
Recovery of Soil Macrofauna Communities after Forest Clearance in Eastern Amazonia, Brazil

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Abstract: *As primary forest is cleared, pastures and secondary forest occupy an increasing space in the Amazonian landscape. We evaluated the effect of forest clearing on a soil macrofauna (invertebrate) community in a smallholder farming system of southeastern Amazonia. We sampled the soil macrofauna in 22 plots of forest, upland rice fields, pastures, and fallows of different ages. In total, we collected 10,728 invertebrates. In cleared plots the species richness per plot of the soil macrofauna fell from 76 to 30 species per plot immediately after forest clearance, and the composition of the new community was different. Ants, termites, and spiders were most affected by the disturbance. In plots deforested several years before, the effect of forest clearance was highly dependent on the type of land use (pasture or fallow). In fallows, the community was similar to the initial state. The species richness per plot in old fallows rose to 66, and the composition was closer to the primary forests than to the other types of land use. On the contrary, in the pastures the species richness per plot remained low at 47. In fallows, all the groups showed a richness close to that in primary forest, whereas in the forest only the richness of earthworms and Coleoptera recovered. Our results show that forest clearing constitutes a major disturbance for the soil macrofauna and that the recovery potential of the soil macrofauna after 6 or 7 years is much higher in fallows than in pastures. Thus, fallows may play a crucial role in the conservation of soil macrofauna.*

Key Words: biodiversity, deforestation, smallholders, soil recovery potential

Recuperación de Comunidades de Macrofauna del Suelo Después de la Tala de Bosques en la Amazonía Oriental, Brasil

Resumen: *A medida que el bosque es talado, los pastizales y la vegetación secundaria cada vez ocupan más espacio en el paisaje Amazónico. Evaluamos el efecto de la tala del bosque sobre una comunidad de macrofauna (invertebrados) del suelo en un sistema agrícola de pequeña propiedad en el sureste de la Amazonía. Muestreamos la macrofauna en 22 parcelas de bosque campos de arroz, pastizales y barbechos de diferentes edades. En total, recolectamos 10,728 invertebrados. En parcelas taladas, la riqueza de especies de macrofauna del suelo por parcela disminuyó de 76 a 30 especies por parcela inmediatamente después de que el bosque fue talado, y la composición de la comunidad nueva fue diferente. Las hormigas, termitas y arañas fueron las más afectadas por la perturbación. El efecto de la tala del bosque fue altamente dependiente del tipo de uso de suelo (pastizal o barbecho) en las parcelas deforestadas varios años antes. En los barbechos, la comunidad fue similar al estado inicial. La riqueza de especies por parcelas en los barbechos viejos se elevó a 66, y la composición fue más cercana a la de bosques primarios que a la de los otros tipos de uso de suelo. Por el*

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contrario, la riqueza de especies por parcela en pastizales permaneció baja en 47. En los barbechos, todos los grupos mostraron una riqueza similar a la del bosque primario, mientras que en el bosque solo se recuperó la riqueza de lombrices y Coleópteros. Nuestros resultados sugieren que la tala de bosques constituye una perturbación mayor para la macrofauna del suelo y que el potencial de recuperación de la macrofauna del suelo después de 6 o 7 años es mucho mayor en los barbechos que en los pastizales. Por lo tanto, los barbechos pueden jugar un papel crucial en la conservación de la macrofauna del suelo.

Palabras Clave: biodiversidad, deforestación, pequeños propietarios, potencial de recuperación

Introduction

Natural succession greatly affects biodiversity and ecosystem functions. In Eastern Amazonia, characteristic successions take place in areas deforested by smallholders. The forest, cleared at the rate of 2 million ha every year in Amazonia (Laurance et al. 2001), is replaced by rice crops and then usually transformed into pastures or fallows (Parayil & Tong 1998). Many pastures are abandoned within 10 to 20 years because of loss of productivity (Costa & Rehman 1999; Desjardins et al. 2000; Alfaiai et al. 2004). This process drives the farmers to enlarge their grazing surface to compensate for the decreasing amount of food for cattle.

