

EARTHWORM COMMUNITIES OF TROPICAL RAIN FORESTS

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Summary—A comparative study of tropical rain forest earthworm communities was carried out to try to identify general patterns of organization. The study included 5 sites in México and Central America, 3 in South America, 2 in Central and Western Africa and 2 in Southeast Asia. Data base comprised 15 biological variables and 11 climatic and edaphic variables.

Average earthworm values of abundance and biomass were 68 ind m⁻² and 12.9 g m⁻² respectively, which were not very different to those values occurring in temperate woods; however, they were considerably lower when compared to temperate and tropical grasslands. Density and biomass showed a bell shape response in function of annual rainfall, with maximal values between 2000 and 4000 mm. Earthworms were mainly concentrated in the first 0-10 cm of soil depth.

Two kinds of communities were differentiated: one dominated by litter-feeding epigeic and anecic and the other one by geophagous endogeic. The former group was associated to oligotrophic soils from South America and Africa, whereas the second one was characteristic of the rich, neutral soils of México and Africa (one site). It is concluded that environmental variables, more than phylogenetic constraints, are the most important factors in determining the structure of these communities.

Comparisons with other soil macrofauna groups revealed that earthworms are the most important group regarding biomass and rank third in terms of abundance.

The importance of these organisms in the dynamics of tropical rain forest soils is discussed in terms of the kind of community found elsewhere.

INTRODUCTION

The role of earthworms in the processes of decomposition, building and maintenance of soil structure have been well documented for soils of temperate climates (see reviews in Edwards and Lofty, 1977; Satchell, 1983; Lee, 1985). In the tropics, considerable research has been carried out in savannas (Lavelle, 1978, 1983a; Martin *et al.*, 1990; Blanchart *et al.*, 1991) and pastures (Lavelle *et al.*, 1981; Dash and Patra, 1979). In contrast, little has been done in tropical rain forest (TRF), and it is not yet possible to answer their role in these processes.

A general view that has limited this research is the current belief that earthworms are little abundant in tropical rain forest and consequently play unimportant roles in the soil dynamics (Golley, 1983; Anderson and Swift, 1983). This belief comes from early studies in which very low abundances were found, mainly due to the use of inadequate formalin sampling methods (Madge, 1965; Block and Banage, 1968), and from the results obtained in Asiatic forests (Kitazawa, 1971; Collins, 1980; Anderson *et al.*, 1983).

In another series of studies in Mexican forests Lavelle and Kohlmann (1984) and Fragoso and

Lavelle (1987) found higher abundances of earthworms, mainly endogeic-soil feeders, suggesting that earthworms probably have an important role in soil dynamics.

In a recent paper about decomposition in tropical rain forests, Swift and Anderson (1989) point out that termites and earthworms are the most relevant macrodecomposer groups; these authors indicate that savanna and some forest earthworms may have profound pedological effects, although they expressed doubts concerning the consumption of litter by earthworms.

The present paper summarizes all the information (published or not) about the ecological aspects of tropical rain forest earthworms, in order to obtain the general patterns of these communities. A brief discussion on the role of earthworms in these ecosystems is also provided.

METHODS

The data set comprised 31 communities from 14 different localities (6 from Central America, 3 from South America, 2 from Africa and 3 from Asia) (Tables 1 and 2). Nine edaphic variables (pH, organic matter, N, C:N, Ca, Mg, sand, clay, and litter) and two climatic variables (annual rainfall and seasonality) described the environment. Communities were characterized by mean absolute values of population density,

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Table 1. Environmental and edaphic variables from different tropical rain forest earthworm communities. All edaphic data from first 0–10 cm layer

Locality	Annual rainfall (mm)	Dry season*	Soil type (FAO)	Organic matter (%)	N (%)	Ca (mq 100 g ⁻¹)	Mg (mq 100 g ⁻¹)	pH	Sand (%)	Clay (%)	C:N	Litter (g m ⁻²)†	Key	References
Chajul;	2963	4	Alluvial	6.1	0.27	12.6	3.5	5.5	32	16	22.5	193	chp	Fragoso, (1985)
Mexico			Gley-ferra	6.5	0.23	6.4	2.8	5	62	9	28.2	241	chs	Fragoso and Lavelle (1987)
Bonampak,	2600	3	Rendzine	2.2	0.11	7.25	3.6	6.5	35	50	20	132	bk	Lavelle and Kohlmann (1984)
Mexico														
Lag. Verde,	1800	6	Vertisol	1.86	0.09	7.25	4.9	6.5	60	15	20	ND	lv7	Lavelle <i>et al.</i> (1981)
Mexico	1500	7	Vertisol	1.38	0.07	8	5.7	6.5	60	15	20	ND	lv1	
Los Tuxtlas,	4725	1	Andosols	15.5	0.47	13.6	4.6	6.1	50	5	33	466	tx1	Fragoso (in preparation)
Mexico				18.4	0.14	24.8	9.3	6.5	34	23	131.4	422	tx2	
				17.8	0.4	24.3	6.3	6.2	50	13	44.5	255	tx3	
				9.3	0.32	16.5	11.2	5.9	19	38	29	456	tx4	
				4.1	0.4	1.2	0.3	4.2	ND	ND	10.1	ND	cr1	Marrs <i>et al.</i> (1988)
Volcan Barva,	4015	ND	ND	9.9	0.9	1	0.6	4.3	ND	ND	10.8	ND	cr5	
Costa Rica	4627	ND	ND	9.9	0.9	1	0.6	4.3	ND	ND	10.8	ND	cr5	
Yurimaguas,	2100	3	Ultisols	1.76	0.07	0.34	0.23	3.9	52	15	25.1	ND	yrp	Lavelle and Pashanasi (1989)
Peru				2.24	0.07	1.01	0.09	4.2	58	15	32	ND	yrs	Lavelle and Pashanasi (in preparation)
Rio Negro,	3521	0	Latosol	9.9	0.06d	0.18a	0.014a	4.3	93.3a	4.3a	32	600c	rnl	a: Jordan (1982)
Venezuela			Podzol	4.7	0.07d	0.3a	1.55b	4.6	ND	ND	25	425	rnp	b: Klinge <i>et al.</i> (1977)
			Lat-pod	4	0.07d	0.24	0.78	4.2	ND	ND	25	425	rny	c: Jordan and Herrera (1981)
														d: Herrera <i>et al.</i> (1978)
														Nemeth, 1981; Nemeth and Herrera (1982)
Panguana,	2403	2	Cambisol	ND	ND	ND	ND	5.6	ND	ND	ND	ND	pan	Rombke and Verhaag (1992)
Peru														
Lamto,	1276	5	Gleys	1.45	0.63	1.68e	2.3e	5	82	15	2.3	ND	lmt	e: Lavelle and Schaeffer (1974)
Ivory Coast														Lavelle (1978)
Dimonika,	1600	5	ND	3.3	0.16	1.2	1.9	3.8	29f	34f	20	411	car	f: Garnier-Sillam (1987)
Congo			ND	1.05	0.04	12.6	6	3.8	ND	ND	25	263	cnb	Montadert (1985)
			ND	2.95	0.07	0.15	0.3	3.4	ND	ND	42	1306	cna	
			ND	3.9	0.13	0.20	0.5	3.6	ND	ND	25.5	547	cnc	
Gunung Mulu,	5087	0	Alluvial	9.7	0.54	8.3	0.59	5	45	10	18.5	900g	gma	g: Proctor <i>et al.</i> (1983b)
Sarawak	5107	0	Podzol	11	0.51	0.04	0.18	4.1	10	10	21.5	1100g	gmd	Proctor <i>et al.</i> (1983a)
	5698	0	Podzol	29	0.91	0.67	1.5	3.6	ND	ND	31.8	1080g	gmh	
	5698	0		42	2.5	6.1	6.1	6.1	ND	ND	16.8	710g	gml	
Gunung Silam,	2011	4	Inceptisol	6.8	ND	7.7	24.6	5.7	ND	ND	ND	651h	gs2	h: Proctor <i>et al.</i> (1989)
Malaysia				7.5	ND	2.3	15.7	5.8	ND	ND	ND	737h	gs3	Proctor <i>et al.</i> (1988)
				7	ND	4.2	11.5	6.1	ND	ND	ND	522h	gs4	Leakey and Proctor (1987)
El Verde,	3280	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	pr	Moore and Burns (1970)
Puerto Rico														
Sepilok	3206	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	sp	Kitazawa (1971)
Borneo														

*Number of months with < 100 mm of rainfall.

