

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 epigeics and anecics and the other one by geophagous endogeics. 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, Mexico	2963	4	Alluvial	6.1	0.27	12.6	3.5	5.5	32	16	22.5	193	chp	Fragoso, (1985)
Bonampak, Mexico	2600	3	Gley-ferra Rendzine	6.5	0.23	6.4	2.8	5	62	9	28.2	241	chs	Fragoso and Lavelle (1987)
Lag. Verde, Mexico	1800	6	Vertisol	2.2	0.11	7.25	3.6	6.5	35	50	20	132	bk	Lavelle and Kohlmann (1984)
Los Tuxtlas, Mexico	1500	7	Vertisol	1.86	0.09	7.25	4.9	6.5	60	15	20	ND	lv7	Lavelle <i>et al.</i> (1981)
	4725	1	Andosols	1.38	0.07	8	5.7	6.5	60	15	20	ND	lv1	
				15.5	0.47	13.6	4.6	6.1	50	5	33	466	tx1	Fragoso (in preparation)
				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	
Volcan Barva, Costa Rica	4015	ND	ND	4.1	0.4	1.2	0.3	4.2	ND	ND	10.1	ND	cr1	Marrs <i>et al.</i> (1988)
Yurimaguas, Peru	4627	ND	ND	9.9	0.9	1	0.6	4.3	ND	ND	10.8	ND	cr5	
Rio Negro, Venezuela	2100	3	Ultisols	1.76	0.07	0.34	0.23	3.9	52	15	25.1	ND	yrp	Lavelle and Pashanasi (1989)
				2.24	0.07	1.01	0.09	4.2	58	15	32	ND	yrp	Lavelle and Pashanasi (in preparation)
				9.9	0.06d	0.18a	0.014a	4.3	93.3a	4.3a	32	600c	rnl	a: Jordan (1982)
				4.7	0.07d	0.3a	1.55b	4.6	ND	ND	25	425	rnp	b: Klinge <i>et al.</i> (1977)
				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)
Panguana, Peru	2403	2	Cambisol	ND	ND	ND	ND	5.6	ND	ND	ND	ND	pan	Nemeth, 1981; Nemeth and Herrera (1982)
Lamto, Ivory Coast	1276	5	Gleys	1.45	0.63	1.68e	2.3e	5	82	15	2.3	ND	lmt	Rombke and Verhaag (1992)
Dimonika, Congo	1600	5	ND	3.3	0.16	1.2	1.9	3.8	29f	34f	20	411	cnr	e: Lavelle and Schaeffer (1974)
			ND	1.05	0.04	12.6	6	3.8	ND	ND	25	263	cnb	Lavelle (1978)
			ND	2.95	0.07	0.15	0.3	3.4	ND	ND	42	1306	cna	f: Garnier-Sillam (1987)
			ND	3.9	0.13	0.20	0.5	3.6	ND	ND	25.5	547	cnc	Montadert (1985)
Gunung Mulu, Sarawak	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)
	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, Malaysia	2011	4	Inceptisol	6.8	ND	7.7	24.6	5.7	ND	ND	ND	651h	gs2	h: Proctor <i>et al.</i> (1989)
				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, Puerto Rico	3280	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	pr	Moore and Burns (1970)
Sepilok Borneo	3206	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	sp	Kitazawa (1971)

*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			Anecics			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
Laguna Verde, Mexico	44	3.2	4		ND		0	0	0	0	0	0	44 (100)	3.2 (100)	4	lv1	Lavelle <i>et al.</i> (1981)
																	This study
Los Tuxtlas, Mexico	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	
	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	
Volcan Barva, Costa Rica	401	35.4	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	crl	Atkin and Proctor (1988)
	280	71.9	ND		ND		ND	ND	ND	ND	ND	ND	ND	ND	ND		
Yurimaguas, Peru	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)
	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)
Rio Negro, Venezuela	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)
	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)
																	This study
Panguana, Peru	68	2.69	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	pan	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	Lavelle (1978)
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	Montadert (1985)
	48	3.1	9		4.5		1.7 (4)	0.6 (19)	2	0	0	0	45.9 (96)	2.52 (81)	7	cnb	This study
	4	0.2	4		6.2		2.4 (67)	0.1 (55)	3	0	0	0	1.2 (33)	0.09 (45)	1	cna	
	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 Mulu, Sarawak	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	
	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	
Gunung Silam, Malaysia	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	
El Verde Puerto Rico	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)
Sepilok, Borneo	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 handsorting 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