Conservation of the soil macrofauna may help keep land productive longer because these organisms maintain nutrient cycling and decomposition processes and modify the physical properties of soil (de Bruyn & Conacher 1990; Lavelle et al. 1997; Ekschmitt & Griffiths 1998). It is already known that soil macrofauna, and earthworms in particular, can lead to dramatic change in soil properties and plant productivity, especially in acid soils that often have low amounts of organic matter (Curry 1987; Lavelle et al. 1994; Chauvel et al. 1999). Little is known, however, about the recovery potential of soil macrofauna after forest clearance in Amazonia, especially in smallholder farming systems. In particular, if the role of fallows, or "secondary forests," in the recovery of many aboveground organisms (invertebrates and vertebrates) is recognized (Dunn 2004), the role of secondary forest in the conservation of soil invertebrates has been poorly investigated.

We quantified the effect of deforestation on the overall soil macrofauna community in a smallholder farming system of southeastern Amazonia. We also compared the recovery potential of the soil macrofauna among areas with different land uses. We identified the groups with the best recovery potential and discuss possible reasons for the differences in recovery potential among land uses.

Methods

Study Site

Benfica is a 10-year-old smallholder community that relies mainly on cattle ranching and rice production. The

community is located in an area of current deforestation in eastern Amazonia (5° 16' S and 49° 50' E), near Marabá, State of Pará, Brazil.

The climate is tropical humid with annual rainfall of 1800 mm (wet season December to March) and an average temperature of 26° C. The landscape is fragmented and consists of small hills separated by a network of rivers and seasonally flooded land. Primary forest and pastures cover most of the area. Pastures are dominated by *Brachiaria bryzantha* (Staph) cv. Marandu sometimes mixed with *Panicum maximum* (Jacq.) cv. Tanzania. Seasonally flooded parts of the pastures are often dominated by *B. humidicola* (Rendle). The remaining space is in temporary rice fields, fallows, and family fruit orchards. Fallows are dominated by very fast-growing plants and look like secondary forests after 5 or 6 years. Clayey ferralsols (i.e., red and yellow weathered soils, whose colors result from an accumulation of metal oxides, formed on geologically old parent materials) are dominant in the study area (Deckers et al. 1998).

Reconstitution of the Chronological Sequence

In this area of Amazonia, a characteristic succession of land use is common to most smallholder farming systems. This kind of agricultural system is characterized by small exploitations (50 ha on average), no mechanization, and low use of insecticides or fertilizers. After deforestation by slash and burn, farmers generally establish rice fields for 1 or, less frequently, 2 years and then transform them into pastures or they are left as fallows.

To study the evolution of soil macrofauna during succession, we sampled 22 plots in different stages of the exploitation sequence: six primary forest plots, five rice fields (1 year old), one young fallow (2 years old), two young pastures (1 year old), four established pastures (6 years old), and four established fallows (7 years old). All the established pastures and fallows had been exploited as rice fields after forest clearance and had the same grazing history. Forest was cleared with slash-and-burn methods, and all pastures were burned annually in a prescribed fire at the end of the dry season. The 1-year-old pasture plots had never been grazed, and the grass cover was high, up to 2 m. Plots of the same type of land use were separated by at least 400 m or by a stream or by both.

In each plot we sampled a set of 10 to 25 points distributed at regular intervals along one to three 50-m-long transects. The number of transects was set so that all the different soil subtypes within the plots would be sampled because the soil type (ferralsol or cambisol) can influence diversity of local soil macrofauna in pastures at the plot scale (Mathieu et al. 2004). We sampled a total of 270 points.

Soil Macrofauna Sampling

At the end of the wet season in 2002, we sampled soil macrofauna (i.e., groups in which more than 90% of individuals are visible to the naked eye) according to the methods of Anderson and Ingram (1993). We focused on the most abundant, broad taxonomic groups of the soil macrofauna (i.e., earthworms, ants, termites, Coleoptera, spiders, chilopods, and diplopods). The samples were blocks of soil (25 × 25 × 30 cm deep) that were dug out quickly. We hand sorted the soil macrofauna and preserved most organisms in 75% alcohol. Earthworms were preserved in 4% formaldehyde. Litter macrofauna was also collected. All individuals were later sorted and identified at the species level with the help of taxonomists.

