Aporrectodea trapezoides	Lumbricidae	Europe	5	19	1200–3300 (2650)
Aporrectodea turgida	Lumbricidae	Europe	5	20	1300–3400 (2570)
Bimastos parvus	Lumbricidae	N. America	5	32	12–1500 (756)
Bimastos tumidus	Lumbricidae	N. America	1	1	1000–1270 (1135)
Dendrobaena octaedra	Lumbricidae	Europe	4	32	1200–4650 (2423)
Dendrodrilus rubidus	Lumbricidae	Europe	5	46	950–4650 (2442)
Diachaeta thomasi	Glossoscolecidae	S. America	1	2	Sea level
Dichogaster affinis	Dichogastrini*	W. Africa	4	24	0–1400 (391)
Dichogaster annae	Dichogastrini*	W. Africa	2	5	60–1940 (1438)
Dichogaster bolaui	Dichogastrini*	W. Africa	5	43	0–1360 (259)
Dichogaster gracilis	Dichogastrini*	W. Africa	2	2	Under 500
Dichogaster modigliani	Dichogastrini*	W. Africa	4	20	0–1100 (339)
Dichogaster saliens	Dichogastrini*	W. Africa	4	17	0–1100 (307)
Drawida barwelli	Moniligastridae	India	2	11	0–1000 (347)
Eisenia fetida	Lumbricidae	Europe	5	45	1300–1500 (1394)
Eiseniella tetraedra	Lumbricidae	Europe	5	45	1300–3820 (3109)

Eudrilus eugeniae	Eudrilidae	W. Africa	4	31	0–60 (15)
Eukerria kukenthali	Ocnerodrilidae	S. America	2	8	n.d
Eukerria mcdonaldi	Ocnerodrilidae	S America	1	1	300
Eukerria peguana	Ocnerodrilidae	S. America	1	1	n.d.
Eukerria saltensis	Ocnerodrilidae	S. America	4	10	550–3875 (1911)
Eukerria zonalis	Ocnerodrilidae	S. America	1	1	300
Gordiodrilus peguanus	Ocnerodrilidae	C. Africa	4	7	n.d.
Hyperiodrilus africanus	Eudrilidae	W. Africa	1	6	n.d.
Lumbricus rubellus	Lumbricidae	Europe	5	34	1500–3750 (2739)
Lumbricus castaneus	Lumbricidae	Europe	3	23	n.d.
Lumbricus terrestris	Lumbricidae	Europe	5	36	n.d.
Metapheretima taprobanae	Megascolecidae	Asia	4	7	10–40 (30)
Metaphire californica	Megascolecidae	Asia	5	21	0–2000 (982)
Metaphire houlleti	Megascolecidae	Asia	5	20	10–853 (408)
Metaphire posthuma	Megascolecidae	Asia	2	12	12–22 (17)
Microscolex dubius	Acanthodrilinae*	S. America	5	16	n.d.
Microscolex phosphoreus	Acanthodrilinae*	S. America	5	28	1500–3600 (1506)
Nematogenia panamaensis	Ocnerodrilidae	C. America	3	12	n.d.
Ocnerodrilus occidentalis	Ocnerodrilidae	C. America	5	22	0–1520 (470)
Octolasion cyaneum	Lumbricidae	Europe	5	30	1050–2430 (1576)
Octolasion tyrtaeum	Lumbricidae	Europe	5	35	1180–4654 (2313)
Periscolex brachycystis	Glossoscolecidae	C. America	1	4	0–500 (192)
Peryonix excavatus	Megascolecidae	Asia	4	19	300–1050 (1077)
Pheretima bicincta	Megascolecidae	Asia	3	12	30–1100 (577)
Polypheretima elongata	Megascolecidae	Asia	4	27	0–1300 (185)
Polypheretima taprobanae	Megascolecidae	Asia	4	7	1360
Pontoscolex corethrurus	Glossoscolecidae	S. America	4	56	0–2000 (463)

*Tribe or subfamily of Megascolecidae; n.d. = not determined.

Table 1.2. Distribution of common exotic earthworms in different tropical land-use systems. No. of records from Mexico, Central America, the Caribbean, Colombia, Rwanda, Congo, Ivory Coast and India.

Species	Natural ecosystems	Crops	Pastures	Tree plantations	Fallows	Organic wastes
Pontoscolex corethrurus	94	31	44	41	6	4
Polypheretima elongata	30	10	39	19	4	5
Dichogaster bolaui	11	7	15	11	3	5
Ocnerodrilus occidentalis	3	6	15	7	2	1
Amynthas gracilis	7	4	6	9	2	2
Amynthas corticis	22	6	7	4	2	2
Hyperiodrilus africanus	2	4	8	5	1	2
Dichogaster affinis	9	5	5	7	1	0
Dichogaster saliens	5	1	9	4	1	0
Drawida barwelli	3	1	9	3	0	0
Eudrilus eugeniae	2	0	3	3	0	4
Dichogaster annae	0	2	2	4	0	1
Amynthas rodericensis	24	1	5	3	0	0
Peryonix excavatus	1	0	1	1	0	5
Metaphire californica	0	0	4	0	0	1
Dichogaster modigliani	1	0	4	1	0	0
Metaphire houlleti	0	0	4	0	0	0
Metapheretima taprobanae	2	0	2	1	0	0
Periscolex brachycystis	6	1	2	1	0	0
Pheretima bicincta	5	0	0	1	0	0
Metaphire posthuma	1	0	0	1	0	0

Table 1.3. Range of environmental conditions tolerated by the most common exotic species.

