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Soil beetles (Coleoptera) of a primary forest, secondary forest and two mixed polyculture systems in central Amazonia

Abstract

The beetle fauna of soil and litter in Amazon forest eco-systems was studied by means of Berlese-Tullgren extractions, at 8 sampling dates during 2 years in four experimental plots (one in primary forest, one in secondary forest and two polyculture plots) of the Embrapa Amazônia Ocidental research centre near Manaus (Brazil). Beetle individuals were found in 99 % of the extracted litter and soil cores. In total, we recorded 47 beetle families, of which 12 contributed to more than 90% of the total individual numbers and beetle biomass, respectively. Most individuals recorded were very small averaging less than 2 mm body length. The total number of predator families was low (6 families, 13 %), when compared to that of the decomposers (29 families, 62 %). Only one family was considered herbivorous (Chrysomelidae, 2 %). 28 % of the decomposer families, but 67 % of the predator families ranged among the 12 most abundant beetle families. Among the 12 dominant beetle families the carnivorous Scydmaenidae, Staphylinidae, Carabidae and Pselaphidae represented 51 % of the abundance and 41 % of the biomass. In comparison to other macroarthropods (Chilopoda, Formicidae, Isoptera, Diplopoda) the contribution of Coleoptera to the total of individual numbers or faunal biomass was rather small. We conclude that although diversity of the soil dwelling beetles seems to be high, their total contribution to nutrient cycling may be of minor importance.

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key words

Beetles, guilds, diversity, Amazonia, polyculture systems

1. Introduction

Beetles are one of the most diverse taxa among the insects (JACOBS & RENNER 1988, ERWIN 1982). Following DUNGER (1964) they are the most important Pterygota in soil biology. SCHUBART & BECK (1968), however, stated that beetles may be very important and dominant in temperate zones, but in the tropics termites and ants appear to be much more abundant and functionally more important. Beetles provide a wide range of functions in ecosystems, occupying almost all types of trophic niches. There are carnivorous, phytophagous (including pollen- and sap-feeders), detritophagous, saprophagous (including scavengers and coprophagous species), xylophagous and fungivorous groups.

In the Amazon region, a series of studies on the functional diversity of the soil fauna has been carried out, considering abundance and partially the biomass at the level of orders (e.g. ADIS 1982, ADIS et al. 1987 a, b, HARADA & BANDEIRA 1994, BANDEIRA & HARADA 1998, LAVELLE & PASHANASI 1989, TAPIA-CORAL et al. 1999). Ants, termites and earthworms are the most studied soil fauna groups at the level of genus or species (BANDEIRA & HARADA 1991, MARTIUS 1994). However, only a few papers show data on the abundance and even less publications offer data on the biomass of litter and soil dwelling beetles at the family level (DIDHAM 1998, DIDHAM et al. 1998a, 1998b). This may be surprising because beetles are also abundant insects of the litter and soil in Amazonia (BECK 1963, HANAGARTH 1981, DIDHAM 1998, DIDHAM et al. 1998 a, b) and in Panama (WILLIAMS 1941). The reason for this low attention given to ground dwelling beetles may be (i) their small body size, (ii) the low status of knowledge of trophic behaviour even in well studied temperate zones and (iii) the poor taxonomic status of many families in the tropics.

The present study was part of the project ENV 52 "Soil fauna and litter decomposition" of the German-Brazilian SHIFT program "Studies on Human Impact on Forests and Floodplains" in the Brazilian Amazonia. Here we analyse the beetle fauna extracted from soil cores with a Berlese-Tullgren apparatus. First we describe the soil beetle fauna and evaluate the importance of different families due to abundance and biomass. Second, we compare the functional position of soil beetles with other groups of soil macroarthropods.

2. Material and methods

The study site is located at the experimental area of the agroforestry research station Embrapa Amazônia Ocidental close to the city of Manaus, Amazonas, Brazil (3°8´S, 59°52'W, BECK et al. 1998, HÖFER et al. 2000; VOHLAND & SCHROTH 1999). The study area is flat without accentuated altitudinal differences (altitude 44 - 50 m a.s.l.). The investigations took place on an abandoned plantation of rubber trees (*Hevea brasiliensis* occulated with *Hevea pauciflora*, Seringueira) which has been used for agroforestry research since 1992. Originally, the area was cleared from primary forest in 1979/1980, and the rubber plantation was abandoned in 1984. The SHIFT experimental area is surrounded by primary and secondary forests. In the SHIFT project ENV 52 a primary forest (FLO), a 12 year old secondary forest plot (SEC), dominated by *Vismia guianensis*, and two 7 year old mixed polyculture systems (POA and POC) were studied. The tree plantations were planted with Seringueira (*Hevea brasiliensis-pauciflora*), Paricá (*Schizolobium amazonicum*), Mogno (*Swietenia macrophylla*) and Andiroba trees (*Carapa guianensis*). After tree planting, second growth was tolerated. Therefore, these plantations corresponded floristically and structurally to improved secondary forests, in which *Vismia* species dominate (PREISINGER et al. 1994, 2000; SKATULLA et al. 2000). The soil properties correspond to a clayey Xanthic Ferralsol according to the FAO/UNESCO classification (FAO/UNESCO 1990) in all four study plots.