Statistical Analysis

Five standard indexes were used to describe the evolution of the community structure: Shannon diversity index, Simpson (inverse: $1/D$) dominance index, frequency of the species, the species richness per sample, and the species richness per plot. We calculated the species richness per sample as the average number of species per sample for a given plot. The species richness per plot was calculated as the average number of species per plot for a given type of land use. Because the number of samples differed among the different types of land use, we used rarefaction methods (in ECOSIM [Gotelli & Entsminger 2001]) to calculate the expected values of the diversity indexes at the minimum number of sampling points per plot (10 samples per plot) (Simberloff 1972; James & Wamer 1982). The frequencies were calculated as the probability of the presence of each species in each plot.

To study the similarity of the soil macrofauna among plots, we analyzed community composition data with a hierarchical ascendant classification (HAC) based on chi-square metrics. This type of distance is asymmetrical (i.e., it does not consider double absence as a similarity between sites) (Legendre & Legendre 1998). Hierarchy was calculated using unweighted arithmetic average clustering (UPGMA), also called the "average link" algorithm. We used the matrix of the frequencies of each species in each plot to reduce the bias introduced by the presence of social insects, which can present locally extremely high densities. We used the ADE-4 program (Thioulouse et al. 1997) for classification. The differences were tested using multiple-mean comparisons with nonparametric tests

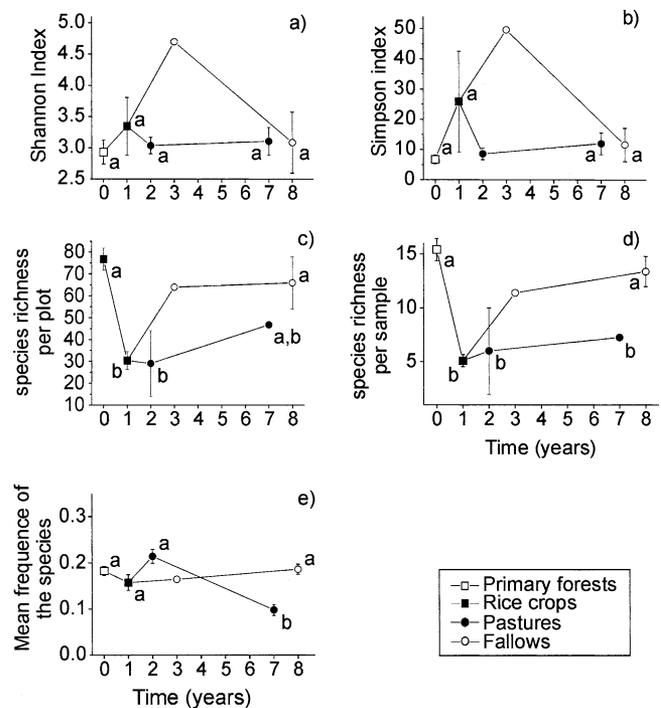


Figure 1. Diversity indices of the soil macrofauna at the different succession stages of smallholders farming systems: (a) Shannon index, (b) Simpson index, (c) species richness per plot, (d) species richness per sample, and (e) mean frequencies of the species per plot. Stages that do not have common letters are different ($p < 0.05$). Error bars: standard error of mean.

(Kruskall and Wallis) followed by Mann-Wittney U tests (Sokal & Rohlf 1995). The data for the young fallow stage were not included in the tests because there was only one plot.

Results

Changes in Community Structure

The value of the Shannon diversity index was higher in the rice fields than in the primary forests (Fig. 1a), but this difference was not significant. In the primary forests the Shannon index was 2.9, whereas in rice fields it reached 3.3 on average, although it was variable. In pastures it remained fairly constant, from 1 year old ($H = 3.0$) to 6 years old ($H = 3.1$). The Shannon index was much higher in the young fallow ($H = 4.9$) than in the forest. In old fallows, however, it decreased to 3.1, which is fairly close to that of primary forests and pastures.