Species	T (°C)	Rainfall (mm)	pH	OM (%)	N (%(× 0.1))	Ca (mEq 100 g^{-1})	Mg (mEq 100 g^{-1})	S (%)	C (%)
Pontoscolex corethrurus	14–28	268–5000	3.8–8.2	0.9–12.6	0.1–9	0.8–16.5	0.1–11.2	3–91	6–87
Polypheretima elongata	21–30	800–4000	5–7.8	1.8–7.6	0.8–3.8	4.4–53	1–2.7	5–93	4–54
Dichogaster bolaui	18–30	800–4725	5–8.2	1–10.2	0.2–8.8	1.7–44	0.06–9	5–93	4–53
Ocnerodrilus occidentalis	16–30	146–4725	5.6–8.9	0.9–7.8	0.7–8.9	0.8–53	0.06–4.5	18–98	2–74
Amynthas gracilis	15–26	670–3500	4.8–8.9	1.7–14.4	0.7–5.9	1.3–3.4	0.7–.46	11–61	9–53
Amynthas corticis	13–26	865–4521	3.9–7.5	2–12.6	2–4.2	1.9–5.8	1.5–3.5	36–61	17–33
Dichogaster affinis	17–28	440–2240	4.5–8.2	1–13.7	0.7–8.8	0.82–53	0.06–4.9	9–98	2–74
Dichogaster saliens	22–28	916–4725	5–8.9	0.6–6.2	0.2–8.9	0.9–12.5	0.06–4.5	18–91	6–47
Drawida barwelli	21–26	1500–4000	5–7.9	3.6–5.4	2–2.5	3.5–5.8	1.1–3.5	3–42	24–87
Eudrilus eugeniae	25–28	1352–1880	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Dichogaster annae	28	1880	3.7–6.3	1.6–4.9	1–2.6	n.d.	n.d.	32–85	11–54
Amynthas rodericensis	20–26	1200–5000	4.7–8	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Peryonix excavatus	15–24	865–2173	7.1–7.5	3	n.d.	n.d.	n.d.	50	33
Metaphire californica	21	2631	5.2–5.6	4.3–5.4	2.2–2.5	3.5–5.8	1.5–3.5	36–42	24–28
Metaphire houlleti	22–26	1314–1996	6.8	2	n.d.	n.d.	n.d.	n.d.	n.d.
Metapheretima taprobanae	26	1450–2000	6.4–8	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Dichogaster modigliani	25	1396	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Periscolex brachycystis	24–28	1880–4725	5–6.5	2.2–7.6	1.1–4.2	4.1–44	1.1–3.6	5–62	9–50
Pheretima bicincta	21–26	2500–3500	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Metaphire posthuma	24	916–1079	8.1	1.2	1	6.6	0.86	46	18

T = temperature, OM = organic matter, N = nitrogen, Ca = calcium, Mg = magnesium, S = sand, C = clay; all values from the upper 10 cm of soil.

Table 1.4. Native earthworm species of tropical agroecosystems.

Species	C	P	T	F	W
Belize					
Diplotrema jenniferae		1			
Bolivia					
Andiorrhinus bolivianus	1				
Enantiodrilus borelli		1			
Eukerria asuncionis	1				
Eukerria eiseniana		1			
Eukerria garmani		1			
Eukerria tuberculatus			1		
Goiascolex vanzolinii			1		
Colombia					
Andiodrilus yoparensis	1	1			
Andiorrhinus sp.nov1		1			
Glossodrilus sikuani	1	1			
***Glossodrilus* sp1**	**1**	**2**	**2**	**3**	
Martiodrilus agricola	1			2	
Martiodrilus carimaguensis	1	1			
Martiodrilus savanicola	1			1	
Martiodrilus sp1	1			3	
Thamnodrilus sp1				2	
Congo					
Dichogaster graffi			1		
Gordiodrilus sp1			1		
Nematogenia lacuum			1		
Costa Rica					
Glossodrilus dorasque			1		
Glossodrilus nemoralis		4			
Glossodrilus orosi		1			
Cuba					
Diplotrema ulrici	1				
Onychochaeta elegans	**1**	**4**	**4**		
Onychochaeta windlei	**2**	**2**	**3**		
Pontoscolex cynthiae	1		3		
Zapatadrilus morenoae	1	1			
Zapatadrilus siboney			1		
Zapatadrilus taina			1		
El Salvador					
Eutrigaster sporadonephra			1		
Guadaloupe					
Pontoscolex spiralis	1	2	1		