The macrofauna at each site has been extracted in a BERLESE-TULLGREN apparatus (DUNGER & FIEDLER 1989, SOUTHWOOD 1966). This extraction method was frequently applied in soil fauna studies in Europe (e.g. BRASSE 1975, HOUSE & PARMELEE 1985, SCHAEFER 1974), as well as in the Amazon rain forest (BECK 1972, 1976; HÖFER et al. 1996, HÖFER et al. 2000, RÖMBKE et al. 1999, SCHUBART & BECK 1968). A major drawback of this method is that large beetle species or those of low abundance may be not representatively extracted because of the small size of the individual samples. Due to this methodological restrictions the beetle fauna is considered as part of a "Berlese soil fauna" However, compared to handsorting methods, the Berlese-Tullgren method offers great advantages, because it permits the extraction of very small and medium sized beetles as well as a large proportion of larvae.

In total 480 samples comprising a total sampling area of 16.6 m^2, were taken from July 1997 to March 1999 during 8 sampling events at the four plots. Samples were taken at random with a soil core sampler (21 cm diameter), subsequently separated in litter and soil (0-5 cm) and extracted during 17 days in a BERLESE-TULLGREN apparatus. During each sampling event 20 samples were taken each in FLO and SEC and 10 cores in POA and POC, respectively.

The extracted beetle specimens were identified to the family level. Their dry weight was estimated by direct individual measurement of total body length or other body size variables and applying body length-body weight regression curves with the formula $y = ax^b$ (y = dry weight in mg, a and b = coefficients, x = body length or other body variable in mm). All regressions were highly significant ($r^2>0.9$, $P<0.001$). For the definition of body length-body weight regression curves, fresh material has been independently measured and weighed. The same specimens were dried at 65°C during 72 hours and weighed (dry weight), using a microbalance (min. >0.0001 g, SARTORIUS). For some species of rarely sampled families with similar body weight-body length relationships, the same length categories have been used for the estimation of their biomass.

The determination of trophic groups was hindered by the low level of knowledge of the feeding behaviour of most species and families. Assuming that most species of the recorded families have similar food preferences than their relatives from temperate zones, the trophic level of the families was determined with reference mainly to literature from the European, southeast Asian, North American and Central American Coleoptera fauna (ARNETT 1993, BORROR et al. 1981, DELVARE & ABERLENC 1989, FREUDE et al. 1965-1983, HAMMOND 1990, JACOBS & RENNER 1988, ZAHRADNIK 1985). Families such as Carabidae and Staphylinidae have to be considered as trophically heterogeneous since some of them are not strictly predaceous (HAMMOND 1990, VANICEK et al. 1994), although conventionally they were considered to be predators (BELL 1990, DUNGER & FIEDLER 1989, NEWTON 1990).

The decomposer families include groups which may act as primary decomposers, feeding on litter similarly to many Myriapoda and Isopoda. However, most species may be fungivorous and micro- or macrosaprophagous thus occupying an inferior trophic level as secondary decomposers.

3. Results and discussion

Diversity of beetle families

In sum, 47 beetle families were identified in the study area. The largest number of families was found in the primary forest (FLO: 36 families), whereas the number of families was smaller at the other plots (28 families in SEC, 24 in POA and 26 in POC).

The total number of families with predatory beetles was low (6 families, 13 %), when compared to that of

Table 1. Mean frequency of ground dwelling beetles in 480 Berlese samples of a) all study plots and b) in the different plots. SD = standard deviation based on eight sampling events during two years.

a) All study plots	Frequency (%)	SD	Median (%)
Litter fraction			
Adults	87.0	12.0	90
Larvae	68.3	15.1	70
Adults + larvae	90.9	9.3	90
Soil fraction			
Adults	83.7	13.1	88
Larvae	61.7	19.2	63
Adults + larvae	90.8	9.2	93
Litter & soil fractions			
Adults	97.2	4.6	100
Larvae	87.2	11.4	90
Adults + larvae	99.2	2.2	100
b) Study plots	**Frequency (%)**	**SD**	**Median (%)**
FLO			
Adults	85.0	12.1	85
Larvae	66.9	8.8	65
Adults + larvae	92.5	7.6	93
SEC			
Adults	86.3	10.3	90
Larvae	75.0	15.4	75
Adults + larvae	91.3	7.9	90
POA			
Adults	92.5	7.1	90
Larvae	75.0	15.4	75
Adults + larvae	93.8	7.4	95
POC			
Adults	83.8	16.9	85
Larvae	67.5	10.4	65
Adults + larvae	86.3	13.0	85

Table 2. Proportion of individuals and biomass of the most abundant beetle families. Data based on 480 Berlese samples. N = 3.629 individuals (adult specimens), 47 families (*remaining families: predators: 2; decomposers: 21; herbivores: 1; other groups: 11).

Trophic group	Family	Individuals %	Individuals Cumulative %	Dry weight (mg) %	Dry weight (mg) Cumulative %
Decomposers	Scolytidae	19.1	19.1	19.2	19.2
Decomposers	Ptiliidae	17.5	36.6	4.5	23.8
Predators	Scydmaenidae	16.7	53.3	6.9	30.7
Predators	Staphylinidae	15.6	68.9	16.7	47.4
Predators	Carabidae	13.1	82.0	13.5	60.9
Predators	Pselaphidae	5.9	87.9	3.4	64.2
Decomposers	Leiodidae	3.4	91.4	3.0	67.2
Decomposers	Platypodidae	0.9	92.3	1.1	68.3
Decomposers	Curculionidae	0.9	93.1	9.3	77.6
Decomposers	Colydiidae	0.8	93.9	0.5	78.1
Decomposers	Tenebrionidae	0.8	94.7	1.4	79.6
Decomposers	Scarabaeidae	0.7	95.4	14.4	94.0
Remaining (*)	35 families	4.6	100.0	6.0	100.0

decomposers (29 families, 62 %). Only one family was considered herbivorous (Chrysomelidae, 2 %).