The Simpson index followed the variation in the Shannon index (Fig 1b). It increased from 6.8 in forests to 25.9 in rice fields. In 1-year-old pastures, the Simpson index was close to that of primary forests (i.e., 8.6) as were the

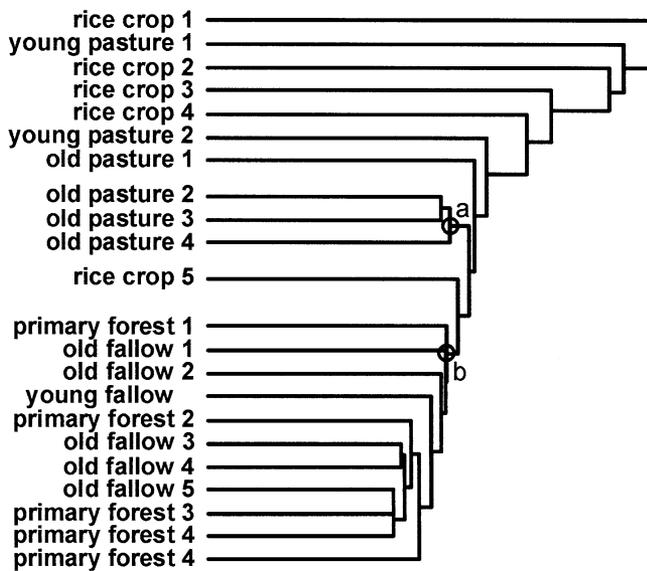


Figure 2. Classification of the plots according to their soil macrofauna community based on a hierarchical ascendant classification (HAC) (a, b are distinct clusters, see text).

Simpson indexes in the old pastures (12.0). In the young fallow, it was 49.6, much higher than in primary forests or rice fields. In the old fallows, however, it was 11.6, a value close to that in primary forests and in old pastures.

Species richness per plot in recently deforested plots was less than half that in primary forest (30 species per plot in rice fields vs. 76 in forests, Fig 1c). In old pastures, the species richness reached 47 species per plot. The species richness in young fallow was very high after 2 years: 64 species per plot, a value even higher than that in the primary forest. In old fallows, the species richness per plot was still high (66 species per plot).

The species richness per sample varied strongly with the type of land use (Fig. 1d) and was highest in the primary forests, with 15 species per sample on average. In 1-year-old deforested plots (rice fields), species richness dropped to 5 species per sample. In pastures richness remained low, reaching 7.2 species per sample in 6-year-old plots. In fallows, richness was much higher than in rice fields and pastures, reaching 11.4 species per sample in 2-year-old fallows and 13.4 species per sample in 7-year-old fallows, respectively.

Forest clearance had a limited effect on species frequencies (Fig. 1e). They changed from 0.18 in the primary forests to 0.15 in the rice fields. Frequencies were very similar in fallows (0.19) and primary forest. In old pastures, however, species frequencies (0.09) were lower than in all the other stages.

The dendrogram shows a strong separation between a cluster formed by the forest and fallow plots and the rest of the plots (Fig. 2, node b). Within the broad cluster,

the forest and fallow plots were not well separated, and the difference between these plots was never high. Outside this cluster nearly all plots were isolated on single branches. Three of the four old-pasture plots formed a distinct cluster (node a). The remaining plots did not form any cluster, and the separation between plots was always high. Interestingly, one rice field plot was situated between the forest and fallow cluster and the pasture cluster.

Changes within the Different Groups with Land-Use Type

Without exception deforestation had a dramatic effect on the species richness per sample of all taxonomic groups (Fig. 3). Richness was halved in the majority of the groups, with ants, termites, and spiders having the greatest difference between primary forest and rice fields. In old fallows, richness of all groups, except for Coleoptera, was close to that in primary forests. In pastures, richness of most taxonomic groups was very low, in both young plots and old ones. Only the species richness of earthworms was slightly higher in old pastures than in rice fields.

Deforestation had a strong effect on species frequencies for half the groups (Fig. 4). Frequencies of earthworms, diplopods, and chilopods were halved in deforested plots. Deforestation had no effect on frequencies of the other groups. In fallows, species frequencies were close to the primary forest values. Only for earthworms were the frequencies lower in old fallows than in primary forest. In old pastures, however, species frequencies were always lower than in primary forest, with the exception of termites. Moreover, the frequencies of ants, Coleoptera, and spiders were even lower in the old pastures than in the rice fields.

