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Species diversity of Enchytraeidae (Oligochaeta) in pastures, regenerating secondary forests, and old-growth forests in the southern Mata Atlântica (Brazil)

Jörg Römbke[1]*, Rut Collado[2], Hubert Höfer[3], Richard Ottermanns[4], Florian Raub[3], Martina Ross-Nickoll[4] and Rüdiger M. Schmelz[1,2]

[1] ECT Oekotoxikologie GmbH, Böttgerstr. 2-14, 61435 Flörsheim, Germany
[2] Department of Animal Biology, Plant Biology and Ecology, University of A Coruña, Alejandro da Sota, 1, 15008 A Coruña, Spain
[3] Staatliches Museum für Naturkunde Karlsruhe, Erbprinzenstr. 13, 76133 Karlsruhe, Germany
[4] Institute for Environmental Research, RWTH Aachen University, Worringerweg 1, 52074 Aachen, Germany
* Corresponding author, e-mail: j-roembke@ect.de

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Abstract

In the framework of the German-Brazilian project SOLOBIOMA ('Soil biota and biogeochemistry in the Southern Atlantic rainforests of Brazil'), soil invertebrates were sampled in different regeneration stages of forest: pastures, young, medium and advanced secondary forests as well as old-growth forests. Thirty-nine study sites were located in two private nature reserves situated in neighbouring regions of the southern Atlantic Forest (Mata Atlântica) in Paraná, Brazil. All sites were characterized in terms of climate, history of use (age), vegetation, and soil properties. Here we report on the species diversity of pot worms (Oligochaeta: Enchytraeidae) in these sites, sampled with ISO standard methods. At each site ten soil cores of 5.7 cm diameter were taken once between 2003 and 2008, wet extracted and all pot worms identified alive soon after sampling. Most of the 61 species found in this study were new to science. The enchytraeid fauna of the region is dominated by species of the genera *Achaeta*, *Guaranidrilus* and *Hemienchytraeus*. To date, six species of the genus Achaeta, three species of the new genus *Xetadrilus* and four species of the species-rich genus Guaranidrilus were described by some of the authors. The terrestrial enchytraeid fauna of Paraná is composed partly of (probably) endemic species (e.g. *Achaeta paranensis*), partly of species with a known wider distribution within South America (e.g. *Hemienchytraeus patricii*). Species-poor genera are *Fridericia*, *Enchytraeus* and *Marionina*. On average, enchytraeid abundance was low (i.e. less than 5000 ind m^{-2}). Highest abundance was found in old-growth forests. Species assemblages respond to soil type and vegetation type, and some preferences at the species or genus level could be identified. Due to their small size, low abundance and resulting low biomass enchytraeid worms seem to have little ecological importance in terms of energy flux and nutrient turnover, especially when compared with earthworms. However, due to their species richness they may be useful to indicate the biological status of a site in terms of biological soil quality or perturbation.

Keywords Pot worms | abundance | Parana | forest regeneration | soil fauna

1. Introduction

Enchytraeidae are known to be an important group of soil invertebrates in temperate regions of the world, but almost nothing is known about their biology and ecology in the humid tropics. Only recently, the available information increased considerably and particularly in Brazil, by a number of publications, including species descriptions from this country (for an overview see Schmelz et al. 2013). However, knowledge of the enchytraeid fauna of the Atlantic Rainforest (Mata Atlântica) – a worldwide recognized 'hotspot of

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biodiversity' (Myers et al. 2000) – is still scarce. The German-Brazilian cooperative project SOLOBIOMA (Höfer et al. 2007, Schmidt et al. 2008, Römbke et al. 2009, Höfer et al. 2011) aimed to assess the ecosystem quality of secondary forests in the coastal region of Paraná and especially their potential for conservation of biodiversity and the related ecosystem services. For this purpose several biota relevant for soil processes were investigated: plants (Liebsch et al. 2007), ants (Bihn et al. 2008), beetles (Hopp et al. 2010, Ottermanns et al. 2011), spiders (Raub et al. 2014) and earthworms (Römbke et al. 2009). Objectives of the enchytraeid studies in this project were (1) to get knowledge of the diversity of enchytraeid assemblages in the southern Mata Atlântica, (2) to assess the potential and mode of recovery of the enchytraeid fauna during the regeneration of forests

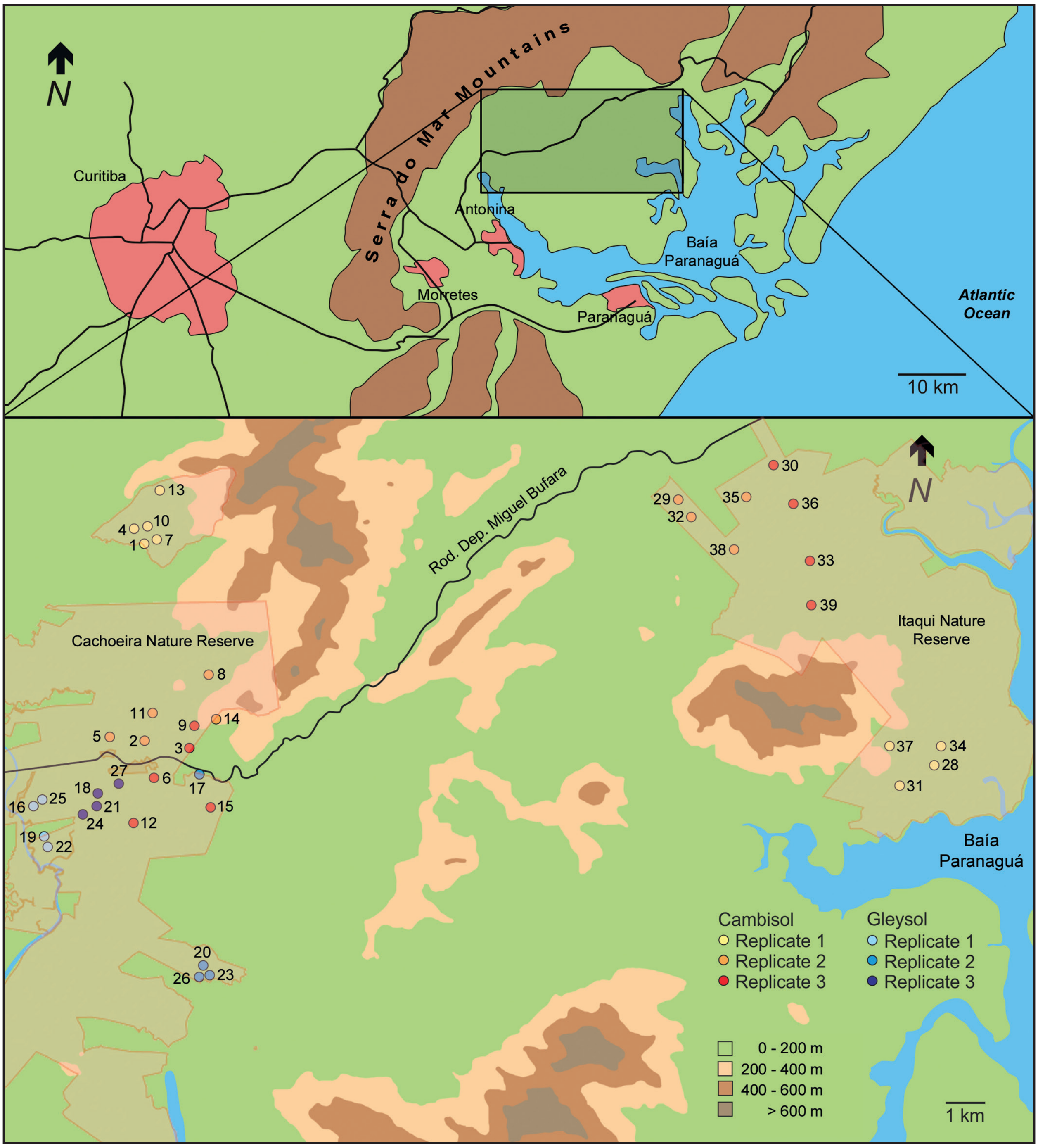


Figure 1: Location of the study sites in the two reserves or areas (Cachoeira, Itaqui) in the coastal plain region of Paraná state, Brazil. Numbers refer to the site numbers in Table 1.

from abandoned pastures, and (3) to identify the site properties (e.g., soil type, land use history, vegetation) that determine abundance and diversity of enchytraeids. Some information on total enchytraeid abundance and their indicative potential in the Atlantic Rainforest has already been published (Römbke et al. 2007, Schmelz et al. 2009). In addition, twelve new species have been described, five of *Achaeta*, four of *Guaranidrilus*, and three of the new genus *Xetadrilus* (Schmelz et al. 2008, 2011). In this contribution, the species composition of the enchytraeid assemblages of secondary forests of different age is compared to that of pastures and old-growth forests.

