SOIL FAUNA DENSITIES AND FLUCTUATIONS IN CENTRAL AMAZONIAN FORESTS AND POLYCULTURES AS AFFECTED BY THE *EL NIÑO* AND *LA NIÑA* EVENTS IN THE YEARS 1997 - 1999

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Abstract

A survey of the soil meso- and macrofauna in three different forest systems (a primary forest and a secondary forest site as well as two polyculture plantation sites) in central Amazonia was carried out between July 1997 and March 1999. Main interest of the study was to reveal the presence, abundance and relative importance of functional groups of the soil fauna in decomposition and nutrient cycling processes in polyculture plantations. Here we describe and analyze the abundance of the meso- and macrofauna in relation with litter quantity and its dependence on regional climate conditions as well as site-specific microclimate. Mean mesofauna density over 8 sampling events in all three forest systems ranged between 13-17,000 ind./m² at the lower end when sampled in the dry seasons and 30-40,000 ind./m² at the higher end when sampled in rainy seasons. Mean macrofauna densities ranged between 2,100 Ind./m² during the La Nina dry season in the polycultures and 9,200 Ind./m² during the El Nino dry season in the primary forest. The assessment of the macrofauna in the plantations showed a substitution of taxa and functional groups dominating in the primary forest. Social insects (ants and termites) were more abundant in the primary forest than in the secondary forest and even less abundant in the polyculture plantations. In contrast, some primary decomposers (diplopods and isopods) were more abundant in the polycultures than in the forests. Litter quantity was an important factor determining abundance of litter fauna, but the association was different for different plots and influenced by the temporal variation of rainfall. The strong rainfall deficits during the El Niño event had no negative effects on the soil macrofauna. Most arthropod groups had higher abundances during the predominance of El Niño, than in the following normal and La Niña events. Thus, the soil macrofauna responded differently from the soil mesofauna. Both, macrofauna and mesofauna migrated from the litter layer to the soil layer during El Niño.

Keywords. Soil fauna, Amazonian forests, polyculture plantations, *El Niño, La Niña*

Introduction

The term "*El Niño*" originally applied to an annual weak warm ocean current that ran southward along the coast of Peru and Ecuador in late December. Only subsequently did it become associated with the unusually large warmings in the Pacific that occur every few years and change local and regional ecology. It is this Pacific basin-wide phenomenon that forms the link to the anomalous global climate patterns. The atmospheric component tied to *El Niño* is termed the "Southern Oscillation". *El Niño* corresponds to the warm phase of

ENSO (*El Niño*-Southern Oscillation). The opposite "*La Niña*" phase consists of a basin-wide cooling of the tropical Pacific and thus the cold phase of ENSO (Trenberth, 1997). During moderate and strong *El Niño* events of the past 30 years, rainfalls were lower in most months of the year at the Embrapa climatic station, whereas higher precipitations were registered during moderate and strong *La Niña* phases.

The primary aim of our investigation was to study the regeneration and more sustainable use of already degraded areas, so as to diminish the human impact on primary rain forest in Amazonia. The basic hypothesis of our investigations was that soil fauna and microorganisms are extremely important for the maintenance of the nutrient cycling processes and consequently for the sustainability of natural as well as anthropogenic ecosystems. Our study of the soil ecosystem compartment included structural and functional endpoints. One of the objectives was to evaluate the specific contribution of the different soil fauna groups to the decomposition of organic matter. Central Amazonia is a climatically variable region with pronounced regional rainfall gradients (Ribeiro and Adis, 1984), Fisch *et al.*, 1998) and a high rainfall variability from year to year and between decades (Hanagarth *et al.* in prep.). Our study, which was carried out between July 1997 and March 1999, was affected by one of the strongest *El Niño* phenomena of the 20th century (Changnon, 2000). High rainfall deficits, extremely high temperatures and high evaporation rates characterised the *El Niño* weather situation between April 1997 and April 1998, whereas in the following period "normal" and *La Niña* conditions (July 1998 through at least December 1999) prevailed. The year 1997 was the second driest year between 1971 and 2000 according to information from the Embrapa climatic station near Manaus. These extreme climatic situations made it necessary to analyze the soil fauna abundances carefully under the effects of the climatic conditions.

