

SOIL MACROFAUNA AND DECOMPOSITION RATES IN SOUTHERN BRAZILIAN ATLANTIC RAINFORESTS

Petra Schmidt¹, Kauana Dickow², Aline Alinéia Rocha², Renato Marques², Ludger Scheuermann¹, Jörg Römbke³, Bernhard Förster³ & Hubert Höfer¹

¹Staatliches Museum für Naturkunde Karlsruhe (SMNK), Germany

²Universidade Federal do Paraná (UFPR), Brazil

³ECT Oekotoxikologie GmbH, Germany

Abstract. We studied abundance, biomass, and structure of soil macrofauna communities and decomposition rates (*k*) in three different regeneration stages of a lowland and a sub-montane rainforest in the southern part of the Brazilian Mata Atlântica. The contribution of soil fauna to the decomposition process was assessed by using litterbags with three different mesh sizes. Decomposition of three leaf species differed strongly. In litterbags admitting faunal activity, leaves of *Tibouchina pulchra* disintegrated almost twice as fast (*k* 2.1–2.8 in lowland, 3.1–4.7 in sub-montane forest) as those of *Sloanea guianensis* (*k* 0.9–1.5), and about three times faster than *Andira anthelminthica* (*k* 0.6–0.9). This is due to the fact that only the decomposition of *T. pulchra* was accelerated by soil fauna. Decomposition rates of all species increased in both areas with the age of the sites (by a factor of 1.24 to 1.66). All six sites were very much alike regarding the structure of their soil macroarthropod communities. Ants strongly dominated in terms of abundance (55–87 %) and biomass (18–62 %), but most are generalists or predators. Ants had a negative effect on decomposition rates, probably by influencing the decomposer community. Beetles were abundant in all sites, but due to their minute size not important in terms of biomass. Abundant decomposers were diplopods (5.5–17 %) and in the older stages also termites (12 and 23 %). In terms of biomass, cockroaches (1–22 %), diplopods (3–15 %), and isopods (2–25 %) were most important. Concerning the abundance or biomass of arthropods, neither the two different forest formations nor the regeneration stages differed considerably and in a way interpretable as succession. By contrast, abundance and biomass of earthworms, e.g. of the peregrine species *Pontoscolex corethrurus*, were much higher in the sub-montane forests than in the lowland forests. The different decomposition rates of *Tibouchina pulchra* in different sites are well explained by the respective biomass of soil decomposer macrofauna, especially earthworms. Accepted 24 October 2008.

Key words: Brazilian Atlantic forest, decomposition, litterbags, Mata Atlântica, secondary forests, soil fauna.

INTRODUCTION

The Brazilian Atlantic forest or Mata Atlântica is among the most diverse and most threatened ecosystems of the world. Its forests originally covered about 1.1 million km², corresponding to 12 % of the land surface of Brazil, extending for more than 3000 km along the eastern Brazilian coast between the latitudes of 6° and 30°S (SOS Mata-Atlântica & INPE 1993). The region was impacted early by colonization, resulting in extensive deforestation, conversion into farmland, and urbanization. Consequently, forest was reduced to about 7 % of its original area or less than 100 000 km² (Schäffer & Prochnow 2002, Ferretti & Britez 2006). Of the remaining forested area, one of the largest remnants is found on

the coast of Paraná. It harbors a mosaic of environments at elevations ranging from sea level to more than 1500 m a.s.l. As a consequence of geomorphological and climatic variations, the Dense Ombrophilous Forest (Veloso *et al.* 1991) is divided into four subformations (lowland, alluvial, sub-montane, and montane forest), each presenting distinct floral and structural characteristics. Two pioneer formation types (restinga and mangrove) are limited to unstable substrates under direct influence of sea and river waters (Ferretti & Britez 2006). As the development of vegetation strongly depends on nutrient cycling, a characterization of the components of the decomposer system (litterfall, nutrient contents, and biomass of soil biota) as well as the processes (decomposition, nutrient release) is fundamental to the understanding of the functioning of these forests and the effects of anthropogenic changes.

* e-mail: petra.schmidt@smnk.de

Organic matter in decomposition is the main source of plant nutrients in tropical forests on nutrient-poor soils. It originates from litter fall, which in these forests is mainly composed of leaves (> 60 % in weight). Another 8 to 20 % usually comes from fine woody material, and another 6 % from flowers, fruits, and seeds (Klinge 1977, Luizão 1989, Brites 1994, Pinto & Marques 2003, Martins 2004, Martius *et al.* 2004b). Litter decomposition dynamics and nutrient release are of particular importance to forest sustainability. The role of soil fauna in the decomposition process seems to be proven for temperate as well as for tropical ecosystems and to be beyond dispute (Edwards & Heath 1963, Swift *et al.* 1979, Heneghan *et al.* 1999, González & Seastedt 2000, Martius *et al.* 2004a, Huhta 2006). However, no data on the importance or contribution of soil fauna have so far been presented from Brazilian Atlantic forest.