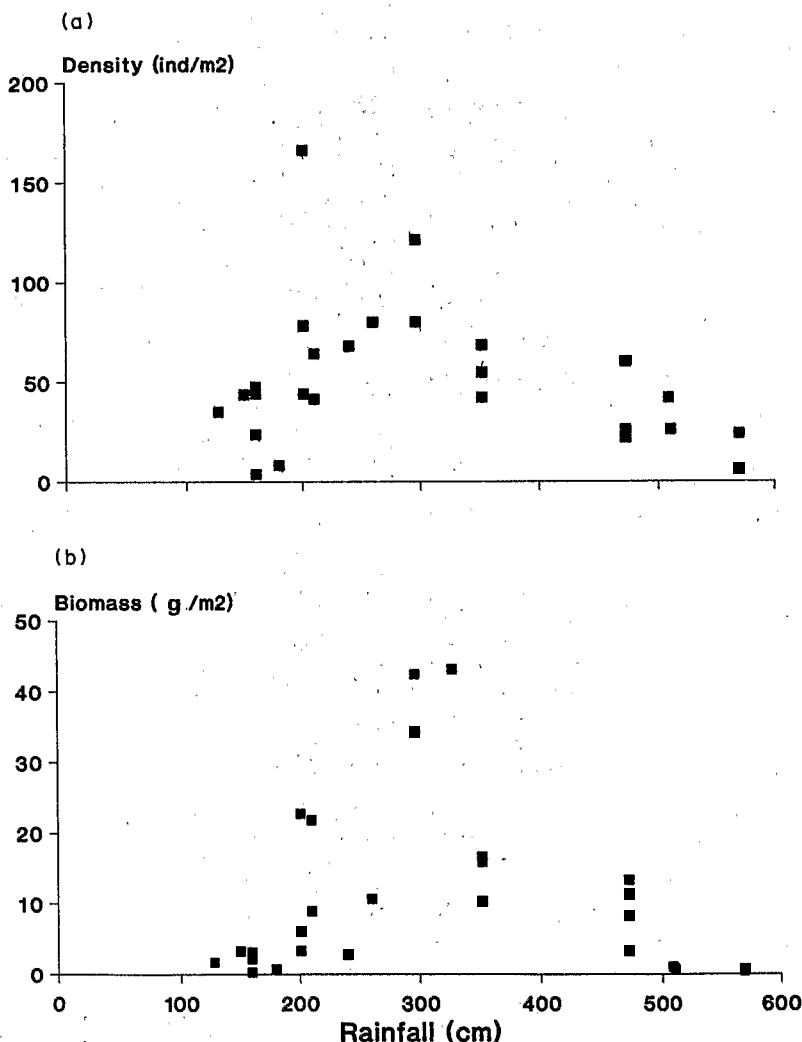


Fig. 1. Relationship between (a) density and (b) biomass vs annual rainfall in earthworm communities from different tropical rainforest. Costa Rica values excluded.