Table 1.4. *Continued.*

Species	C	P	T	F	W
India					
Curgiona narayani	3				
Drawida ampullacea	**1**	**3**	**1**	**2**	
Drawida assamensis				1	
Drawida calebi	**1**	**1**	**2**		
Drawida fakira	1				
Drawida ferina	2		1		
Drawida ghatensis			1		
Drawida japonica	1	1	1		
Drawida kanarensis	1		1		
Drawida lennora	1			1	
Drawida modesta	1			1	
Drawida nepalensis	**1**	**2**			
Drawida paradoxa	**1**	**10**	**1**	**1**	
Drawida pellucida	2		1	1	
Drawida sp1	1				
Drawida sp2		1			
Drawida scandens		1	1		
Drawida sp3		4	1		
Drawida sulcata	1		1	1	
Drawida thurstoni		4		1	
Drawida willsi	**1**	**3**	**1**		
Eutyphoeus festivus				2	
Eutyphoeus incommodus	**2**	**3**			
Eutyphoeus orientalis		1			
Eutyphoeus sp1	1				
Eutyphoeus waltoni	1				
Gen.nov1 sp.nov1		**8**	**1**		
Gen.nov1 sp.nov2		2			
Gen.nov2 sp.nov1		1		1	
Gen.nov3 sp.nov1		3			
Glyphidrilus tuberosus		2			
Glyphidrilus annandalei	1			2	
Hoplochaetella kempi	1		1	1	
H. sanvordemensis		1			
Hoplochaetella suctoria			1		
Hoplochaetella sp1		1			
Hoplochaetella sp2		2			
Karmiella karnatakensis		**6**	**1**		
Karmiella sp1		1			
***Konkadrilus* sp1**		**6**	**1**	**1**	
Konkadrilus sp2		8	2		
Konkadrilus tirthahalliensis			6		
Lampito mauritii	**3**	**2**	**5**	**1**	
Lennogaster chittagongensis		1			

Continued

Table 1.4. *Continued.*

Species	C	P	T	F	W
Lennogaster pusillus	**3**	**3**			
Lennogaster sp1			1		
Lennoscolex sp1			1		
Lennogaster dashi			2		
Mallehulla indica		1	1	1	
Megascolex felicisetae	1				
Megascolex sp1	3				
Megascolex insignis	1		1	1	
Megascolex konkanensis		**2**	**2**	**3**	
Megascolex lawsoni	1		2		
Nelloscolex strigosus				1	
Notoscolex sp1	1				
Octochaetona beatrix	1	1	1		
Octochaetona rosea	1		1	1	
Octochaetona surensis		1	1		
Pellogaster bengalensis	1		1		
Perionyx sp1		1			
Plutellus tumidus	1		1		
Ramiella bishambari	1				
Tonoscolex horaii				2	
Travoscolides duodecimalis	1				
Wahoscolex sp1		4			
Ivory Coast					
Agastrodrilus opisthogynus			1		
Chuniodrilus palustris	**10**	**1**	**1**	**3**	
Chuniodrilus zielae	**10**	**1**	**1**	**3**	
Dichogaster agilis	**9**	**1**	**2**	**2**	
Millsonia anomala	**9**	**1**	**1**	**3**	
Millsonia lamtoiana	1		1	1	
Millsonia schlegeli		2			
Jamaica					
Eutrigaster grandis	1				
Martinique					
Pontoscolex cuasi		1			
Pontoscolex spiralis	**1**	**2**	**2**		
Mexico					
Balanteodrilus pearsei	**4**	**10**	**1**	**2**	**2**
Diplocardia eiseni		1			
Diplocardia sp.nov1		6			
Diplocardia sp.	1				
Diplocardia sp.nov2	3		6	1	
Diplotrema sp.nov1		1			
Diplotrema murchiei	**1**	**11**		**3**	

Table 1.4. *Continued.*

Species	C	P	T	F	W
Diplotrema papillata		4			
Gen.nov4 sp.nov1		3			
Gen.nov5 sp.nov1		1			
Larsonidrilus microscolecinus		2	1		
Larsonidrilus orbiculatus		3			
Lavellodrilus maya		3			1
Lavellodrilus parvus	**5**	**5**	**1**	**1**	
Lavellodrilus riparius		1			
Mayadrilus rombki	1				
Phoenicodrilus sp.nov1		1		1	
Phoenicodrilus taste	**1**	**16**	**2**		
Protozapotecia australis	**1**	**6**	**1**	**1**	
Ramiellona sp.nov1			1		
Ramiellona sp.nov2		1		1	
Ramiellona sp.nov3		1			
Ramiellona sp.nov4		1			
Ramiellona sp.nov5				1	
Ramiellona sp.nov6				1	
Ramiellona sp.nov7		1			
Ramiellona strigosa		**1**	**2**		
Ramiellona wilsoni		1			
***Zapatadrilus* sp.nov1**	**3**	**3**	**9**	**3**	
Zapotecia amecameca				1	
Zapotecia nova		**4**		**3**	
Zapotecia sp1		3		1	
Peru					
Diachaeta xepe	1	2	1	1	
Rhinodrilus lavellei	1		1		
Rhinodrilus pashanasi	**1**	**1**	**1**		
Rwanda					
Dichogaster itoliensis	2	1	1		
Dichogaster sp1	1	1	2		1
Eminoscolex lavellei	**3**	**1**	**5**		
***Gordiodrilus* sp1**	**4**	**1**	**15**		
Stuhlmannia variabilis	1		2		1

No. of records from EWDBASE. C=crops, P=pastures, T=tree plantations, F=fallows,W=organic wastes.