We were interested in the contribution of soil fauna to the functioning of Brazilian coastal rainforests and have chosen decomposition rate as a measure for it. Our hypotheses, arrived at from our own experiences with decomposition processes in Amazonian forests and agroforestry sites (Höfer *et al.* 2001, Martius *et al.* 2004a,b, Brown *et al.* 2006a) and earlier studies in some of the sites studied herein (Wisniewski 1997, Boeger & Wisniewski 2003, Pinto & Marques 2003, Boeger *et al.* 2005), were the following. A) Decomposition rates are strongly determined by faunal activity. Exclusion of macrofauna and mesofauna by means of litterbags with different mesh sizes should therefore decrease decomposition rates (Höfer *et al.* 2001, Brown *et al.* 2006a). B) Floristic species composition of Atlantic forests strongly depends upon soil properties and influences leaf nutrient content, degradability, organic matter building, and nutrient availability (Boeger & Wisniewski 2003, Boeger *et al.* 2005). This should also lead to differences in soil macrofauna community structure as well as in total abundance and biomass of soil macrofauna in the two different forest formations stocking on different soil types, and as a consequence decomposition rates should also differ. C) Soil macrofauna is dependent upon microclimatic (Martius *et al.* 2004a) and resource conditions (litter fall, litter stocks, nutrient content of leaves) (Martius *et al.* 2004b) and should therefore develop along the observed secondary forest succession (forest regenerating from pastures or agricultural sites). Sites representing different regeneration stages should therefore differ in macrofauna community structure.

MATERIAL AND METHODS

Study sites. The two study areas covered by the different forest types were close to the coast of Paraná, about 100 km distant from the capital Curitiba and about 50 km distant from each other. The climate of the coastal region of Paraná can be described as mesothermic subtropical humid, corresponding to the *Cfa*-type, according to Köppen's classification (Schröder 2000, Strahler & Strahler 2005). Mean annual temperature is above 18 °C and monthly precipitation over 60 mm. Frost rarely occurs in areas from sea level to 700 m a.s.l. (IPARDES 2001). Annual rainfall in the region varies between 2000 and 3000 mm (Roderjan & Kunyoshi 1988) and shows seasonality. Lower rainfall occurs from the end of autumn to winter (April to August), higher rainfall during the warmer summer (September to March) (IPARDES 2001).

"Dense ombrophilous forests of the lowlands" *sensu* IBGE (1992) stock on sandy Podzol soils of the coastal plain. Our corresponding study sites were situated in the municipality of Paranaguá (25°35'S, 48°32'W) within the "Floresta Estadual do Palmito" (530 ha, herein called Palmito forest), a reserve administered by the environmental institute of Paraná (IAP), State of Paraná. Soils in Palmito forest can be characterized as non-hydromorphic Spodosols (soil taxonomy of Soil Survey Staff 2006; Podzols of WRB, FAO 1998). In most places soils are well drained, which leads to severe leaching and very low nutrient contents ($\text{Ca} < 3.3 \text{ cmolc dm}^{-3}$, $\text{K} < 0.21 \text{ cmolc dm}^{-3}$, $\text{P} < 11.6 \text{ g dm}^{-3}$, $\text{N} < 2.5 \text{ g kg}^{-1}$; from Wisniewski 1997). They have a moderate sandy texture and plain relief, a generally low base saturation, and a high toxic aluminum concentration (EMBRAPA 1984). A hard layer of sesquioxides in the B horizon inhibits rooting and makes the soil partly water-impermeable.

The Palmito forest was in the past intensively exploited for wood and palm hearts ("palmito" *Euterpe edulis* Martius). Some parts were completely cleared of trees and used for agriculture. Due to the low fertility of the soil agriculture was abandoned soon after, allowing a secondary succession. The three study sites were established in the course of previous studies in this reserve (Wisniewski 1997) and represent forest patches close to each other but belonging to three chronologically different regeneration stages. At the beginning of our study in 2003 they had regenerated for 20, 33, and 58 years respectively since the abandonment of manioc cultivation (Boeger *et*

al. 2005). They differ floristically and in vegetation structure and were named according to their successional aspect as “initial”, “intermediate”, and “advanced”. Tree species typical for the initial stage were *Ilex theezans* Mart. ex Reissek. (Aquifoliaceae), *Ternstroemia brasiliensis* Camb. (Theaceae), *Andira anthelminthica* Benth. (Fabaceae), and *Ocotea pulchella* Mart. (Lauraceae). In the intermediate stage, *Ilex theezans*, *Ternstroemia brasiliensis*, *Rapanea venosa* (DC) Mez. (Myrsinaceae), and *Gomidesia fenzliana* Berg. (Myrtaceae) occurred frequently. In the advanced stage, distinctive species were *Ocotea aciphylla* (Ness) Mez. (Lauraceae), *Tapirira guianensis* Aubl. (Anacardiaceae), *Andira anthelminthica*, and *Euterpe edulis* Mart. (Palmae). Other epiphytes and vines were common. In the two older sites bromeliads were very abundant. Trees reached heights of up to 14 meters in the advanced stage, in the other stages they were much lower (Wisniewski 1997).

Roughly corresponding to these stages, three sites were selected in an area of sub-montane forest in the “Reserva Natural do Rio Cachoeira” (herein called Cachoeira forest), owned and administered by the regional NGO “Society for Wildlife Research and Environmental Education” (SPVS). The reserve is located in the municipality of Antonina (25°25'S, 48°40'W) and within the Environmental Protection Area (EPA) of Guaraqueçaba. It contains many patches of forest naturally regenerating from pasture. These secondary forests in Cachoeira are mostly in the plain and under groundwater influence (hydromorphic gleysols), or are located on slightly inclined hillsides on soils originating from neo-precambrian acid rocks. Depending on the soil development conditions, Entisols, Inceptisols or Ultisols (Soil Survey Staff 2006) occur. For this study we selected sites on well-drained Inceptisols (WRB: Cambisols). Nutrient contents were also low (Ca < 2.5 cmolc dm⁻³, K < 0.36 cmolc dm⁻³, P < 6.6 g dm⁻³, N < 3.4 g kg⁻¹; Corrêa unpublished).