†Data from rain season except rnl, Gunung Mulu, Gunung Silam (annual estimations) and Dimonika (average of dry and rain seasons).

Table 2. Biological variables from different tropical rain forest earthworm communities

Locality	Density (ind m ⁻²)	Biomass (g m ⁻²)	No. spp Comm. Loc.		Diversity Comm. Loc.		Epigeics			Aneics			Endogeics			Key	References
							D (%)	B (%)	Spp	D (%)	B (%)	Spp	D (%)	B (%)	Spp		
Chajul, Mexico	80	34.2	11	17	4.5	4.55	0.8 (0.9)	0.3 (1)	1	0	0	0	79.2 (99)	33.8 (99)	10	chp	Fragoso (1985)
	121	42.4	7		2.58		0.8 (0.9)	0.4 (1)	2	0	0	0	120 (99)	42 (99)	2	chs	Fragoso and Lavelle (1987)
Bonampak, Mexico	80	10.6	8	8	4.1	4.1	14 (18)	0.5 (0.5)	2	0	0	0	66.6 (82)	10 (99.5)	6	bk	Lavelle and Kohlmann (1984)
	8	0.6	2	5	ND	ND	0	0	0	0	0	0	8 (100)	0.6 (100)	2	lv7	This study Lavelle <i>et al.</i> (1981)
Laguna Verde, Mexico	44	3.2	4		ND		0	0	0	0	0	0	44 (100)	3.2 (100)	4	lv1	This study
	60	11.2	5	9	2.7	4.1	1.3 (2)	2.6 (23)	2	0	0	0	58.7 (98)	8.6 (77)	3	tx1	
Los Tuxtlas, Mexico	26	8.2	5		3.2		4 (15)	3.2 (40)	2	0	0	0	22 (85)	4.9 (60)	3	tx2	Fragoso (in preparation)
	22	3.2	5		2.25		0.8 (4)	0.9 (29)	2	0	0	0	21.2 (96)	2.28 (71)	3	tx3	
	26	13.3	5		4.88		2.3 (9)	5.3 (40)	1	0	0	0	23.2 (91)	7.98 (60)	4	tx4	
	401	35.4	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	crl	Atkin and Proctor (1988)
Volcan Barva, Costa Rica	280	71.9	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND		
	64	21.8	5	ND	ND	ND	49.8 (78)	13.9 (64)	2	1.79 (3)	0.9 (4)	1	12.4 (19)	7 (32)	2	yrp	Lavelle and Pashanasi (1989)
Yurimaguas, Peru	42	8.9	5				19.9 (46)	7.5 (81)	2	0.05 (2)		1	21.6 (52)	1.36 (15)	2	yrp	Lavelle and Pashanasi (in preparation)
	55	15.8	6	8	3.07	3.3	38.5 (70)	5.7 (36)	2	0	0	0	16.2 (30)	10 (64)	4	rnl	Nemeth (1981)
Rio Negro, Venezuela	68	16.6	8		3.2		46.9 (69)	3.2 (20)	2	0.6 (1)	6.8 (40)	1	20.9 (30)	6.55 (40)	5	rnp	Nemeth and Herrera (1982)
	42	10.3	7		3.07		33.2 (79)	2.7 (26)	2	0.77 (1)	5 (49)	1	8.2 (20)	2.59 (25)	4	rny	Lavelle (1983a)
Panguana, Peru	68	2.69	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	pan	This study
Rombke and Verhaagh (1992)																	
Lamto Ivory Coast	35	1.6	7	7	1.7	1.7	4.6 (13)	0.5 (31)	3	0	0	0	30.4 (87)	1.13 (69)	4	lmt	Rombke and Verhaagh (1992)
Dimonika, Congo	44	2.1	14	17	6.5	8.9	22.6 (51)	1.6 (79)	7	0	0	0	21.7 (49)	0.43 (21)	7	cnr	Lavelle (1978)
	48	3.1	9		4.5		1.7 (4)	0.6 (19)	2	0	0	0	45.9 (96)	2.52 (81)	7	cnb	Montadert (1985)
Gunung Mulu, Sarawak	4	0.2	4		6.2		2.4 (67)	0.1 (55)	3	0	0	0	1.2 (33)	0.09 (45)	1	cna	This study
	24	2.4	8		2.2		16.2 (69)	2.1 (88)	4	0	0	0	7.5 (31)	0.3 (12)	4	cnc	
Gunung Silam, Malaysia	42	1	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	gma	Collins (1980)
	26	0.6	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND	gmd	
El Verde Puerto Rico	24	0.4	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND	gmh	Anderson <i>et al.</i> (1983)
	6	0.6	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND	gml	
	64	6	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	gs2	Leakey and Proctor (1987)
	166	22.7	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND	gs3	
Sepilok, Borneo	78	3.3	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND	gs4	
	ND	43.1	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	pr	Moore and Burns (1970)
	3	2.57	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	sp	Kitazawa (1971)

biomass, species richness and diversity (1/Simpson index; Smith, 1980). Number of species, abundance and biomass (absolute and relative values) of the three ecological categories as defined by Bouché (1977) were also included. Separation of species into these categories was made as follows: the epigeic included all those litter-feeding worms with dorsal pigmentation and spasmodic movements that live in the litter or in the first 5 cm of soil. Anecics were soil-burrowing species with antero-dorsal pigmentation and a flattened posterior end that live in the soil but feed on litter. The endogeics were all those unpigmented soil-dwelling species with slow movements which feed on soil.

Data from ecosystems derived from formerly tropical forests (Cook *et al.*, 1980) and from studies which only used formalin as sampling method (Madge, 1965; Block and Banage, 1968; Standen, 1988) were discarded. Only studies which used the hand-sorting method were considered.

Using data of Tables 1 and 2 the communities were ordinated and classified by means of PCA (principal component analysis) and no hierarchical clustering (average-linkage, UPGMA) methods (Gauch, 1982). In the first case the matrix association was obtained with correlation coefficients whereas in the second case Gower index was used. These analyses were made using PATN (Belbin, 1986) and STATGRAPHICS software.

RESULTS

Species richness and diversity

These parameters were calculated on a community basis (α diversity) and at the regional scale (landscape diversity).