Study sites and methods

Site description

The Brazilian research institute, Embrapa-Amazônia Ocidental, where this study was carried out, is situated in Central Amazonia, about 30 km outside Manaus (02°53'S, 59°59'W, 40-50 m a.s.l.). The natural vegetation is dominated by a dense primary lowland rainforest (*terra firme*) on nutrient-poor soils classified as yellow clayey latosol (Xanthic Ferralsol; FAO/ UNESCO 1991).

The study sites were plots of two forest sites and one plantation type with two plots. A first plot of 40 x 40 m was marked out in a primary forest (FLO). A second plot of the same size was marked out in a nearby secondary forest (growing since 1984, SEC). The two other plots (POA, POC) of 32 x 48 m were marked out in large polycultures where, in 1992, four different tree species of commercial use had been planted in rows and secondary regrowth had occurred. In these plots the tolerated secondary vegetation (mainly *Vismia* spp., Guttiferae) dominated the stand and especially litter production (Beck *et al.*, 1998; Höfer *et al.*, 2000; Höfer *et al.*, 2001). Therefore these plantations are similar to improved young secondary forests. All plots were situated within a distance of less than 500 m from each other.

Local climate characteristics and microclimate

According to Köppen´s classification (Heyer, 1984; Schröder, 2000) the climate in the study region corresponds to the Af-type (A = mean temperature of all months over 18 °C; f = monthly precipitation over 60 mm). Spanning 30 years (1971 - 2000) the average annual rainfall was 2,554 mm (SD ± 273). The mean climate conditions are characterised by a very strong wet season with over 200 mm rainfall per month from December to May and a short dry (or "low rainfall"), but not arid season from July to September when the prevailing monthly precipitation is still slightly over 100 mm. Therefore, the general climate condition can be designated as perhumid (precipitation of all months is over 100 mm), without a real dry season. Average monthly temperatures varied between 25 and >28 °C with a 30-year mean of 26.0 °C (SD ± 0.9) (Hanagarth *et al.*, in prep.).

The microclimate in the four plots was measured using small data loggers ("Stowaway XTI Internal/External Temperature Logger" in air-tight "submersible" cases; "Stowaway RH Relative Humidity Logger" from Onset Computer Corporation, Porasset, MA, USA). We recorded temperature in the litter layer above the soil and in the soil at a depth of 5 cm, and relative air humidity at about 10 cm above the soil. Data were obtained in three subsets: August 1997 to March 1998, May 1998 to November 1998, and November 1998 to April 1999. A detailed evaluation of the microclimate is presented in Martius *et al.* (2004a).

The microclimate showed some strong differences between the plots (Fig. 1). Mean litter temperatures in FLO and SEC were similar, but in the plantation plots the means were consistently higher (about 2 - 4 °C). The highest maximum temperatures at the litter level were achieved in POA. Temperatures at the soil surface were similar to temperatures in litter in FLO, SEC and POC, but in POA litter temperature was considerably higher than the soil temperature (Martius *et al.*, 2000). The microclimatic differences between the two plantation plots are due to different structural characteristics of the vegetation cover and shading effects of neighbouring plots (see design of the whole experimental area in Lieberei and Gasparotto, 1998). In POA vegetation was sparser and the site always received high insolation during the mostly cloudless morning hours, because the neighbouring secondary forest and other plantations did not throw enough shade. The POC plot is located beside a tall primary forest and achieved shading in the morning and less solar radiation in the afternoon, because of the higher cloud cover in the later day hours.