In “dense sub-montane ombrophilous forests” *sensu* IBGE (1992) trees reach heights of 20 to 25 meters. Characteristic species are *Virola bicuhyba* (Myristicaceae), *Schizolobium parahybum* (Caesalpinioideae), *Alchornea glandulosa* or *A. triplinervia* (Euphorbiaceae), and *Hyeronima alchorneoides* (Euphorbiaceae), with an understory rich in palms of *Euterpe edulis*, *Bactris* spp., and *Geonoma* spp., epiphytes and (tree) ferns.

Each of the 0.1-ha sites in both areas was subdivided into ten 10 x 10 m plots for the sampling of soil fauna and microbial biomass.

Decomposition experiment. The role of soil fauna in determining litter decomposition rate was studied using a litterbag series. Litterbags (25 x 25 cm) of three different mesh sizes (fine = 0.02 mm, medium = 0.5 mm, and coarse = 4 mm) were filled with one of two leaf species typical for most, and occurring in all stages of the same forest formation. In lowland forest *Andira anthelminthica* (local name: jacarandá; Papilionoideae) and in sub-montane forest *Sloanea guianensis* (laranjeira-do-mato; Elaeocarpaceae) were chosen. *Tibouchina pulchra* (jacatirão; Melastomataceae) was used in all sites as one of the few frequent species occurring in both forest formations. Leaf material was collected from the trees in March 2004, at a time when the leaves are mature (Brazilian autumn). Leaves were air-dried in the laboratory and between 8 and 14 g were inserted in each litterbag. The experiment was initiated in both areas in August 2004 with the distribution of 40 litterbags of each mesh-size and plant species at random in the respective sites, resulting in 240 bags per site. Within one year 8 litterbags per site were retrieved on each retrieval date: 42, 85, 126, 257, and 365 days after exposure for *Andira* and *Sloanea* leaves; 42, 85, 126, 193, and 257 days for *Tibouchina* leaves. The retrieved material was oven-dried and subsequently weighed. Bias by contamination of leaf material with soil particles was avoided by determining ash content and subsequently using ash-free retrieval mass. Ash free dry mass (AFDM) values from the different retrievals were submitted to regression using the exponential decay model (SigmaPlot 8.2., $M_t = M_0 e^{-k}$; Olson 1963). All correlation coefficients were high ($R^2 > 0.7$) and highly significant ($p < 0.0001$) thus producing reliable k -values as decomposition rates. The effect of mesh size on k was tested with ANOVA after testing the requirements. Fisher's LSD test was used as Post-Hoc test (Statistica 7). To reveal relationships between decomposition rate and the occurrence of functional soil fauna group at the sites, a multiple regression was calculated using the k -rate of *Tibouchina pulchra* in coarse litterbags as the dependent variable, and biomass of ants, arthropod decomposers and earthworms as independent variables.

Soil fauna. Arthropods were sampled once in all forest sites. In each of the ten plots per site one sample was taken. Litter fauna was collected from the litter of 1-m² quadrats by first sieving the material through a 1-cm mesh and subsequently storing the sieved material in Winkler bags for three days (Bestelmeyer *et al.* 2000). Edaphic fauna was collected by digging

TABLE 1. Decomposition rates (k per year) for the three leaf species in the different regeneration stages of lowland forest (Palmito) and sub-montane forest (Cachoeira), calculated by regression (exponential decay) from ash-free dry weights of the retrieved material.

Leaf species	Area	Mesh size	Regeneration stage/site		
			initial	intermediate	advanced
<i>Andira anthelminthica</i> - jacarandá	Palmito	coarse	0.6	0.7	0.9
		medium	0.5	0.6	0.7
		fine	0.5	0.6	0.7
<i>Tibouchina pulchra</i> - jacatirão	Palmito	coarse	2.1	2.3	2.8
		medium	1.4	1.9	1.8
		fine	1.2	1.6	1.6
<i>Tibouchina pulchra</i> - jacatirão	Cachoeira	coarse	3.8	3.1	4.7
		medium	2.0	2.4	3.1
		fine	1.6	1.9	2.0
<i>Sloanea guianensis</i> - laranjeira-do-mato	Cachoeira	coarse	0.9	0.9	1.5
		medium	0.9	0.9	1.5
		fine	0.8	1.4	1.8

out 20 x 20 cm quadrats of soil to a depth of 10 cm and subsequent extraction of the fauna with Berlese funnels (see Southwood 1966) over 14 days. Litter fauna and edaphic fauna were pooled to obtain soil fauna abundance and biomass per m² for further analyses. All macroarthropods were stored in 70 % ethanol, thereafter identified, sorted to order, and counted. All non-social arthropods were measured individually for biomass determination using factors from mass-length-regressions originating from our own studies (for arachnids: Höfer & Ott in press; other groups unpublished) on Amazonian fauna. Ants were sorted to genera, to which specific size-mass factors resulting from the same investigations were applied. For termites, an average individual weight of 0.7 mg ind.⁻¹ from the literature (Martius 1994) was used. Cockroaches, diplopods, isopods, and termites were considered as decomposers. Coleopteran larvae (mostly staphilinids) were considered predators. Earthworms were captured by hand-sorting 50 x 50 cm quadrats of soil to a depth of 20 cm, followed by formalin extraction (Lee 1985, ISO 2006). Five samples were taken in a systematic way in each site, four from the corners and one from the center. Dry mass was calculated from fresh mass, determined by weighing and a factor (dry = 0.15 fresh mass) derived from the literature (Peterson & Luxton 1982).

Microbial respiration. In March 2004, ten soil samples of 5-cm depth (one per plot) were taken from

each site after removal of the litter layer, sieved (4 mm) and combined to one composite sample per site (Palmito) or measured separately (Cachoeira). After an equilibration period of 10 days at approx. 20–25° C the basal respiration (BR) and the substrate-induced respiration (SIR) were measured from four aliquots each, via infra-red gas analysis in an open flow system with ambient air (Heinemeyer *et al.* 1989) according to ISO (1997) guidelines.