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

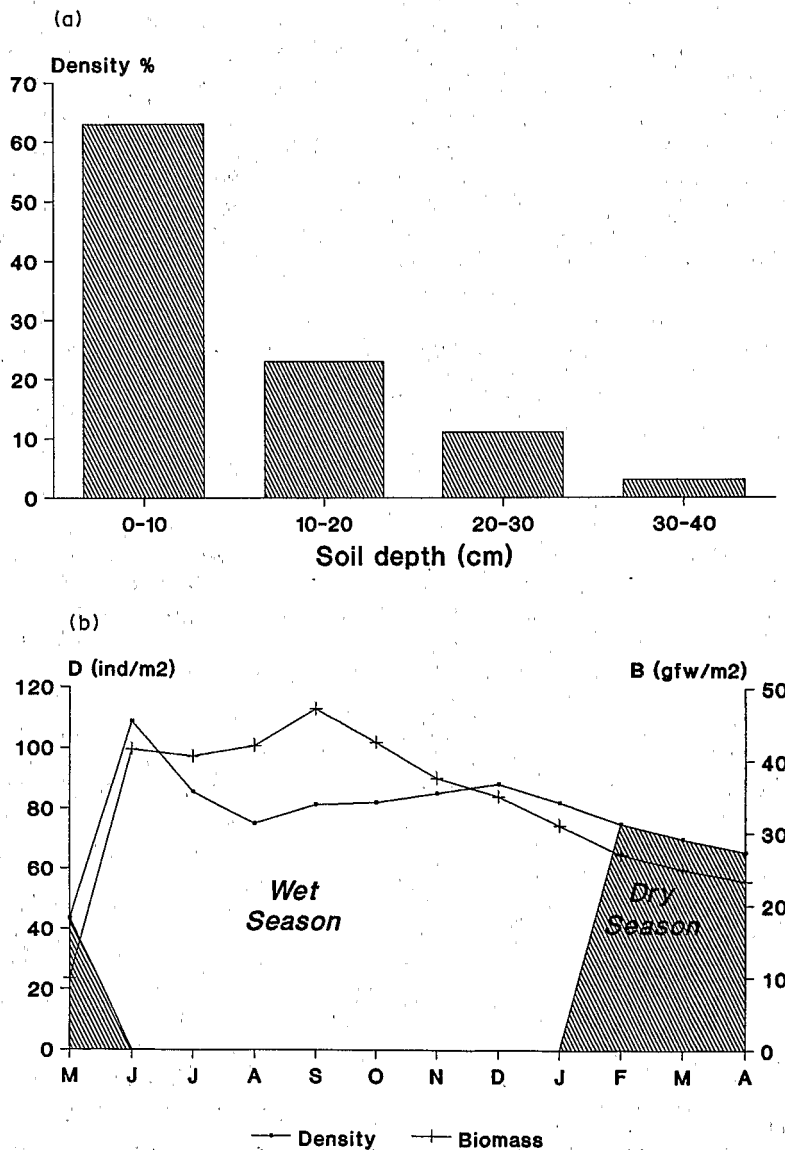


Fig. 2. (a) Vertical distribution of earthworm communities from seven tropical rain forest localities [Chajul, Bonampak, Los Tuxtlas, Laguna Verde (México), Yurimaguas (Perú), San Carlos Río Negro (Venezuela) and Dimonika (Congo)], expressed as average percentages of density. (b) Temporal patterns of 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	South America	Chajul ... CHP	Central America
Yurimaguas ... YRS		Chajul ... CHS	
Rio Negro ... RNL		Bonampak ... BK	
Rio Negro ... RNP		Lag. Verde ... LV7	
Rio Negro ... RNY		Lag. Verde ... LV1	
		Tuxtlas ... TX1	
Dimonika ... CNR	Africa	Tuxtlas ... TX2	
Dimonika ... CNA		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%) ordinales 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