Soil fauna sampling

The "basic sampling program for soil fauna" consisted in 8 sampling events: 23-24 July 1997, 1-2 September 1997, 1-2 December 1997, 2-3 March 1998, 1-2 June 1998, 1-2 September 1998, 1-2 December 1998, 2 and 4 March 1999. Each sampling event took two days to be accomplished. Four different sample types were taken with the following methods: small soil core samples (6.5 cm diameter) were taken twice, for extraction of the arthropod mesofauna with a Kempson apparatus, and for the extraction of microdrilid worms by a wet-extraction-method (Römbke 2000); large soil core samples of 21 cm diameter were taken for the extraction of macrofauna (arthropods) with a Berlese apparatus. Already in the field all these samples were separated in two sub-samples, the litter layer including the root-mat and the upper 5 cm of the soil core. Earthworms were collected by formalin extraction from 4 m² large quadrats (Römbke, 2000; Römbke *et al.* 1999) . In each of the studied systems (primary forest, secondary forest, polyculture) ten samples of each type were taken at the first day, starting with the polyculture POA and continuing in SEC and FLO and ten samples at the second day, starting with POC and continuing in SEC and FLO. As such, 60 samples were taken in total per sampling event, ten samples each from POA and POC; 20 samples each from SEC and FLO.

Fig. 1. Litter and soil monthly mean temperatures in the different study plots from August 1997 to March 1998 (97/98) and from May 1998 to March 1999 (98/99), n.d. = no data.

Classification of functional groups

The small soil cores were used to assess the groups with most of the specimens below 2 mm body length, e.g., Acari, Collembola, Symphyla, Protura, Pauropoda and Enchytraeidae, herein called mesofauna. From the large soil cores, specimens of all arthropod groups except those of the above-mentioned groups were treated as macrofauna, independent from their size. These include and differentiate all macrofauna core taxa as defined recently in the report of an international workshop on soil macrofauna held in 2000 at Bondy, France (Lavelle and Fragoso, 2000.), except the earthworms (Oligochaeta: Opisthopora), which were sampled separately.

Further classification of the macrofauna into predators, decomposers, herbivores and others (not clearly belonging to the above groups) was done following common knowledge accomplished in the case of ants and beetles by our expert knowledge on Amazonian fauna (for beetles see Hanagarth and Brändle, 2001). In this study, only arthropod meso- and macrofauna extracted from the soil core samples are investigated.

Litter fall and litter stock

Litter fall was recorded as weight of dried litter from weekly samples from 10 (POA and POC) or 20 (SEC and FLO) collectors with a basal area of 0.25 m² each. Litter stocks were recorded monthly by weighing dried litter which was taken with the macrofauna soil cores.

For the analysis of litter stock - macrofauna relationships, data on litter stock and macrofauna abundance were both taken from the same Berlese samples. Only data of six sampling events were considered (from December 1997 to March 1999). The litter samples were separated by sieving into five fractions: leaves (not passing mesh width of 5 mm), fine organic matter (fine litter, passing mesh width of 5 mm), wood and twigs of >1 cm diameter and of <1 cm diameter, and roots.

The "El Niño" and the "La Niña" phenomena

The classification of "*El Niño*", "*La Niña*" and "normal" climate conditions during our study period follows Trenberth (1997). During our study period strong *El Niño* weather conditions prevailed from April 1997 to April 1998, while "normal" situations existed in May and June 1998. *La Niña* conditions began in July 1998 and ended in late 1999.

For the evaluation of inter-annual and seasonal variation and the vertical distribution of soil fauna abundance in relationship to weather conditions, the fauna sampling events were grouped into the following categories according to rainfall deviation patterns and the duration of the *El Niño* event (Fig. 2):

1. Sampling under *El Niño* conditions:

a. in the dry season 1997 after months with strong rainfall deficits (first sampling in July and second in September 1997);

b. in the rainy season 1997/1998 after months with moderate deficits (third sampling in December 1997 and fourth in March 1998);

2. Sampling under normal and *La Niña* conditions:

   in the dry season 1998 preceeded by close to average rainfall patterns (fifth sampling in June and sixth in September 1998);

3. Sampling under *La Niña* conditions:

   in the rainy season 1998/1999 preceeded by excessive rainfalls (seventh sampling in December 1998 and eight in March 1999).