RESULTS

Decomposition rates. The three leaf species decomposed at different rates in the litterbag experiment (Table 1). *Tibouchina pulchra* leaves showed the highest mass (AFDM) loss: 257 days after exposure, 94–99 % in the sub-montane forest sites and 63–82 % in the lowland sites had disappeared from coarse-meshed litterbags. *Sloanea guianensis* had lost between 69 and 81 % of initial mass and *Andira anthelminthica* only between 50 and 62 % after 365 days in coarse-meshed litterbags. *T. pulchra* leaves were decomposed to 50 % in a period of 53 to 122 days, which for the same mesh size varied for *Sloanea guianensis* from 173 to 289 days and for *A. anthelminthica* even from 289 to 433 days. The difference between the species was significant in both areas ($F_{1,12} = 122$; $F_{1,12} = 27.4$, $p < 0.001$) (Fig. 1), with *T. pulchra* leaves decomposing almost twice as fast as those of *S. guianensis* and about three times as fast as *A. anthelminthica*. Differences in decomposition be-

tween the two forest types were tested with *Tibouchina pulchra* leaves only, and showed a significant difference, i.e. a higher decomposition rate in the submontane Cachoeira forest ($F_{1,12} = 19.0$, $p < 0.001$). Taking only litterbags with coarse mesh size into account, the advanced stages showed significantly higher decomposition rates than the two younger stages ($F_{2,6} = 5.6$, $p < 0.05$).

Effects of soil fauna on decomposition. Results of the litterbag experiment with the species *Tibouchina pulchra*, *Andira anthelminthica*, and *Sloanea guianensis* demonstrated different effects of the fauna on the different plant species (Fig. 1). Mesh size, i.e. exclusion of macro- and mesofauna, had a significant effect on *T. pulchra* decomposition rates ($F_{2,12} = 18.0$, $p < 0.001$), whereas no soil fauna effect was found in the decomposition of *S. guianensis* or *A. anthelminthica*, which consequently was much slower. The k -rates (k_{year}) for *T. pulchra* in the three regeneration stages were between 2.1 and 4.7 (Table 1) when

faunal access was not restricted (coarse mesh). In the litterbags with medium mesh size, where macrofauna was excluded, decomposition rates were significantly lower (1.4–3.1; 52–84 % of unhindered decomposition) (Table 1). Further exclusion of the mesofauna by fine mesh did not reduce decomposition rates significantly. *S. guianensis* decomposition rates varied between 0.8 and 1.8 (Table 1) without significant differences between mesh sizes and were in the same range as *T. pulchra* with fauna excluded (fine mesh). The same was observed for *Andira anthelminthica* (Table 1, Fig. 1), leading to the assumption that both plant species are unpalatable or at least not attractive for the soil macrofauna.

Soil arthropod communities. The structure of the soil macrofauna communities in the different sites was very similar. Ants dominated the samples in terms of abundance (Cachoeira 55, 58, 87 %; Palmito 78, 74, 71 % of all individuals) and biomass (Cachoeira 53, 18, 35 %; Palmito 62, 28, 51 %). Most abundant at

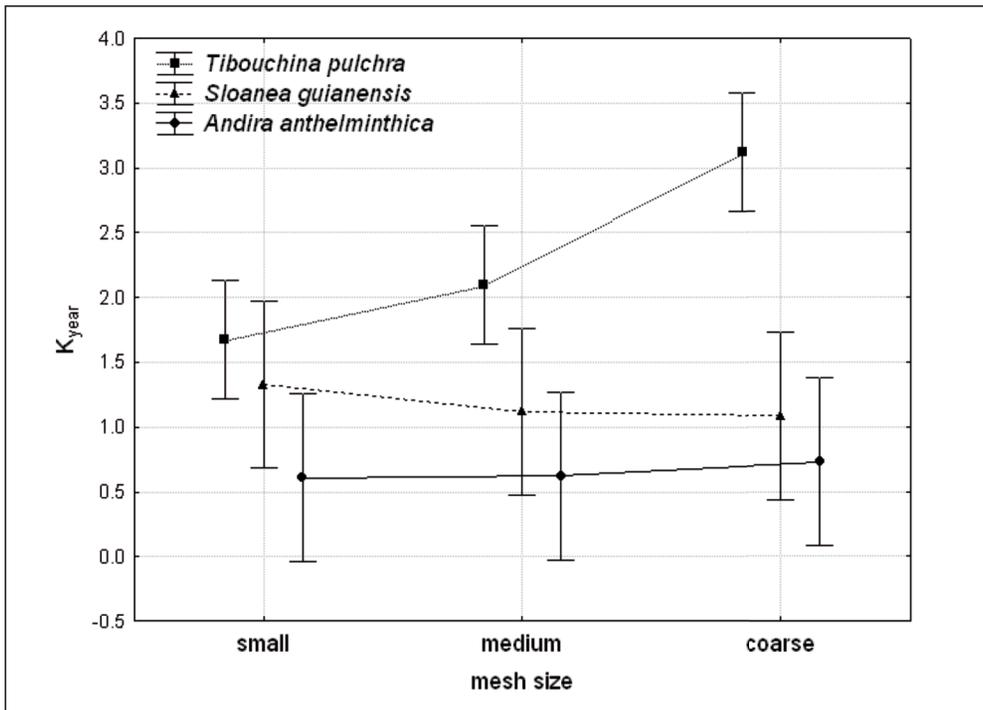


FIG. 1. Effect of mesh size on the decomposition rates of *Tibouchina pulchra* (jacatirão), *Andira anthelminthica* (jacarandá), and *Sloanea guianensis* (laranjeira) leaves in both forest types (Cachoeira and Palmito); bars show 0.95 confidence intervals.