Table 1.5. Environmental tolerance ranges (climatic and edaphic) of selected tropical native earthworms (data from EWDBASE).

Species	T (°C)	Rainfall (mm)	pH	OM (%)	N (% (× 0.1))	Ca (mEq 100 g^{-1})	Mg (mEq 100 g^{-1})	S (%)	C (%)
Cuba									
O. elegans	28	1880	n.d.	7.6	n.d.	44	9	5	50
India									
D. ampullacea	22	5000	4.6–5.8	4.3–11	0.17–0.48	2.5–14	1–3.7	15–43	18–53
D. paradoxa	22	5000	4.4–5.1	3.6–9.3	0.19–0.33	2.4	0.93	23	40
D. willsii	30–31	1150–2363	5.9–6.8	0.9–2.4	0.08–0.38	n.d.	n.d.	83–95	2–7
E. incommodus	16–30	1014–1600	5.9–6.8	1–3	n.d.	n.d.	n.d.	n.d.	n.d.
D. nepalensis	16–26	1014–1600	6.7–6.8	1–2	n.d.	n.d.	n.d.	n.d.	n.d.
K. karnatakensis	22	5000	4.7–5.5	4.2–7.5	0.17–0.33	5.04	1.71	28	18–40
L. mauritii	24–31	865–2166	6–6.7	1–3.2	0.08–0.19	n.d.	n.d.	83–91	4–7
L. pusillus	16–30	1014–1700	5.9–6.8	1–5	n.d.	n.d.	n.d.	47	34
O. beatrix	16–24	865–1314	6.8–7.1	2	n.d.	n.d.	n.d.	n.d.	n.d.
K. sp1	22	5000	4.4–5.8	4.2–11	0.17–0.48	14.8	3.74	n.d.	18–53
K. sp2	22	5000	4.4–5.8	3.6–10.8	0.17–0.48	2.4–15	0.9–3.7	15–43	18–53
Mexico									
B. pearsei	24–27	916–2963	5.5–8.2	1–14.4	0.09–0.59	0.9–23	0.06–5	9–82	10–86
D. murchiei	24–27	916–2160	7.5–8.9	0.2–2.6	0.06–0.88	1.3–21	0.06–3	22–98	2–74
D. papillata	25–27	814–2130	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
L. parvus	24–27	1156–4725	5.3–8.1	0.9–10.1	0.07–0.42	4.5–17	0.65–11	19–63	13–74
P. taste	19–27	600–2963	5–8	1–14.4	0.08–0.42	4.1–23	0.06–6	9–78	9–86
P. australis	14–25	600–2522	5.3–7.9	1.4–11.8	0.07–0.42	5.6–14	1–6.1	11–63	12–73
R. strigosa	24–27	1000–2963	5–6.5	2.2–6.5	0.11–0.42	4.1–13	1.7–3.6	32–62	9–50
Z. sp.nov 1	24–25	916–1349	7.7–8.3	1.1–7.3	0.02–0.48	0.87–24	0.18–3	9–46	26–62

Ivory Coast									
C. palustris	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
C. zielae	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
D. agilis	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
M. anomala	28	1276	5–7	0.75–1.3	0.08–1.3	1.7–2.8	1–2.3	55–82	5–15
Rwanda									
E. lavellei	n.d.	n.d.	3.7–7.4	1.6–4.9	0.08–0.24	n.d.	n.d.	32–60	29–54
G. sp1	n.d.	n.d.	3.5–7.8	1.4–41.2	0.06–1.4	n.d.	n.d.	2–92	10–67
S. variabilis	n.d.	n.d.	3.7–4.4	3.5–4.7	0.13–0.26	n.d.	n.d.	42–85	11–48

T = temperature, OM = organic matter, N = nitrogen, Ca = calcium, Mg = magnesium, S = sand, C = clay; all values from the upper 10 cm of soil.

however, are common in tropical agroecosystems (Table 1.4, 31 species in bold). This group includes species widely distributed at the regional level (e.g. *Onychochaeta elegans* in Cuba, *Balanteodrilus pearsei* in southeastern Mexico or *Lampito mauritii* in India) or locally abundant (*Ramiellona strigosa*, *Zapatadrilus* sp.nov1 in Mexico and *Millsonia anomala* in Ivory Coast). Table 1.5 shows the environmental (precipitation, temperature) and edaphic (pH, organic matter, nitrogen, sand and clay) tolerance ranges of some of these species, according to the country in which they occur. Species listed in this table are those for which these data were available.