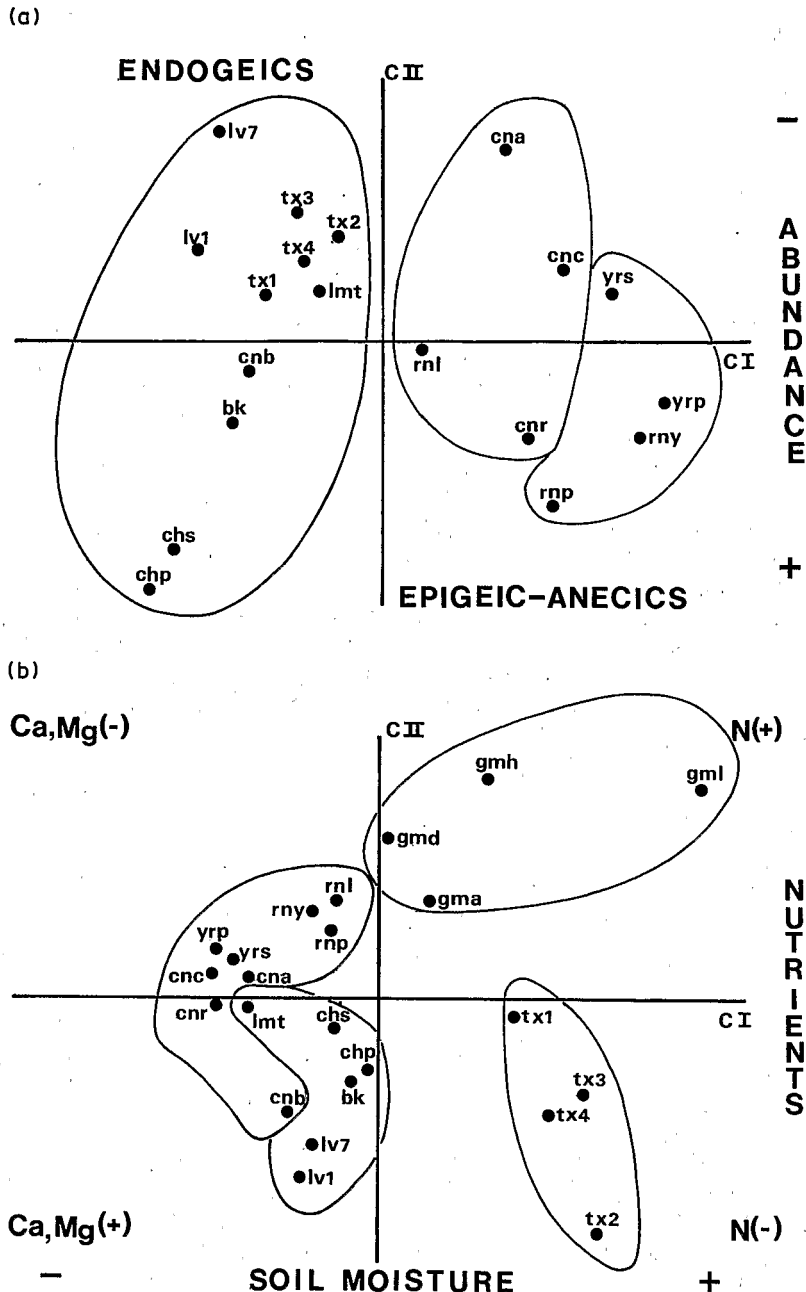


Fig. 3. Ordination (PCA) and Clustering (UPGMA) of TRF earthworm communities on the basis of:
(a) biological variables and (b) climatic and edaphic variables.

taxa must have the same strategy. In Central America almost all native species belong to the family Megascotidae 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 Ocerodrilidae (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