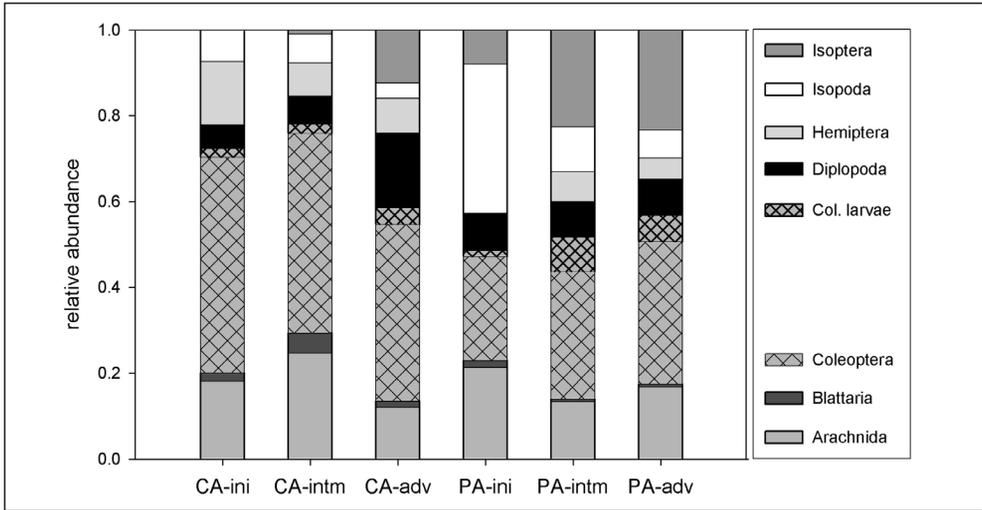


FIG. 2. Structure of the soil fauna community (abundance, arthropods without ants) in the six study sites (CA – Cachoeira forest, PA – Palmito forest, ini – initial stage, intm – intermediate stage, adv – advanced stage).

all sites were ants of the genera *Solenopsis*, *Pyramica*, *Paratrechina*, *Crematogaster*, and *Pheidole*. *Wasmannia* ants were abundant at all sites in Palmito forest and the initial stage in Cachoeira forest, but not in the other two sites. Ants of all these genera are considered predators or generalists and were not expected to have a direct effect on leaf decomposition rates. *Acropyga*, subterranean ants relying on mealybugs or aphids to provide their nutritional needs, only appeared in samples from the intermediate and advanced stages in Palmito forest. Detritivorous ants like *Cyphomyrmex* and *Trachymyrmex*, which could have a strong effect on leaf litter decomposition, were only rarely sampled.

Excluding ants from the macrofauna in total, beetles dominated in terms of abundance at all sites (Fig. 2), but due to their small size not in terms of biomass (Fig. 3). The predatory arachnids (Araneae, Opiliones, and Pseudoscorpionida) were abundant at all sites, and due to large harvestmen dominated the biomass at most sites (Figs. 2, 3). Abundant decomposer taxa, which contributed considerably to the total biomass, were millipedes (Diplopoda: 5.5–17 % of individuals, 3–15 % of biomass) and woodlice (Isopoda: 3–35 % of individuals, 1–25 % of biomass). One large millipede with 121 mg dry mass was excluded as an outlier from the evaluations. Cockroaches (Blattaria) contributed much more to biomass (1–22 %) than to abundance (0.5–4.6 %;

Figs 2, 3). Termites were abundant in all Palmito sites (8–23 %) and the advanced stage in Cachoeira (12 %). Neither total abundance nor total biomass of the arthropods (excluding ants) differed much between the sites (Figs. 4, 5).

Earthworms. The structure of the earthworm community was very simple: more than 90% of all worms caught belonged to the peregrine species *Pontoscolex corethrurus* (Müller, 1857) (Glossocoelidae), while the rest were members of the families Acanthodrilidae (*Dichogaster* sp.) and Megascolecidae (*Amyntas* sp.). In contrast to the arthropods, earthworm abundance differed strongly between sites. In the Cachoeira forest sites, 664 earthworms were caught (initial: 214.4, intermediate 72.0, advanced stage 246.4 inds. m⁻²), while only 25 earthworms were found in Palmito (initial: 2.4, intermediate: none, advanced stage 17.6 inds. m⁻²). Biomass of earthworms was therefore very high in the Cachoeira forest sites, about 2–5 times the biomass of all arthropods together. In Palmito forest the biomass of earthworms was lower than the biomass of the arthropods. Earthworm biomass did strongly correlate ($R^2 = 0.77$) with the k-rates of *T. pulchra* (coarse mesh; Fig. 6). A multiple regression showed the highest contribution of the earthworms (beta = 1.33) and much lower contributions of arthropod decomposers (0.53) and ants (–0.51) to a linear model ($R^2 = 0.97$, $p < 0.05$) explaining the decomposition rate.

