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Original article

Litter manipulation and associated invertebrate fauna in secondary forest, central Amazonia, Brazil

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ABSTRACT

Plant litter from selected tree species has been used for improving soil productivity in low-input systems of secondary vegetation in Central Amazon, leading to different conditions for invertebrates. Soil invertebrate assemblages were monitored to test the effects of adding litter types of contrasting nutritional quality and periods of exposure on the development of the community. We established four second growth plots with 80 subplots of 3 m^2 from which the original litter was removed and replaced in 60 subplots. Twenty subplots received *Hevea brasiliensis* leaves, 20 others *Carapa guianensis* leaves, and another 20 an equal mixture of *H. brasiliensis*, *C. guianensis* and *Vismia guianensis*. Twenty subplots were left with the original litter. Litter and mineral soil (5 cm deep) sub-horizons were collected after 45, 100, 160, 240 and 300 days of exposure. The invertebrates were extracted using Kempson apparatus. At the day 210, the litter was replenished to match the surrounding litter. Regression analyses showed no significant effect of litter type, but the period of exposure did affect the community in both sub-horizons. Only after the litter replenishment, the type of litter and periods of exposure affected the community in the litter sub-horizon. Because we tried to isolate the effects of litter composition from other large-scale phenomena, several factors interfered in the experiment and potential problems were identified to optimize the investigation. The sampling design must be improved by using a larger number of subsamples for each kind of litter within each plot. Coarse parameters of Order and Family were suited to detect major environmental patterns on soil invertebrates, but taxonomic resolution to species and/or morphospecies is required to detect more subtle effects. Future manipulations should also be done on a longer time scale, and the replicates need to be spread over larger areas to capture the natural variations within the ecosystems.

1. Introduction

The litter system includes the above-ground litter which serves as energy source, a rich microflora dominated by fungi and the epigeic invertebrates and surface roots, which act as regulatory macro-organisms (Lavelle and Spain, 2001). The chemical composition of plant residues and the nature of the decomposer community play an important role in

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decomposition and nutrient availability to plants (Tian et al., 1993). Faunal influences are strongest in the tropics (Haneghan et al., 1998), and the amount and quality of the litter layer may control the diversity and action of important soil organisms (Crossley et al., 1992; Wall and Moore, 1999; Wardle et al., 1999). Since the use of such organic nutrients improves crop production (Tian, 1998), there is increasing interest in using plant residues for maximizing soil productivity in agricultural systems in the tropics which use low external inputs (Tian et al., 1992; Wanner et al., 1994). Applications of plant residues as mulch are known to attenuate the temperatures and retain higher soil moisture content (Lal et al., 1980), thus protecting the soil (Ross et al., 1990), in addition to providing food for soil animals. Above-ground manipulation, such as residue management or planting soil-cover vegetation has potentially important effects on soil arthropods (Paoletti et al., 1991; Wanner et al., 1994; Wardle et al., 1999; Sayer, 2006).

In Central Amazonia, a suitable crop association and the maintenance of adequate litter layer may be a more important management tool for the development of an abundant and diverse litter fauna than the quantity of inorganic fertilizers applied to a cropping system (Vohland and Schroth, 1999). In this region, edaphic organisms such as invertebrates, roots, and microflora play an important role in soil structural organization, both by building and destroying aggregates and altering their assemblage in the profile (Barros et al., 2004).

In Amazonia, the importance of ''capoeiras'' (local term for spontaneous secondary forests) for carbon accumulation in biomass and soil recovery is widely recognized (Williamson et al., 1998; Barlow et al., 2007), but this natural rehabilitation process may take several decades before the area is suitable for a new use. Improved fallows can be a good alternative to accelerate the natural process, partly by producing litter with higher nutritional value for the decomposer organisms. As part of the SHIFT project ENV-052 (Beck et al., 1998; Höfer et al., 2001), a polyculture system composed of rubber trees (*Hevea* spp.), ''paricá'' (*Schizolobium amazonicum* Huber), ''mogno'' (*Swietenia macrophylla* King) and ''andiroba'' (*Carapa guianensis* Aubl.) was compared to a natural ecosystem (primary forest) in central Amazonia. The polyculture was enriched by planting rows of four selected valuable native tree species, just after the initial burn treatment, growing together with the spontaneous secondary vegetation after initial burn treatment. The structure and function of soil fauna communities in these ecosystems were studied in parallel studies by Franklin et al. (2001, 2004), Höfer et al. (2001), and Martius et al. (2004a,b).

There is little experimental data on the consequences of varying above-ground substrates (litter manipulation) on soil invertebrate communities in the tropics (Sayer, 2006). Also, studies on the effect of second growth enrichment with valuable tree species and its consequent litter mixture with better nutritional value are not known in the Amazon up to date. Most leaf-decay experiments use litter enclosed in nylon mesh-bags, which may exclude some faunal groups (Coleman et al., 2004), and have several limitations as a method of measuring litter decomposition (Hector et al., 2000). In Central Amazonia, mesh-bags create an artificial and moister environment, thus influencing the decomposition rates (Franklin et al., 2004), indicating the need to perform field studies on litter dynamics and associated fauna in nearly natural conditions. In the present study, we manipulated litter in four plots of secondary forests of similar structure, to study the effect of adding four contrasting substrates (litter of distinct nutritional value) in the development of soil invertebrate communities after 45, 100, 160, 240 and 300 days in the litter and mineral soil (5 cm deep) sub-horizons. The periods of exposure before and after litter replenishment at 210 days were also evaluated.

2. Materials and methods

The investigation was made during November 1998–October 1999 in an abandoned rubber tree (*Hevea brasiliensis*, ''seringueira'') plantation, located at the Experimental Station of ''Embrapa-Amazônia Ocidental'', 29 km north of Manaus, in Central Amazonia, Brazil (3°8′S; 59°52′ W), about 44–50 m a.s.l. Accumulated rainfall was 3000 mm during the period. From January to June, the monthly rainfall varied from 270 to 430 mm, with 17–25 rain days, and the daily temperature from 26 to 27 °C. During the dry season (July–November), the monthly rainfall varied from 79 to 260 mm, with 12–23 rainy days, and the daily temperature from 26.5 to 28.5 °C (Meteorological Station of Embrapa/CPAA, Manaus, Amazonas). Rainy days were considered those days with the rainfall volume greater than the average daily evaporation (Medina et al., 1978). The microclimatic records, litter stock and decomposition rates in the neighboring experimental areas were studied by Martius et al. (2004a,b).