2. Materials and methods

2.1. Study sites

The study sites were located within an area of about 30 × 80 km^2, along the coast of Paraná, in two private reserves situated in the municipalities of Antonina and Guaraqueçaba, within the Environmental Protection Area (EPA) of Guaraqueçaba (Ferretti & Britez, 2006) (Fig. 1). Climate of this coastal region of Paraná is mesothermic subtropical humid, corresponding to Köppen's Cfa-type (Schröder 2000, Strahler & Strahler 2005). Mean annual temperature varies between 20 and 22°C, mean annual precipitation around 2545 mm (Roderjan & Kunyoshi 1988), both presenting seasonality. Lower rainfall occurs from the end of autumn to winter (April to August), higher rainfall during the warmer Brazilian summer (September to March) (IPARDES 2001). The submountain forests in the region are found mostly on slightly inclined hillsides and stock on soils originating from neo-precambric acid rocks. Depending on the soil developmental conditions and groundwater influence, Entisols ('Neossolos litólicos'), Cambisols, Ultisols ('Argissolos') and Gleysols occur. For this study only sites on well-drained Cambisols and Gleysols were selected (Soil World Reference Base, FAO 1998). These are characterized by low pH (3.5–4.3 ($CaCl_2$), under pastures sometimes reaching 5.0), C/N-ratios of 15–40 and organic matter contents of 2–5% in the upper 20 cm of soil.

One group of study sites (Nos 1-27 in Tab. 1) was located within the 'Reserva Natural do Rio Cachoeira' (herein called Cachoeira (CA); 25.3142°S, 48.6958°W). Here, pastures and secondary forests were found on the two most frequent soil types: on Cambisol (Nos 1-15) and Gleysol (Nos 16-27), but old-growth forest only on Cambisol. The successional gradient from pastures to forest was categorized into four regeneration stages, following Liebsch et al. (2007): pastures (P in the following), young herbaceous stage (H), young arboreal stage (A), medium old arboreal stage (M). Three replicate sites for each stage of secondary forest on each soil type were selected, plus three replicates of old-growth forest (F) on Cambisol, resulting in a total of 27 study sites (Tabs 1, 2). The second group of sampling sites (Nos 28-39) was located approximately 30 km to the east, within the 'Reserva Natural do Itaqui' (herein called Itaqui (IT); 25.2733°S, 48.4872°W). Here, secondary forests of the three regeneration stages and old-growth forests on Cambisols were found and 12 sites selected (Tabs 1, 2).

These 39 sites within the submountain forest range represent the natural regeneration process starting from buffalo pastures, which were abandoned in different years, creating mosaic-like distributed patches of forest differing in age since abandonment of use (from 0 to > 100 years). The regeneration stages may also represent a gradient of decreasing anthropogenic influence (disturbance). All sites are owned and administrated by the Brazilian NGO 'Society for Wildlife Research and Environmental Education' (SPVS).

2.2. Sampling of enchytraeids

At each of the 39 sites (Tab. 2), Enchytraeidae were sampled once, taking ten soil core samples (diameter 6.4 cm) during six sampling campaigns between 2003 and 2008 (always in spring or autumn), following the ISO standard (ISO 2006). For practical reasons the cores were subdivided into litter or root layer (thickness 1–4 cm) and mineral layer (4 cm depth), and the layers were stored separately. Samples were transported to the laboratory and kept in a refrigerator until further processing, not longer than one month. Worms were extracted using a cold/wet extraction method according to the standard ISO guideline (2006); extraction time was 1–2 days (litter layer) and 3–4 days (mineral soil). Numbers of extracted animals from the two layers were aggregated to one sample. Individuals per sample were counted and abundance per square meter (ind m^{-2})was calculated multiplying the numbers by the factor of 311).

2.3. Species determination

Worms were inspected with a dissecting microscope and a compound microscope at the Department of Soils and Agricultural Engineering, Federal University of Paraná (UFPR), Section Agrosciences, Curitiba. Light-microscopical identification of specimens included a careful morphological inspection of each specimen, because of the lack of identification literature and the

Table 1. Location, site characteristics and coordinates of the 39 sampling sites (see also Fig. 1), (P – Pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest).

Site nr.	Municipality	Area	Stage	Soil	Vegetation Stage	Age (2003)	Altitude m a.s.l.	UTM coordinates (SAD69)	
								Easting	Northing
1	Antonina	Cachoeira	pasture	Cambisol	P	0–2	30	734334	7204529
2	Antonina	Cachoeira	pasture	Cambisol	P	0–2	70	734238	7199013
3	Antonina	Cachoeira	pasture	Cambisol	P	0–2	50	735508	7198781
4	Antonina	Cachoeira	forest	Cambisol	H	5–8	40	734061	7204934
5	Antonina	Cachoeira	forest	Cambisol	H	5–8	70	733288	7199183
6	Antonina	Cachoeira	forest	Cambisol	H	5–8	30	734496	7197937
7	Antonina	Cachoeira	forest	Cambisol	A	10–15	40	734616	7204648
8	Antonina	Cachoeira	forest	Cambisol	A	10–15	90	736041	7200815
9	Antonina	Cachoeira	forest	Cambisol	A	10–15	150	735667	7199405
10	Antonina	Cachoeira	forest	Cambisol	M	35–50	60	734398	7204990
11	Antonina	Cachoeira	forest	Cambisol	M	35–50	120	734443	7199717
12	Antonina	Cachoeira	forest	Cambisol	M	35–50	120	733866	7196682
13	Antonina	Cachoeira	forest	Cambisol	F	> 100	140	734752	7206000
14	Antonina	Cachoeira	forest	Cambisol	F	> 100	260	736219	7199635
15	Antonina	Cachoeira	forest	Cambisol	F	> 100	90	736052	7197080
16	Antonina	Cachoeira	pasture	Gleysol	P	0–2	10	731087	7197204
17	Antonina	Cachoeira	pasture	Gleysol	P	0–2	20	735760	7198041
18	Antonina	Cachoeira	pasture	Gleysol	P	0–2	30	732899	7197464
19	Antonina	Cachoeira	forest	Gleysol	H	5–8	10	731383	7196323
20	Antonina	Cachoeira	forest	Gleysol	H	5–8	10	735777	7192646
21	Antonina	Cachoeira	forest	Gleysol	H	5–8	20	732881	7197245
22	Antonina	Cachoeira	forest	Gleysol	A	10–15	10	731445	7196189
23	Antonina	Cachoeira	forest	Gleysol	A	10–15	10	735922	7192419
24	Antonina	Cachoeira	forest	Gleysol	A	10–15	20	732514	7196985
25	Antonina	Cachoeira	forest	Gleysol	M	35–50	10	731297	7197343
26	Antonina	Cachoeira	forest	Gleysol	M	35–50	10	735748	7192354
27	Antonina	Cachoeira	forest	Gleysol	M	35–50	30	733457	7197827
28	Guaraqueçaba	Itaqui	forest	Cambisol	H	5–8	13	756475	7197916
29	Guaraqueçaba	Itaqui	forest	Cambisol	H	5–8	46	749433	7205484
30	Guaraqueçaba	Itaqui	forest	Cambisol	H	5–8	8	752108	7206406
31	Guaraqueçaba	Itaqui	forest	Cambisol	A	10–15	26	755490	7197369
32	Guaraqueçaba	Itaqui	forest	Cambisol	A	10–15	36	749752	7205013
33	Guaraqueçaba	Itaqui	forest	Cambisol	A	10–15	~20	753102	7203698
34	Guaraqueçaba	Itaqui	forest	Cambisol	M	35–50	28	756712	7198457
35	Guaraqueçaba	Itaqui	forest	Cambisol	M	35–50	27	751327	7205532
36	Guaraqueçaba	Itaqui	forest	Cambisol	M	35–50	8	752667	7205328
37	Guaraqueçaba	Itaqui	forest	Cambisol	F	> 100	93	755254	7198485
38	Guaraqueçaba	Itaqui	forest	Cambisol	F	> 100	31	750950	7204080
39	Guaraqueçaba	Itaqui	forest	Cambisol	F	> 100	20	753109	7202469

fact that most of the species found were new to science. Specimens were sorted into morphospecies labelled with informal codes (e.g., He2a, Ac01, etc.). A large proportion of identified worms was fixed in formaldehyde or heated Bouin's fluid, preserved in 70 % ethanol, and deposited in the collections of the Zoological Museum of the University of São Paulo (CA material) and at the Entomological Collection in the Zoological Department of the University of Curitiba (UFPR) (IT material). The material was loaned for reinvestigation at the University of A Coruña, Spain, where formal descriptions of species were prepared (Schmelz et al. 2008, 2011). In the following, species with codes but without names still await scrutiny and formal description.