Discussion

Shannon and Simpson Diversity Indexes

The values of the diversity (Shannon) and dominance (Simpson) indexes did not show clear patterns. Both Shannon and Simpson indexes increased in young plots, especially in the young fallow, but were not significantly different between old plots and primary forest plots, whether in pastures or in fallows. Because there was only one young fallow and only two young pastures it was difficult to evaluate the real significance of these hump-shaped curves.

Effect of Forest Clearance on Soil Macrofauna Community

Forest clearance had a strong effect on the soil macrofauna. The community in the rice fields appeared impoverished, with low species richness per sample and per plot. The species richness and frequencies of all groups were affected by deforestation. Moreover, the classification showed that the soil macrofauna communities of the

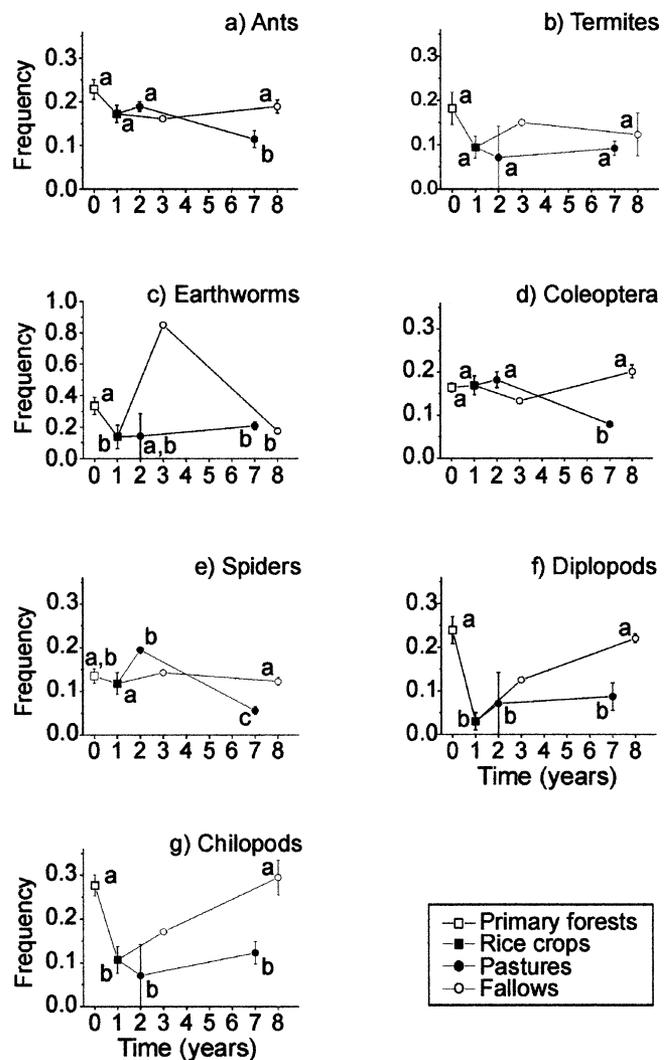
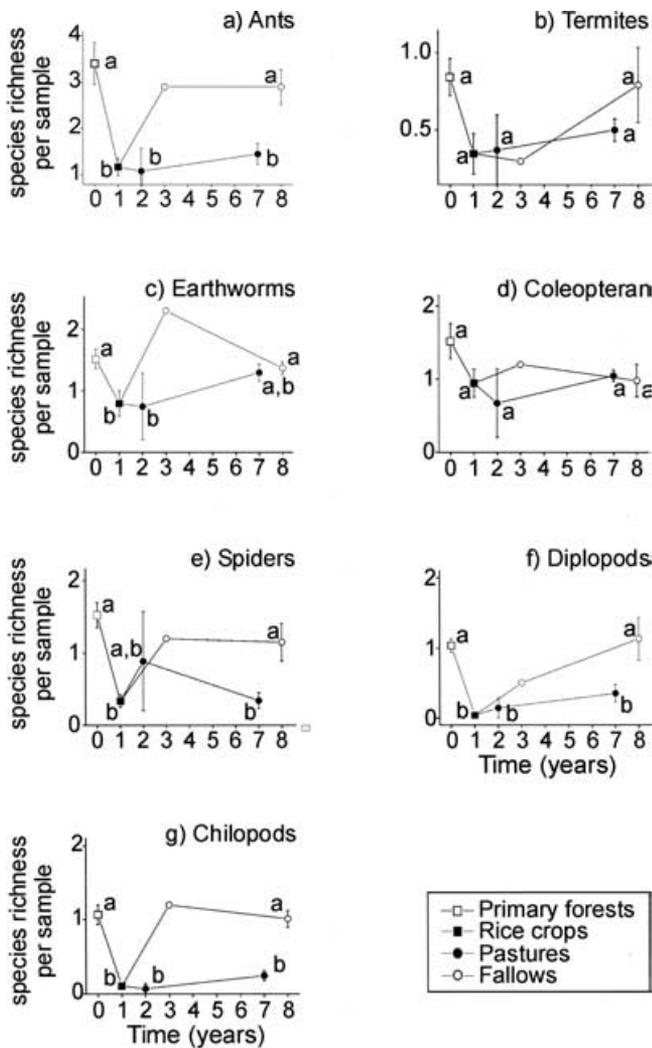