Originally, the area was dominated by dense primary lowland rainforest (''terra firme'') (Klinge et al., 1975) on nutrient-poor soils classified as Yellow clayey Latosol (FAO: xanthic Ferralsol). The primary forest of the experimental area was cleared and burned in 1970, but it was not used. The secondary forest grew naturally until 1980, when the vegetation was removed using tractors, displacing the superficial soil layer, to establish a rubber tree plantation. The plantation was fertilized during 5 years, and then abandoned, after been severely affected by the fungus *Microcyclus ulei*, thus growing together with the spontaneous secondary growth. In 1992, the 8-year old secondary vegetation and the surviving rubber trees were again cut and burned. Since then, the area of 17 ha was divided into 90 plots of 32 × 48 m each (Fig. 1A), to grow mono- and poly-cultures, interspersed with plots of secondary forest as fallow lands. This area has been used for a cooperative agroforestry research program between the Embrapa-Amazônia Ocidental, Manaus (Brazil) and the Institute of Applied Botany, University of Hamburg (Germany) (Lieberei and Gasparotto, 1998). To develop the present study, we choose four plots (32 × 48 m) of 7-year old secondary forests (''capoeira''; Fig. 1B) among the 90 plots. The plots have similar forest structure and during the study period they were dominated by *Vismia guianensis*, as usually occurs on areas that suffered mechanization or more intense use of soil in Amazonia (Williamson et al., 1998), *Miconia* spp., and *Bellucia* spp. Within the plots, 80 randomly distributed subplots of 3 m^2 were established. In each one of the four plots, 20 subplots of 3 m^2 were randomly selected (Fig. 1C). Twenty subplots were left with the native litter (C:N ratio = 42; soluble components = 13.8%) as controls. This native litter was composed by a mixing of several plant

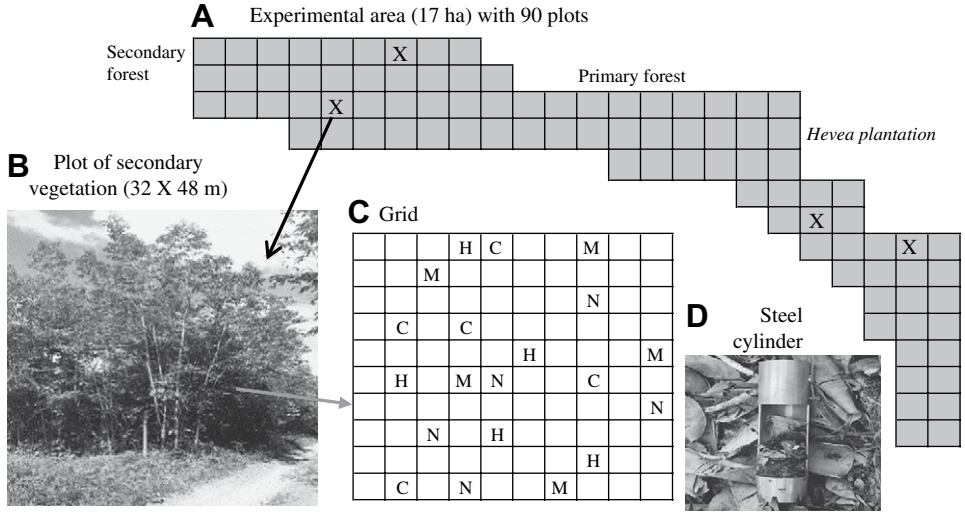

Fig. 1 – (A) Layout of the experimental area showing 90 plots and the position of the plots of secondary forest (×); (B) plot of secondary forest; (C) layout of the grid installed in each plot, showing an example of a random position of 20 subplots (C = *Carapa guianensis*; H = *Hevea brasiliensis*; M = mixed litter; N = native litter); (D) steel cylinder showing the litter and soil sub-horizons. Images: Project SHIFT ENV-052.

species, mainly *V. guianensis*, *Miconia* spp., *Bellucia* spp. and *Cecropia* spp., among 200 species of vascular plants which can be found in the area (Preisinger et al., 1998; Martius et al., 2004a). *Vismia* spp. would represent 40–45% of total litter in the four selected plots. The original litter was removed and replaced in the remaining 60 subplots. Twenty subplots received leaves of *H. brasiliensis* (C:N ratio = 23; soluble components = 26.8%), 20 others received leaves of *C. guianensis* (C:N ratio = 37; soluble components = 19.2%), and another 20 an equal mixture (on dry weight basis) of *H. brasiliensis*, *C. guianensis* and *V. guianensis* (C:N ratio = 34; soluble components = 19.5%). The species *H. brasiliensis* and *V. guianensis* were selected because they are frequent species in the polyculture systems, and represented contrasting litter (soft and small leaves *vs.* big and coriaceous leaves). Thus, they could indicate the potential role of introducing valuable tree species to the spontaneous second growth following land abandonment in the Amazon region, resulting in an enrichment of native litter by continuously adding leaves with better or differential nutritional value to the soil surface.

To estimate the initial litter stock on the surface and the amount of litter to be added at the beginning of the experiment, the original litter sub-horizon in the secondary forest plots was measured at the end of the dry season of 1998. Seventy-two litter samples were taken at random surrounding the subplots, from 20 × 20 cm quadrats, and the result extrapolated for a subplot of 3 m^2, resulting in 377 g (dry weight) of *H. brasiliensis* and *C. guianensis* leaves and 126 g (dry weight) of each leaf type added to the mixture treatment. The leaves were air dried and weighted. In the subplots, except the natural litter subplots and the remaining area of the plots, the original loose litter layer was removed, to simulate the perturbation occurred when a plot is prepared for agricultural use in the region, and then replaced by the new substrates.