Comparisons between exotic and widely distributed native earthworm species

So far, we have identified 20 exotic and 27 native species that commonly occur in tropical agroecosystems of Asia, Africa and America (Tables 1.2 and 1.5). Data from Tables 1.3 and 1.5 suggest that these species apparently have wide ranges of climatic and edaphic tolerances. Figure 1.1 shows that the degree of tolerance (i.e. the environmental plasticity) is larger in the group of exotics, both at the regional (range of annual precipitation) and local level (range of pH). In this figure, however, environmental plasticity is analysed with range values (difference between maximum and minimum) of only two variables. In order to determine whether this pattern is maintained with more variables, two multivariate analyses were performed using the climatic (two) and edaphic (seven) variables of Tables 1.3 and 1.5. The input matrix consisted of 47 rows (native and exotic species) and nine columns (environmental variables), data being standardized in both cases. The first analysis was a principal component analysis (PCA), that ordinated species along two components which together explained 76% of the total variance (C1 = 62%, C2 = 14%). C1 and C2 correlated, respectively, with edaphic and climatic ranges. The second analysis was a cluster analysis, performed using unweighted pair-groups method analysis (UPGMA) as an average-linkage clustering method. PCA and UPGMA were made respectively, with STATGRAPHIC and PATN (Belbin, 1976) software.

Figure 1.2 shows the result of these analyses that ordinated and grouped the native and exotic species listed in Tables 1.3 and 1.5, into four main groups:

1. G1 includes those native species with wide edaphic and medium climatic tolerances (high local plasticity but low regional plasticity), which correspond to the majority of native widespread Mexican species.
2. G2 are the common exotic species of the tropics that exhibit wide climatic and edaphic tolerances (high regional and local plasticity).
3. G3 includes species (natives and exotics) with narrow edaphic tolerances that are resistant to climatic variations (low local but high regional plasticity).

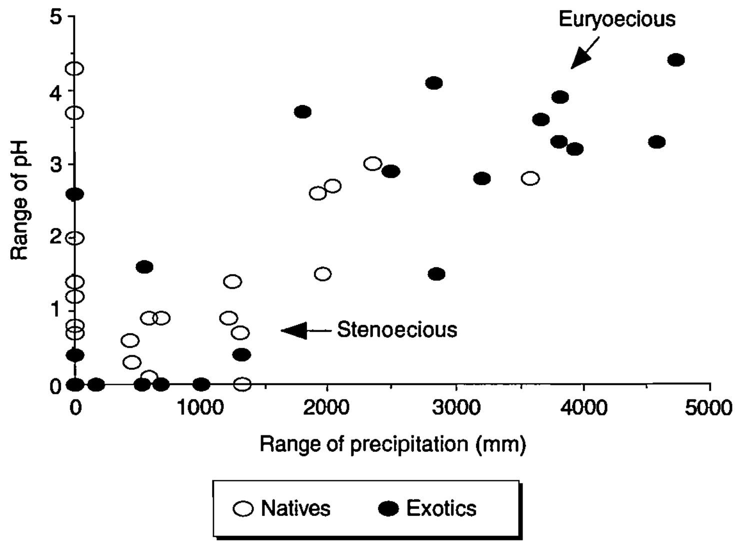

Fig. 1.1. Example of climatic (annual precipitation) and edaphic (pH) plasticity of exotic and native widespread tropical earthworm species. Each point represents a species. Those situated in the upper right corner indicate euryoecious species, whereas those situated in the lower left corner indicate stenoecious species. Both precipitation and pH are range values.

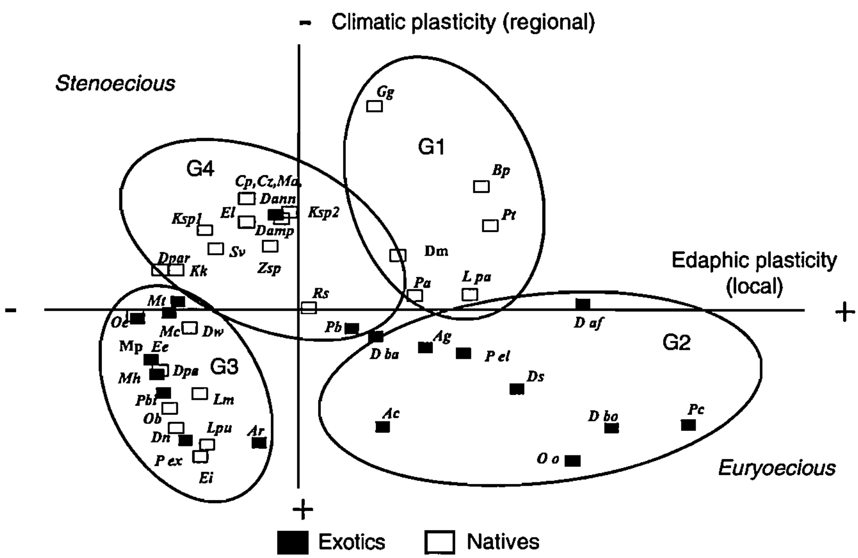

Fig. 1.2. Ordination (PCA) and clustering (UPGMA) of widespread native and exotic species on the basis of climatic and edaphic range values. For initials see Table 1.6.