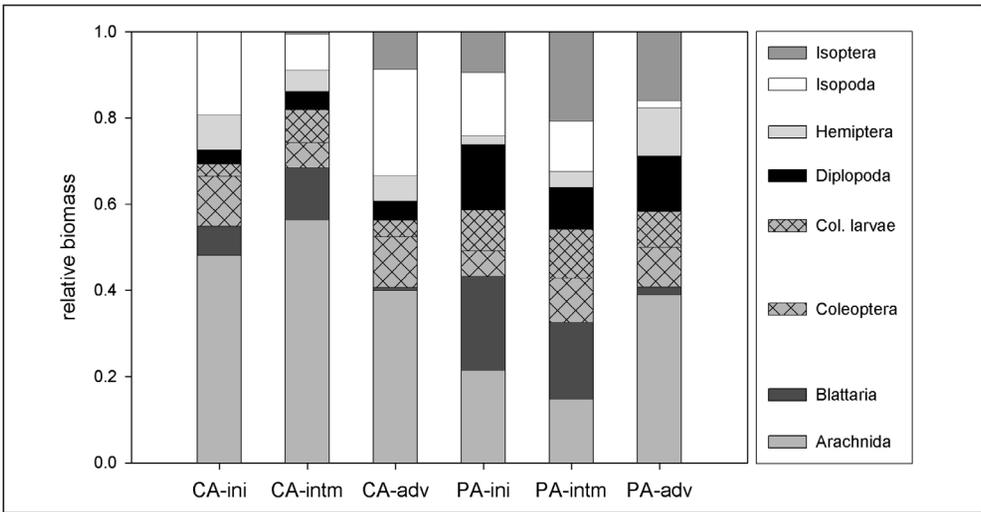


FIG. 3. Structure of the soil fauna community (biomass, arthropods without ants) in the six study sites (CA – Cachoeira forest, PA – Palmito forest, ini – initial stage, intm – intermediate stage, adv – advanced stage).

Microbial respiration. SIR and basal respiration were in the same range as in temperate forests (Anderson & Jörgensen 1997). In Cachoeira forest, soil basal respiration varied between 0.9 and 1.1 $\mu\text{L CO}_2 \text{ h}^{-1}$

g^{-1} soil, and differences between the stages were not statistically significant. SIR, however, decreased with increasing age of the forest (initial 17.0, intermediate 13.6, advanced 11.5 $\mu\text{L CO}_2 \text{ h}^{-1} \text{ g}^{-1}$ soil). Thus

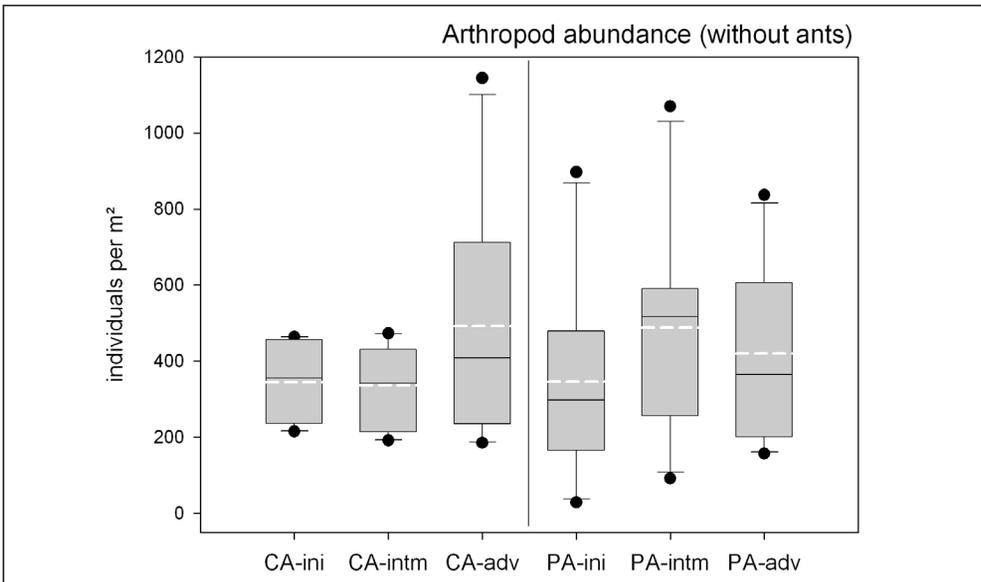


FIG. 4. Arthropod abundance (inds. m^{-2} , without ants) in the six study sites (box plots show medians, 25 and 75 % percentiles, 10 and 90 % percentiles and outliers; white dashed lines are means).

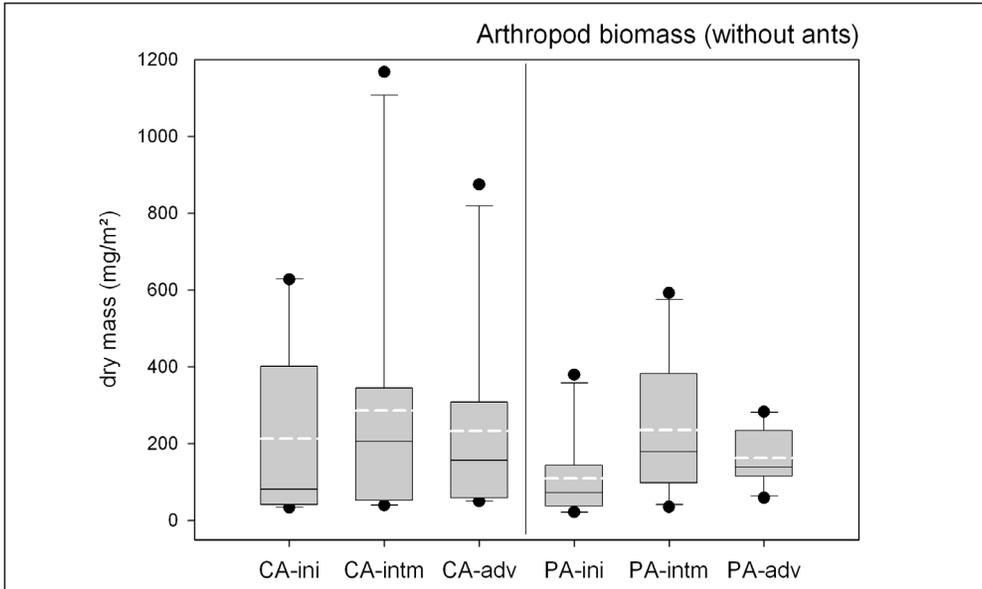


FIG. 5. Arthropod biomass (inds. m^{-2} , without ants) in the six study sites (box plots show medians, 25 and 75 % percentiles, 10 and 90 % percentiles and outliers; white dashed lines are means).