2.4. Design and statistics

An unconstrained ordination analysis (CA) with all 39 sites and all species (61, including unidentified species lumped to one) was executed with CANOCO 5 (Ter Braak & Šmilauer 2012). To ordinate the 24 forest sites on Cambisol (Tab. 2) a NMDS based on a Bray-Curtis distance matrix with a solution based on 3 axes from 50 perturbations was executed with CANOCO 5. Inferential statistics could only be realized with data from the forest sites on Cambisol (core design, see Tab. 2), because pastures were not studied in Itaqui and on Gleysol no old-growth forest could be found for comparison. Analyses of variance were made for effects of area and stage on total abundance and species number per site, based on Generalized Linear Modelling (GLM, R statistical language, R Core Team, 2014). After testing for overdispersion [function dispersion test from the package AER (Kleiber & Zeileis 2008)], a negative binomial model was used for abundance data (function glm.nb), whereas a Poisson model was used for the number of species [in both cases by using the package MASS (Venables & Ripley 2002)]. Significances were calculated by likelihood ratio tests of models including both factors with interaction (function lrtest from package lmtest; Zeileis & Hothorn 2002), eventually dropping one of the factors to enhance the explained information of the model. GLMs were calculated with R (MASS package). The raw data used in this analysis as well as the dominance spectrum (see next subchapter) are provided in the Annexes 1–3, i.e. the number of enchytraeids per sample.

3. Results

3.1. Species number and composition

The total number of morphospecies so far distinguished is 61: 43 species were found in sites on Cambisol and 25 on Gleysol sites in Cachoeira, 46 species were found in Itaqui (Cambisol). In total, 39 species of the genus *Guaranidrilus* (only four of them named so far) could be distinguished, meaning that this was the most diverse genus in the whole study area. All other genera were represented by far less species (numbers in parentheses): *Hemienchytraeus* (9), *Achaeta* (6), *Xetadrilus* (5), *Fridericia* (2), *Tupidrilus* (1) and *Enchytraeus* (1). All these numbers have to be taken as preliminary, which is most obvious in the case of *Enchytraeus* sp., which is a still unresolved complex of species similar to *E. buchholzi* Vejd. and *E. bigeminus* Niels.& Christ., for convenience considered as one species in the following. Although taxonomic work is still in progress, formalised descriptions (including figures) are already available for all species and distinguishable forms. In addition, keys to genera and as well to species have been prepared. However, named species are still rare. In Tab. 3, these species, the original reference and notes about their geographical distribution are compiled.

Per site between 0 and 21 species were found. In Cachoeira, the mean number of species per site was 9.8 on Cambisol and 8.9 on Gleysol, but the difference is not significant. In Itaqui, the respective number (only

Table 2. Sampling design with number of replicates per area, soil type and stage: P – pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest. The sites of a balanced core design to evaluate the effect of stage and region on the assemblages on Cambisol are shaded.

Areas and soil types	Vegetation stages → increasing age and decreasing human impact →				
Itaqui	**P**	**H**	**A**	**M**	**F**
Cambisol	-	3	3	3	3
Cachoeira	**P**	**H**	**A**	**M**	**F**
Cambisol	3	3	3	3	3
Gleysol	3	3	3	3	-

Cambisol) was considerably higher: 13.4. All species occurring at the Gleysol sites in Cachoeira also occurred at the Cambisol sites. However, when comparing the fauna on Cambisol in Cachoeira and Itaqui, species composition differed: 14 species were exclusively found in Cachoeira and 17 species exclusively in Itaqui (i.e. about one third of all species in each region). The differentiating species mainly belong to the genus *Guaranidrilus*. However, with one exception ('GUA21' in Itaqui, see Annex 3) these species were not dominant.

Mean species number per site increased with the age of the forest on Cambisol, but not on Gleysol (Tab. 4). Variance analysis (GLM based on a Poisson model) showed a significant effect ($p = 0.018$) on the species number for area (i.e a difference between Cachoeira and Itaqui), whereas Spearman rank correlation revealed a significant increase in species number ($p = 0.017$) along the gradient of decreasing human impact on Cambisol in Itaqui.

3.2. Multivariate ordination of sites

The unconstrained ordination of all 39 sites by all species (including the collective species) showed a clear separation of the pastures on Gleysol from all other sites on the second axis (Fig. 2). Most of the other sites on Gleysol were also ordinated away from the sites on Cambisol on the second axis, but all close to the center of the first axis. In contrast, the sites on Cambisol showed a separation of the different stages along the first axis. Total variation was 3.76, of which 11.8 %

Table 3. List of named enchytraeid species found in the study region, with indications of their biogeographical distribution and occurrence in the study regions [Cachoeira (CA), Itaqui (IT)].

Species	Occurrence
Achaeta hanagarthi Schmelz, 2008	CA, IT
Achaeta neotropica Černosvitov, 1937	CA, IT, Brazil, Argentina, Mexico
Achaeta paranensis Schmelz, 2008	CA, IT
Achaeta piti Bittencourt, 1974	CA, IT, Brazil
Achaeta singularis Schmelz,. 2008	CA, IT
Guaranidrilus andreolii Schmelz, Collado & Römbke, 2011	CA, IT
Guaranidrilus cingulatus Schmelz, Collado & Römbke, 2011	CA, IT
Guaranidrilus hoeferi Schmelz, Collado & Römbke, 2011	CA, IT
Guaranidrilus marquesi Schmelz, Collado & Römbke, 2011	CA, IT
Hemienchytraeus patricii Schmelz & Römbke, 2005	CA, IT, Brazil
Hemienchytraeus tanjae Schmelz & Römbke, 2005	CA, IT, Brazil
Xetadrilus aphanus Schmelz, Collado & Römbke, 2011	CA, IT
Xetadrilus fabryi Schmelz, Collado & Römbke, 2011	CA
Xetadrilus maacki Schmelz, Collado & Römbke, 2011	CA, IT

Table 4. Mean (and min/max) number of species per site in the different areas, soils and stages (P – pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest).

Areas and soil types	Vegetation stages → increasing age and decreasing human impact →				
Itaqui	**P**	**H**	**A**	**M**	**F**
Cambisol	-	10 (7–13)	11 (8–14)	15 (9–19)	18 (17–21)
Cachoeira	**P**	**H**	**A**	**M**	**F**
Cambisol	7 (1–11)	8 (5– 2)	8 (4–12)	11 (4–16)	12 (5–20)
Gleysol	5 (4–5)	5 (2–9)	5 (1–8)	6 (1–13)	-

were explained by the first axis and further 8.2 % by the second axis.

For a better distinction of the sites on Cambisol a second ordination was done based on a nMDS (Fig. 3). The low stress value (0.12) means that the graphic ordination of the sites reflects the Bray-Curtis distances quite well. The first axis separates the younger from the older stages. The second axis shows unexplained variation within the stages. Whereas old-growth sites are well separated from the medium arboreal stage in Cachoeira, these two stages strongly overlap in Itaqui. The Itaqui M-sites are characterized by an assemblage typical of old-growth forests. Younger sites show a higher variability in species composition.

3.3. Abundance: total community and single species

Abundances of enchytraeids in the different stages are given in Fig. 4 for both areas, Cachoeira and Itaqui. On average, 1,600 ± 1,200 ind m^{-2} were found in Cachoeira on Gleysol, 2,500 ± 1,200 ind m^{-2} in Cachoeira on Cambisol, and 3,200 ± 1,000 ind m^{-2} in Itaqui on Cambisol. In a GLM analysis with negative binomial model, only the old-growth forest stage (F) differed from the youngest stage (H) ($p = 0.015$); area had no significant effect.