The number of species for a given community (*ca* 1 ha) varied from 4 to 14, with a mean value of $6.5 \text{ spp} \pm 1.3$ ($P < 0.05$, $n = 19$); diversity showed a mean value of 3.6 ± 0.7 ($P < 0.05$, $n = 15$), ranging

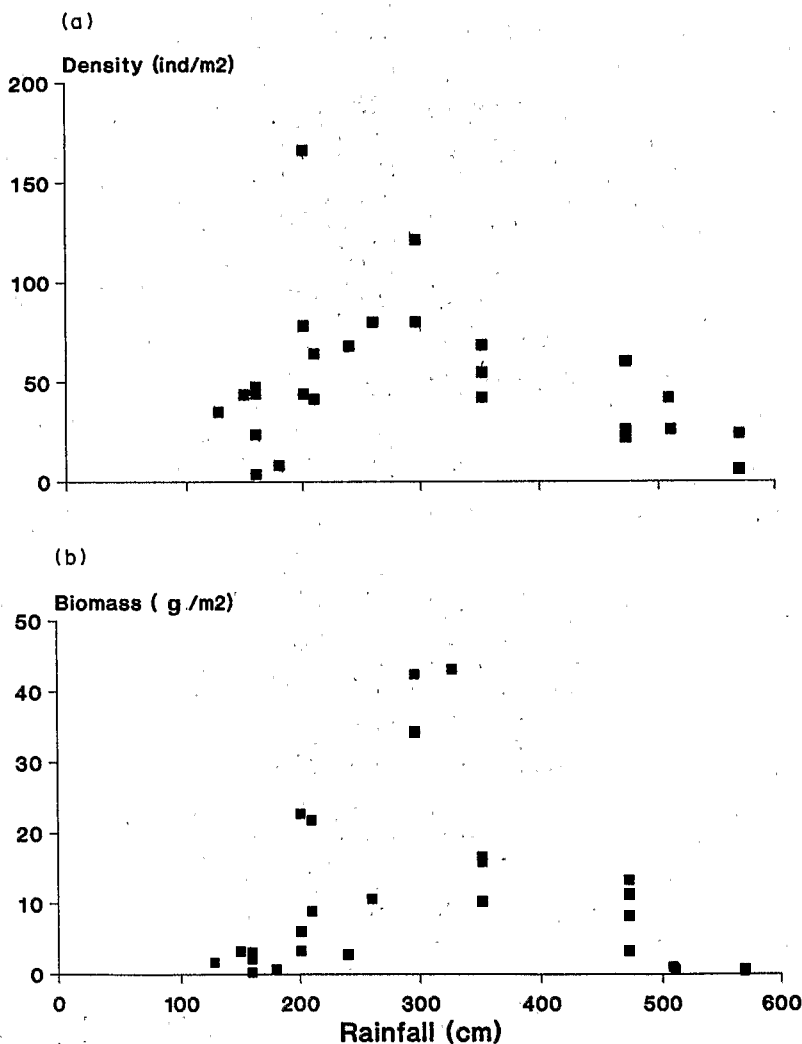


Fig. 1. Relationship between (a) density and (b) biomass vs annual rainfall in earthworm communities from different tropical rainforest. Costa Rica values excluded.

from 1.7 to 6.5 (Table 2). At the regional scale (ca 100 ha) both species richness and diversity increased, with mean values of $10.7 \text{ spp} \pm 4$ ($P < 0.05$, $n = 7$ and range of 7-17) and 4.4 ± 2.5 ($P < 0.05$, $n = 6$ and range of 1.7-8.9) respectively.

Differences between communities and localities indicates that environmental heterogeneity within the same locality (β diversity) is important in promoting earthworm diversity in tropical rain forests, as it has been shown by Fragoso and Lavelle (1987) in the forests of Chajul, México.

Population density and biomass.

Average values for density and biomass were $68 \text{ ind m}^{-2} \pm 32$ ($P < 0.05$, $n = 30$, range of 4-401)

and $12.9 \text{ g m}^{-2} \pm 6.22$ ($P < 0.05$, $n = 31$, range of 0.2-71.9) respectively. Central American forests of Chajul (México) and Volcan Brava (Costa Rica) presented the highest values, mainly due to the presence of the exotic earthworm *Pontoscolex corethrurus* (Fragoso, 1985; Fragoso and Lavelle, 1987; Lavelle, pers. obs.). This species probably colonized these forests in the past, when disturbances (e.g. human settlements) destroyed natural vegetation. If Costa Rica values are excluded these averages decrease to 49 ind m^{-2} and 10.09 g m^{-2} .

In the same locality rich soils supported greater densities and biomasses of native earthworms than poor soils (Gunning Mulu and Chajul forests). A bell shape response of density and biomass to increasing

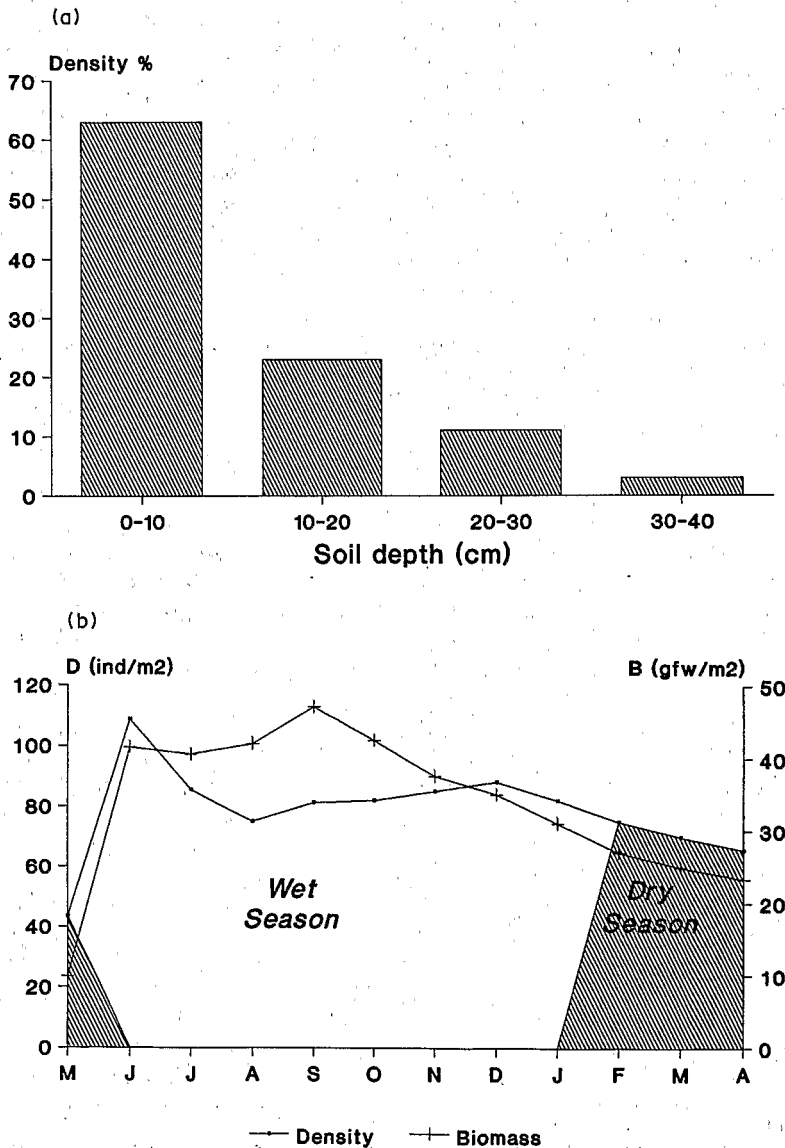


Fig. 2. (a) Vertical distribution of earthworm communities from seven tropical rain forest localities [Chajul, Bonampak, Los Tuxtlas, Laguna Verde (México), Yurimaguas (Perú), San Carlos Río Negro (Venezuela) and Dimonika (Congo)], expressed as average percentages of density. (b) Temporal patterns of density and biomass of earthworm populations from alluvial soils in Chajul (México) tropical rain forests.

annual rainfall (Fig. 1) was the only relationship of these parameters with edaphic and environmental variables. Maximal values of density and biomass were found in forests with precipitations of 2000–4000 mm. These results indicate that tropical forests with annual rainfall below 2000 mm are too dry to support optimum earthworm populations; forests with rainfall >4000 mm or with periodical flooding are too wet for earthworms to inhabit the soils. In the later situation Lavelle and Barois (1988), Adis and Righi (1990) (in the Amazonian forests) and Lee (1969) (in the Solomon Islands) have observed that earthworms change their habitat towards epiphytes and decaying logs.