All subplots, including controls, were covered with nylon netting (2 mm mesh) and the newly fallen litter on the nylon covering was removed weekly. The plots were surrounded by a nylon netting 'fence' (2 mm mesh; 10 cm high) in order to retain the substrate within the subplot.

When the added litter substrates reached half of their initial weight, a replenishment of new litter was made in the treatments, in order to match the surrounding litter sub-horizon of the secondary forest. The replenishment occurred after 210 days (July 28th, 1999), and the amount of dried leaves added was equivalent to the difference between the initial weight and the average of the litter weight loss. The replenished litter was prepared in the same way as in the initial addition, 7 months before. Litter replenishment was made because the remaining stocks of the fast-decomposing litter (*H. brasiliensis*) were too low, causing local alteration (less available substrate to soil animals, as well as lower soil protection and moisture), masking potential effects of litter additions in the last sampling periods.

Samplings of litter and soil sub-horizons were done after 45 (February), 100 (April), 160 (June) 240 (August), and 300 (October) days of exposure. The first two periods represented the wet season, the third the transition to the dry season, and the last two periods corresponded to the dry season.

Soil animal assemblages were monitored to test the effects of different qualities of the litter on the development of the invertebrate community during five periods of exposure. In each period, for each kind of litter treatment, one subplot was selected in each secondary forest plot, and two samples were randomly taken within the subplot using a steel cylinder measuring 6.4 cm in external diameter, to a depth of 5 cm in the mineral soil. The cylinder was then opened to separate the sample into litter and mineral soil sub-horizons (Fig. 1D). The invertebrates were extracted using Kempson apparatus (Kempson et al., 1963). The material was placed in sieves measuring 8 cm in diameter and 5 cm in height, with a mesh size of 1.5 mm having four holes of 4 mm, to allow the active extraction of larger animals. The sieves were placed on the

top of the container with the killing-preserving agent (one part of saturated picric acid solution to three parts of water plus detergent). After the extraction, the animals of each two samples taken in each subplot were pooled together to make a compound sample.

We classified the invertebrates within taxonomic levels of Class, Sub-class, Order, Sub-order or Family. Acari were sorted into Oribatida and non-Oribatida. Diptera, Coleoptera, Hemiptera–Homoptera, Hemiptera–Heteroptera and Thysanoptera were separated into adults and juveniles. Hymenoptera was sorted into ants and other Hymenoptera. The sampling method was not efficient to catch Nematoda, Enchytraeidae and invertebrates larger than 1 cm.

For comparison of the means of the invertebrate population between periods of exposure in the litter and soil sub-horizons we calculated Tukey's significant differences, using Bonferroni adjustment. We used ordination methods to summarize the major patterns in the data, undertaken in the Non-Metric Hybrid Multidimensional Scaling (SSH-NMDS) module of the PATN Program (Belbin, 1992). This method is a graphical representation (''ordination'') of dissimilarities between objects in as few dimensions (axes) as possible. The *a priori* decision was made to use two dimensions (SSH1 and SSH2), to capture the major gradients. We tested whether substrate or period (before or after replenishment) significantly affected species composition. In order to avoid a strong influence of the more numerically dominant taxa on the analysis, ordinations were produced for $\log(x+1)$ transformed quantitative data. The Bray–Curtis Association Index was used to indicate the dissimilarity between the samples. Ordination with NMDS and the Bray–Curtis distance is generally effective at detecting ecological gradients (Kenckel and Orloci, 1986; Minchin, 1987) and it is well suited to soil fauna (Caruso et al., 2005). A measure of 'stress' and r^2 statistic was calculated. The r^2 statistic is descriptive of the proportion of the variance in the original distances captured by the ordination and is generally comparable among analyses. The smaller the stress value, the better the fit of the reproduced distance matrix to the observed distance matrix (Clarke, 1993).

Five periods of exposure were analyzed initially. However, taking into consideration that the replenishment litter sub-horizon at 210 days from the beginning of the experiment affected the invertebrate community, we compared two periods before (45 and 160 days) and after (240 and 300 days) the replenishment. We used MANOVA to test the effects of adding four substrates on the development of invertebrate communities, and also the effects of periods of exposure.

3. Results

3.1. Abundance and diversity of the invertebrates in the decomposing litter

Forty-two faunal community variables (taxa) were found (Appendices I and II). In the litter sub-horizon, Acari Oribatida, Acari non-Oribatida and Collembola were the most abundant and frequent groups, followed by Diplopoda, Diptera juveniles, Araneae, Coleoptera adults, Coleoptera juveniles and Formicidae. In the mineral soil, Acari and Collembola also presented the highest abundance and frequency, followed by Diplopoda, Pauropoda, Protura, Symphyla, Araneae, Diplura, Pseudoescorpionida, Coleoptera adults, Coleoptera juveniles and Formicidae.

In the total for litter and soil sub-horizons, the whole populations of invertebrates were higher in miniplots covered with leaf of *H. brasiliensis* leaves (8358 individuals), followed by native litter (7749), mixed litter (6079) and *C. guianensis* (5284). Considering only the litter sub-horizon, the native litter supported highest populations (52% of total fauna for litter and soil sub-horizons) against 36% in *H. brasiliensis*, 40% in mixed litter, and 28% in *C. guianensis*. Overall, the number of invertebrates in the soil sub-horizon was greater than in the litter sub-horizon (mean ± SD $\log(x+1)$; litter: 1.844 ± 0.450 individuals; soil: 2.160 ± 0.305; $t = -5.188$; $df = 139.0$, $P < 0.001$).

In the litter sub-horizon, the most accentuated weight loss was always registered for *H. brasiliensis* litter followed by mixed litter, *C. guianensis* litter and native litter. In all litter substrates, the most accentuated weight loss coincided with the period of highest precipitation and lower temperature (Fig. 2). The abundance of invertebrates for the whole period of the experiment was not significantly different among the substrates in both sub-horizons (ANOVA, litter: $F_3 = 1.061$, $P = 0.371$; mineral soil: $F_3 = 1.833$, $P = 0.148$).