Numbers of individuals found per site (i.e. the sum of the ten soil cores taken per site) differed considerably: the minimum was 4 individuals, i.e. 124 ind m^{-2} (site

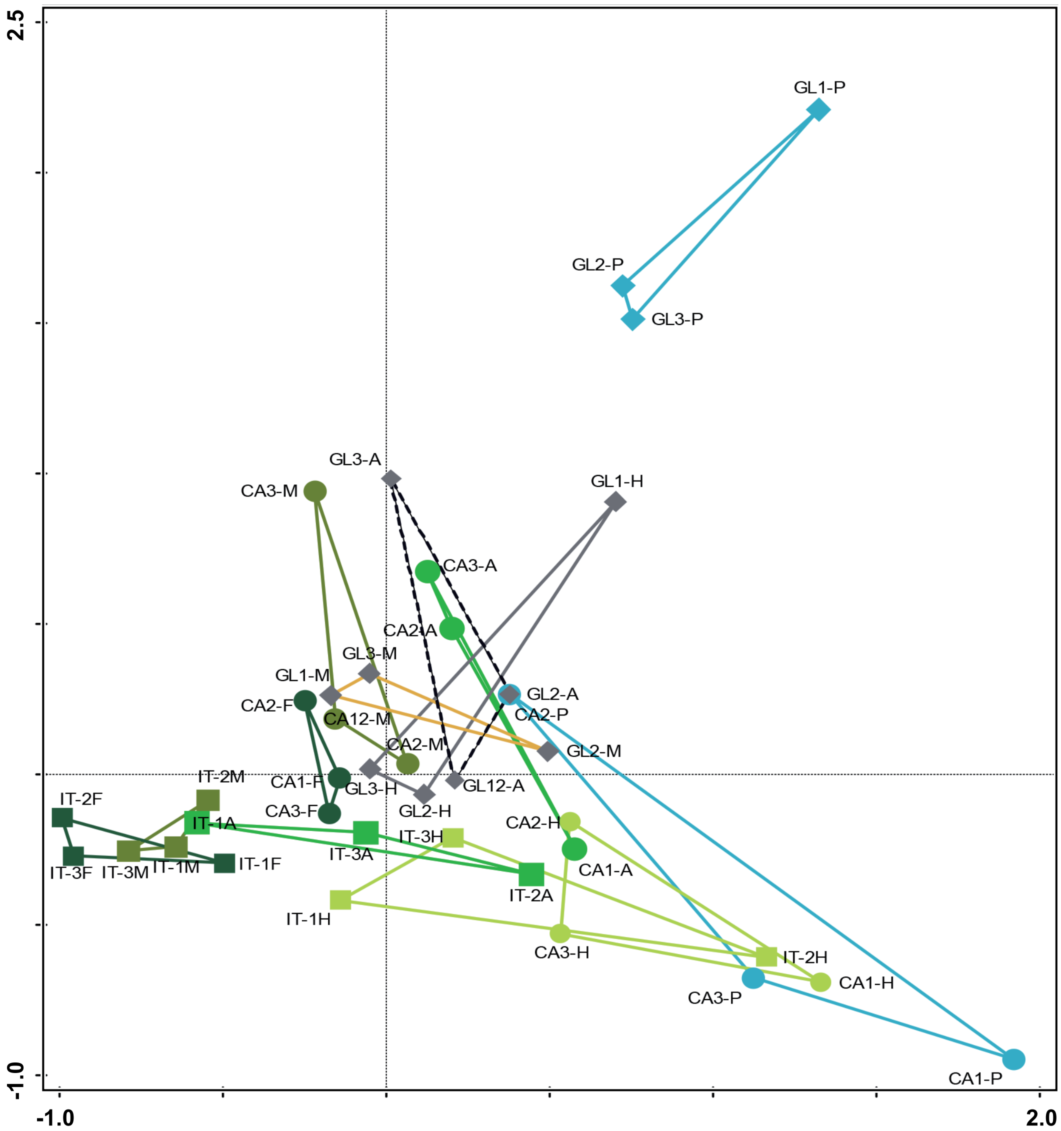


Figure 2. Ordination of all sites, based on a Correspondence Analysis (CA, unconstrained) with all 61 species. Total variation 3.76, eigenvalues 0.445 (axis 1), 0.309 (axis 2). Envelopes drawn on sites of the same category (stage, soil, area). Abbreviations: IT – Itaqui, CA – Cachoeira Cambisol sites, GL – Cachoeira Gleysol sites; 1-3 replicate number; P, H A, M, F for the stages (see Table 1).

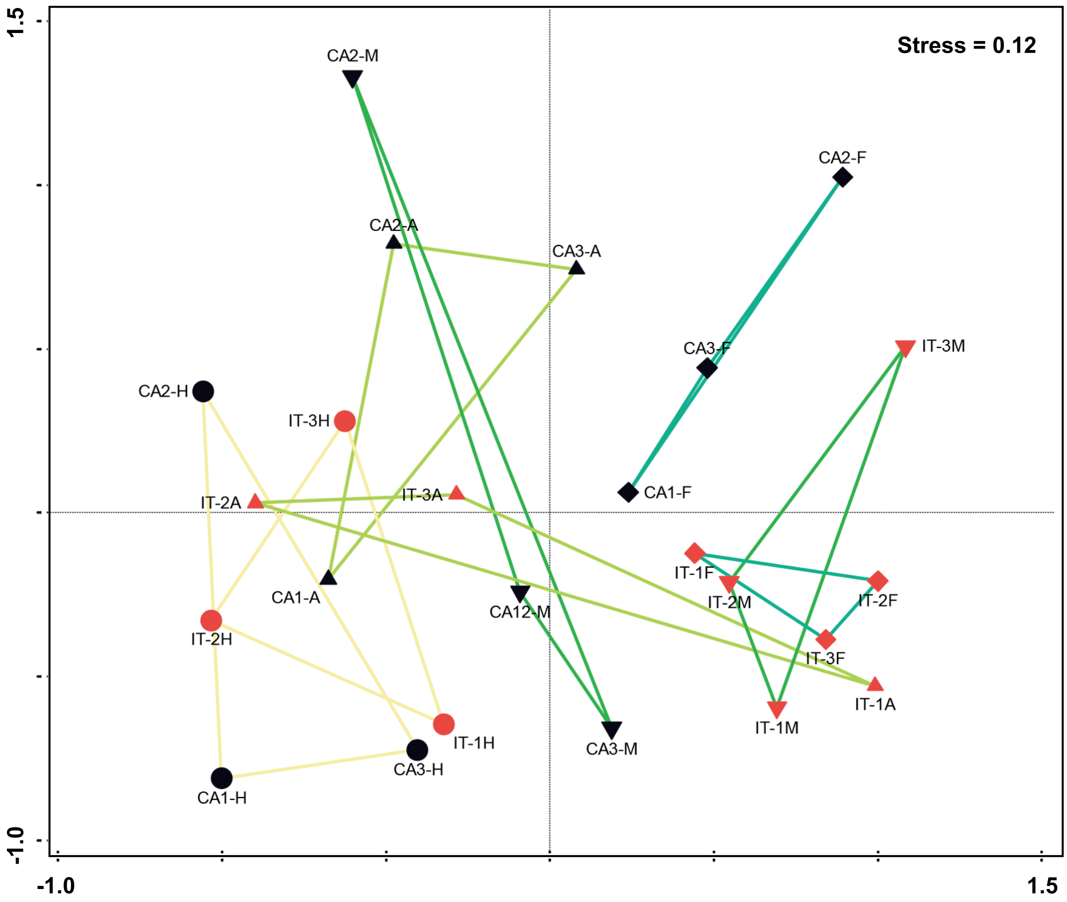


Figure 3. Ordination of sites on Cambisol, based on a nMDS analysis with Bray-Curtis distances. Abbreviations and envelopes as in Fig. 2.

GL2-A) and the maximum was 167 individuals, i.e. 5,194 ind m^{-2} (site IT2-M). Numbers per species differed as well: in most cases very few enchytraeids were found in one sample. An exceptional outlier were 58 specimens of *Enchytraeus* sp. found in one soil core (out of 10) at site CA1-P. Five species were represented with more than 5% of all individuals collected at all sites: *Achaeta hanagarthi* Schmelz, 2008, *Enchytraeus* sp., *Guaranidrilus marquesi* Schmelz, Collado & Römbke, 2011, *Hemienchytraeus patricii* Schmelz & Römbke, 2005, and *Hemienchytraeus tanjae* Schmelz & Römbke, 2005; these dominant species are considered in detail in Fig. 5A–E. The following patterns can be observed, indicating possible specific preferences of these species.