Spatio-temporal patterns

Horizontal distributions. The only detailed study of horizontal patterns of distribution has been made by Fragoso and Lavelle (1987) in the forest of Chajul. They found that almost all species presented aggregative distributions, mainly explained by soil texture, organic matter and litter quality. In relation to the last parameter Nemeth (1981) and Nemeth and Herrera (1982) proposed that differences of earthworm abundance between laterite and podzols soils of San Carlos Río Negro could be explained by the presence of polyphenols in soil litter.

Vertical distributions. Earthworms of tropical rain forests generally occur at depths of 0–40 cm with a clear concentration in the upper 10 cm [Fig. 2(a)]. The average vertical niche overlap (Pianka index: Pianka, 1974) calculated for the forests of San Carlos de Río Negro-SCRN (Venezuela) (0.50, Lavelle, 1983b after Nemeth, 1981), Chajul (México) (0.47, Fragoso and Lavelle, 1987) and Dimonika (Congo) (0.74, Montadert, 1985) gives a value of 0.57 which is lower than the mean value of 0.91, calculated for temperate climates (Lavelle, 1983b). This is a clear indication of an extended vertical distribution of earthworms in tropical forests as compared to temperate equivalents.

Temporal distributions. At Chajul (México), earthworm populations showed clear seasonal variations with maximal values concentrated in the wet season (Fragoso, 1985) [Fig. 2(b)]. Vertical distribution was also influenced by seasonality, with worms migrating to deeper layers in the dry season. This pattern also occurs in other forests with seasonal rainfall cycles (Dimonika: Montadert, 1985; SCRN: Nemeth, 1981); in non-seasonal forests a more uniform pattern is expected to prevail.

Community structure

Earthworm communities were classified into epigeic-anecics (surface-litter feeding) or endogeics (geophagous) on the basis of the contribution of each group to the total density and biomass. The community was considered as epigeic-anecic or endogeic when any one of these groups accounted for 50% or more of total density and biomass. Table 3 indicates that all the Central American and two African (Lamto and

Table 3. Epigeic-anecic [(%D + %B)/2 > 50%] and endogeic [(%D + %B)/2 > 50%] earthworm communities from different tropical rain forests. See Table 2 for keys and original values

Epigeic-anecics		Endogeics	
Yurimaguas ... YRP		Chajul ... CHP	
Yurimaguas ... YRS		Chajul ... CHS	
Rio Negro ... RNL	South America	Bonampak ... BK	
Rio Negro ... RNP		Lag. Verde ... LV7	
Rio Negro ... RNY		Lag. Verde ... LV1	Central America
		Tuxtlas ... TX1	
Dimonika ... CNR		Tuxtlas ... TX2	
Dimonika ... CNA	Africa	Tuxtlas ... TX3	
Dimonika ... CNC		Tuxtlas ... TX4	
		Lamto ... LMT	Africa
		Dimonika ... CNB	

Dimonika b) communities are endogeics whereas all South American and the other African communities are epigeic-anecics. Asian communities were not classified due to the lack of data. In order to confirm this separation a PCA was realized with data of Table 2, excepting the absolute values of the ecological categories (Fig. 3(a)). Two factors were extracted which explained 63% of total variance. The first factor (41%) clearly opposed the epigeic-anecic communities to endogeic ones, whereas the second factor (22%) opposed communities with low abundances to the ones with high abundances. A cluster analysis further identified three groups: the first comprised all the endogeic communities whereas the second and third ones grouped the epigeic-anecic communities.

Later patterns can be explained at least by two factors: (1) environmental and soil variables and (2) phylogenetic determinants.

In the first case a PCA and a cluster analysis were made with edaphic and climatic variables of Table 1 (excepting litter, sand, and clay). PCA produces two factors [Fig. 3(b)] that accounted for 73% of total variance. The first factor (45%) ordines the localities along an axis of soil moisture contents (relatively wet vs very wet soils); second factor (28%) separates the forests on the basis of their nutrient status. Cluster analysis produced four groups: the first grouped the Mexican forests of Los Tuxtlas, characterized by rich soils with abundant rainfall; the second isolates the Asiatic forests from Sarawak, located over soils with high nitrogen and organic matter contents and with heavy rainfalls; the third grouped Lamto and Mexican forests characterized by rich soils with seasonally low rainfalls; the fourth comprises South American and African forests in low nutrient soils with seasonally low rainfalls. The comparison of Fig. 3(a) with (b) indicates that geophagous endogeic communities are characteristic of rich nutrient soils, whereas surface litter-feeding epigeic-anecic are normally present in oligotrophic soils. Significant relationships of density and biomass of epigeics with litter, pH, Ca, Mg and N [Fig. 4(a)–(e)] confirms the edaphic factor as an important determinant in the structure of earthworm communities.

If the feeding strategy (litter vs soil) is the result of a common inherited genetic pattern then closer

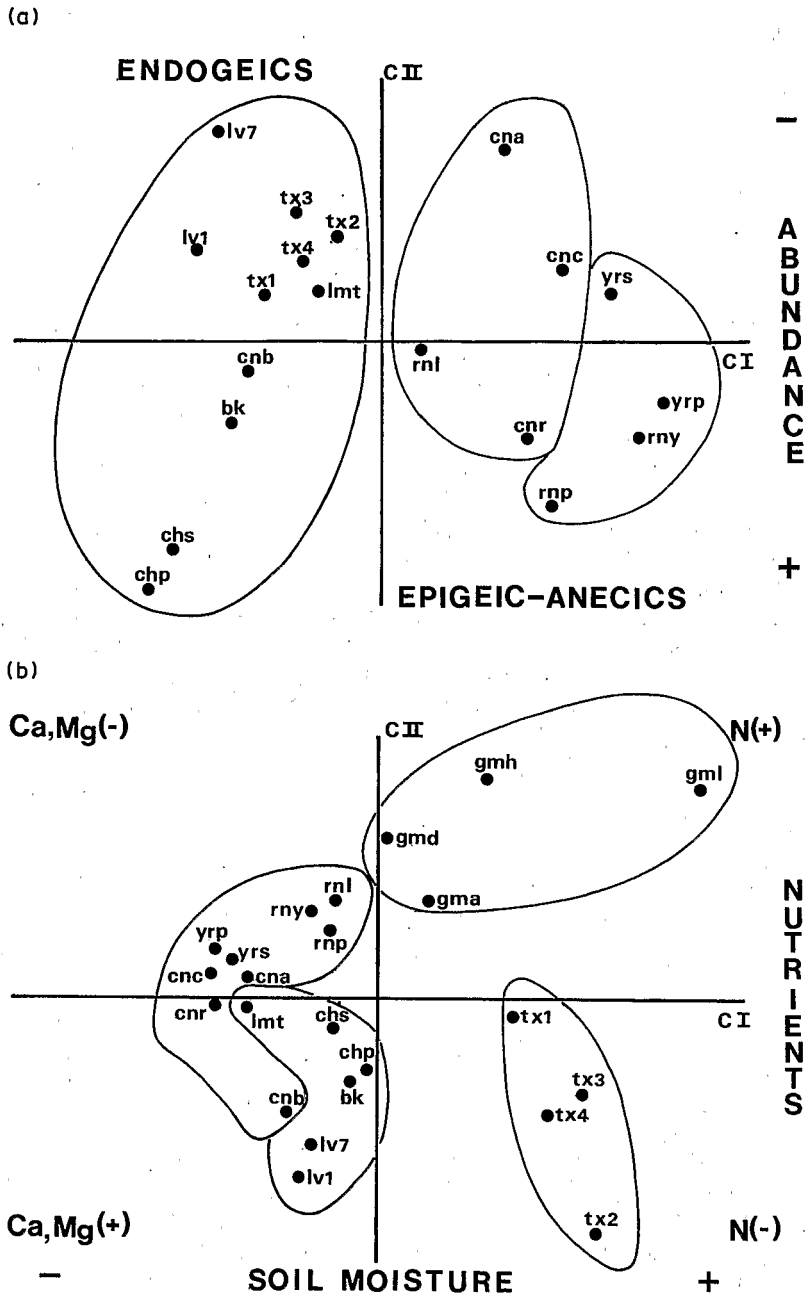


Fig. 3. Ordination (PCA) and Clustering (UPGMA) of TRF earthworm communities on the basis of: (a) biological variables and (b) climatic and edaphic variables.