In all substrates, the invertebrate populations in the litter sub-horizon were higher in the first three periods. In the soil sub-horizon, an inverse pattern was detected in the substrates composed by *H. brasiliensis* leaves and native litter, whose invertebrate populations were higher in the last two periods (Fig. 3). Using Tukey's test, and applying Bonferroni adjustment, we did not detect a significant effect of sampling period for both sub-horizons.

3.2. Comparing types of leaves and periods of exposure

In the litter and soil sub-horizons, multivariate multiple regression data indicated no statistically significant effect of the litter type on the invertebrate composition (litter: MANOVA; Pillai Trace = 0.466, $P = 0.332$; soil: MANOVA; Pillai Trace = 0.311, $P = 0.626$).

However, the period of exposure did affect the community in both sub-horizons (litter: MANOVA; Pillai Trace = 0.040, $P = 0.012$; soil: MANOVA; Pillai Trace = 1.273, $P = 0.001$). For the litter sub-horizon, the variation was principally on the NMDS axis 1 (ANOVA; $F_{4,\ 12} = 5.60$; $P = 0.009$; stress: 0.310, $r^2 = 0.623$) (Fig. 4), and the separation was clear mainly within the period corresponding to 300 days of experiment, which represented a characteristic community. For the soil, the variation was principally on the NMDS axis 2 (ANOVA; $F_{4,\ 12} = 12.283$; $P < 0.001$; stress: 0.337, $r^2 = 0.571$) (Fig. 4), and the separation was clear mainly within the period corresponding to 45 and 160 days.

3.3. Comparing periods of exposure before and after litter replenishment

Before litter replenishment (i.e. 45 and 160 days) in the litter sub-horizon, the regression data indicated that the litter type (MANOVA; Pillai Trace = 1.377; $P = 0.179$) and the periods of exposure (MANOVA; Pillai Trace = 0.220; $P = 0.780$) did not

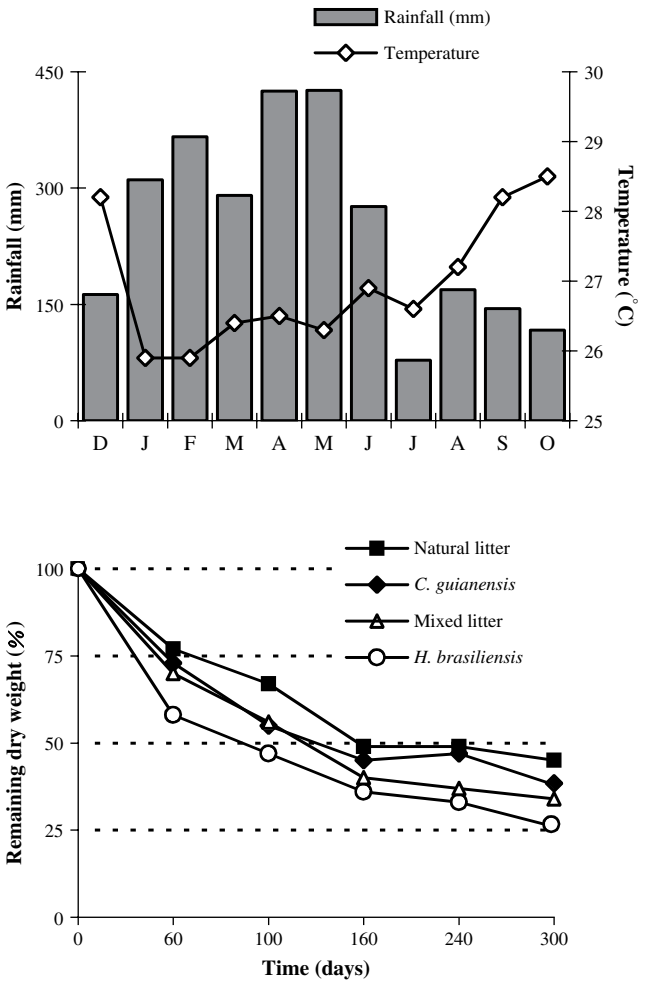

Fig. 2 – Monthly rainfall and mean temperature during the study period (December 1998–October 1999) and remaining dry weight (%) in relation to the initial weight of litter after five periods of exposure. Data after Silva (2000) and Mota (2003). Note that except for the period corresponding to 60 days of exposure corresponding to February, the remaining periods are equivalent to the period of this study: 100 (April), 160 (June), 240 (August) and 300 (October) days of exposure.

affect the invertebrate community. In the soil sub-horizon, the invertebrate community also did not differ neither among litter types (MANOVA; Pillai Trace = 0.615; $P = 0.827$), nor among periods of exposure (MANOVA; Pillai Trace = 0.925; $P = 0.075$). However, the low value of the null hypothesis associated with period ($P = 0.075$) and a significant difference on axis 2 (ANOVA; $F_{1,\ 3} = 25.87$; $P = 0.015$) in individual analyses of each axis indicate a possible type II error (acceptance of null hypothesis when it is false).

After litter replenishment (240 and 300 days) in the litter sub-horizon, all litter types were significantly different from each other (MANOVA; Pillai Trace = 1.876; $P = 0.002$), and the variation was found on both axes (ANOVA; SSH1: $F_{3,\ 3} = 18.94$; $P = 0.019$; SSH2: $F_{3,3} = 11.16$; $P = 0.039$; stress: 0.216, $r^2 = 0.804$) (Fig. 5). There were also differences among both periods of exposure (MANOVA; Pillai Trace = 0.976; $P = 0.024$), and variation was detected on both axes (ANOVA; SSH1: $F_{1,\ 3} = 31.86$; $P = 0.011$; SSH2: $F_{1,\ 3} = 25.22$; $P = 0.015$). The pattern detected was a decreasing abundance from 240 days to 300 days in all litter types. In the mineral soil, neither the litter type (MANOVA; Pillai Trace = 0.796; $P = 0.686$) nor the periods of exposure (MANOVA; Pillai Trace = 0.010; $P = 0.990$) affected the invertebrate community.