biomass specific respiration (qCO_2) calculated from SIR-based biomass and basal respiration was highest in the advanced stage. Basal respiration and SIR of soil from Palmito forest were higher than in Cachoeira forest and differed significantly between the three sites in the order initial < intermediate < advanced (SIR: 12.5, 56.0, 61.5 $\mu L CO_2 h^{-1} g^{-1}$ soil). The biomass specific respiration (qCO_2) increased slightly from initial (Cachoeira 0.13, Palmito 2.6 $\mu L CO_2 h^{-1} mg^{-1}$ Cmic) to intermediate (Cachoeira 0.18, Palmito 2.8 $\mu L CO_2 h^{-1} mg^{-1}$ Cmic), and strongly from intermediate to advanced stages (Cachoeira 0.23, Palmito 3.9 $\mu L CO_2 h^{-1} mg^{-1}$ Cmic).

DISCUSSION

The litterbag experiment demonstrated strong differences in decomposition rates of different litter species. Soil fauna did not influence the decomposition of the species *Andira anthelminthica* and *Sloanea guianensis*, since their leaves remained almost untouched in litterbags of all mesh sizes. Low k-values, and the lack of influence of the fauna at all sites, may be caused by recalcitrant substances in the leaves of these two species (as the name suggests, *Andira anthelminthica* is known as a remedy against parasiticial worms; see Lorenzi & Matos 2002). In any case,

leaves of both species show sclerophyllic characters. Lower decomposability of leaf litter in younger stages of secondary forests is indicated by several studies in the region. Boeger & Wisniewski (2003) report on a higher degree of sclerophylly in leaves of trees from the early successional stage in Palmito forest. Wisniewski (1997) calculated k-rates ($-\ln(\text{remaining mass after 1 year} / \text{initial mass})$) for mixed litter material exposed in coarse litterbags at the same Palmito sites as 0.51 (initial), 0.48 (intermediate), and 0.60 (advanced stage). These are rather low rates for tropical sites, indicating the resistant strength of most of the leaf material, resulting in litter accumulation of 9 t ha^{-1} (initial), 71 t ha^{-1} (intermediate), and 147 t ha^{-1} (advanced) (Wisniewski 1997). The amount of organic matter in the humus horizon, determined through soil incineration in a muffle furnace, also strongly increased from the initial to the advanced stage (13 %, 34 %, 59 %, Peña *et al.* 2005). Compared with the plots in the Palmito forest, the k-rates in the young succession stages of the sub-montane rainforest of the Mata Atlântica were either slightly higher at 0.68–0.95 for mixed leaf litter (Scheer 2006) or considerably higher (this study). The difference between the two study sites might go back to the very low pH of Palmito forest soils (2.9–3.8,

Wisniewski 1997) in comparison with the Cachoeira sites (pH 4.1–5.6, our measures). Also, sclerophylly is generally lower in the mesophyllic sub-montane forests (Boeger & Wisniewski 2003). The rapidly decomposed species *T. pulchra* was relatively rare at the Palmito forest sites, but is one of the most important plant species in sub-montane forests (Scheer 2006: 9 % of litter fall in younger stages and 24 % in older stages).

While basal respiration in the Cachoeira soil slightly decreased with the age of the stages, SIR showed an opposite tendency. This indicates that microorganisms in the old stage are less C-limited than those from younger stages, and that younger stages harbor a different microbial community that reacts faster to glucose amendment. Differences in microbial respiration and biomass between the stages at the Palmito sites are assumed to be mainly the result of differences in soil organic matter content (Peña *et al.* 2005). In both forest types the highest metabolic activity was found in the advanced stages, indicating that the nutrient status is less C-limited than in the initial and intermediate stages. Sampaio *et al.* (1993) have shown by modeling litterfall, litter layer losses, and mass transfer in a humid Neotropical forest that it takes many years until freshly fallen leaves are incorporated into the soil organic matter,

which further explains the C-limitation of young successional stages. Bihn *et al.* (2008a) explained different bait preferences of ants along a successional gradient in the region of Cachoeira by increasing nitrogen availability, which in fact is linked to a higher availability and quality of dead organic matter and thus C.

Since a strong and significant effect of the macrofauna on the decomposition rates of *Tibouchina pulchra* was proven for both forest formations and therefore, based on the assumption that at least some of the other leaf species will be accepted by soil fauna, we question our hypothesis of a strong influence of soil macrofauna on decomposition rates in young secondary forests of the Mata Atlântica. But the high biomass of the peregrine earthworms in the sub-montane forests is likely to mask the effect of the arthropod decomposers. Generally the abundance and biomass values of the macrofauna (except the ants) were rather low when compared with sites in the Brazilian Amazon region (Höfer *et al.* 2001), where abundances of 2500 inds. m⁻² (without ants) were frequent. The proportion of ants, on the other hand, was much higher in the forests of the Mata Atlântica than in Amazonian forests (Höfer *et al.* 2001).