taxa must have the same strategy. In Central America almost all native species belong to the family Megascoclecidae tribes Acanthodrilini and Dichogastrini (Gates, 1982; Jamieson, 1971). In Central Africa the communities are dominated by species of the family Eudrilidae and of the tribe Dichogastrini (mainly *Dichogaster*), whereas in West Africa acanthodrilins and dichogastrins are more important than eudrilids (Omodeo, 1958; Sims, 1987). South American communities, on the other hand, are dominated by the families Glossoscolecidae and Ocnodrilidae (Righi, 1971; Jamieson, 1971; Brinkhurst and Jamieson,

1971). In terms of phylogenetic relationships the earthworm fauna of Central America is closer to the earthworms of Central and West Africa than to the earthworms of South America, e.g. African dichogastrins are very closely related to Central American ones, whereas South American glossoscolecids are very distant from African Eudrilidae (Jamieson, 1989).

Without discarding at all phylogenetic constraints it seems clear that environmental variables are very important in the determination of the structure of TRF earthworm communities. Such an environmental determinism is not specific to TRF. In temperate

forests from Belgium, Muys *et al.* (1992) have also demonstrated that the nutrient status of soil is the main determinant of the structure of earthworm communities.

Relative importance of earthworms in tropical rain forest macro-invertebrate communities

Comparing 12 communities from different tropical rain forests, we found that termites and earthworms are the most important groups of soil macrofauna. Earthworms account for 51% of total biomass whereas termites make up 13%; regarding abundance, termites dominate with 37% followed by ants (23%) and earthworms (9%) [Fig. 5(a)].

It has been proposed that earthworms and termites occupy the same niche, and that termites are the tropical equivalent of temperate earthworms (Drummond, 1886, quoted in Lee and Wood, 1971; Anderson and Swift, 1983; Golley, 1983). This hypoth-

esis can be tested by looking for the kind of relation between these two groups. Using data from Lavelle and Fragoso (1992) no relationship is found between absolute values of density and biomass of both groups. When this analysis is extended to include savanna, grassland and cultivated soils an inverse correlation between relative values of these groups is clear [Fig. 5(b)]. This relation is explained by the dominance of termites and the near absence of earthworms in soils with less than 900 mm annual rainfall and with a dry season of more than 5 months (Lavelle, 1988b).

With the precedent evidence we cannot conclude that in soils of TRF earthworms and termites are in competition. To reach this conclusion it would be necessary to make some kind of laboratory or field experiment (removal of one or another group). More than competitive exclusion, the likely explanation is that when environmental conditions exclude one of

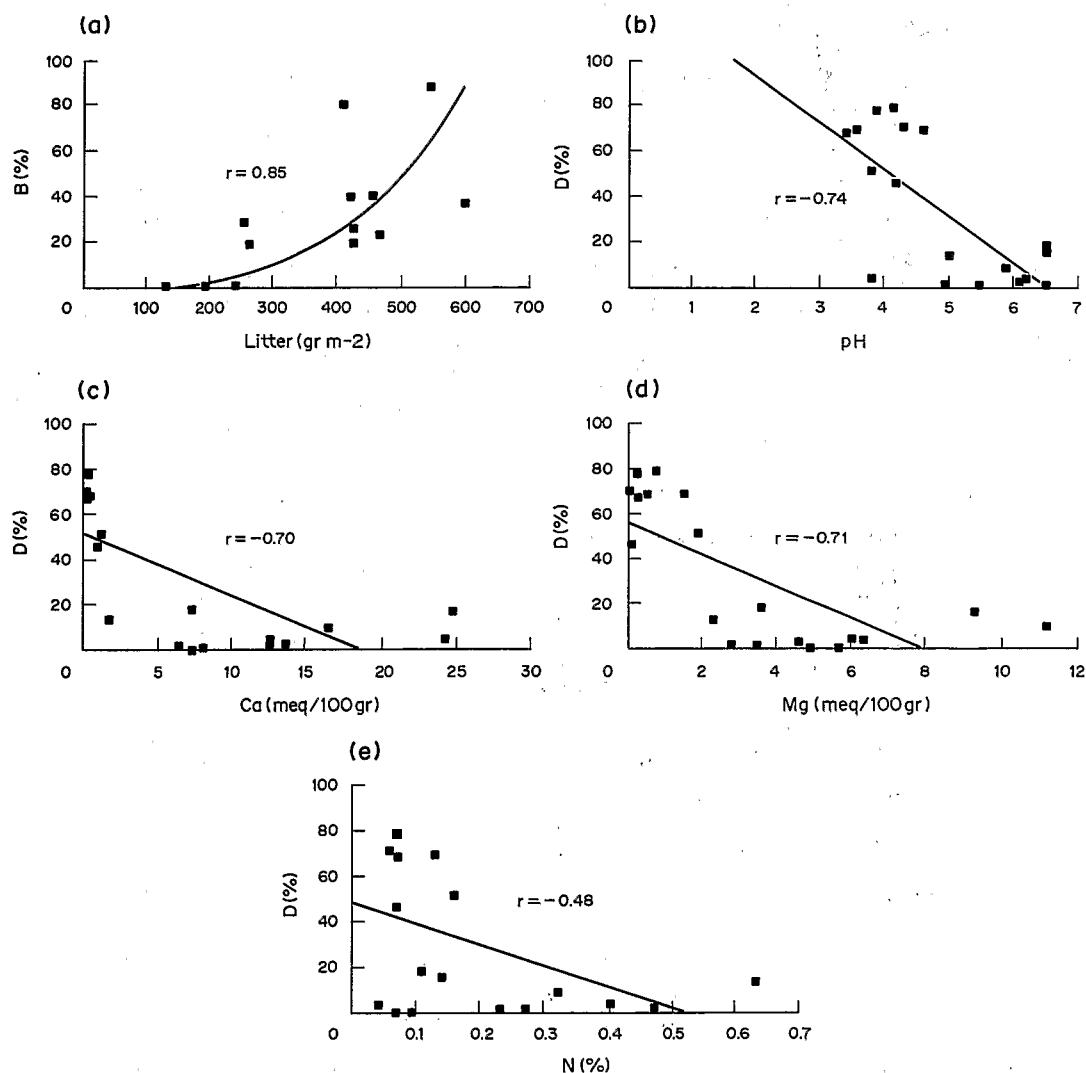


Fig. 4. Relationship between percentage of biomass (B%) and density (D%) of TRF epigeic worms and different soil variables: (a) B% vs litter, (b) D% vs pH, (c) D% vs Ca, (d) D% vs Mg and (e) D% vs N (r significantly at $P < 0.05$).

these two groups, the other one occupies the empty niche.

On the other hand earthworms of TRF are the most important group in terms of biomass, no matter if termites have high or low abundances.