Fig. 2. Deviation of monthly precipitation (in %) of the mean (1971 - 2000) in the preceding 3 months of every sampling event during the study period, underlayed by the usual classification in dry and rainy seasons and the simultaneous occurrence of *El Niño* and *La Niña* phenomena.

Results

Mesofauna

Mean mesofauna density in all three forest systems ranged between 13,000 and 17,000 ind./m² at the lower end when sampled in the dry seasons and 30,000 - 40,000 ind./m² at the higher end when sampled in rainy seasons (Table 1). Exceptionally high densities (50,500 and 78,500 ind./m²) were reached at two sampling events in polyculture POA (March 1998 and December 1998). Highly dominant in all plots were the primary decomposers oribatid mites (43-62 %), followed by enchytraeids (14 - 23%) and collembolans (6-13 %). The predatory non-oribatid mites were also abundant (15 - 20%). More detailed information on mesofauna biomass has been presented by Franklin *et al.* (2001).

The very high densities in March and December 1998 in POA were caused by extreme oribatid mite densities in several single samples. Nonetheless oribatid mite densities were often and also in total higher in all three anthropogenic plots than in the primary forest (Table 1). The contrary was observed for springtails (Collembola)

In the primary forest and both polyculture plots the mesofauna moved down from the litter layer into the upper soil layer during the dry season in 1997. This was not observed in the secondary forest, where a much higher litter cover probably prevented the fauna from the drought (Franklin et al. 2001).

Macrofauna

The macrofauna included a total of 29 high order arthropod taxa, of which 9 important groups (predators: spiders, chilopods, pseudoscorpions, diplura; decomposers: diplopods, isopods and diptera; larvae and adults of beetles) were considered. Macroarthropods were abundant in all three systems studied. Mean densities over all eight sampling events were highest in the primary forest (FLO) with nearly 5,000 ind./m^2 and lowest in the secondary forest area (SEC) with nearly 4,000 ind./m² (Fig. 3). Highest densities during the whole sampling period of 21 months were observed in July 1997 in FLO and December 1997 in both polyculture plots (POA and POC). With the exception of the primary forest, arthropods were always more abundant in samples taken in December, at the beginning of the rainy season and less abundant in June, at the beginning of the dry season.

Predatory arthropods made up between 46 and 53% of the individuals, and decomposers between 34 and 43%. The most abundant predators were pseudoscorpions, diplura, spiders and beetles. Predatory ants were more abundant in the forest areas, especially in the primary forest, than in both polycultures. Termites (Isoptera) were the most abundant decomposers in FLO and

Table 1: Mean densities (ind./m²) of the functional mesofauna groups during the study period 1997 - 1999.