Regarding soil type, *A. hanagarthi*, *G. marquesi*, and *H. tanjae* seem to prefer Cambisol, since they were found rarely and/or in low numbers on Gleysol. *Enchytraeus* sp. and *H. patricii* did occur in both soil types. Regarding the stages, *G. marquesi* was not found in pastures, while *Enchytraeus* sp. reached the highest abundance of all enchytraeid species in pastures on Cambisol (about 1,000 ind m^{-2}). However, at the time of sampling there was no obvious relationship between soil properties (most likely: high amount of organic matter, (i.e. food) and the occurrence of *Enchytraeus* sp. was visible. The high

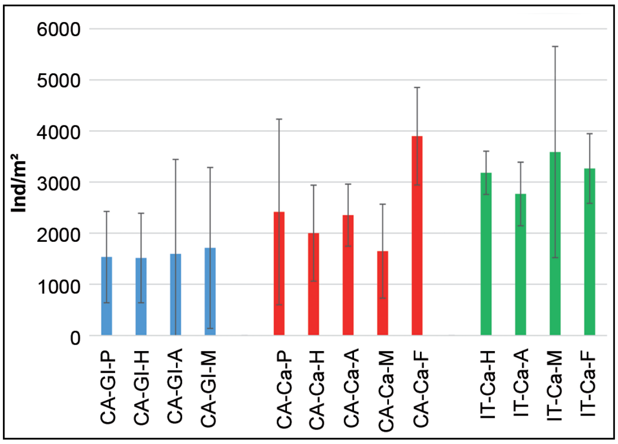
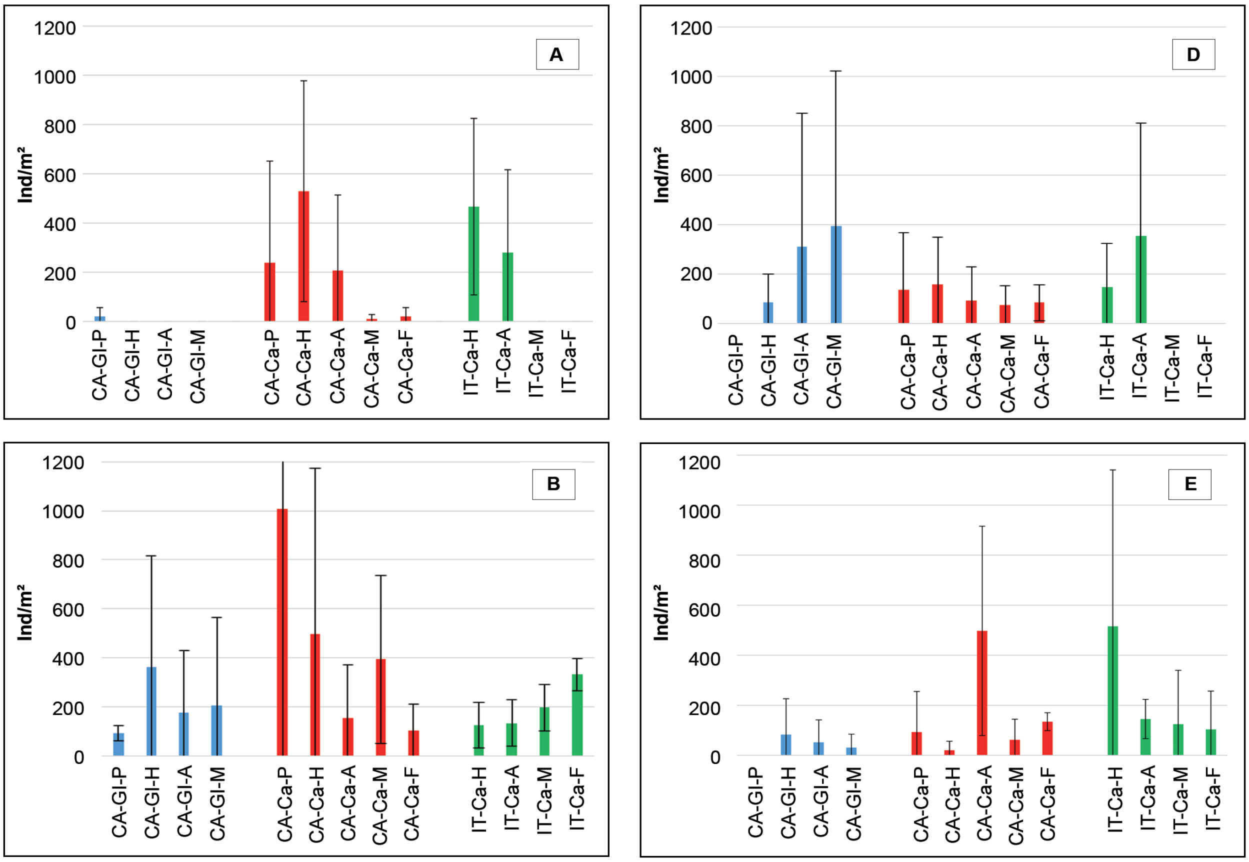


Figure 4. Mean enchytraeid abundance and standard deviation in the investigated combinations of region, soil type and vegetation stage. CA – Cachoeira, IT – Itaqui, Gl – Gleysol. Ca – Cambisol. P – pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest.

followed by *Guaranidrilus* sp. 31 (not known from outside Itaqui). In the next stage (A) the same species did occur in a more evenly distributed way, meaning that their abundances were mostly similar (only *A. neotropica* and *Guaranidrilus* sp. 31 were less often found). Almost the same percentage of seven species was observed in the M-stage; no other stage had such an even distribution of the most dominant species (only *A. hanagarthi* and *H. patricii* did not occur any more). The same seven species as in the M-stage did also dominate the oldest forst stage (F), but the individual percentages differed: especially in the case of *Guaranidrilus* sp. 3 and sp. 31 decreased, while those of *H. tanjae* and *G. marquesi* increased. In general, the dominance pattern at the older stages of Itaqui seems to be quite stable.

3.5. Other oligochaete taxa

While the focus of this contribution is on enchytraeids it should be noted that also a diverse and abundant naidid and tubificid fauna was found at many sampling sites, belonging mostly to species of the genera *Pristina* and *Bothrioneurum* (Naididae) (Römbke et al. 2007).



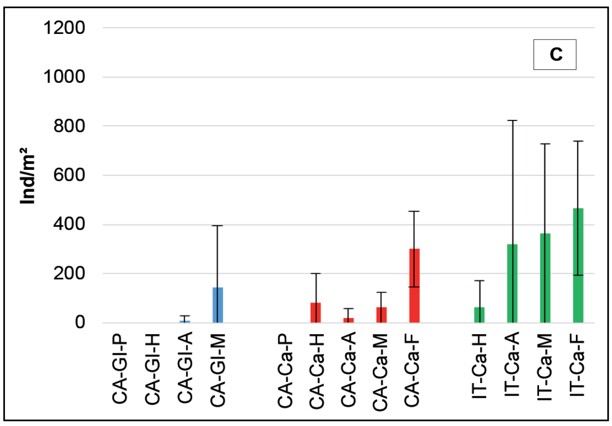


Figure 5A–E. Mean abundance and standard deviation of five dominant enchytraeid species (**A**: *Achaeta hanagarthi*; **B**: *Enchytraeus* sp.; **C**: *Guaranidrilus marquesi*; **D**: *Hemienchytraeus patricii*; **E**: *Hemienchytraeus tanjae; **D**: Hemienchytraeus patricii*; **E**: *Hemienchytraeus tanjae*) for the different categories (area, soil type, stage) (CA – Cachoeira. IT – Itaqui, Gl – Gleysol, Ca – Cambisol, P – pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest). Note that the standard deviation of the abundance of *Enchytraeus* sp. at one site (CA-Ca-P) is so high (+/- 1,609) that it is outside of the range of the figure.

variability in time and space is at least partly explainable by the fact that this (collective) species reproduces partly by fragmentation; i.e. it is much quicker than the other enchytraeid species. The other three species were found at pasture sites, but (with one small exception: *A. hanagarthi*) only on Cambisol. On the genus level, only *Achaeta* species were (almost) exclusively found in Cambisols.

When considering the four stages of forest regeneration, *A. hanagarthi* was found more often in the two young stages, both in Cachoeira and Itaqui. The same pattern, but less clear, is seen for *H. tanjae* – this species occurs rarely but regularly in older stages (M and F) in both regions. *G. marquesi* seems to prefer old forests, but while this is clear in Cachoeira its occurrence is less pronounced in Itaqui, i.e. this species does not really fit into the young/old differentiation. The same is true for *H. patricii*, since in Cachoeira it does occur in all stages in similar numbers but only in the young stages in Itaqui. Note that on Gleysol *H. patricii* mainly occurs in the older young and the younger old stages. No clear pattern is observed for *Enchytraeus* sp., which occurs in all stages of forest regeneration in both regions in comparable numbers. Summarising these results it seems that individual species have different ecological preferences, but soil type and vegetation stage alone are not sufficient to identify them clearly. This is at least partly caused by the high standard deviations, indicating considerable differences in enchytraeid numbers at the three sites belonging to each vegetation stage.