DISCUSSION

Species richness and diversity of TRF earthworm communities are not significantly different from those of temperate forests. The average value of 5.7 spp (± 2.02) calculated from 15 temperate forest communities (quoted by Lee, 1985), is very similar to our estimates for TRF. At a larger regional scale

(ϵ diversity), however, tropical countries harbour more species than temperate ones: e.g. India has more than 400 species (Senapati, 1980) whereas in England and France only 27 (perhaps 28) and 97 species respectively have been reported (Sims and Gerard, 1985; Bouché, 1972). This is partly explained by the depauperative effect that glaciations had on Northern earthworm fauna, and the several evolutionary and environmental patterns responsible for the large species diversity of tropical countries.

Tropical rain forest earthworm communities have lower abundances and biomasses than temperate pastures (reviewed in Lee, 1985) and tropical savannas and grasslands (Lavelle, 1983a). Temperate deciduous

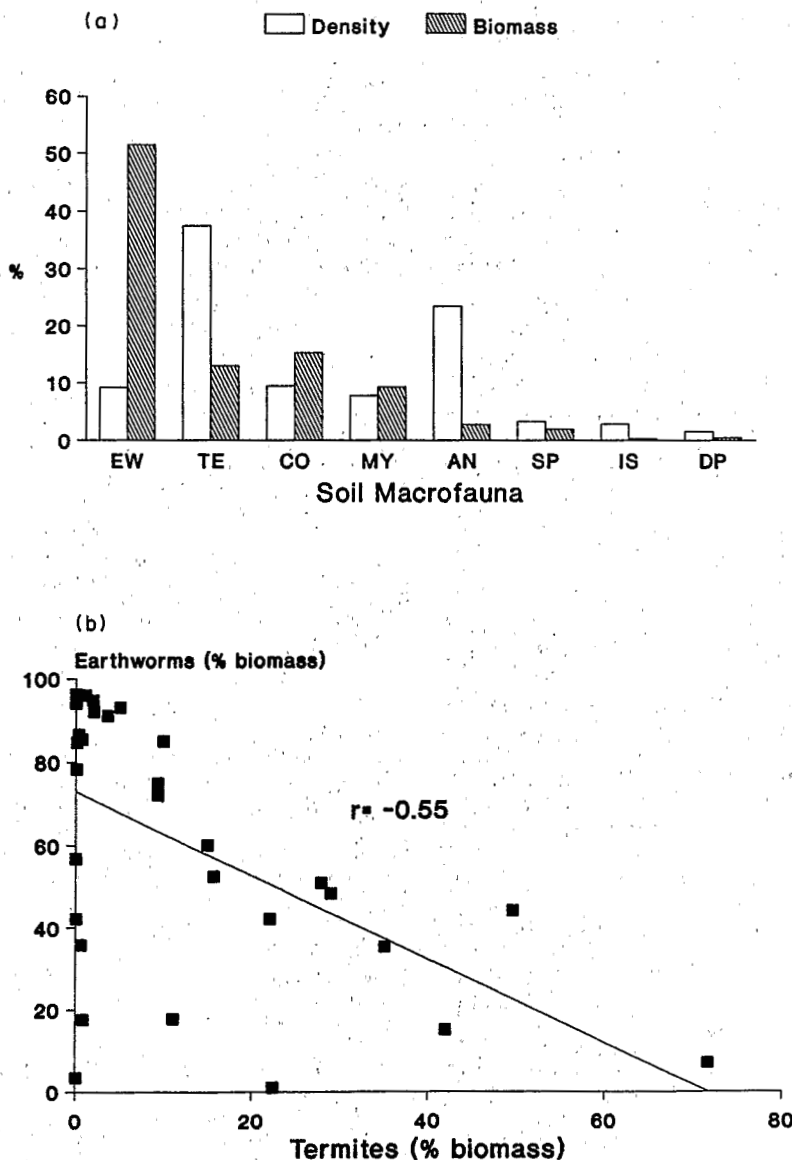


Fig. 5. (a) Main soil macroinvertebrate groups (D and B >1%) from different tropical soils. EW: earthworms; TE: termites; CO: coleoptera; MY: Myriapoda; AN: ants; SP: spiders; IS: isopoda; DP: diptera. (b) Relationship between relative biomass of earthworms and termites in different tropical soils (savannas, forests and disturbed lands).

and cold coniferous forests, on the other hand, show similar values of density ($64 \text{ ind m}^{-2} \pm 19$), with biomass twice as high ($30 \text{ g m}^{-2} \pm 20$) as those of TRF (calculated from data of Lee, 1985; Pop, 1987; Römcke, 1987).

Lavelle (1983b) has found that the structure of world earthworm communities is mainly determined by the temperature. However, when temperature is the same in markedly different edaphic or environmental conditions, other factors tend to predominate. In TRF, temperature remains nearly constant all year (Lauer, 1989); under these conditions we found that the nutrient status of soils is the variable that determines the structure of the community. Since a wide range of nutrient status have been observed in soils of TRF (Sánchez, 1989), it is expected that epigeic and endogeic populations will dominate respectively in poor and rich soils. In soils with comparable nutrient status, seasonality of rains emerges as a further determining variable, e.g. the majority of soils of Mexican TRF (Bonampak, Chajul, Laguna Verde) are rich in nutrients and their communities are composed by endogeic worms. At Los Tuxtlas Mexican forest, however, epigeic populations comprise almost 50% of total biomass; the main difference with the other Mexican TRF is a shorter dry season.

It is thus clear that the structure of earthworm communities is determined by a suite of hierarchical organized factors: temperature operates at the higher hierarchical level, followed by edaphic (nutrient status) and environmental (seasonality) factors.

The effect of earthworms on decomposition and mineralization processes in TRF depends on the composition of their community. In communities dominated by epigeic and anecic species, worms feed on leaf litter mixed with some soil. Epigeics act as efficient agents of comminution and fragmentation of leaf litter that they transform in stabilized organic matter. Anecics have two main effects on the soil: (1) to modify the soil physical properties by their burrowing activity and (2) to enhance decomposition of plant debris by burying and mixing them to the soil (Lavelle, 1988a). Endogeic communities, on the other hand, are dominated by worms that live in the soil and mainly feed on soil organic matter that they digest in association with soil microflora (Barois and Lavelle, 1986; Lavelle, 1984; Lavelle *et al.*, 1989). These worms have an important impact on soil aggregation. As a result in South American and some African forests epigeic earthworms probably affect significantly the decomposition of litter, whereas in Central American forests endogeic ones must have important interactions with soil microflora, affecting the process of soil organic matter decomposition and the nutrient cycling.

The response of earthworm communities to the clearing of tropical forests also varies as a function of the ecological category. In communities dominated by epigeics most species disappear, whereas in communities dominated by endogeics and anecics some

species may survive, as it occurs with *Ramiellona strigosa* in induced pastures of Chajul. After native earthworms have disappeared the disturbed soils of the humid tropics may be colonized by a few peregrine species, which soon overdominated the community. This is the case of *Pontoscolex corethrurus* in Peru and México soils (Lavelle *et al.*, 1981; Lavelle and Pashanasi, 1989) and *Polypheretima elongata* in soils of New Guinea (Standen, 1988) and Martinique (Barois, pers. commun.). It is hypothesized that one feasible way to recover and improve the fertility of disturbed tropical soils would be to manipulate these communities, by introducing a mixture of native and alien savanna-like species (well adapted to low nutrient conditions and with a wide physiological and ecological plasticity) (Lavelle *et al.*, 1989).

CONCLUSIONS

The present study is a synthesis of the current information available on earthworm communities from TRF. Some general patterns have been observed which exemplify the plastic response of these communities towards environmental factors. More research is needed to consolidate or to change these observations. Studies on Indian forests might change some of these patterns, as suggested by the preliminary data of Ferry (in preparation), who found high biomasses of earthworms (up to 90 g m^{-2}) in very wet Indian forests (5000–7000 mm of annual rainfall).