4. Discussion

Unexpectedly, in comparing the five periods of exposure there were no significant differences between the litter types, showing that the invertebrate communities were generally similar, independent of the texture and nutritional quality of the leaves. However, the influence of the periods over the invertebrate community was detected both in the litter and soil sub-horizons. Before the litter replenishment (i.e. 45 and 160 days), a possible difference ($P = 0.075$; quantitative data) was detected between periods in the soil, meaning that the pattern was not strong enough to capture the influence of the treatments. Only for the periods after the replenishment (i.e. 240 and 300 days) differences among litter types and periods of exposure in the litter sub-horizon were detected. To explain this factor, in these last two periods, there was a reversal of the invertebrate's density among the litter and soil sub-horizons: density in the soil was higher than in the previous periods. These periods correspond to the dry season in the region and the reduction of precipitation can be another reason for such results. Although it was not measured in the present experiment, we also suppose that during unfavorable microclimatic conditions, a short-term vertical migration of the invertebrates can occur, as already registered for mesofauna (Franklin et al., 2001) and macrofauna (Martius et al., 2004b) in the same experimental area.

Despite the limited differences observed among litter types, it is worthy to notice that total invertebrate population in the two upper layers considered here (litter + surface soil) was ~8% greater in the subplots with addition of *H. brasiliensis* than in subplots with native litter (control). On the other hand, subplots with *C. guianensis* had a total population ~32% lesser than in the control. These results may be related to the nutritional quality of the substrates, *H. brasiliensis* being of finer texture and better quality than *C. guianensis* and, thus, easier to decompose and to release carbon and nutrients.

It is difficult to interpret the results produced by manipulative experiments since the depth and structure of the manipulated litter layer can significantly affect the arthropod density (Chen and Wise, 1999). The lack of a clear response should not be a surprise since litter manipulation experiments made over 150 years have shown contrasting results regarding different aspects and functions of the litter layer (Sayer, 2006).

Quantitative changes to the litter layer affect the population dynamics and community structure of soil animals that in turn affect the breakdown of organic matter and its incorporation into the soil (Hector et al., 2000; Sayer, 2006). In this experiment, the initial amount of litter added to each subplot was equivalent to the mass of the native litter sub-horizon sampled during the early dry season of 1998. In this period, the litter sub-horizon was likely low because the

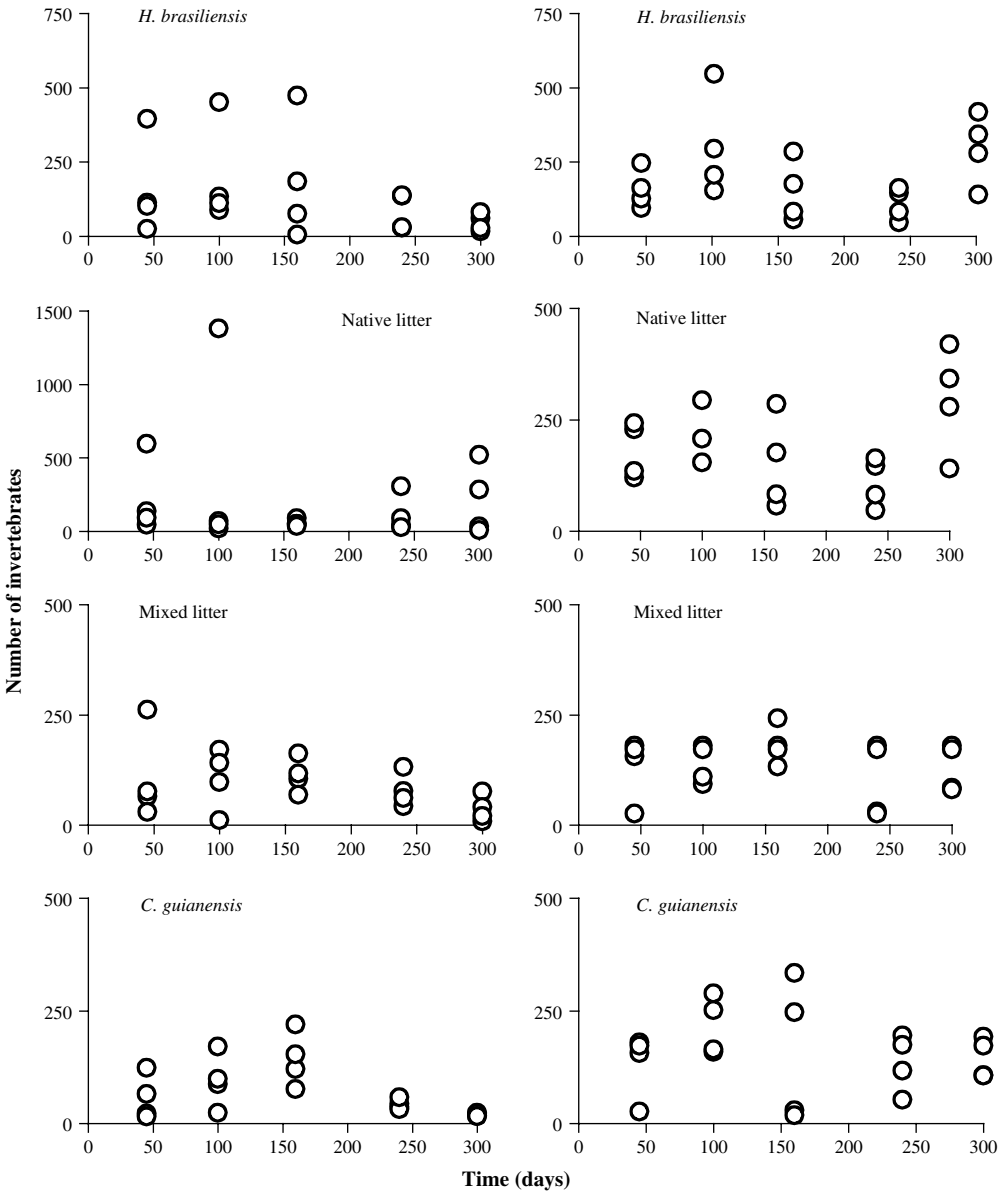

Fig. 3 – Total number of invertebrates sampled in the litter (left column) and in the soil (right column) sub-horizons in the plots of secondary forest, under four leaves substrates (mixed litter; *H. brasiliensis*; *C. guianensis*; native litter) at five periods of exposure. At the day 210 the litter was replenished. Note differences in scales.

decomposition was enhanced during the previous rainy period in the rainforest (Luizão and Schubart, 1987; Cornu et al., 1997). We suppose that the amount of litter added in the manipulated substrates may not have been enough to maintain or enhance the original soil invertebrate community.