Primary forest FLO taxon	Jul'97	Sep'97	Dec'97	Mar'98	Jun'98	Sep'98	Dec'98	Mar'99	Mean	SD in %	Median
Acari: Oribatida	7,838	10,078	16,595	11,726	11,509	5,490	9,860	10,093	10,399	31%	10,086
Acari Non-Oribatida	5,257	5,956	5,215	5,863	4,323	2,535	5,303	5,552	5,001	22%	5,280
Collembola	2,519	2,986	1,775	1,882	5,785	995	4,308	5,197	3,181	54%	2,753
Pauropoda	46	39	95	85	27	81	79	32	61	45%	63
Protura	121	105	59	72	66	107	136	49	90	36%	89
Symphyla	192	175	92	92	83	16	267	192	139	58%	134
Enchytraeida	5,500	2,400	1,700	3,300	8,100	5,800	10,400	7,300	5,563	54%	5,650
Total Mesofauna	21,474	21,740	25,531	23,021	29,894	15,024	30,353	28,416	24,431	21%	24,276
Secondary forest SEC	Jul'97	Sep'97	Dec'97	Mar'98	Jun'98	Sep'98	Dec'98	Mar'99	Mean	SD in %	Median
Acari: Oribatida	4,152	7,527	10,964	20,233	16,547	8,880	17,885	14,308	12,562	44%	12,636
Acari Non-Oribatida	3,313	4,603	5,412	5,739	5,552	1,851	7,092	6,454	5,002	34%	5,482
Collembola	793	1,431	793	5,442	3,499	700	2,893	4,510	2,508	74%	2,162
Pauropoda	17	4	16	40	30	33	22	40	25	50%	26
Protura	33	36	66	149	43	123	167	45	83	66%	56
Symphyla	92	58	142	167	17	17	291	200	123	78%	117
Enchytraeida	7,000	2,700	1,800	3,000	9,900	3,900	8,700	12,500	6,188	63%	5,450
Total Mesofauna	15,401	16,360	19,194	34,770	35,589	15,504	37,049	38,057	26,491	40%	26,982
Polyculture POA	Jul'97	Sep'97	Dec'97	Mar'98	Jun'98	Sep'98	Dec'98	Mar'99	Mean	SD in %	Median
Acari: Oribatida	9,518	8,523	20,529	34,588	20,778	12,784	63,266	16,983	23,371	78%	18,756
Acari Non-Oribatida	3,328	6,812	10,700	6,656	4,541	1,089	5,754	6,998	5,735	50%	6,205
Collembola	1,306	1,275	1,711	2,240	5,163	747	1,835	4,728	2,376	69%	1,773
Pauropoda	375	29	29	29	0	0	29	577	134	164%	29
Protura	87	87	58	115	87	462	635	173	213	101%	101
Symphyla	500	525	992	624	467	250	275	967	575	49%	513
Enchytraeida	2,500	3,300	1,900	6,300	9,900	1,800	6,700	8,600	5,125	62%	4,800
Total Mesofauna	17,614	20,550	35,918	50,552	40,936	17,131	78,494	39,027	37,528	55%	37,472
Polyculture POC	Jul'97	Sep'97	Dec'97	Mar'98	Jun'98	Sep'98	Dec'98	Mar'99	Mean	SD in %	Median
Acari: Oribatida	9,051	6,687	11,384	19,347	19,751	10,669	11,913	12,970	12,722	36%	11,649
Acari Non-Oribatida	4,635	3,701	3,764	6,874	2,022	7,589	3,701	7,838	5,016	43%	4,199
Collembola	1,369	550	2,613	2,686	342	1,337	2,706	5,039	2,080	73%	1,991

Pauropoda	29	144	260	664	318	1,357	144	635	444	98%	289
Protura	895	144	1,675	1,732	491	1,501	173	1,155	971	67%	1,025
Symphyla	408	466	216	550	158	308	92	808	376	62%	358
Enchytraeida	3,900	2,100	2,100	3,700	6,600	2,300	7,000	6,500	4,275	50%	3,800
Total Mesofauna	20,286	13,793	22,011	35,553	29,682	25,062	25,730	34,946	25,883	29%	25,396

Fig. 3.

Abundance (ind./m^2) of the whole macrofauna in the litter and soil fraction of the core samples during the study period from 1997 to 1999.

SEC (24 and 14% of all arthropods) and clearly less abundant in the polycultures, whereas in the polycultures diplopods dominated the decomposer group (7 and 9% of all arthropods). Ants classified as decomposers made up 7 to 11% of all arthropods (Verhaagh *et al.*, 2001). For more details and information on macrofauna biomass and diversity see Höfer *et al*,. (2001).

Litter fall, litter stock and macrofauna abundance relationships

The highest weekly litter fall quantities, together with the highest variability, were recorded in the dry season of 1997 (September/October) (Fig. 4). The high difference of the mean monthly litter fall in the second half of 1997 to the means of other years becomes apparent as in previous years (1993-96) no significant inter-annual variation was detected in a neighbouring primary rain forest (Martius *et al.*, 2004b). This already points to an effect of the strong *El Niño* of 1997. The variation of litter fall in FLO was higher than in the other plots, best explained by a higher heterogeneity of the vegetation structure at this plot. Litter fall was low from February to March 1998, and increased again during the dry season 1998 (September) (Fig. 4). In FLO, annual litter fall was higher in 1997 - 1998 than in 1998-99, but this trend was not observed in the other plots.