Earthworms are an important component of tropical rain forest ecosystems. However, we do not know yet their exact role in the global dynamics of energy and matter fluxes. Further research must be focused on this aspect. This must be urgently achieved in the near future because tropical forests are disappearing at very high rates (Mabberley, 1983; Myers, 1983), with many of their patterns and processes still remaining unknown.

REFERENCES

- Adis J. and Righi G. (1990) Mass migration and life cycle adaptation—a survival strategy of terrestrial earthworms in Central Amazonian forests. *Amazoniana* 11, 23.
- Anderson J. M. and Swift M. J. (1983) Decomposition in tropical forests. In *The Tropical Rain Forests* (S. L. Sutton, T. C. Whitmore and L. C. Chadwick, Eds), pp. 287–309. Blackwell, Oxford.
- Anderson J. M., Proctor J. and Vallack H. W. (1983) Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. III. Decomposition processes and nutrient losses from leaf litter. *Journal of Ecology* 71, 503–527.
- Atkin L. and Proctor J. (1988) Invertebrates in the litter and soil on Volcán Barva, Costa Rica. *Journal of Tropical Ecology* 4, 307–310.
- Barois I. and Lavelle P. (1986) Changes in respiration rate and some physico-chemical properties of a tropical soil during transit through *Pontoscolex corethrurus* (Glossoscolecidae, Oligochaeta). *Soil Biology & Biochemistry* 18, 539–541.
- Belbin L. (1987) *PATN Pattern analysis package*. CSIRO, Division of Wildlife and Rangelands Research, Canberra.

- Blanchart E., Lavelle P. and Spain A. V. (1991) Effects of two species of tropical earthworms (Oligochaeta: Eudrilidae) on the size distribution of aggregates in an African soil. *Revue d'Écologie et de Biologie du Sol* **26**, 417–425.
- Block W. and Banage W. B. (1968) Population density and biomass of earthworms in some Uganda soils. *Revue d'Écologie et de Biologie du Sol* **5**, 515–521.
- Bouché M. B. (1972) *Lombriciens de France. Écologie et Systématique*. Annales de l'institut National de Recherche Agronomique, Numéro hors série, Paris.
- Bouché M. B. (1977) Stratégies lombriciennes. In *Soil Organisms as Components of Ecosystems* (U. Lohm and T. Persson, Eds), Vol. 25, pp. 122–132. Ecological Bulletin, Stockholm.
- Brinkhurst R. O. and Jamieson B. G. M. (1971) *Aquatic Oligochaeta of The World*. Oliver & Boyd, Edinburgh.
- Collins N. M. (1980) The distribution of soil macrofauna on the west ridge of Gunung (Mount) Mulu, Sarawak. *Oecologia* **44**, 263–275.
- Cook A. G., Critchley B. R., Critchley U., Perfect T. J. and Yeaton R. (1980) Effects of Cultivation and DDT on earthworm activity in a forest soil in the subhumid tropics. *Journal of Applied Ecology* **17**, 21–29.
- Dash M. C. and Patra V. C. (1979) Worm cast production and nitrogen contribution to soil by a tropical earthworm population from a grassland in Orissa, India. *Revue d'Écologie et de Biologie du Sol* **16**, 79–83.
- Edwards C. A. and Lofty J. R. (1977) *Biology of Earthworms*, 2nd Edn. Chapman & Hall, London.
- Fragoso C. (1985) Ecología general de las lombrices terrestres (Oligochaeta: Annelida) de la región Boca del Chajul, Selva Lacandona, Estado de Chiapas. Thesis Universidad Nacional Autónoma de México, México.
- Fragoso C. and Lavelle P. (1987) The earthworm community of a Mexican tropical rain forest (Chajul, Chiapas). In *On Earthworms* (A. M. Bonvincini Paglai and P. Omodeo, Eds), pp. 281–295. Mucchi, Modena.
- Garnier-Sillam E. (1987) Biologie et rôle des termites dans les processus d'humification des sols forestiers tropicaux du Congo. Thèse d'État, Université de Paris Val de Marne, Paris.
- Gates G. (1982) Farewell to North American Megadriles. *Megadrilogica* **4**, 12–77.
- Gauch H. G. (1982) *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Golley F. B. (1983) Decomposition. In *Tropical Rain Forest Ecosystems* (F. Golley, Ed.), pp. 137–156. Ecosystems of the World—14A. Elsevier, The Netherlands.
- Herrera R., Jordan C. F., Klinge H. and Medina E. (1978) Amazon ecosystems. Their structure and functioning with particular emphasis on nutrients. *Interciencia* **3**, 223–231.
- Jamieson B. G. M. (1971) A review of the Megascolecoid earthworm genera (Oligochaeta) of Australia. Part I. Reclassification and checklist of the megascolecoid genera of the world. *Proceedings of the Royal Society of Queensland* **82**, 75–86.
- Jamieson B. G. M. (1989) On the phylogeny and higher classification of the Oligochaeta. *Cladistics* **4**, 367–400.
- Jordan C. F. (1982) The nutrient balance of an amazonian rain forest. *Ecology* **63**, 647–654.
- Jordan C. F. and Herrera R. (1981) Tropical rain forests: are nutrients really critical? *The American Naturalist* **117**, 167–180.
- Kitazawa Y. (1971) Biological regionality of the soil fauna and its function in forest ecosystems types. In *Productivity of Forest Ecosystems* (P. Duvigneaud, Ed.), pp. 485–498. UNESCO, Brussels.
- Klinge H., Medina E. and Herrera R. (1977) Studies on the ecology of amazon caatinga forest in southern Venezuela. *Acta Científica Venezolana* **28**, 270–276.
- Lauer W. (1989) Climate and Weather. In *Tropical Rain Forest Ecosystems* (H. Lieth and M. J. A. Werger, Eds), pp. 7–54. Ecosystems of the World—14B. Elsevier, The Netherlands.
- Lavelle P. (1978) Les vers de terre de la savane de Lamto (Côte d'Ivoire). Peuplements, populations et fonctions de l'écosystème. *Publications du laboratoire de Zoologie de l'École Normale Supérieure* **12**, 1–301.
- Lavelle P. (1983a) The soil fauna of tropical savannas. II. The earthworms. In *Tropical Savannas* (F. Bourliere, Ed.), pp. 485–504. Ecosystems of the World—13. Elsevier, The Netherlands.
- Lavelle P. (1983b) The structure of earthworm communities. In *Earthworm Ecology* (J. Satchell, Ed.), pp. 449–466. Chapman & Hall, London.
- Lavelle P. (1984) The soil system in the humid tropics. *Biology International* **9**, 2–17.
- Lavelle P. (1988a) Earthworm activities and the soil system. *Biology and Fertility of Soils* **6**, 237–251.
- Lavelle P. (1988b) Assessing the abundance and role of invertebrate communities in tropical soils: aims and methods. *Journal of African Zoology* **102**, 275–283.
- Lavelle P. and Barois I. (1988) Potential use of earthworms in tropical soils. In *Earthworms in Waste and Environmental Management* (C. A. Edwards and E. F. Neuhauser, Eds), pp. 273–279. SPB, The Hague.
- Lavelle P. and Fragoso C. (1992) Food-webs in the soils of the humid tropics: importance of mutualistic relationships. In *The Soil Food-Webs* (N. Ingham, Ed.).
- Lavelle P. and Kohlmann B. (1984) Etude quantitative de la macrofaune du sol dans une forêt tropicale humide du Mexique (Bonampak, Chiapas). *Pedobiologia* **27**, 377–393.
- Lavelle P. and Pashanasi B. (1989) Soil Macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia* **33**, 283–291.
- Lavelle P. and Schaefer R. (1974) Les sources de nourriture des organismes du sol dans les savanes de Lamto. In *Analyse d'un Ecosystème Tropical Humide: La Savane de Lamto (Côte d'Ivoire). V. Les Organismes Endogés*. Bulletin de liaison des chercheurs de Lamto. Numéro spécial.
- Lavelle P., Maury M. E. and Serrano V. (1981) Estudio cuantitativo de la fauna del suelo en la región de Laguna verde Veracruz. Epoca de lluvias. In *Estudios Ecológicos en el Trópico Mexicano* (P. Reyes Castillo, Ed.), pp. 75–105. Instituto de Ecología, México.
- Lavelle P., Barois I., Martin A., Zaidi A. and Shaefer R. (1989) Management of earthworm populations in agroecosystems: a possible way to maintain soil quality? In *Ecology of Arable Land* (M. Clarholm and L. Bergström, Eds), pp. 109–122. Kluwer, Dordrecht.
- Leakey R. J. G. and Proctor J. (1987) Invertebrates in the litter and soil at a range of altitudes on Gunung silam, a small ultrabasic mountain in Sabah. *Journal of Tropical Ecology* **3**, 119–129.
- Lee K. E. (1969) Earthworms of the British Solomon Islands Protectorate. *Philosophical Transactions of the Royal Society B* **255**, 345–354.
- Lee K. E. (1985) *Earthworms. Their Ecology and Relationships with Soils and Land Use*. Academic Press, Sydney.
- Lee K. E. and Wood T. G. (1971) *Termites and Soils*. Academic Press, London.
- Mabberley D. J. (1983) *Tropical Rain Forest Ecology*. Blackie, London.
- Madge D. S. (1965) Leaf fall and litter disappearance in a tropical forest. *Pedobiologia* **5**, 273–288.
- Marrs R. H., Proctor J., Heaney A. and Mountford M. D. (1988) Changes in soil nitrogen-mineralization and nitrification along an altitudinal transect in tropical rain forest in Costa Rica. *Journal of Ecology* **76**, 466–482.
- Martin A., Mariotti A., Balesdent J., Lavelle P. and Vuattoux R. (1990) Estimate of organic matter turnover rate in a savanna soil by ¹³C natural abundance measurements. *Soil Biology & Biochemistry* **22**, 517–523.