Roots and living organisms play important role in the recycling of nutrients in Amazon forest ecosystems (Chauvel et al., 1987), but roots are often a neglected component of the litter system in humid climates (Lavelle and Spain, 2001). In central Amazonia, the organic matter input to soil through fine roots (up to 5 cm in diameter) can be equivalent to fine litter fall produced in forest systems (Luizão et al., 1992) and, therefore, it would have affected the soil microorganisms, as microbial activity is limited by its relative immobility and its high sensitivity to environment constraints (Lavelle and Spain, 2001). The microbial biomass of the present manipulation experiment was evaluated by Silva (2000), who concluded that the treatment with a mixing of various litter types (mixed litter) showed soil microbial biomass significantly higher than the native litter. Apart from litter, soil microbial biomass was likely fueled by organic carbon inputs from roots which in all treatments likely belonged mainly to *V. guianensis*, the dominant pioneer species which has vegetative propagation through its root system (Preisinger et al., 1998). Although it was not measured, we suppose that fine root growth had also affected the soil invertebrates, which respond to the growth of the microbiota. Both fine root and microbial biomass are affected by soil moisture (Luizão et al., 1992) which in turn is influenced by the litter cover (Ross et al., 1990). In the present experiment,

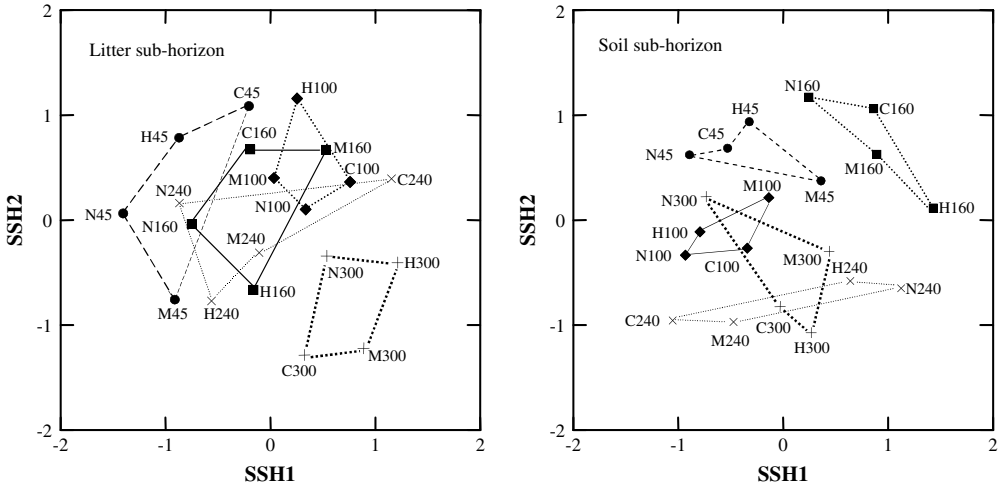

Fig. 4 – SSH-NMDS ordination of the survey data from the litter and soil sub-horizons in four plots of secondary forest. Symbols represent leaf substrates (C = *C. guianensis*; H = *H. brasiliensis*; M = mixed litter; N = native litter) and periods of exposure (days): 45 (●), 100 (◆), 160 (■), 240 (×) and 300 (+). Different pattern of lines shows the grouping according the periods of exposure.

the replaced litter was probably insufficient to produce better conditions for fine root growth and its associated organisms. The area covered by each manipulation (3 m^2) was small and, besides the effects of roots, the effect of migration of fauna from surrounding area may have masked any endogenous change within the treatments.

It is also possible that the duration of our experiment (300 days) was not enough to quantify the effects of the manipulated substrates, which may appear only after several years (Tian et al., 1992; Wardle et al., 1999). A former pioneer study, in primary forest of central Amazon (Ducke Reserve, near Manaus city), has shown that a lag phase occurs for faunal colonization of litter added to the system, even in the case of maintenance of the native litter (Höfer et al., 1996). It implies that a long period is required for detecting changes in the invertebrate fauna in case the original litter is removed and replaced as in the present study (Wardle et al., 1999), even though under natural conditions in central Amazon, it has been shown that the effect of the fauna on decomposition rates is noticeable in less than 1 year (Luizão and Schubart, 1987; Cornu et al., 1997; Luizão, 2004).

Apparently, the replenishment of the original and semi-decomposed litter sub-horizon by an equal weight of leaves was not beneficial to the soil organisms, failing to enhance their activities. This suggests that a retrieval of the litter sub-horizon from a neighboring forest site for agricultural uses should leave the old broken litter and root mat on site in order not to disrupt the biological activity of the forest soil. Besides the intimate relationship between environmental conditions and spatial distribution of soil animals (Caruso et al., 2005), soil animals can move and make their own choices (Eijackers, 2001), even thought discrete changes in