4. G4 groups species with low tolerance to both climatic and edaphic variables (low regional and local plasticity). It is this group in which the majority of the other native species of Table 1.4 should be placed.

Although this analysis is somewhat biased by the amount of records and/or data available (some species have very few records and consequently low ranges), the output ordination and classification is useful because it provides a framework for the classification of earthworms with potential for manipulation, according to their ecological plasticity.

Thus, G2 (euryoecics) includes those exotic species that can be manipulated in the majority of tropical agroecosystems, both if they are introduced and if they are already present. They represent the species best adapted to unsuitable edaphic environments: *Amynthas gracilis* (*Ag*), *A. corticis* (*Ac*), *Dichogaster affinis* (*Daf*), *D. bolaui* (*Dbo*), *D. saliens* (*Ds*), *Ocnerodrilus occidentalis* (*Oo*), *Pontoscolex corethrurus* (*Pc*) and *Polypheretima elongata* (*Pe*). The last two species are endogeic mesohumic species (see Chapter 2 for a definition of these terms) which, due to their abundances, cast production and burrowing activities, have important effects on soil processes. In the same way, G1 (euryedaphic species) corresponds to native species that, for a given country and/or region, should be ranked first in manipulative practices because they represent the original adapted fauna: *Balanteodrilus pearsei* (*Bp*), *Lavellodrilus parvus* (*Lpa*), *Phoenicodrilus taste* (*Pt*), *Diplotrema murchiei* (*Dm*) and *Protozapotecia australis* (*Pa*) in Mexico and *Hyperiodrilus africanus* for several African countries (this species was not analysed for plasticity, but is very common in different land-use systems). G3 (stenoedaphic species) comprises species that could be manipulated in different regions but in the same type of soil substrate, e.g. epigeic native (*Drawida willsii, Dw*) and exotic species (*Perionyx excavatus, Pex; Eudrilus eugeniae, Ee*) on organic rich substrates. Finally, G4 (stenoecic species) represents the more local scale of management: native species that only survive in a given locality and in a given type of soil. They might be manipulated at a local level, provided no intensive or destructive practices are used (see Chapter 2). This is the case, for example, for some of the savanna species of Lamto (*Millsonia anomala, Ma*), some (but not all) forest species of Yurimaguas and several Indian (*Konkadrilus* sp1 and sp2, *Ksp1* and *Ksp2; Drawida ampullacea, Damp*) and Mexican (*Ramiellona strigosa, Rs; Zapatadrilus* sp.nov1, *Zsp*) species.

In general, this analysis shows that exotic species are better adapted than natives to factors that change both at the regional–continental level (e.g. rainfall, temperature) and at the local level (edaphic changes); the majority of natives, on the other hand, are incapable of adapting to regional variations, but some species are still able to withstand variations at a more local level.

Besides environmental plasticity, there are at least two other variables that could explain the wider distribution of exotics and the absence of native species in other regions.

1. Parthenogenetic reproduction: almost all exotic species in Table 1.2 are considered to be facultatively parthenogenetic, meaning that they may produce viable unfertilized cocoons. Native species in Table 1.4, on the other hand, only produce viable cocoons after fertilization (with a few exceptions such as *P. taste* and *O. elegans*). Parthenogenesis, therefore, appears to be an essential determinant of the wide geographic distribution of exotics, as was originally proposed by Reynolds (1974) and Lee (1987). If mating is not obligatory, one single individual (even a cocoon) may establish a new population.
2. Historical dispersal by man: the distribution of exotics has been greatly favoured by the spread of plants worldwide and such practices as the use of soil as ballast, in the days of long sea voyages. Gates (1972, 1982) intercepted, over several years, the worms that were introduced to the United States in pots containing imported plants. He found all the exotic species of Table 1.2 and many native species from several tropical and temperate countries; these species, of course, did not have any chance to establish in North American soils, but we can infer that, in the past, this situation occurred repeatedly, being the main cause for the presence of exotic species.

In some cases, it is possible to relate the distribution of some exotics to the origin of introduced plants. The African exotic species *Gordiodrilus peguanus* and *Eudrilus eugeniae*, for example, are present mainly in former European colonies (e.g. Greater Antilles; Gates, 1972) that were, in the past, dominated by an African slave population; they are not present, for example, in Mexico, Peru and other countries where this population was practically non-existent. In a number of cases, the absence of euryoecious native species in a given tropical country may, therefore, better be explained by human activities than by factors related to ecological plasticity.

Conclusions

The list of most common earthworm species of tropical agroecosystems includes a set of euryoecious exotic species, common in the majority of tropical countries, and native species that are common for a given country at local or regional levels. Table 1.6 lists these species, their ecological categories and the geographic level at which management of their populations should be considered.