The litter stocks on the forest floor were by far highest in SEC and lowest in FLO (< 50 %;). The stocks in POA and POC were intermediate between FLO and SEC and did not differ significantly from each other (Fig. 5). Litter stocks did not differ significantly between the two years, but in FLO, the monthly litter stocks were somewhat higher in the first twelve months (1997-98). In SEC the contrary was observed. Obviously there is no immediate effect of *El Niño* on litter stocks, which is not surprising because the stocks are integrating a much longer period.

Inter-annual and seasonal fluctuations of abundance

Despite the harsh weather conditions during the "*El Niño*" months, our data show that the litter and soil macrofauna did not respond with a decrease in densities, as could be expected. At all sites the total macrofauna showed in an inter-annual comparison significantly higher densities during the *El Niño* situation (sampling July 97 to March 98) than during the normal and *La Niña* situations (sampling June 98 to March 99). Spiders, diplopods, isopods, pseudoscorpions and Diplura particularly had higher densities in samples during *El Niño* at all sites, whereas Diptera larvae for example showed the contrary in all four and chilopods

Fig. 4. Mean weekly litterfall in the four plots (dry weight in g/0.25 m²).

Fig. 5. Litter weight (litter stock) in the soil core samples in the four plots (dry weight in g/0,364 m²), values are means of 20 (FLO, SEC) or 10 (POA, POC) samples.

and beetles in at least one of the plots (Fig. 3**).** Comparison of the *El Niño* dry season 1997 with the following normal dry season 1998 reveals that total macrofauna had significantly higher individual numbers in all plots. We assume that most taxa responded positively to rainfall deficits, resulting in higher densities during the dry season of 1997, than in the (following) normal dry season. Spiders, pseudoscorpions and Diplura obviously did better during low rainfall periods than during a surplus of precipitation under *La Niña* influence. Interesting are differences between the different plots. In FLO and SEC, several groups (larvae of beetles, diplopods, Diptera larvae, and chilopods) were less abundant during 1997, whereas in POA and POC only Diptera larvae were less numerous in 1997.

When comparing the abundances sampled during the two wet seasons, differences were not so large (Fig. 3). The whole macrofauna was more abundant in the wet season under *El Niño* influence in 1997/98 and most groups showed significant differences, e.g., higher densities in the *El Niño* wet season, but only for diplopods and isopods this was true for all plots. Spiders, isopods and diplura had significantly higher densities in three of the four plots. When the differences in densities between the samples from dry and wet seasons were compared, no clear tendency could be detected.

Seasonal variation of vertical distribution

The selected macrofauna groups reacted to rainfall fluctuations (to seasons) by migrating between the litter and the soil layer. In the dry season of 1997 more individuals of most taxa were extracted from the soil fraction of the samples (soil/litter ratios: >1.0). Ratios were very high (>5) for the predatory taxa in the primary forest and in one of the plantations (POA), the two plots with lower litter quantity (Martius *et al.* 2004b). In the secondary forest, where the litter layer was distinctly higher throughout the study period, a larger portion of most macroarthropod taxa was extracted from the litter and soil/litter-ratios were closer to 1 (Fig. 3). During the rainy season 1997/98 the portion of the fauna extracted from the litter fraction had increased in nearly all taxa and plots. Arthropods obviously had moved from the upper soil layer to the moist litter, where most of them fed on organic matter or predated upon the decomposers. Principally the same pattern was observed in 1998/1999, but the differences between the dry and rainy season seem to be more accentuated in the rainy season 1997/98 than in 1998/99, with the exception of the POA plot. The differences between the years reflect the more accentuated dry period under the influence of *El Niño*. The predatory groups especially chilopods, pseudoscorpions and diplura and the isopods reacted strongly to the rainfall deficits by downward migration. In the rainy season influenced by *La Niña*, the densities of most groups were higher in the litter layer in relation to the preceeding rainy season.