A preliminary estimation of species richness applying the morphospecies concept (data not shown) indicates that Staphylinidae, Pselaphidae, Scydmaenidae and Carabidae might be the species richest families, whereas species richness of the decomposer families seemed to be low. However, in comparison to a study from western Amazonia (HANAGARTH 1981), the species richness of Carabidae seemed to be low in all plots studied here. DIDHAM et al. (1998b) also recorded low species richness of Carabidae in the leaf litter of forest fragments north of Manaus.

Frequency of beetles

Beetle individuals (adults and larvae) were found in 99 % of the Berlese samples, attaining a frequency value of 91 % both in the litter and soil fraction, respectively (tab. 1a). They occurred in very similar frequencies in all four study plots (tab. 1b). The frequency of adult beetles ranged between 83 and 87 % in soil and litter fractions. The frequency of the larvae was lower (62 – 68 %). These differences might be caused by sampling artefacts: larvae are expected to be more sensible to the sample handling.

Abundance and biomass

In the whole sample, adult beetles dominated in abundance and biomass compared to the larvae, attaining 64 % and 61 %, respectively.

Out of the 47 families, 12 families (26 %) represented 95 % of all individuals registered and 94 % of the biomass of adult beetles (tab. 2). Among them, the xylophagous Scolytidae and the very small detritivorous Ptiliidae (0.5 - 0.8 mm) were the most abundant families. However, Scarabaeidae (mainly Aphodiini) occupied the second rank in the decomposers biomass and the third when all families were considered. Only 28 % of the decomposer families, but 67 % of the predator families ranged among the 12 most abundant beetle families. Among the 12 dominant beetle families the carnivorous Scydmaenidae, Staphylinidae, Carabidae and Pselaphidae represented 51 % of the abundance and 41 % of the biomass. The remaining 35 families only represented 5 % of the abundance and 6 % of the biomass.

In the four plots total mean abundance of the beetles, including larvae, were 321 individuals per m^2 with a mean biomass of 121 mg. In the primary forest (FLO) and in POC the total abundance was low, and high in SEC and POA (tab. 3a), whereas total beetle biomass was high in FLO and low in the other study plots (tab. 3b). However, no statistically clear differences, either in abundance nor in biomass, were found between the primary forest and the tree plantations (tab. 3a and 3b). Predators and decomposers shared about the same proportion of individuals (53 % and 46 %) and biomass (48 % and 50 %), respectively. There were no strong differences of abundance of predators between the primary forests and the tree plantations, whereas predator biomass was slightly higher in the primary forest than in the secondary forest and in the tree plantations. No strong differences in abundance were found for the decomposers, whereas larger differences existed in their biomass. However, their mean biomass was 1.5 – 3 times higher in the primary forest when compared to the other plots (tab. 5).

Body length

Figure 1 shows the body length distribution of a total of 3.575 adult individuals of predators and decomposers. The $\log_{10}$-transformed body length distribution of both groups was right-skewed and differed significantly from the normal distribution (tab. 4). Most of the beetles

Table 3. a) Mean abundance (individuals/ m^2) and b) mean biomass (dry weight mg/ m^2) of functional groups, based on 480 Berlese samples.

a) Functional group	FLO Mean	SEC Mean	POA Mean	POC Mean
Predators	157.2	179.3	189.9	148.7
Decomposers	121.2	147.5	207.7	117.1
Herbivores	0.0	1.7	4.2	0.9
Others	4.6	2.5	2.3	0.0
Sum	282.9	331.0	404.1	266.6
b) Functional group	FLO Mean	SEC Mean	POA Mean	POC Mean
Predators	72.7	60.7	41.4	58.2
Decomposers	99.4	39.3	67.6	35.0
Herbivores	0.0	0.4	1.3	0.2
Others	3.7	0.3	0.2	1.6
Sum	175.8	100.7	110.5	95.0

recorded had relatively small to very small body sizes. The mean length of 5.283 specimens from 47 families, including all adults and larvae recorded in the samples, was 2.04 mm. They achieved maximum and minimum lengths of 42.0 and 0.4 mm, respectively (Appendix, tab. 1). Following the classification of VAN DER DRIFT (1951), and the Tropical Soil Biology and Fertility Programme (TSBF) (LAVELLE & PASHANASI 1989, ANDERSON & INGRAM 1993) most of them would be characterised as mesofauna (< 2 mm body length) rather than macrofauna (> 2 mm body length). The adults of 23 families (48 %) had a mean body size equal or larger than 2 mm, whereas the mean body length of 22 families (46 %) was between 1.0 and 2.0 mm and that of adults of 3 families only (6 %) was below 1 mm. Almost all individuals of families with a minimum body length larger than 2 mm were singletons, doubletons or tripletons. Exceptions were the Platypodidae and Scarabaeidae with 33 and 25 individuals, respectively. The Scarabaeidae had the largest mean body length. Among the twelve most abundant families only five had a mean body size larger than 2 mm. Even the Staphylinidae achieved only a mean length of 3.0 mm. Nevertheless, in this family the smallest adult specimens were not longer than 0.4 mm, and the largest one measured 42 mm. Carabidae are commonly considered as relatively large predators (THIELE 1977). However, in our study plots, the mean body length of 474 individuals was 1.7 mm, attaining a minimum length of 0.9 mm and a maximum length of 11.5 mm. A high proportion of the ground beetle species is part of the very small Bembidiini (Tachyina and Anillina, ERWIN 1984) with body length ranges of 0.9 to 1.1 mm, or of small Scaritini species (2.0 mm).