Most species with potential for manipulation are large species, mainly mesohumic endogeics and epi-endogeics that live in the soil and ingest a mixture of soil and surface litter. These species can be considered as ecosystem engineers because they transform the edaphic profile through the production of casts and burrows; in this regard they are keystone species in the agroecosystem. Small polyhumic species may play a role in the system (e.g. as 'decompacting' species; see Chapter 5) but may not be crucial in the short term as their activities do not dramatically affect soil profile and other subordinated

Table 1.6. List of tropical earthworm species with potential for manipulation in annual cropping systems.

Species	Ecological category	Region	Management
Dichogaster bolaui (Dbo)	Epigeic	Humid tropics	Worldwide
Dichogaster saliens (Ds)	End. polyhumic	Humid tropics	Worldwide
Dichogaster affinis (Daf)	End. polyhumic	Humid tropics	Worldwide
Dichogaster annae (Dann)	End. polyhumic	Humid tropics	Worldwide
Drawida barwelli (Dba)	End. polyhumic	Humid tropics	Worldwide
Eudrilus eugeniae (Ee)	Epigeic	Humid tropics	Worldwide
Metapheretima taprobanae (Mt)	End. mesohumic	Humid tropics	Worldwide
Metaphire californica (Mc)	Epi–endogeic	Humid tropics	Worldwide
Metaphire houlleti (Mh)	Epi–anecic	Humid tropics	Worldwide
Metaphire posthuma (Mp)	End. mesohumic	Humid tropics	Worldwide
Ocnerodrilus occidentalis (Oo)	End. polyhumic	Humid tropics	Worldwide
Periscolex brachycystis (Pb)	End. polyhumic	Humid tropics	Worldwide
Peryonix excavatus (Pex)	Epigeic	Humid tropics	Worldwide
Pheretima bicincta (Pbi)	Epi–endogeic	Humid tropics	Worldwide
Polypheretima elongata (Pel)	End. mesohumic	Humid tropics	Worldwide
Pontoscolex corethrurus (Pc)	End. mesohumic	Humid tropics	Worldwide
Balanteodrilus pearsei (Bp)	End. Poly-mes.	SE Mexico	Regional
Diplotrema murchiei (Dm)	End. Poly-mes.	SE Mexico	Regional
Phoenicodrilus taste (Pt)	End. polyhumic	SE Mexico	Regional
Lavellodrilus parvus (Lpa)	End. polyhumic	SE Mexico	Regional
Protozapotecia australis (Pa)	End. polyhumic	SE Mexico	Regional
Eminoscolex lavellei (El)	End. polyhumic	Rwanda	Regional
Stuhlmannia variabilis (Sv)	End. mesohumic	Rwanda	Regional
Gordiodrilus sp1 *(Gg)*	End. polyhumic	Rwanda	Regional
Dichogaster itoliensis (Di)	Anecic	Rwanda	Regional
Onychochaeta elegans (Oe)	End. mesohumic	Cuba, Caribbean	Regional

Onychochaeta windelei (Ow)	End. mesohumic	Cuba, Caribbean	Regional
Pontoscolex spiralis (Ps)	End. mesohumic	Lower Antilles	Regional
Chuniodrilus zielae (Cz)	End. polyhumic	Lamto, Ivory Coast	Regional
Chuniodrilus palustris (Cp)	End. polyhumic	Lamto, Ivory Coast	Regional
Hyperiodrilus africanus (Ha)	Epiendogeic	Tropical Africa	Regional
Lampito mauritii (Lm)	Anecic	India, SE Asia	Regional
Drawida paradoxa (Dpa)	End. mesohumic	Karnataka, India	Regional
Drawida ampullacea (Damp)	Endogeic	Karnataka, India	Regional
Drawida willsii (Dw)	Epianecic	Karnataka, India	Regional
Drawida nepalensis (Dn)	End. mesohumic	Karnataka, India	Regional
Karmiella karnatakensis (Kk)	End. poly-mes.	Karnataka, India	Regional
Megascolex konkanensis (Mk)	Endogeic	Karnataka, India	Regional
Eutyphoeus incommodus (Ei)	Anecic	Northern India	Regional
Ramiellona strigosa (Rs)	End. mesohumic	Chiapas, Mexico	Local
Zapatadrilus sp.nov *(Zsp)*	Endoanecic	Veracruz, Mexico	Local
Rhinodrilus pashanasi (Rp)	End. mesohumic	Peru, Yurimaguas	Local
Millsonia anomala (Ma)	End. mesohumic	Lamto, Ivory Coast	Local
Millsonia lamtoiana (Ml)	Anecic	Lamto, Ivory Coast	Local

soil organisms. This aspect, linked to the issue of the functional value of biodiversity, is considered in Chapters 4 and 5.