Discussion

Litter quantity was an important factor determining abundance of litter fauna, but the association was different for different plots and influenced by the temporal variation of rainfall. Clumped distribution, especially of social insects and population size and growth factors (intrinsic ones like seasonal reproduction and extrinsic ones like predation and competition) certainly interferred, as well as other abiotic variables like microclimate, litter quality and litter moisture, which beside influencing the litter quantity also can have direct effects on the soil fauna. The differences in the strength of the litter - abundance association between predators and decomposer fauna showed that litter quantity (acting through its volume) is an important (and sometimes limited) space resource factor for litter inhabiting predatory arthropods, but is probably never limited as a food resource for the primary decomposers.

Total litter weight might also not be the best indicator of litter quantity; sometimes large wood pieces in the samples increased the weight without representing space nor food resources. The abundance of the soil fauna is influenced by many other factors. Positive correlations between litter quantity and abundance of litter inhabiting spiders have been found in another primary forest near Manaus (Höfer unpubl.) and in other agroforestry systems of the Embrapa station (Vohland and Schroth, 1999). Experimental increase of litter resulted in higher densities of spiders and other arthropods (Höfer *et al.*, 1996), but it was also shown that such experimental litter accumulations were decreased to the normal amounts through rapid decomposition, promoted by the faunal activity.

In a widely accepted hierarchical model proposed by Lavelle *et al.*, (1993) for soil processes, climate is the top factor which determines the differentiation of the next level, which is the soil type and its nutrient content, followed by vegetation and resource quality, and finally the macro- and microorganisms and their biological interactions. Although climate is primarily seen as a factor acting on the highest time and space scale, the short term cycles, seasonal weather patterns and day-to-day sequences such as rainfall and drainage and the regime of heating and cooling during the day are important factors (Lavelle *et al.*, 1997). The inter-annual climatic variations described as *El Niño* and *La Niña* events, are responsible for the changing conditions for the soil fauna and lastly for the ecosystems. As well as the normal seasonal variations, they could have direct and indirect impacts on the macrofauna and mesofauna taxa (and microorganisms), causing opposite alternations in functional groups. They alter litter fall intensity and therefore litter stocks on the ground, influence the quality and determine the forest floor moisture, which is one of the most important environmental factors for the soil fauna.

However, contrary to our expectation, strong negative effects on the abundance of the soil macrofauna did not occur as a consequence of the extraordinarily dry conditions during the *El Niño* prevailing from April 1997 to April 1998. We recorded inter-annual and seasonal variations of macrofauna abundance as well as vertical movements between the litter and soil layer as responses to weather variation. The total macrofauna abundance was higher during the dry season under *El Niño* influence at all plots. Spiders, diplopods, isopods, pseudoscorpions and diplura in particular were more abundant in nearly all plots and in both the dry and the wet seasons under *El Niño* influence than under normal or *La Niña* conditions. By contrast, diptera larvae showed clearly lower densities during the normal dry season and the *La Niña* wet season. During the dry periods, a large portion of the litter dwelling macrofauna moved downwards to the upper soil layer whereas during more humid periods, more animals inhabited the litter layer. A comparison of the data of the two years showed that the macrofauna groups exhibited very complex reactions depending on the preceeding weather and site conditions (like seasonal litter fall and litter stock fluctuations), certainly originating from their species composition and the specific ecological requirements. Some site characteristic differences in abundances of the taxa may be interpreted as the result of reactions of several or a few dominant species at each study site, as a response to microclimatic site characteristics (Höfer et al., 2001, Martius *et al.*, 2004a). Even at the level of orders and families of diplopods and isopods Höfer *et al.*, (2001) shows that there were some strong differences in species composition at the study sites. Species may have responded differently to weather variations. Approximately the same number of macrofauna groups reacted clearly on climatic changes, even in the primary forest plot (FLO) where microclimatic conditions are moderate. However, the largest differences were measured in the plantation plot POA which also revealed a more extreme (hot and dry) microclimate.