The functional position of beetles within the soil fauna table 5 summarizes the biomass data of all considered soil macroarthropods (HÖFER et al. 2000). Among the predators, beetles (adults and larvae) attained a biomass roughly similar (41 73 mg/m^2) to that of the Araneae (8 59 mg/m^2) and of Pseudoscorpiones (34 - 62 mg/m^2) in the four study plots. The beetles occupied 3 - 4 % of the biomass of the total macroarthropods and 8 - 15 % of that of the predators. In all plots the Chilopoda were the most important predators, attaining high biomasses (168 - 504 mg/m^2) and dominances (7 - 37 % of the macroarthropods; 42 - 66 % of

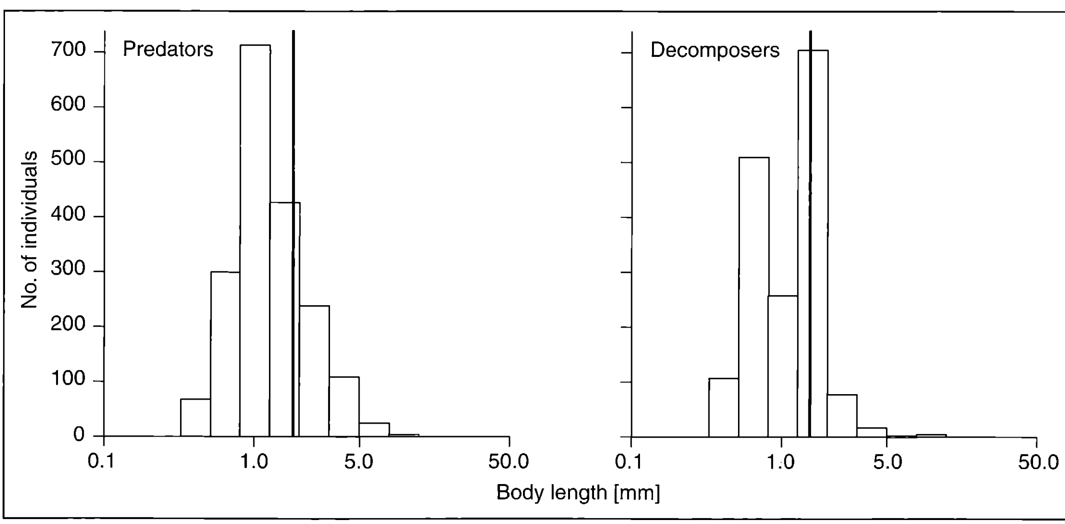

Figure 1. Body length distributions of predatory and decomposer beetle individuals. The mean of the trophic guilds is marked by a vertical line. Note that the body length axis is log_{10}-transformed.

Table 4. Characteristics of the distribution of log_{10}-transformed body length of predatory and decomposer beetles. N = number of individuals; SD = standard deviation; SE = standard error; K.-S. = probability level for the hypothesis that the distribution of the log10-transformed data is significantly different from the normal distribution (KOLMOGOROV-SMIRNOV test).

Trophic group	N	Mean	SD	Skewness	SE Skewness	Kurtosis	SE Kurtosis	K.-S.
Predators	1883	0.18	0.25	0.72	0.06	0.47	0.11	< 0.01
Decomposers	1692	0.13	0.24	0.13	0.06	-0.78	0.12	< 0.01

Table 5. Functional position of beetles. Mean biomass of taxonomic groups was calculated among all Berlese samples at four plots. Note that biomass was standardized to mg per m^2 (Data from HÖFER et al. 2000).

Functional group	Biomass dry weight (mg/ m^2)			
	FLO	SEC	POA	POC
Predators				
Coleoptera (part.)	72.7	60.7	41.4	58.2
Chilopoda	434.2	503.5	183.6	167.5
Formicidae, adults (part.)	145.2	68.5	26.0	62.3
Araneae	58.5	46.8	7.6	40.4
Pseudoscorpionida	62.3	61.6	33.7	55.5
other predators	16.7	16.6	11.9	14.8
Total	789.5	757.7	304.2	398.8
Decomposers				
Coleoptera (part.)	99.4	39.3	67.6	35.0
Isoptera	654.4	306.0	108.7	303.6
Diplopoda	219.6	107.1	247.1	275.9
Isopoda	287.2	33.7	227.0	993.7
Diptera, Larvae	33.5	25.7	64.1	41.6
Formicidae, adults (part.)	22.8	10.4	12.1	8.1
other decomposers	128.3	11.5	19.4	24.7
Total	1445.2	533.7	746.0	1682.6
Herbivores				
Coleoptera (part.)	0.0	0.4	1.3	0.2
Formicidae, adults (part.)	13.2	5.1	4.2	13.2
Rhynchota	43.0	56.4	28.1	75.8
Lepidoptera, larvae	12.1	8.9	20.0	12.9
other herbivores	0.6	1.5	1.3	1.6
Total	69.0	72.3	54.9	103.7
Other groups				
Coleoptera (part.)	3.7	0.3	0.2	1.6
Formicidae, adults (part.)	6.7	3.8	3.6	7.3
Total	10.4	4.1	3.9	8.8
Macrofauna (total)	2314.1	1367.9	1108.9	2193.9

the predators). The ants (Formicidae) had markedly higher biomasses and dominances in the primary forest (145 mg/m^2; 18.4 %), than in the other plots (26 - 69 mg/m^2; 9 % in POA and SEC, respectively).