3.4. Dominance spectra of single species

In order to characterize each site category (area, soil type and stage) (see Tab. 2), the eudominant, dominant and subdominant species [i.e. those with > 3.2% abundance; (Engelmann 1978)] for these 13 combinations of area, soil type and vegetation stage were selected. In addition to the five species used in the previous chapter (*A. hanagarthi*, *Enchytraeus* sp., *G. marquesi*, *H. tanjae* and *H. patricii*) seven more species were considered: *Achaeta neotropica* Černosvitov, 1937, *Guaranidrilus hoeferi* Schmelz, Römbke & Collado, 2011, *Guaranidrilus* sp. 3, sp. 7, sp. 9, sp. 31, and *Hemienchytraeus* sp. 5.

The average species number per Gleysol site (Tab. 4) did not increase with age, but the number of dominant species per vegetation stage was clearly higher in the oldest stage (M) compared to the two younger stages and in particular the pasture sites (Fig. 6A–D). In Gleysols of the Cachoeira region, the pasture (P) sites were characterized by five species, mainly *Hemienchytraeus* sp. 5 (about 50%), followed by *Guaranidrilus* sp. 9 and *Enchytraeus* sp. In the youngest forest stage (H), *Guaranidrilus* sp. 9 and *Enchytraeus* sp. dominated the assemblage, while no *Hemienchytraeus sp.* 5 was found. Instead, *H. tanjae* and *H. patricii* were sampled. The latter as well as *Enchytraeus* sp. were by far the most abundant species in the arboreal stage, meaning that these two 'young' stages did differ in their dominance pattern. In the M-stage of the forest, *H. patricii* and *Enchytraeus* sp. were still the most abundant species, but two *Guaranidrilus* species (*G. marquesi* and *G.* sp. 7) as well as *A. neotropica* occurred in relevant percentages. The appearance of an *Achaeta* species is conspicuous, since members of this genus did not occur in other sites on Gleysol

At sites with Cambisol in Cachoeira and Itaqui, the species number per site increased with the age of the vegetation (and was always higher than the number in Gleysols) (Tab. 4). However, in Cachoeira a pattern with only one highly dominant species was found at all stages except the oldest forest (F) (Fig. 7). On Cambisol in Cachoeira, the pasture (P) sites were dominated by three species, mainly *Enchytraeus* sp., *A. hanagarthi*, and *H. patricii* (Fig. 7A–E): This pattern did not change considerably in the next stage (H): only the number of dominant species increased by one (*H. tanjae*). This species became by far the most dominant species in the A-stage (almost 50%), followed by the three species dominating the previous stages plus *A. neotropica*. The number of dominant species increased to nine. This value did not change in the M-stage, but surprisingly this medium old forest was strongly dominated by *Enchytraeus* sp. again. Still both *Hemienchytraeus* species (*H. patricii*, *H. tanjae*) occurred in considerable numbers as did also two *Guaranidrilus* species (*G.* sp. 3 and *G. marquesi*), while *Guaranidrilus* sp. 7 and *Achaeta hanagarthi* were only rarely found. In the old-growth forest stage (F) the species number increased to nine and the dominance pattern changed again: *A. neotropica*, followed by *G. marquesi* and *Guaranidrilus* sp. 7 were most dominant. Relevant percentages were also reached by *H. tanjae*, *H. patricii* and, still, *Enchytraeus* sp., while *A. hanagarthi*, *Guaranidrilus* sp. 3 and *G. hoeferi* occurred more rarely. In general, a steady increase in diversity took place in parallel with increasing age of the vegetation.

The dominance structure along the forest regeneration in Itaqui appears to be different from that in the Cachoeira sites (Fig. 8A–D). Already in the young stages more species were sampled and the dominant species had lower portions than in Cachoeira. On average, no species dominated with more than 50% of all enchytraeids.

H. tanjae, followed closely by *A. hanagarthi*, was most dominant in the young herbaceous stage (H). Even less dominant was *H. patricii* and, with a surprisingly low percentage for this early stage, *Enchytraeus* sp., closely

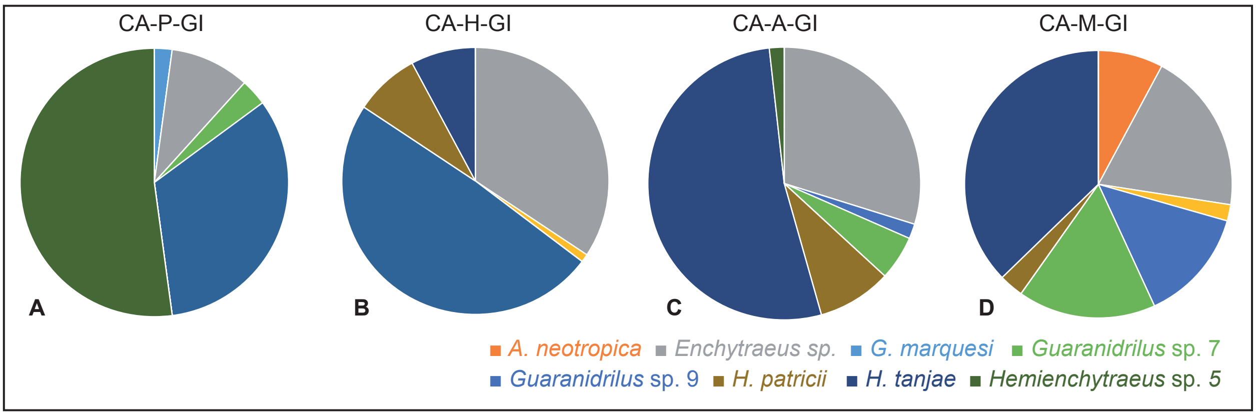


Figure 6A–D. Dominance structure of the enchytraeid assemblages of the different stages (mean of three sites) in Cachoeira (CA) on Gleysol (Gl). P – pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage.

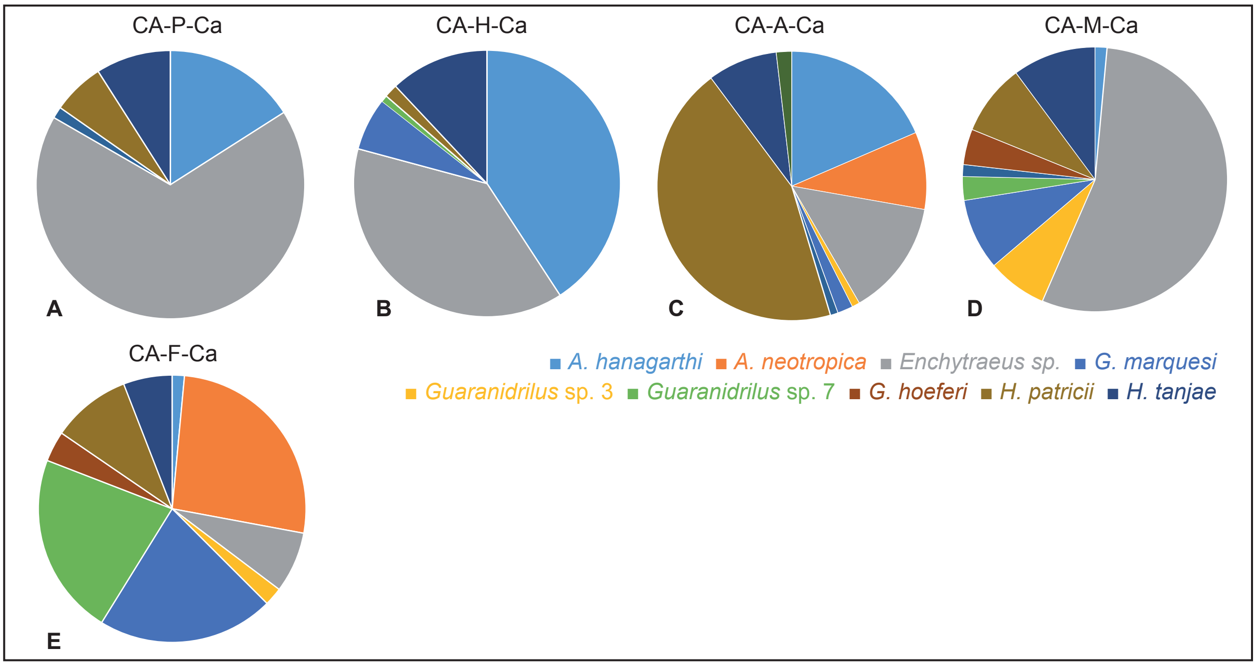


Figure 7A–E. Dominance structure of the enchytraeid assemblages of the different stages (mean of three sites) in Cachoeira (CA) on Cambisol (Ca) .P – pasture, H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest.