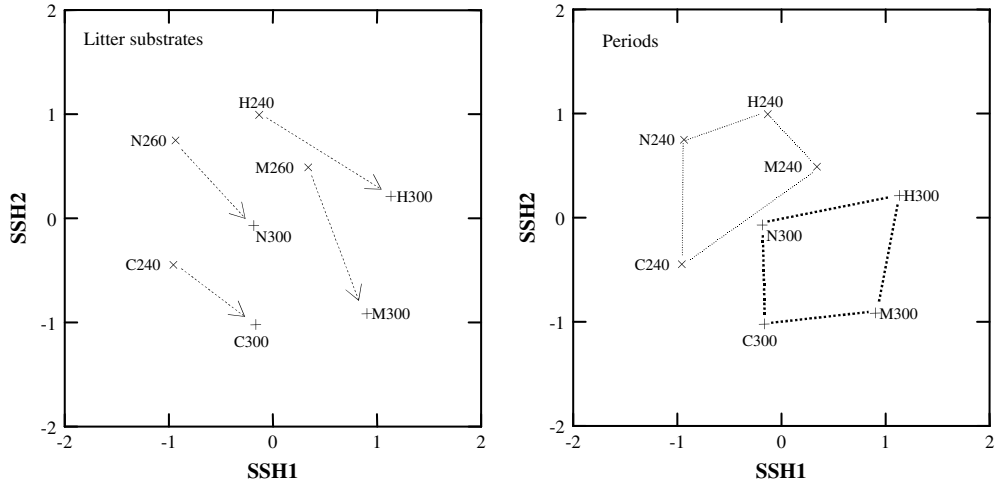

Fig. 5 – SSH-NMDS ordination of survey data from four plots of secondary forest in the litter sub-horizon, showing differences among leaves substrates and among periods (punctuated seta show unidirectional pattern of changing). Symbols represent leaves substrates (C = *C. guianensis*; H = *H. brasiliensis*; M = mixed litter; N = native litter) and periods (days) after exposure: (×) 240 and (+) 300.

soil and plants can be broad transition zones for many invertebrate taxa, which do not perceive these changes in the same way that environmental managers do (Dangerfield et al., 2003). This would be the case of the fauna already installed before the litter replenishment, which could have either moved away or migrated vertically into soil profile.

In the Brazilian Amazonia, coarse parameters of Order and Family were suited to detect major environmental patterns for the soil invertebrates, like the influence of the system context of plant species on the litter and litter fauna in agroforestry and monoculture plantations (Vohland and Schroth, 1999), the changes on soil fauna communities following deforestation and subsequent land-use systems (Höfer et al., 2001), the effects of land-use (Barros et al., 2002), and the main differences of the spatial variation in community structure in savanna (Franklin et al., 2005). Otherwise, soil communities are collection of organisms and species will respond individualistically to temporal and spatial variation (Levin, 2005). For example, it has been showed that coarse parameter was not suitable for evaluating the effect of environmental change on soil Collembola (Pflug and Wolters, 2001). Habitats' partitioning occurring at species level is very complex, and our results are not showing the differences among species. We suppose that taxonomic resolution to species and morphospecies will improve our ability to detect the effects of litter manipulation on the associated invertebrate fauna.

We identified potential problems in following the research procedure. Therefore, we can use these results to optimize the sampling design in order to maximize our ability to detect the effects of different litter qualities on the development of the invertebrate community. The sampling strategy can be improved by using a larger number of subsamples for each kind of litter within each plot to increase the chance to detect an effect of the added substrates. In our experiment, we tried to isolate the effects of litter composition from other large-scale phenomena, such as root production by trees and the general ecosystem processes that affect the site. Even thought the scale of study was similar to other experiments involving soil organisms in central Amazonia (Höfer et al., 1996, 2001; Beck et al., 1998; Vohland and Schroth, 1999; Franklin et al., 2001, 2004; Barros et al., 2004; Martius et al., 2004a,b), one major conclusion is that the scale was too small for our objectives, and it is not possible, or desirable, to isolate leaf-litter decomposition from other ecosystem processes. Thus, future manipulations should be done on much larger scale so that their effects on ecosystem processes can be evaluated, and the replicates need to be spread over much larger areas to realistically capture the natural variations in Amazonian ecosystems. Overall, the time scale of the present work (less than 1 year long) was not enough to produce more significant changes in litter layer and surface soil, matching those expected to occur after several years of growing valuable tree species together with the spontaneous second growth following land abandonment.

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Appendix I

Relative abundance and frequency of the soil invertebrate groups sampled on the litter layer under four substrates (native litter, mixed litter, *H. brasiliensis* and *C. guianensis*) in four plots of secondary forest after 45, 100, 160, 240 and 300 days of litter exposure. The abundance is categorized as 5 (> 10%), 4 (> 5%, < 10%), 3 (> 2%, < 5%), 2 (< 2%, > 1%) and 1 (< 1%). The parenthesis indicates relative frequency higher than 50% (presence in at least two of the four plots of secondary forest studied)

Invertebrate groups	Native litter					Mixed litter					*H. brasiliensis*					*C. guianensis*				
	Time (days)																			
	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300
1 Acari non-Oribatida	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
2 Acari Oribatida	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
3 Araneae	1	(1)	1	1	(1)	(1)						1				(2)		1		2
4 Chilopoda				1								1	1							
5 Coleoptera adults	1	(1)	(1)	1	1		(1)	1	1		1	(1)	(1)	1		(1)	1	1	1	
6 Coleoptera immatures	1	1	1	1	1	(1)	1		(2)	(2)	(1)	1	(1)		1		1			2
7 Collembola	(5)	(5)	(5)	(5)	(5)	(4)	(4)	(5)	(5)	(4)	(4)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
8 Crustacea (Copepoda)	1	1	1				1	1	1			1		(1)		2	1	(1)		
9 Crustacea (Ostracoda)[a]																				
10 Dermaptera	1																			
11 Diplopoda	(1)	(1)	3	1	(2)	(2)	(4)	2	1		(1)	(1)	1	(2)		1	(3)	1	2	
12 Diplura	1	1	1				1	1			1		(1)			(2)	2	1		
13 Diptera adults	1			(1)		1	1	1			1		1	(1)	1	1		1		

(continued on next page)

Appendix I (*continued*)