The biomass of the decomposer beetles was rather similar compared to that of the predatory beetles (39 - 99 mg/ m^2, see above). Their contribution to the total biomass was, however, low (2 - 4 % of the macroarthropods; 2 - 9 % of the decomposers) especially when compared to those of termites, Diplopoda and Isopoda (tab. 5). Termites (Isoptera) attained a very high absolute biomass value (654 mg/ m^2) and dominance (28 % of the macroarthropods, 45 % of the decomposers) in the primary forest plot (FLO), and medium to high values in the other plots (109 – 306 mg/ m^2; 15 – 57 % of the decomposers in the corresponding plots). Other important decomposers in all plots were the Diplopoda and Isopoda whose dominances ranged between 26 and 76 %. In all plots (with exception of the POC plot) decomposer beetles had higher biomasses than decomposer ants and Diptera larvae.

Herbivorous beetles occupied only a small proportion in biomass and dominance, represented by a single family, the Chrysomelidae. Among the other arthropods, the Rhynchota, especially the Homoptera, were the most important herbivores, followed by moth larvae (Lepidoptera) and ants (mainly leaf-cutting species of the genus *Acromyrmex* and *Atta*).

4. Conclusions

Our study indicate that ground dwelling beetles are one of the most diverse taxa of Arthropoda in Amazon forest ecosystems. These results support the findings of ADIS (1982a), ADIS (2000), ADIS & RIBEIRO (1989), DIDHAM et al. (1998b), FRIEBE (1984), SCHUBART & BECK (1968). Ground dwelling beetles are found to be a very diverse group in family richness also in other parts of the tropics (DAMMERMAN 1925, HAMMOND 1990, WILLIAMS 1941) as well as in temperate forests (ELLENBERG et al. 1986, FRIEBE 1983). For example, the latter author found 40 families in soil and litter of a beech forest applying hand sorting and photo eclectors which is very similar to our findings in the primary forest (36 families). SCHUBART & BECK (1968) applying hand sampling and Berlese extractions recorded in the organic layers of terra firme forests and floodplain forests rather similar numbers (27 and 29, respectively).

The Staphylinidae, Ptiliidae, Pselaphidae, Carabidae and Scydmaenidae were among the most dominant families. These results support the findings of ADIS (1982), ADIS & RIBEIRO (1989), FRIEBE (1984), DIDHAM (1998), DIDHAM et al. (1998a, 1998b), SCHUBART & BECK (1968), as well as ADIS (2000). Additionally, as in SCHUBART & BECK 's samples the xylophagous Scolytidae were dominant in all our four plots, corresponding to the high quantity of dead wood. Of lesser importance but nevertheless among the most dominant families, they mentioned also the Tenebrionidae and Curculionidae. Also among the forest soil beetle fauna of the Barro Colorado Island, Panama, the first four families mentioned above dominated (WILLIAMS 1941). Most other families were uncommon. A very high proportion of the total abundance and biomass may be concentrated on a few families, of which some such as the Staphylinidae are very rich in species (see also DIDHAM et al. 1998a, b).

In total, the biomass of the Berlese beetle fauna was low, although abundance and frequency was high. This might be related to the high proportion of species of very small to small body sizes (see also DIDHAM et al. 1998a). The causes of this phenomenon, which was found also in spiders and Diplopoda (HÖFER et al. 2000), is still unknown. Previous evaluations of the ground beetle fauna in western Amazonia (HANAGARTH 1981) indicated, that the Carabidae assemblages had similar body size ranges compared to that in Central European environments, but the proportion of very small and small species (<3.5 mm) was higher in the tropical site.

Applying the macrofauna definition (>2 mm body length) of VAN DER DRIFT (1951) and the Tropical Soil Biology and Fertility Programme (LAVELLE & PASHANASI 1989, ANDERSON & INGRAM 1993) the greatest proportion of the ground dwelling beetles would be part of the mesofauna (<2 mm) (VAN DER DRIFT 1951). Therefore, there are large differences between the abundance of macrofauna collected with handsorting methods (e.g. TAPIA-CORAL et al. 1999, LAVELLE & PASHANASI 1989) and with the Berlese-Tullgren method (e.g. HÖFER et al. 2000) or the similar Kempson method (ADIS 2000). Handsorting methods only take a small spectrum of the beetle fauna. The efficiency of handsorting methods for macrofauna was studied by FRANKE et al. (1988) in a German beech forest. Over 67 % of the important groups of the macrofauna were recorded. The authors applied an efficiency value for the estimation of the total abundance.

The Berlese-Tullgren extraction and the Kempson extraction method may offer the most representative results for beetles of very small and medium body size, but there are doubts if the abundance, species richness and especially the biomass of large species may be approximately realistically estimated. There are indications based on the comparison with results obtained with handsorting methods, pitfall traps and other methods applied in western Amazonia (HANAGARTH 1981) and in a German beech forest (BECK et al. 1998), that the importance of large highly mobile ground species may be underestimated even by handsorting methods (BECK pers. com.). Taking into account the small body size of many species data gained with handsorting methods present only a small spectrum of the beetle fauna. This is shown also by unpublished data of our SHIFT project (HÖFER et al. 2000) and may explain the low abundances of beetles presented in other publications (e.g. TAPIA-CORAL et al. 1999). As in the case of the ants and termites, the abundance and biomass of large beetles is surely underestimated.