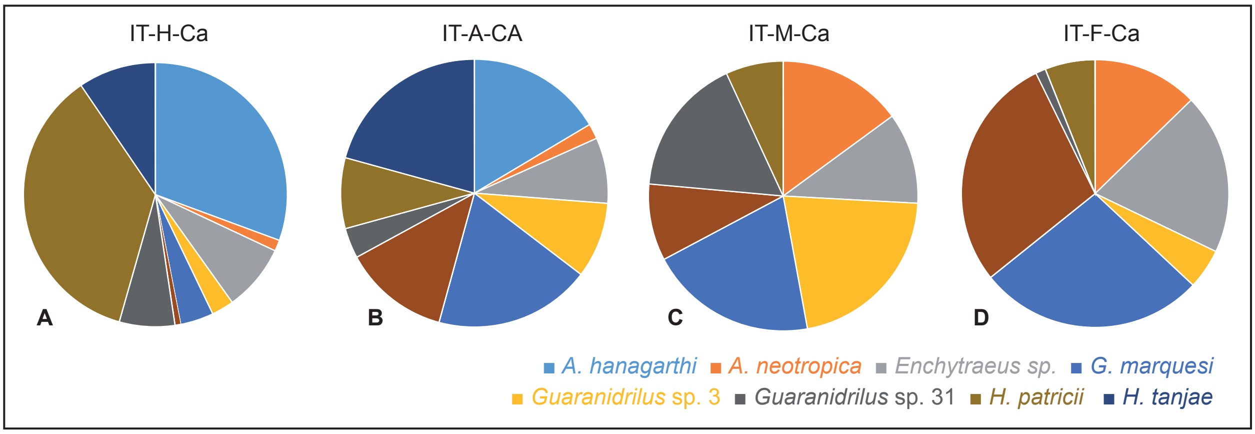


Figure 8A–D: Dominance structure of the enchytraeid assemblages of the different stages (mean of three sites) in Itaqui (IT) on Cambisol (Ca) . H – young herbaceous stage, A – young arboreal stage, M – medium old arboreal stage, F – old-growth forest.

Actually, similar experiences concerning the microdrile community were also made in the Amazon (Collado & Schmelz 2000). Maybe their occurrence may indicate sites with higher moisture levels. However, at the time of sampling there was no obvious relationship between soil moisture and naidid/tubificid occurrence was visible. Results of the earthworm sampling were presented in Römbke et al. (2009).

4. Discussion

4.1. Biodiversity: Comparison with literature data

In the study region, represented by 39 study sites distributed in two areas (reserves) of the Atlantic Forest of Eastern Paraná, 61 morphospecies of Enchytraeidae were found. This number is in the same order of magnitude as the total number of terrestrial or semi-aquatic enchytraeid species known in whole Latin America (Schmelz et al. 2013). Only four of the species were described (Tab. 3): three of them from other Brazilian states and one from the different Neotropical regions. Ten species have been described by some of us within the SOLOBIOMA project, three in a new genus (*Xetadrilus,* Schmelz et al. 2008, 2009, 2011). For predictions on the distribution of species and possible endemisms, the data basis is still too weak. A preliminary survey of enchytraeids in soils of an *Araucaria* forest near Curitiba, carried out in 2010, yielded many of the species listed in Tab. 1 (Schmelz et al. forthcoming), suggesting a wider distribution of the species at least in the State of Paraná. One species, *Achaeta singularis*, considered as a true representative of the old autochthonous forest fauna (Schmelz et al. 2008) was not found at the EMBRAPA site, but was abundant in a collection from river sediments in the State of São Paulo (Schmelz et al. forthcoming). The find of *Achaeta piti* Bittencourt, 1974 is a further link to the fauna of this neighbouring state. The fauna of eastern Paraná may also have relations to other parts of Brazil, especially Central Amazonia, as indicated by two *Hemienchytraeus* species (Schmelz & Römbke 2005). In addition, there are relations to various Brazilian states (e.g. Amazonas, Mato Grosso, Minas Gerais, Sao Paulo) due to findings of *A. neotropica* [a species complex that includes *A. iridescens* Christoffersen, 1979 and *A. becki* Schmelz & Collado, 2005 (Schmelz et. al 2009)]. This species is also known from Argentina and Mexico.

Peregrines are to be expected in *Fridericia*, a genus present in pastures and early successional stages on Cambisol (see Annex 2 and 3). The material from the study sites remained unidentified for the lack of sexually mature individuals, but two probably peregrine species, *Fridericia pretoriana* Stephenson, 1930 and *F. chonqingenis* Xie et al., 1999, were found in additional samples from a pasture near the study sites in Itaqui (Schmelz, pers. obs.). There is evidence that at least in Brazil the occurrence of *Fridericia* is dependent on open landscapes created by human activity (Römbke et al. 2007). In *Enchytraeus* DNA data are needed to evaluate species identity and distribution type. The specimens found belong to the cosmopolitan species aggregates *E. buchholzi* and *E. bigeminus*. In summary, the terrestrial enchytraeid fauna of Paraná is composed partly of (probably) endemic species (e.g. *Achaeta paranensis* Schmelz, 2008), partly of species with a known wider distribution within South America (e.g. *Hemienchytraeus patricii*), plus a few peregrine species, probably introduced from other continents.

4.2. Ecology: Comparison with literature data

Recently, Schmelz et al. (2013) reviewed the knowledge on enchytraeid ecology in Latin America, compiling data from various habitats. Despite some recent progress (e.g. regarding the use of standard protocols for sampling enchytraeids), there are still almost no quantitative data available which could be used for comparison in the context of this study, i.e. numbers per square meter for different forest stages or pastures based on standard sampling techniques, preferably species-specific (Tab. 5). In fact, the only comparable study has been performed in another German-Brazilian cooperative project in Central Amazonia in the late Nineties of the last century– and

Table 5. Comparison of own data on enchytraeid abundance in tropical secondary forests with literature data (range per vegetation type, abundances are means for one site).

Land use type	Abundance (Ind m^{-2})		
	Own data	Literature	Reference
Pastures	500 – 4,100	?	None
Young Secondary forests (A / H stage)	100 – 3,700	1,700 – 9,300	Römbke & Meller 1999
Old-growth forests (M / F stage)	200 – 5,200	1,600 – 8,600	Römbke & Meller 1999

even from that study so far only abundances for the whole assemblage are available (Römbke & Meller 1999, Römbke 2007). Despite the fact that the numbers are somehow higher in Amazonia (which might be caused by the fact that sampling was repeated seven times within two years at these sites), the order of magnitude is comparable (i.e. all numbers are below 10,000 Ind m^{-2}). With few exceptions, this seems to be the 'normal range' of abundance of enchytraeids in tropical forests (Römbke 2007). Of course, in specific habitats with high accumulation of organic material, much higher numbers are possible – but these sites (e.g. in the Columbian Andes or on 'Tafelbergen' in Venezuela; see Schmelz et al. 2013) have not yet been studied in detail (e.g. almost nothing is known about their species number and composition). Furthermore, soil samples collected during a field course at a research station (Embrapa Florestas, located close to Curitiba, Paraná, Brazil) in October 2010 revealed abundances of appr. 15,000 Ind m^{-2} in a fragment of mixed Araucaria Forest and appr. 30,000 Ind m^{-2} in another site close to a stream, suggesting that subtropical areas in Brazil may harbour densities within the range normally found in temperate regions (Schmelz et al. 2013). A possible hypothesis to be tested would be that soil carbon content determines the density of enchytraeids worldwide. To conclude, in most tropical forests the enchytraeids do occur, but due to their low numbers and biomass their ecological role (e.g. regarding stimulating microbial activity improving soil structure) is considered to be limited, especially when compared with earthworms. However, due to their species richness they may be useful to indicate the biological status of a site in terms of biological soil quality or perturbation.