The results of the macrofauna contrasted in some aspects to those of the mesofauna. Franklin et al. (2001) recorded lower densities of mites (oribatids and non-oribatids) and collembolans in the same study sites during the *El Niño* period in 1997 than under normal conditions in 1998, whereas the macrofauna had higher densities in the same period. Compared to 1997, the densities of the three mesofauna groups increased by 30% in 1998. The macrofauna and mesofauna groups reacted similarly to dry conditions in the litter layer by downward movements to the soil layer. This is indicated by a higher soil/litter ratio of abundance in the drier than in the wetter months. Franklin et al. (2001) registered a clear pattern in the dominant mesofauna groups (Acari Oribatida, Acari Non-Oribatida and Collembola) with higher densities in the soil fraction during 1997, principally in FLO, POA and POC. In 1998 and 1999, the soil/litter ratio in 1997 was inverted due to high densities of the mesofauna in the litter layer for all plots.

In the central Amazon region, the vertical distribution and abundance of arthropods (meso- and macrofauna) in the litter and the soil layer may depend on the prevailing weather conditions and on the litter quantity. Adis *et al.*, (1987a,b) did register similar high abundances in both litter and soil of a secondary *terra firme* forest during the rainy and dry season. Neither during the dry season nor during the wet season was the abundance of arthropods in the soil higher in response to the changing humidity in organic layers, probably because of the moderate dry season conditions. They did not record strong differences in densities between both seasons. However, Morais (1985) also found a lower density of arthropods during the rainy season in a primary and a secondary forest in the same region. Another short term study on macroarthropods in an Ecuadorian mesothermic rainforest (Silva del Pozo and Blandin, 1991) showed no dramatic changes of the vertical distribution of the soil fauna during the low rainfall period, but the mesofauna density was lowest during the driest season in the litter and soil layer.

In a 40-month study of the soil fauna in a Panamanian tropical deciduous forest, Levings and Windsor (1985) showed that among years, the rank order of abundance in seasonal comparisons was highly correlated. All groups tended to have high or low populations in the same year. The major arthropod groups showed three main patterns of seasonal changes in abundances: dry season increase, like in several of our macrofauna groups; early wet season maxima (in most of the groups studied) as detected in some of our plots; and no fluctuations or fluctuations in dependence of seasonal patterns.

Considering the regional climate conditions, the results may be understandable due to the prevailing perhumid Af-climate (Schröder 2000; Hanagarth *et al.* in prep.). There are on average no arid "dry" season conditions with a general long-term water stress at least in these forests. Under those regional climate conditions, the litter/soil macrofauna and the mesofauna may react similarly strong (but contrary in abundance) on seasonal as well as on short-term weather events and in dependence on microclimatic site characteristics and litter and soil moisture. Obviously, the regional climate conditions of the study region move on a dry-wet gradient, where rainfall deficit favors, but heavy rainfalls and extreme soil moisture conditions limit the development of the soil macrofauna. That moist litter and soil conditions prevailed in the study sites was shown by the presence of microdrilid oligochaeta families of Naididae and Tubificidae (Römbke 2000), because the species of these families are considered to be confined to aquatic or to at least semi-aquatic sites like inundation forests (Irmler 1989). The evaluation of climatic data of the Embrapa climatic station over 30 years showed large inter-annual differences in precipitation and a high variability of monthly rainfall patterns (Hanagarth *et al.* in prep.). Annual rainfall sums ranged between 1958 and 3193 mm, and during the dry season (July to September) perhumid conditions with high precipiations prevailed. By contrast, similar strong situations of droughtness, compared to that of 1997 were rarely recorded. These variations may suggest a moderate to high inter-annual variation of the populations of the soil fauna, which may be at least as strong as or even stronger than the seasonal variations.

These results are also of agricultural interest. The soil fauna (and microorganisms) are extremely important for the maintenance of the nutrient cycling processes and consequently for the sustainability of ecosystems. Their occurrence depend essentially on the litter layer, which fulfills multiple functions such as provision of conducive food and shelter requirements and consequently, microclimatic buffer.

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