In sum, the presented results are a first approach to understand the functional diversity of ground dwelling beetles in Amazon forest systems. Compared to other arthropod taxons, ground-dwelling beetles contribute to a large part of the soil arthropod biodiversity, but may play a minor role as predators and decomposers.

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4. Literature

ADIS. J. (1982): Zur Besiedlung zentralamazonischer Überschwemmungswälder (Varzea-Gebiet) durch Carabiden (Coeloptera). – Arch. Hydrobiol. **95**: 3-15.

ADIS, J. (2000): Terrestrial arthropods in soils from inundation forests and deforested floodplains of white water rivers in Central Amazonia. – In: JUNK, W. J., OHLY, J. J., PIEDADE, M. T. F., SOARES, M. G. M. (eds.): The Central Amazon Floodplain: Actual Use and Options for a Sustainable Management: 464-476; Leiden (Backhuys Publishers).

ADIS, J., MORAES, J. W. DE & RIBEIRO, E. F. (1987a): Vertical distribution and abundance of arthropods in the soil of a neotropical secundary forest during the dry season. – Stud. Neotrop. Fauna Environm., **22** (4): 174-181.

ADIS, J., MORAES, J. W. DE & GUIMARÃES DE MESQUITA, H. (1987b): Vertical distribution and abundance of arthropods in the soil of a neotropical secondary forest during the rainy season. – Stud. Neotrop. Fauna Environm., **22** (4): 189-197.

ADIS, J. & RIBEIRO, M. O. A. (1989): Impact of deforestation on soil invertebrates from Central Amazonia inundation forests and their survival strategies to long-term flooding. – Water Quality Bulletin, **14** (2): 88-98 & 104.

ANDERSON, J. M. & INGRAM, J. (1993): Tropical soil biology and fertility: A handbook of methods. – 2nd. Edition, 221 pp.; Oxford (CAB).

ARNETT, R. H. (1993): American insects, a handbook of the insects of America north of Mexico. – Gainesville (The Sandhill Crane Press).

BANDEIRA, A. G. & HARADA, A. Y. (1991): Cupins e Formigas da Amazônia. – In: VAL, A. L., FIGLIUOLO, R. & FELDBERG, E. (eds.): Bases Científicas para Estratégias de Preservação e Desenvolvimento da Amazônia: Fatos e Perspectivas, Vol. 1: 387-395; Manaus, Brazil (Instituto Nacional de Pesquisas da Amazônia, INPA).

BANDEIRA, A. G. & HARADA, A. Y. (1998): Densidade e distribução vertical de macroinvertebrados em solos argilosos e arenosos na Amazônia central. – Acta Amazônica, **28** (2): 191-204.

BECK, L. (1963): Zur Ökologie und Taxonomie der neotropischen Bodentiere I. Zur Oribatiden-Fauna Perus. – Zool. Jb. Syst., **90**: 299-392.

BECK, L. (1972): Der Einfluss der jahresperiodischen Überflutungen auf den Massenwechsel der Bodenarthropoden im zentralamazonischen Regenwaldgebiet. – Pedobiologia, **12**: 133-148.

BECK, L. (1976): Zum Massenwechsel der Makro-Arthropodenfauna des Bodens in Überschwemmungswäldern des zentralen Amazonasgebietes. – Amazoniana, **6** (1): 1-20.

BECK, L., HÖFER, H., MARTIUS, C., GARCIA, M., FRANKLIN, E. & RÖMBKE, J. (1998): Soil fauna and litter decomposition in primary and secondary forests and a polyculture system in Amazonia – study design and methodology. – SHIFT Workshop (Manaus). Proceedings III Workshop SHIFT, Manaus, Brazil, 15.-19.3.1998: 463-469; Bonn (BMBF).

BELL, R. T. (1990): Insecta: Coleoptera, Carabidae, Adults and Larvae. – In: DINDAL, D. L. (ed.) Soil Biology Guide. Chap. 38: 1053-1092; New York, Toronto (John Wiley & Sons).

BORROR, D. J., LONG, D. M. DE & TRIPLEHORN, C. A. (1981): An introduction to the study of insects. – 5. Edition; Philadelphia (Saunders College Publ.).

BRASSE, D. (1975): Die Arthropodenfauna von Getreidefeldern auf unterschiedlichen Böden im Braunschweiger Raum. – Pedobiologia, **15**: 405-414.

DAMMERMANN, K. W. (1925): First contribution to a study of the tropical soil and surface fauna. – Treubia, **6**: 107-139.

DECAËNS, T., LAVELLE, P JIMENEZ JAEN, J. J., ESCOBAR, G. & RIPPSTEIN, G. (1994): Impact of land management on soil macrofauna in the Oriental Llanos of Colombia. – Eur. J. Soil. Biol., **30** (4): 157-168.

DELVARE, G. & ABERLENC, H. P (1989): Les insects D'Afrique et d'Amérique tropicale – clés pour la reconnaissance des familles. –Montpellier, France (Cirad-Gerdat).

DIDHAM, R.K. (1998) Altered leaf-litter decomposition rates in tropical forest fragments. – Oecologia, **116**: 397-406.

DIDHAM, R. K, HAMMOND, P. M. & LAWTON, J. H. (1998a): Beetle species responses to tropical forest fragmentation. – Ecol. Monogr., **68**: 295-323.

DIDHAM, R. K., LAWTON, J. H., HAMMOND, P. M. & EGGLETON, P. (1998b): Trophic structure and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. – Phil. Trans. R. Soc. Lond. B, **353**: 437-451.

DRIFT, J. VAN DER (1951): Analysis of the animal community in a beach forest floor. – Tijdschr. Entomol., **94**: 1-118.