4.3. Conclusions and Outlook

So far, the evaluation of the enchytraeid data compiled in the SOLOBIOMA project is clearly preliminary. However, the following statements can already be made today:

- Eastern Paraná is a hotspot of enchytraeid diversity;
- so far, only 10 % of the species are described;
- endemic species of the genus *Guaranidrilus* are dominant in the region;
- few 'peregrine' species do occur, mainly in pastures.

It seems that the ecological importance of enchytraeids is rather low, since their abundance and biomass is low independent from the stage (i.e. the age of the respective vegetation, mainly forests). Depending on the site (mainly soil) properties their numbers are on average in a range between 1,000 and 5,000 ind m^{-2}. This range seems to be normal for tropcial regions but they are far lower than the average numbers in temperate forests soils, which range usually between 10,000 and 140,000 ind/m^2 (Didden 1993).

Their taxonomic richness, however, makes enchytraeids good diversity indicators in the Mata Atlântica. Specific assemblages, characterized by their diversity (i.e. species number) but more importantly by their species composition (i.e. dominance pattern) have been identified in this preliminary work. An elaborated assessment of these data, together with more information on, for example, soil properties, is necessary to refine assemblage descriptions. In fact, a detailed statistical evaluation of the enchytraeid data is currently in preparation (Ottermanns, pers comm.). This work will focus mainly on two questions:

- which environmental factors influence the enchytraeid distribution patterns;
- which role do these organisms play in the food web at the SOLOBIOMA sites.

Clearly, this data set will also play an important role when assessing the status of invertebrate diversity (e.g. ants, beetles, spiders) in this part of the Mata Atlântica.

5. Acknowledgements

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Annex 1. Individual data of enchytraeids per sample: Cachoeira – Gleysol sites

Species	GL1-P	GL1-H	GL1-A	GL1-M	GL2-P	GL2-H	GL2-A	GL2-M	GL3-P	GL3-H	GL3-A	GL3-M	Sum
Ach1	2												2
Ach3												8	8
Enc1	4	7	15	20	2				3	28	2		81
Gua1				3						2			5
Gua2			8	1							3		12
Gua3		1		2									3
Gua4						3							3
Gua5				6							6		12
Gua6			1	14									15
Gua7				2	3						3	15	23
Gua8			1							2			3
Gua9	29	50			1				1				81
Gua11			1										1
Gua14				1									1
Gua17										3			3
Gua22										1		5	6
Hem1			3	8					2				13
Hem2a		8	5	3									16
Hem2b						2				4		1	7
Hem4a		1	30	36				1		7		1	76
Hem4b										1			1
Hem58	43				1				5		1		50
Hem67				1						2	2		5
X1				5							1		6
X2	2								1				3
Rest	0	12	54	6	16	14	4	6	33	2	14	20	181
Total	80	79	118	108	23	19	4	7	45	52	32	50	617
Ind m^2	2488	2457	3670	3359	715	591	124	218	1400	1617	995	1555	19189

The tables in Annex 1–3 list the species with informal genus and species codes. The valid genus and species names are as follows: Ach. *Achaeta*. Ach1: *Achaeta hanagarthi* Schmelz, 2008. Ach2, Ach3: *Achaeta neotropica* Černosvitov, 1937. Ach4: *Achaeta piti* Bittencourt, 1974. Ach6: *Achaeta singularis* Schmelz, 2008. Ach7: *Achaeta paranensis* Schmelz, 2008. Enc: *Enchytraeus*. Fri: *Fridericia*. Gua: *Guaranidrilus*. Gua5: *Guaranidrilus andreolii* Schmelz, Collado & Römbke, 2011. Gua 6: *Guaranidrilus marquesi* Schmelz, Collado & Römbke, 2011. Gua8: *Guaranidrilus cingulatus* Schmelz, Collado & Römbke, 2011. Gua10: *Guaranidrilus hoeferi* Schmelz, Collado & Römbke, 2011. Hem: *Hemienchytraeus*. Hem2a: *Hemienchytraeus patricii* Schmelz & Römbke, 2005. Hem4a: *Hemienchytraeus tanjae* Schmelz & Römbke, 2005. X1: *Xetadrilus maacki* Schmelz, Collado & Römbke, 2011. X2: *Xetadrilus aphanus* Schmelz, Collado & Römbke, 2011. X4: *Xetadrilus fabryi* Schmelz, Collado & Römbke, 2011. Tupi: *Tupidrilus*. The rest of the species is still unidentified or undescribed.

Annex 2. Individual data of enchytraeids per sample: Cachoeira – Cambisol sites

Species	CA1-P	CA1-H	CA1-A	CA1-M	CA1-F	CA2-P	CA2-H	CA2-A	CA2-M	CA2-F	CA3-P	CA3-H	CA3-A	CA3-M	CA3-F	Sum
Ach1		33	18		2		5	2			23	13		1		97
Ach3			2		1					4			8		31	46
Ach4	4	3	1								1	7				16
Ach6					3										7	10
Ach7													2			2
Enc1	92	41	13	18	7		2				5	5	2	20	3	208
Fri1	18										2				1	21
Fri2	2															2
Fri4													1			1
Gua1				1	2							2				5
Gua2	1		1	3	3			1								9
Gua3				3	3								1	2		9
Gua4					16											16
Gua5					5			2					3			10
Gua6				2	13		1	2		4		7		4	12	45
Gua7					14					16		1		2		33
Gua8				1	2				1					1		5
Gua9	2												1	1		4
Gua10				1	5									2		8
Gua11	4				2		1									7
Gua12					1											1
Gua13	1															1
Gua14										5						5
Gua15												5				5
Gua17															5	5
Gua19												2				2
Gua22														2	11	13
Gua23											3	6				9
Gua25														2		2
Gua26														11		11
Gua27														3		3
Gua28				2					1					1		4
Hem1				3	7		1	9					9	4	4	37
Hem2a			31	1	5			5	5	3	9	2	12		5	78
Hem2b							2				2	6	4			14
Hem4a		3	1	5	4		12	8	2		13				4	52
Hem4b														2		2
Hem58								1					1			2
Hem67				2				1								3
X1				3	3									2		8
X2			5	1							2	1	2			11
X3	1				1						6					8
X4	1	3														4
Rest	6	7	4	16	19	16	7	64	11	127	19	15	10	17	16	354
Gesamt	132	90	76	62	118	16	31	95	20	159	85	72	56	77	99	1188
Ind m²	4105	2799	2364	1928	3670	498	964	2955	622	4945	2644	2239	1742	2395	3079	36947

Annex 3. Individual data of enchytraeids per sample: Itaqui – Cambisol sites.

Sites	IT1-H	IT1-A	IT1-M	IT1-F	IT2-H	IT2-A	IT2-M	IT2-F	IT3-H	IT3-A	IT3-M	IT3-F	Sum
Ach1	16				26	21			3	6			72
Ach2	18												18
Ach3		1	7	4		2	5	15	2		14	2	52
Ach4					17								17
Ach6							1	1				2	4
Ach7		1					8	1			1	1	12
Enc1	1	1	9	13	7	5	7	9	4	7	3	10	76
Fri1					10	1							11
Gua1	12		5				2			2			21
Gua2		2		6			18	6			2	2	36
Gua3	3	12	12	6		3	25	1	1			1	64
Gua4			3				2						5
Gua5							4	7			1	2	14
Gua6	6	29	25	9			7	25		2	3	11	117
Gua8		4		5			1					1	11
Gua10	1	3	5	3			11	19		18		25	85
Gua12												1	1
Gua14								4		1	2	4	11
Gua15	3						1						4
Gua17				4				9					13
Gua19			4	8				2			7		21
Gua21			2									8	10
Gua22		2										7	9
Gua28			6					1					7
Gua 31	8	6	16				13	2	2				47
Gua32	14	3	3	3					3				26
Gua33		1											1
Gua34								1					1
Gua36			1					5				3	9
Gua37			3									1	4
Gua38			1							2	6		9
Gua39								8					8
Gua40								1					1
Gua41								2					2
Gua42												8	8
Hem1			6				2	2					10
Hem2a	5	2		9	5	5	12		43	7		1	89
Hem2b				2					2				4
Hem4a					3	28			11	6			48
Hem4b	7	3					7			2			19
Hem08												1	1
Hem09						5						1	6
X1							4	1					5
X2	5		13		5				6	1			30
X5				8			7						15
Tupi				2									2
Rest	18	18	10	13	22	38	30	10	13	15	0	3	190
Total	117	88	131	95	95	108	167	132	90	69	39	95	1226
Ind m^{-2}	3639	2737	4074	2955	2955	3359	5194	4105	2799	2146	1213	2955	38129