The main conclusion of this survey is that native species are found frequently in tropical agroecosystems, particularly in some countries (e.g. India) where apparently low-input agricultural techniques prevail (see Chapter 2 for more on this point), or in localities with low annual precipitations that do not permit the invasion of exotics (such as Mexican localities with annual precipitations below 1300 mm, where the native endoanecic *Zapatadrilus* sp.nov1 dominates and no mesohumic exotics have been able to establish). Taking into account the fact that several native species survive in agroecosystems at a very local level (Table 1.4), the number of species to be manipulated in tropical farming systems turns out to be considerably greater than the 10–15 major exotic species identified in Table 1.1. In this regard, and at least for tropical regions, it is no longer possible to maintain Lee's (1987) statement that only exotic species are important in agricultural lands. In addition, it is highly probable that the number of native species with potential for management in agroecosystems will increase as a function of the intensity of sampling effort.

So far, we have presented the list of earthworms with potential for manipulation in tropical soils. In agricultural lands, however, manipulation practices should be considered at the community level, because mixtures of species are generally more common than single species. In the next chapter, we will analyse these species assemblages in relation to their ecological and agricultural determinants and potential for manipulation.

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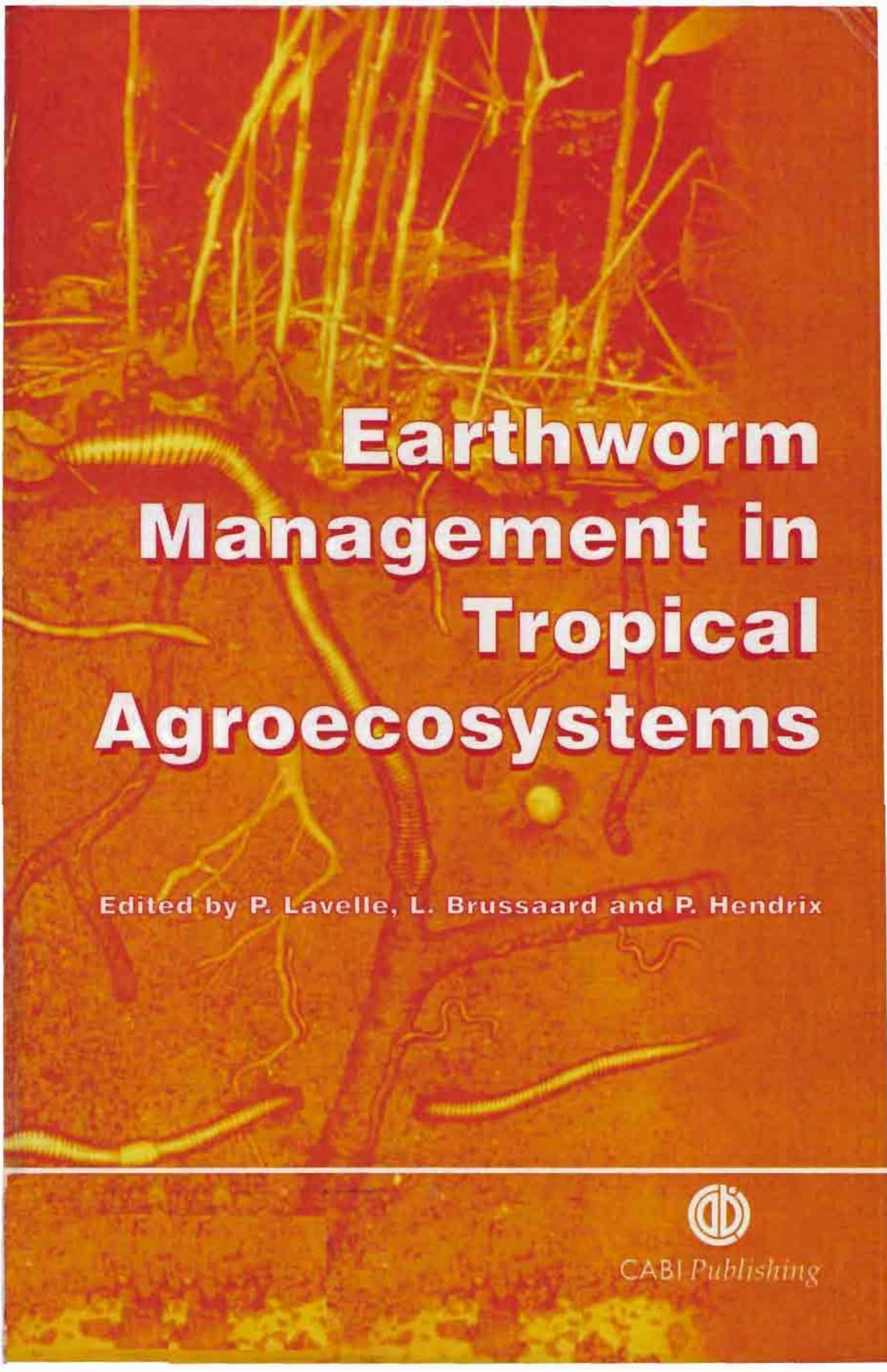

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