DUNGER, W. (1964): Tiere im Boden. – Neue Brehm-Bücherei, **327**; Wittemberg-Lutherstadt (A. Ziemsen).

DUNGER, W. & FIEDLER, H. J. (1989): Methoden der Bodenbiologie. – 432 pp.; Stuttgar (G. Fischer-Verlag).

ELLENBERG, H., MAYER, R. & SCHAUERMANN, J. (1986): Ökosystemforschung – Ergebnisse des Sollingprojektes 1966 – 1986. – 507 pp.;Stuttgart (Ulmer).

ERWIN, T.L. (1982): Tropical forests: their richness in Coleoptera and other arthropod species. – Coleopterists Bulletin, **36**: 74-75.

ERWIN, T.L. (1984): Small terrestrial ground-beetles of the Amazon Basin (Coleoptera: Bembidiini: Tachyina and Anillina). – Amazoniana, **8** (4): 511-518.

FAO-UNESCO (1990): Soil Map of the World, Revised Legend: Food and Agriculture Organization of the United Nations, Rome.

FRANKE, U., FRIEBE, B. & BECK, L. (1988): Methodisches zur Ermittlung der Siedlungsdichte von Bodentieren aus Quadratproben und Barberfallen. – Pedobiologia, **32**: 253-264.

FREUDE, H., HARDE, K. W. & LOHSE, G. A. (1965-1983): Die Käfer Mitteleuropas. – Vol. 1-11; Krefeld (Goecke & Evers).

FRIEBE, B. (1983): Zur Biologie eines Buchenwaldbodens. 3. Die Käferfauna. – Carolinea, **41**: 45-80.

FRIEBE, B. (1984): Vergleichende Betrachtungen zur Käferbesiedlung von Weisswasser- und Schwarzwasserüberschwemmungswäldern (Várzea, Igapó) Zentral-Amazoniens. – Biogeographica, **19**: 101-109.

HAMMOND, P.M. (1990): Insect abundance and diversity in the Dumoga-Bone National Park, n. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. – In: KNIGHT, W. J. & HOLLOWAY, J. D. (eds.): Insects and the rain forests of the south east Asia (Wallacea): 197-254. London (The Royal Entomological Society)

HANAGARTH, W. (1981): Vergleichend-ökologische Untersuchungen an epigäischen Arthropoden aus Naturbiotopen und Kulturland im tropischen Regenwald Perus. Ein Beitrag zur Agrarökologie der Tropen. – 240 pp.; Dissertation, Universität Hamburg.

HARADA, A. Y. & BANDEIRA, A. G. (1994): Estratificação e densidade de invertebrados em solo arenoso sob floresta primária e plantios arbóreos na Amazônia central a estação seca. – Acta Amazônica **24** (1/2): 103-118.

HÖFER, H., MARTIUS, C. & BECK, L. (1996): Decomposition in an Amazonian rain forest after experiment litter addition in small plots. – Pedobiologia, **40**: 570-576.

HÖFER, H., MARTIUS, C., HANAGARTH, W., GARCIA, M., FRANKLIN, E., RÖMBKE, J. & BECK, L. (2000): Soil fauna and litter decomposition in primary and secondary forests and a mixed culture system in Amazonia. – Final report of SHIFT project ENV 52: 299 pp.; Bonn (BMBF).

HÖFER, H., HANAGARTH, W., GARCIA, M., MARTIUS, C., FRANKLIN, E., RÖMBKE, J. & BECK, L. (2001): Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems. – Eur. J. Soil Biol. (in press).

HOUSE, G. J. & PARMELEE, R. W. (1985): Comparison of soil arthropods and earthworms from conventional and no-tillage agroecosystems. – Soil Till. Res., **5**: 351-360.

JACOBS, W. & RENNER, M. (1988): Biologie und Ökologie der Insekten. – 690 pp.; Stuttgart (G. Fischer)

LAVELLE, P. & PASHANASI, B. (1989): Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). – Pedobiologia, **33**: 283-291.

LAVELLE, P., DANGERFIELD, M., FRAGOSO, C., ESCHENBRENNER, V., LOPEZ-HERNANDEZ, D., PASHANASI, B. & BRUSSARD, L. (1994): The relationship between soil macrofauna and tropical soil fertility. – In: WOOMER, P L. & SWIFT, M. J. (eds.): The Biological Management of Tropical Soil Fertility. TSBF, Wiley-Sayce.

MARTIUS, C. (1994): Diversity and ecology of termites (Isoptera) in Amazonian forests. – Pedobiologia, **38**: 407-428.

NEWTON, A.F. Jr. (1990): Insecta:Coleoptera Staphylinidae, Adults and Larvae. – In: DINDAL, D.L. (eds.): Soil Biology Guide. Chap. 38: 1137-1174; New York, Toronto (John Wiley & Son),.

PREISINGER, H., COELHO, L. F., SIQUEIRA, S. G. DO M. & LIEBEREI, R. (1994): Analysis of growth form types and floristic composition of the spontaneous vegetation in an agricultural test area near Manaus, Amazonas, Brazil. – Angew. Botanik, **68**: 40-46.

PREISINGER, H., GILVAN, G. C. & COELHO, L. F. (2000): Structural traits of an eight year old secondary forest in the Central Amazon. – Poster, Program and Abstracts, German-Brazilian Workshop on Neotropical Ecosystems, SHIFT-WAVES, Hamburg.