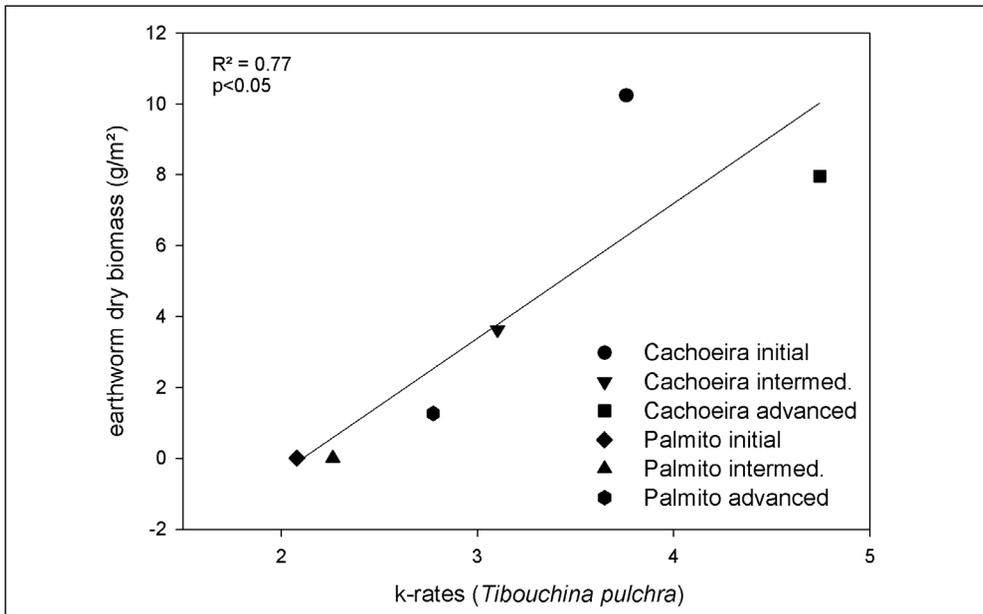


FIG. 6. Linear regression of k-rates (*Tibouchina pulchra*, coarse litterbags) versus earthworm biomass.

Though plant species diversity increased considerably with the age of the site (15, 23, 50 tree species in Palmito) there was no clear succession picture, i.e. change in community structure of the arthropod soil fauna. Rather unexpectedly, there are not even strong differences in abundance or biomass between the regeneration stages. Nevertheless, a few observations in combination with data from the literature and theory allow us to maintain our hypothesis of successional development of the soil fauna.

Increasing decomposition rates along the succession could be an effect of conditions independent of fauna colonization, like nutrient availability in leaves, amount of sclerophylly, or microclimate, but might also reflect faunal activity not visible in our samples and at the identification level of orders. Termites were distinctly more abundant in the advanced stages, where the amount of dead wood is higher (Wisniewski 1997). A study of the ant assemblage in different (replicated) succession stages in the Cachoeira forest revealed a nested pattern for the distribution of ant genera along the stages (Bihn *et al.* 2008b).

Earthworms, at least, seem to play an important role within the process of fauna-driven decomposition in the forest formations studied. In the submontane rainforest the biomass of earthworms was about 3–7 times higher than in the lowland forest, resulting in decomposition rates 1.4–1.8 times higher. The importance of earthworms in tropical soils has rarely been identified so clearly as in this study. On the other hand, our own collections of earthworms from now more than 30 sites in the study region show that a hypothetical original (autochthonous) earthworm fauna of the southern Mata Atlântica has disappeared and has clearly been replaced by the peregrine species *Pontoscolex corethrurus* (Römbke *et al.* 2005). This species has spread throughout the Neotropics during the European expansion and is actually colonizing plantations and secondary forests in Amazonia (Righi 1984, Zicsi *et al.* 2001, Brown *et al.* 2006b). The coastal region of Brazil was substantially colonized earlier than the Amazon region and, consequently, this species has been reported in almost every agricultural area of the Mata Atlântica for about 150 years (Müller 1857, James & Brown 2006, Sautter *et al.* 2006), including near-natural old-growth forests. Although obviously enhancing the decomposition rate, the value of *P. corethrurus* in these regenerating forests is still not certain. The species has already been associated with negative effects on soil structure (Barros *et al.* 2004), plant

production (Brown *et al.* 1999), and native earthworm communities (Lapied & Lavelle 2003).

The very low abundance and biomass of earthworms in all stages of the Palmito forest are readily explained by the sandy soils (90 % to 98 % sand; Wisniewski 1997). They dry out quickly in the upper part due to drainage, while in the lower part the high groundwater level leads to anoxic situations, both fatal conditions for worms. The lack of available nutrients (organic matter, C-limitation), due to the relatively low input (litter fall) from the sparse plant cover and very irregular (clumped) distribution of litter in the youngest stage, together with the high recalcitrance (Wisniewski 1997, Pinto & Marques 2003), might also negatively influence earthworm abundance (Lee 1985, Edwards & Bohlen 1996). Arthropod decomposers (cockroaches, millipedes) partly compensate for the lack of earthworms in Palmito forest. Termites possibly gain importance in this forest formation, while ants seem to have a low and possibly negative effect on decomposition rates. However the soil macrofauna, and not only the decomposers but also the very abundant predators (ants, arachnids), should have long-term effects on the availability of nutrients by their influence on the chemistry of litter and organic matter during decomposition (Blair & Crossley 1988, Heneghan *et al.* 1999, González & Seastedt 2001, Hunter *et al.* 2003), which is very important for the regeneration of forests in the Atlantic forest. Recently it has been shown that in the southern Mata Atlântica the recovery of diversity during succession from pastures to old growth forest needs 50 to several hundred years (Liebsch *et al.* 2008, Bihn *et al.* 2008b), and that the resource availability for soil animals changes along the succession (Bihn *et al.* 2008a).

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