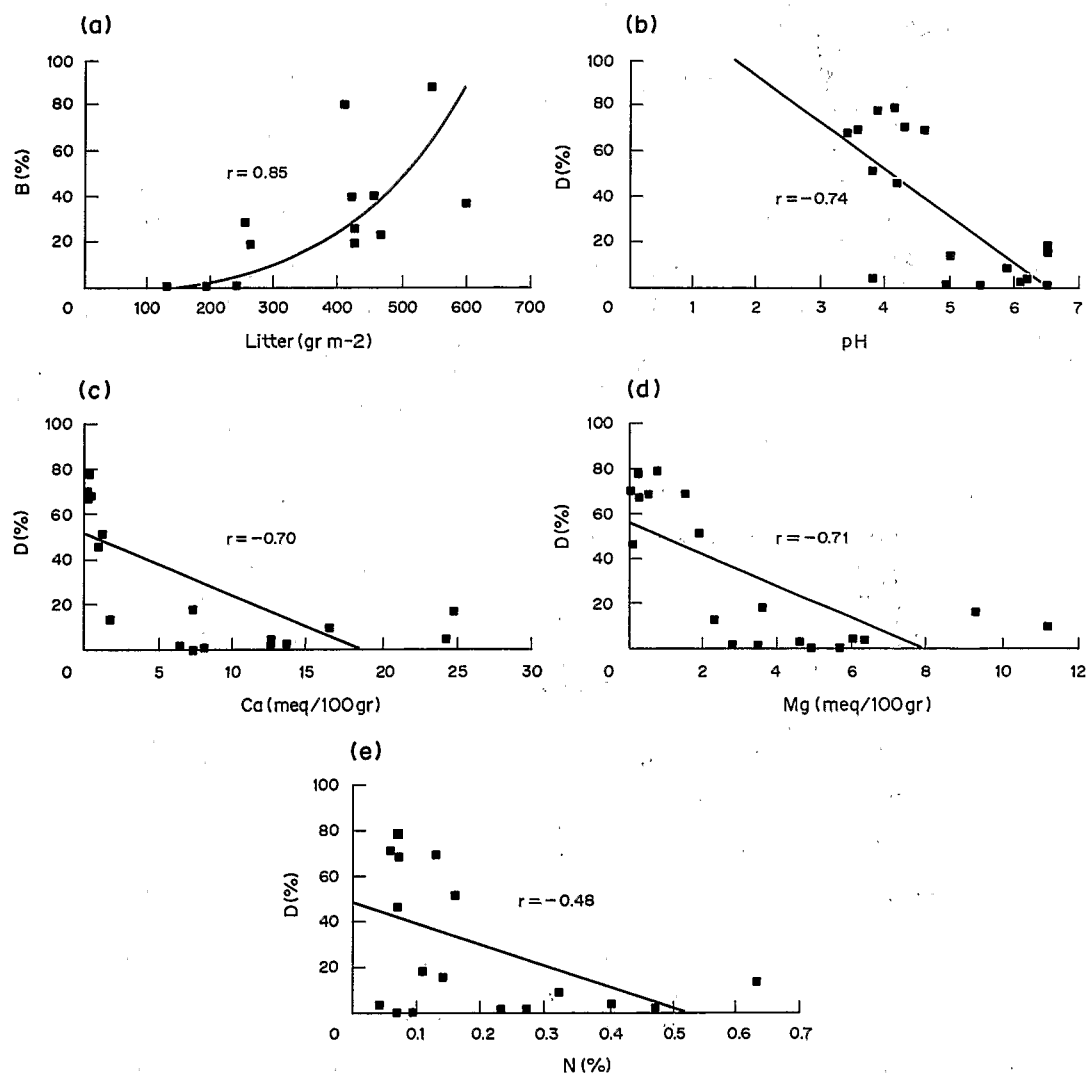


Fig. 4. Relationship between percentage of biomass (B%) and density (D%) of TRF epigeic worms and different soil variables: (a) B% vs litter, (b) D% vs pH, (c) D% vs Ca, (d) D% vs Mg and (e) D% vs N (r significantly at $P < 0.05$).

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

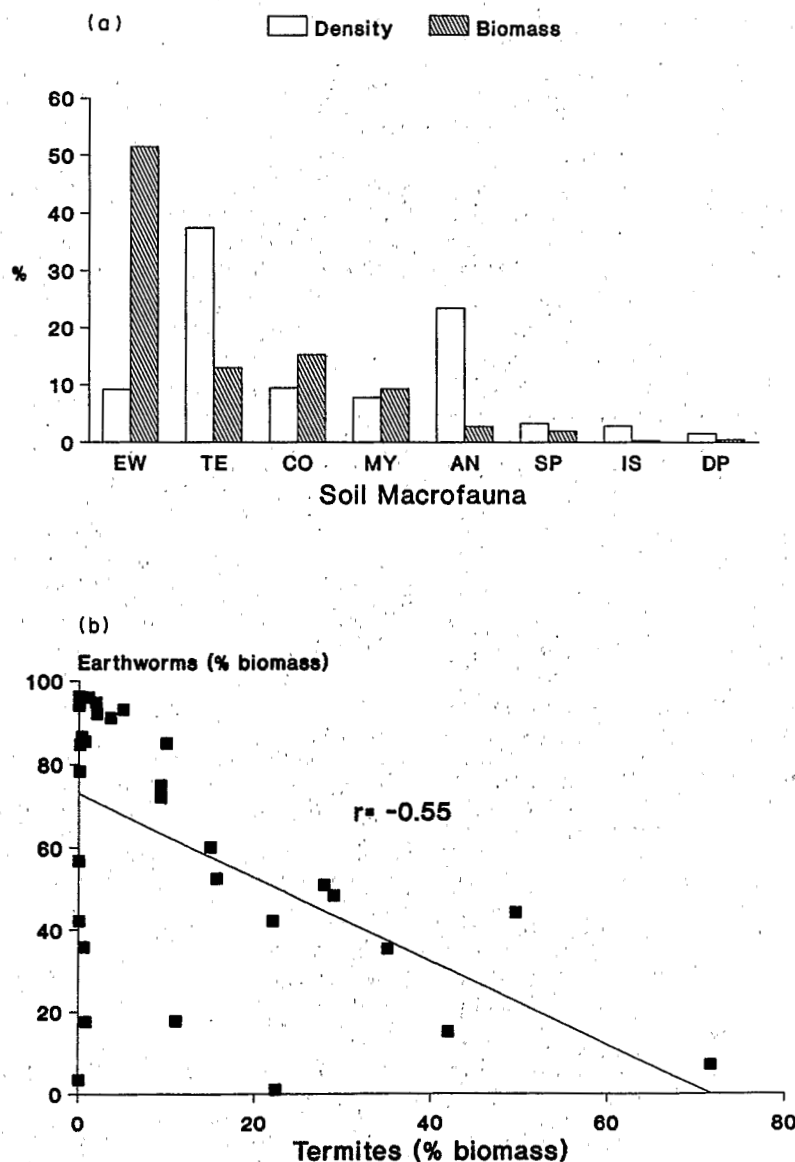


Fig. 5. (a) Main soil macroinvertebrate groups (D and B >1%) from different tropical soils. EW: earthworms; TE: termites; CO: coleoptera; MY: Myriapoda; AN: ants; SP: spiders; IS: isopoda; DP: diptera. (b) Relationship between relative biomass of earthworms and termites in different tropical soils (savannas,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

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