RÖMBKE, J., HÖFER, H., MARTIUS, C., FÖRSTER, B., GARCIA, M., FRANKLIN, E. & BECK, L. (1999): Die Rolle der Bodenfauna beim Streuabbau in Primär- und Sekundärwäldern und einer Holz-Mischkulturfläche in Amazonien (SHIFT Projekt ENV 52): Methodische Überlegungen. – In: OEHLMANN, J. & MARKERT, B. (eds.): Ökotoxikologie: Ökosystemare Ansätze und Methoden: 268-275; Landsberg (ecomed).

SCHAEFER, M. (1974): Auswirkung natürlicher und experimenteller Störungen in Grenzzonen von Ökosystemen untersucht am Beispiel der epigäischen Arthropodenfauna. Pedobiologia, **14**: 51-60.

SCHUBART, H. & BECK, L. (1968): Zur Coleopterenfauna amazonischer Böden. – Amazoniana, **1** (4): 311-322.

SKATULLA, M., COELHO, L. F., GOTTSBERGER, G., LIEBEREI, R. & PREISINGER, H. (2000): Structural traits and regeneration mechanisms in three successional stages of Terra-Firme-forest in the Central Amazon. – Poster, Program and Abstracts, German-Brazilian Workshop on Neotropical Ecosystems, SHIFT-WAVES, Hamburg.

SOUTHWOOD, T R. E. (1966): Ecological Methods. – 391 pp.; London (Chapman and Hall).

TAPIA-CORAL, S. C., LUIZÃO, F. J. & WANDELLI, E. V. (1999): Macrofauna da liteira em sistemas agroflorestais sobre pastagens abandonadas na Amazônia central. – Acta Amazônica, **29** (3): 477-495.

THIELE, H. U. (1977): Carabid Beetles in Their Environments. A Study of Habitat Selection by Adaptations in Physiology and Behaviour. – 369 pp.; Berlin (Springer-Verlag).

VANICEK, M., ADIS, J. & PAARMANN, W. (1994): Untersuchungen zur Biologie dreier Laufkäferarten (Coleoptera, Carabidae, Harpalini) aus amazonischen Regenwäldern. – Andrias, **13**: 161-168.

VOHLAND, K. & SCHROTH, G. (1999): Distribution patterns of the litter macrofauna in agroforestry and monoculture plantations in central Amazonia as affected by plant species and management. – Appl. Soil Ecol., **13**: 57-68.

WILLIAMS, E. C. (1941): An ecological study of the floor fauna of the Panama rain forest. – Bull. Chicago Acad. Sc., **6**: 63-124.

ZAHRADNIK, J. (1985): Käfer Mittel- und Nordeuropas. – Hamburg, Berlin (Paul Parey).

Appendix. Body lengths (mm) of litter and soil beetle families, based on 480 Berlese samples from four sites (FLO, SEC, POA and POC).

Trophic group/ taxon	Individuals	Min.	Max.	Mean
Predators				
Carabidae	474	0.9	11.5	1.7
Dytiscidae	6	1.4	3.8	2.1
Histeridae	11	1.8	3.9	2.3
Pselaphidae	215	0.8	3.3	1.5
Scydmaenidae	606	0.4	13.0	1.1
Staphylinidae	566	0.4	42.0	3.0
Decomposers				
Anthicidae	7	1.4	2.1	1.8
Bostrichidae	1	2.3	2.3	2.3
Byrrhidae	8	1.4	1.9	1.7
Cerylidae	1	1.4	1.4	1.4
Clambidae	1	1.1	1.1	1.1
Colydiidae	29	1.0	6.3	1.7
Corylophidae	11	0.7	1.8	1.2
Cucujidae	6	1.0	1.8	1.4
Curculionidae	31	1.4	5.0	2.9
Elmidae	9	1.1	2.1	1.9
Endomychidae	6	1.1	9.3	2.6
Erotylidae	1	1.2	1.2	1.2
Hydrophilidae	4	1.6	3.4	2.5
Lagriidae	1	0.9	0.9	0.9
Languriidae	2	1.5	2.5	2.0
Lathridiidae	9	1.3	1.5	1.5
Leiodidae	125	0.9	2.3	1.4
Mordellidae	3	1.3	2.8	2.2
Mycetophagidae	1	1.6	1.6	1.6
Nitidulidae	14	1.6	4.3	2.7
Platypodidae	33	2.2	4.3	3.2
Ptiliidae	636	0.5	4.8	0.8
Rhizophagidae	2	1.8	1.8	1.8
Salpingidae	1	1.2	1.2	1.2
Scaphidiidae	6	1.1	2.2	1.7
Scarabaeidae	25	2.1	14.0	4.9
Scolytidae	694	0.7	2.7	2.0
Sphaeridae	1	1.9	1.9	1.9
Tenebrionidae	29	1.2	6.6	2.6
Herbivors				
Chrysomelidae	14	1.4	3.5	2.2
Others				
Aderidae	1	1.9	1.9	1.9
Cholevidae	5	1.8	2.1	1.9
Dasyceridae	1	0.4	0.4	0.4
Euglenidae	1	3.9	3.9	3.9
Heteroceridae	3	2.3	2.6	2.5
Laemophloidae	1	1.8	1.8	1.8
Lyctidae	1	2.3	2.3	2.3
Notiopygidae	1	2.5	2.5	2.5
Scirtidae	2	1.7	2.5	2.1
Silvaniidae	1	2.0	2.0	2.0
Troscidae	1	2.1	2.1	2.1
Unclassified Larvae	22	0.4	3.5	1.1
all families	1655	0.5	38.0	2.7