Invertebrate groups	Native litter					Mixed litter					*H. brasiliensis*					*C. guianensis*				
	Time (days)																			
	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300
14 Diptera immatures		(1)	2	1	1		2	(2)	1			1		1	(2)			1	2	
15 Enchitraeidae	1										(1)									
16 Formicidae	(2)	1	(2)	(1)	(1)	(4)	1	(1)	(2)		(1)	(1)	(1)	(2)	1	(2)		(1)	(2)	(4)
17 Hemiptera–Heteroptera adults	1	1	1	1			1											1		
18 Hemiptera–Heteroptera immatures	1	1	1	1	1	1											1			
19 Hemiptera–Homoptera adults	(3)	1		1				1			1	2								
20 Hemiptera–Homoptera immatures		1			1		1		1	2		1			1			1		
21 Hymenoptera non-Formicidae		1			1		1					2		1		(1)	1			
22 Isopoda	1	1					1				1					1	1		1	2
23 Isoptera	5		1																2	
24 Lepidoptera	1					1									1					
26 Lumbricidae	1		1			1		1			1		1				1			
27 Nematoda[a]																				
28 Onychophora											1									
29 Blattodea												1				1		1		
30 Orthoptera											1									
31 Palpigradi[a]																				
32 Pauropoda	1	1	1			1	1	1	1		(1)	2	1		1		1	(1)		
33 Phalangida			2	1														1		
34 Protura	1	1				1			1	2	1		(1)	(1)				1		
35 Pseudoscorpionida	2		(2)	1		1	1		1	1	1	1	1	1		(3)		1		
36 Psocoptera	1		1	1	(1)			1	1		2		1	1		1				2
37 Ricinulei							1													
38 Symphyla		1		2	1	1	1	(1)	1		(1)	(1)			1		1	1	2	
39 Thysanoptera adults		1			1		1			3		1				(1)	1		1	1
40 Thysanoptera immatures	1		1	1										1						
41 Thysanura						1														
42 Trichoptera[a]																				

a Taxa recorded only in the soil layer.

Appendix II

Relative abundance and frequency of the soil invertebrate groups sampled from the upper soil layer (5 cm) under four substrates (control, mixture, *H. brasiliensis* and *C. guianensis*) in four plots of secondary after 45, 100, 180, 240 and 300 days of litter exposure. The abundance is categorized as 5 (>10%), 4 (>5%, <10%), 3 (>2%, <5%), 2 (<2%, >1%) and 1 (<1%). The parenthesis indicates relative frequency higher than 50% (presence in at least two of the four plots of secondary forest studied)

Invertebrates groups	Native litter					Mixed litter					*H. brasiliensis*					*C. guianensis*				
	Time (days)																			
	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300
1 Acari non-Oribatida	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
2 Acari Oribatida	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
3 Araneae	2	1	1	1	1	1	(1)		(1)	(1)		2	1	1	1	1	(1)		(1)	(1)
4 Chilopoda			1			1	1	1		1	1	1		1		1		(1)	1	
5 Coleoptera adults	1	1	(1)	1		(2)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)	(1)		(1)	1
6 Coleoptera immatures	(1)				(1)	(2)	1		1	(1)	(1)	(1)		(1)	(1)	(2)	1	1	(1)	(1)
7 Collembola	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
8 Crustacea (Copepoda)			(1)	1		1	1	1					1					1		
9 Crustacea (Ostracoda)				1																
10 Dermaptera[a]																				
11 Diplopoda	(2)	(2)	1	1	(1)	1	(3)	(1)	(2)	2	(3)	(1)	(1)	1	(3)	(2)	(4)	1	(1)	(2)
12 Diplura	(2)	(2)	(1)	(3)	(1)	(3)	(1)	(1)	(2)	(1)	2	1		2	2	(2)	3	(3)	(1)	(2)
13 Diptera adults				1					1			1			1			1	(1)	1
14 Diptera immatures				1				1						1				1		

Appendix II (*continued*)

Invertebrates groups	Native litter					Mixed litter					*H. brasiliensis*					*C. guianensis*				
	Time (days)																			
	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300	45	100	160	240	300
15 Enchitraeidae				1																
16 Formicidae	(3)	(3)	(1)	(2)	(1)	(2)	(1)	(2)	(2)	(3)	(2)	(1)	(2)	(2)	(1)	(1)	(1)	(1)	(1)	(4)
17 Hemiptera–Heteroptera adults	1	1	1		1	1		(1)			1		1		1	1				
18 Hemiptera–Heteroptera immatures								1		1			1						1	
19 Hemiptera–Homoptera adults	(2)	1				1				1			1			(1)				
20 Hemiptera–Homoptera immatures		1	1	(2)					1	2		1			(1)		1			(1)
21 Hymenoptera non-Formicidae			1	1					1				1		1					
22 Isopoda	1	1	1					(1)		1	1					1	1			
23 Isoptera		2		(2)								1	3	1	3				(1)	1
24 Lepidoptera						1									1				1	
25 Lumbricidae			1	1				(1)		1	(1)		1	1	1	1				
26 Nematoda						1														1
27 Onychophora[a]																				
28 Blattodea												(1)	1			1				
29 Orthoptera[a]																				
30 Palpigradi											1								1	
31 Pauropoda	(1)	(3)	(1)	(2)	(3)	(1)	(2)	(2)	(1)	(3)	1	(3)	1	(2)	(1)	(2)	(3)	(2)	(1)	(3)
32 Phalangida										1					1					
33 Protura	1	(3)	1	1	(2)	(2)	(1)	(1)	1	(2)	1	(3)		(3)	(3)	(1)	(1)		(3)	(3)
34 Pseudoscorpionida	(1)	(2)	(1)	1	(1)	(1)	(3)	1	(2)	(2)	(1)	(1)		1	(1)	(2)	(2)	1	1	(1)
35 Psocoptera	1			1									1	(2)	1					
36 Ricinulei[a]																				
37 Schizomida																1				
38 Symphyla	(1)	(2)	1	(2)	(2)	(2)	(2)	(1)		(1)	(2)	(3)	(1)	3	(2)	2	(1)	(1)	(1)	(1)
39 Thysanoptera adults									1		1									
40 Thysanoptera immatures[a]																				
41 Thysanura			1												1					
42 Trichoptera		1																	1	

a Taxa recorded only in the litter layer.

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