- Montadert M. (1985) *Le Peuplement de Vers de Terre et Autres Macro-Invertébrés du Sol d'une Forêt Équatoriale Humide. Forêt du Mayombe, Station Biologique de Dimonika, Congo*. DEA d'Écologie, Faculté d'Orsay, Paris.
- Moore A. M. and Burns L. (1970) Preliminary observations on the earthworm populations of the forest soils at El Verde. In *A Tropical Rain Forest. A Study of Irradiation and Ecology at El Verde* (H. T. Odum and R. F. Pigeon, Eds), pp. 283–284. Division of technical information. U.S. Atomic Energy Commission, Tenn.
- Muys B., Lust N. and Granval Ph. (1992) Effects of grassland afforestation with different tree species on earthworm communities, litter decomposition and nutrient status. *Soil Biology & Biochemistry* **24**, 1459–1466.
- Myers N. (1983) Conservation of rain forests for scientific research, for wildlife conservation and for recreation and tourism. In *Tropical Rain Forest Ecosystems* (F. Golley, Ed.), pp. 325–334. Ecosystems of the World—14A. Elsevier, The Netherlands.
- Nemeth A. (1981) Estudio Ecológico de las lombrices de tierra (Oligochaeta) en ecosistemas de bosque húmedo tropical en San Carlos de Río Negro, territorio federal Amazonas. Universidad Central de Venezuela, Tesis, Caracas, Venezuela.
- Nemeth A. and Herrera R. (1982) Earthworm populations in a Venezuelan tropical rain forest. *Pedobiologia* **23**, 437–443.
- Omodeo P. (1958) Oligochètes de la réserve naturelle intégrale du Mont Nimba. *Memoires de l'Institut Français d'Afrique Noire* **53**, 9–109.
- Pianka E. (1974) Niche overlap and diffuse competition. *Proceedings of the U.S.A. National Academy of Sciences* **71**, 2141–2145.
- Pop V. V. (1987) Density and biomass of earthworm synusia in forest ecosystems of the Romanian Carpathians. In *On Earthworms* (A. M. Bonvincini Paglai and P. Omodeo, Eds), pp. 183–190. Mucchi, Modena.
- Proctor J., Anderson J. M., Chai P. and Vallack H. W. (1983a) Ecological studies in four contrasting lowland rain forests in Gunung Mulu national Park, Sarawak. I. Forest environment, structure and floristics. *Journal of Ecology* **71**, 237–260.
- Proctor J., Anderson J. M., Fogden S. C. L. and Vallack H. W. (1983b) Ecological studies in four contrasting Lowland rain forests in Gunung Mulu national Park, Sarawak. II. Litterfall, litter standing crop and preliminary observations on herbivory. *Journal of Ecology* **71**, 261–283.
- Proctor J., Lee Y. F., Langley A. M., Munro W. R. C. and Nelson T. (1988) Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. I. Environment, forest structure and floristics. *Journal of Ecology* **76**, 320–340.
- Proctor J., Phillips C., Duff G. K., Heaney A. and Robertson F. M. (1989) Ecological studies on Gunung Silam, a small ultrabasic mountain in Sabah, Malaysia. II. Some forest processes. *Journal of Ecology* **77**, 317–331.
- Righi G. (1971) Bionomic considerations upon the Glosso-scolecidae (Oligochaeta). *Pedobiologia* **12**, 254–260.
- Römbke J. (1987) Population dynamics of earthworms in a moder soil beech forest. In *On Earthworms* (A. M. Bonvincini Paglai and P. Omodeo, Eds), pp. 199–214. Mucchi, Modena.
- Römbke J. and Verhaagh M. (1992) About the earthworm community in a recently developed pasture in comparison with a rain forest site in Peru. *Amazoniana*.
- Sánchez P. (1989) Soils. In *Tropical Rain Forest Ecosystems* (H. Lieth and M. J. A. Werger, Eds), pp. 73–88. Ecosystems of the World—14B. Elsevier, The Netherlands.
- Satchell J. E. (Ed.) (1983) *Earthworm Ecology: From Darwin to Vermiculture*. Chapman & Hall, London.
- Senapati B. K. (1980) Aspects of ecophysiological studies on tropical earthworms. Distribution, Population dynamics, Production, Energetics and their role in decomposing process. Ph.D. thesis. Sambalpur University, Sambalpur.
- Sims R. W. (1987) Review of the central African earthworm family *Eudrilidae* (Oligochaeta). In *On Earthworms* (A. M. Bonvincini Paglai and P. Omodeo, Eds), pp. 359–388. Mucchi, Modena.
- Sims R. W. and Gerard B. M. (1985) Earthworms. In *Keys and notes for the identification and study of the species. Synopsis of the British fauna (New Series)* (D. M. Kermack and R. S. K. Barnes, Eds), pp. 1–171, Vol. 31. The Linnean Society of London & The Estuarine and Brackish-Water Sciences Association, London.
- Smith R. L. (1980) *Ecology and Field Biology*, 3rd Edn. Harper & Row, New York.
- Standen V. (1988) Oligochaetes in fire climax grassland and conifer plantations in Papua New Guinea. *Journal of Tropical Ecology* **4**, 39–48.
- Swift M. J. and Anderson J. M. (1989) Decomposition. In *Tropical Rain Forest Ecosystems* (H. Lieth and M. J. A. Werger, Eds), pp. 547–569. Ecosystems of the World—14B. Elsevier, The Netherlands.