Figure 3. Species richness of the major taxonomic groups of soil macrofauna at the different stages of smallholders farming systems: (a) ants, (b) termites, (c) earthworms, (d) Coleoptera, (e) spiders, (f) diplopods, and (g) chilopods. Stages that do not have common letters are different ($p < 0.05$).

Figure 4. Species frequencies of the major taxonomic groups of soil macrofauna at the different stages of smallholders farming systems: (a) ants, (b) termites, (c) earthworms, (d) Coleoptera, (e) spiders, (f) diplopods, and (g) chilopods. Stages that do not have common letters are different ($p < 0.05$).

rice fields were very different from the communities of the other types of land use. Recently cleared plots of natural vegetation have already been identified as containing depleted soil macrofauna communities (Fragoso et al. 1999). In the Peruvian Amazon the density of soil macrofauna is also much lower in rice fields and pastures than in the primary forest (Lavelle & Pashanasi 1989). In the plots we studied, changes in the soil macrofauna community may have been caused either by the direct effect of fire during the slash-and-burn process or by resulting modification of the vegetation cover.

Results of previous studies do not show a consistent effect of fire on the soil macrofauna. After burning savannas in Colombia, the soil macrofauna community recovered after only 6 months (Decaëns et al. 1994). In Australia the

surface arthropods were greatly affected by the first fire but not by subsequent fires (Collet 1998). In a controlled experiment, some species of earthworms benefited from the fire whereas others disappeared (Callham et al. 2003). Ants were affected by fire in a tropical deciduous forest in Mexico (Castano-Meneses & Palcios-Vargas 2003). During a fire, the soil temperature can reach 200° C at a depth of 15 cm (Gimeno-Garcia et al. 2004). Nonmobile invertebrates such as some larvae may not escape from the heat. Very mobile invertebrates, however, such as Coleoptera or spiders, may escape the fire and come back later. In our study, ants, termites, and spiders were the groups most sensitive to deforestation. Ants and termites are protected from fire by their mounds, which are largely subterranean.

Spiders are very mobile organisms and are probably not directly affected by fire.

On the other hand, slash-and-burn fires may have an indirect effect on soil macrofauna by destroying the numerous microhabitats on which many soil invertebrates rely. Decaying wood, fine twigs, dead plant stems, and local accumulations of leaves are sources of food and habitat for numerous species. This loss of plant cover exposes the soil to direct solar radiation, which modifies the climatic conditions of the soil (Strehlow et al. 2002). Most forest-dwelling organisms are adapted to shady and humid environments. In the deforested plots, a large part of this fauna probably was unable to tolerate the shift in microclimatic conditions. For instance, in a Neotropical forest, logging without fire affected the ant community (Castano-Meneses & Palcios-Vargas 2003).

The Soil Macrofauna Community after Rice-Cropping Stage

After the rice-crop stage the soil macrofauna communities were completely different depending on the type of land use. In pastures the communities were impoverished even after 6 years. Moreover, the species became less frequent than in the other stages. Only the termites and the earthworms recovered slightly. The different pasture plots, on the other hand, had a relatively homogenous community, well separated from the communities associated with other types of land use. These results suggest that the soil macrofauna community in pastures developed in a distinctive, homogeneous fashion that is different from the communities associated with the rice fields or fallows. In Amazonia establishing pastures usually leads to an impoverishment of the soil macrofauna community (Fragoso et al. 1999). In Colombia the density of the soil macrofauna is also lower in improved pastures than in the primary forest (Decaëns et al. 1994). In central Amazonia the species richness per sample fell from 156 species in forest to 40 in 15-year-old pastures (Decaëns et al. 2004). Litter invertebrate density was much lower in pastures than in primary forest on Martinique (French West Indies) (Loranger et al. 1999). The ant diversity was halved when pastures were established in another area of central Amazonia (Vasconcelos 1999). In Amazonia the transformation of forest into pasture is also often accompanied by a massive proliferation of earthworms, especially the locally invasive species *Pontoscolex corethrurus* (Lavelle & Pashanasi 1989; Höfer et al. 2001; Barros et al. 2002). We did not, however, find this trend, maybe because the plots were too young.

There are probably numerous causes of degradation in these communities. Change in the environmental conditions, leading to modifications of the soil microclimate and the loss of microhabitat, is certainly an important factor. The remaining microhabitats, such as decaying trunks and grass tufts, are local hotspots of biodiversity in Amazonian pastures (Mathieu et al. 2004). High soil com-

paction due to trampling by cattle has been reported as a strong limiting factor for the soil macrofauna (Radford et al. 2001). The loss of litter, organic matter (Schroth et al. 2002; Barros et al. 2004), and soil nutrients (McGrath et al. 2001) probably has an effect on the soil macrofauna. The disappearance of some ecosystem engineers such as earthworms (Decaëns et al. 1999; Lavelle et al. 2001) and termites (Jones et al. 1994) that produce biogenic structures used as microhabitats by other species may also accelerate the process of community degradation.

The soil macrofauna community in the fallows showed a very different pattern. It appeared to be a community returning to its initial state after considerable disturbance. The diversity indexes were close to the primary forest values, as were the species frequencies. Most of the groups recovered, especially in terms of diversity. Moreover, the composition of the soil macrofauna of the fallows converged with that of the forest community. The soil macrofauna has a good recovery potential in fallows. For instance, in central Amazonia, the biomass and the diversity of the soil macrofauna in secondary forests are not significantly different from those in the primary forest (Höfer et al. 2001). In a primary forest on Martinique (French West Indies) the litter invertebrate density is higher in fallows than in the primary forest (Loranger et al. 1999). Ants and termites have good recovery potential in fallows. In central Amazonia, the diversity of ants in fallows is close to that in primary forest, although it is halved in pastures (Vasconcelos 1999). In Cameroon, Africa, the composition of the termite community in secondary forests is similar to the composition of the community in primary forest in several studies (Eggleton et al. 1996; Eggleton et al. 2002). This high recovery potential in fallows suggests that fallows are good habitats for the soil macrofauna.

When a plot is abandoned after a rice-crop stage, fast-growing plants such as *Cecropia*, with high litter biomass, grow rapidly (Baar et al. 2000). After 2 or 3 years there is a thick litter layer, and the canopy is already well developed. A microclimate with a low light level and high humidity, similar to a forest microclimate, appears quickly. Moreover, the presence of numerous plant stems and trunks and the thick litter layer provide numerous microhabitats and abundant trophic resources. In the deforested areas of Amazonia, the forest is cleared in patches, creating mosaic landscapes in which deforested plots and primary forest are often close to each other. In such a situation, the soil macrofauna from the remaining forest plots may colonize habitats such as fallows.

Conclusion

Forest clearance was a major disturbance for the soil macrofauna in Amazonia. Immediately after forest clearance, the soil macrofauna community was extremely impoverished and no group seemed to escape this change.

Fallows offered favorable conditions for the soil macrofauna, but the soil fauna in pastures seemed to have a very low recolonization potential. Consequently, in Amazonia, fallows may play an important role in the conservation of soil macrofauna.

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