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Decreasing fallow duration in tropical slash-and-burn
agriculture alters soil macro-invertebrate diversity: A
case study in southern French Guiana

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Abstract

In the humid tropics, slash-and-burn cultivation causes changes in the composition of soil biota communities. We investigated the soil macro-invertebrates (body length ≥ 2 mm) in five sites, two at Maripasoula, an Aluku village along the Maroni river (French Guiana), with short fallow (≈ 8 years), and the other three at Elahe, a Wayana village along the same river, with long fallow (≈ 25 years). We report observed species richness, the corresponding estimates by bootstrap and its associated standard deviation. At both sites the cultivation led to impoverished communities. The overall observed species richness i.e. γ diversity was ca. twice as larger in Elahe than in Maripasoula. The landscape at Maripasoula was dominated by highly disturbed areas with the direct consequence that local species richness relied on

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colonization from an impoverished regional species pool. On the contrary, in Elahe, crops formed small patches scattered across a landscape essentially constituted of rich undisturbed or slightly disturbed forests hence higher γ diversity. The proportion of rare species ranged from 44% to 54%. We found 6 indicator species amongst which 5 were associated to the old secondary forest in Elahe and one, the earthworm *Pontoscolex corethrurus* was associated to crop fields in Maripasoula (short fallow system). Results are discussed in a landscape context in terms of conservation and management of soil macrofaunal diversity in agro-ecosystems.

Key words: Soil macrofauna, species richness, slash-and-burn agriculture, agriculture intensification, landscape, biodiversity.

1. Introduction

Soil invertebrates are key mediators of soil functions in agro-ecosystems. They substantially affect many important processes that take place below-ground like comminution and incorporation of litter into the soil, building and maintenance of structural porosity and aggregation in soils through burrowing, casting and nesting activities and control of microbial activities (Lavelle et al., 2006, and references therein). Invertebrates therefore contribute to the ecosystem services provided by soils and for this reason, they are increasingly considered as a resource to be managed and protected. Amongst soil biota, macrofauna (animals with body length ≥ 2 mm (Anderson and Ingram, 1993)) are dramatically affected by cultural practices and various authors have discussed the utility of managing their populations to improve the sustainability of soil fertility especially in countries or regions where farm-

ers have limited access to mineral fertilizers (Matson et al., 1997; Brussaard et al., 2007; Rossi and Blanchart, 2005).

In the tropics, the traditional slash-and-burn system (shifting cultivation) consists of cutting the forest, burning the trees and settling familial agriculture for several years. Long fallow periods follow the cropping period and the regeneration of the vegetation combined with the recovery of soil fauna contribute to restore soil organic content and structure which in turn affect soil water and nutrient dynamics. These processes require a long fallow period (Grandisson, 1997). Unfortunately, the changes from a traditional to a permanent agriculture that accompany a population demographic growth generally lead to a decrease in the fallow duration (Fleury, 1998). Ultimately, the cropping period is followed by the establishment of permanent pastures used for cattle ranching instead of fallows. This is the case for huge surfaces of land in Brazil where these practices have a strong detrimental impact upon soil physical and chemical properties of the soil as well as diversity and activity of soil biota with dramatic impacts on the sustainability of agriculture (Mathieu et al., 2005).

In French Guiana, the demographic pressure threatens the long-lasting equilibrium between slash-and-burn agriculture and nature conservation, due to the progressive disappearance of shifting cultivation. In southern Guiana near the Suriname border, the duration of fallow in the slash-and-burn system has decreased from 15 to 7-8 years in the last 30 years (Topoliantz et al., 2006). The traditional shifting cultivation is still practised in that region by Amerindian communities and the duration of the fallow ranges from 15 to more than 100 years (Fleury, 1998). The aim of this study was to assess the

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10 39 impact of slash-and-burn cultivation upon the diversity of soil macrofauna in
11 40 two agricultural systems that differed by the duration of the fallow period.
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13 41 We investigated a traditional shifting cultivation system in a small Wayana
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15 42 Amerindian village and an accelerated rotation cycle in a larger Aluku village
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17 43 where the demographic pressure is strong. Crops are mostly manioc (*Manihot*
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19 44 *esculenta* Cranz) i.e. cassava in both villages and the studied systems are
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21 45 good examples of traditional shifting cultivation (Wayana Amerindians) and
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23 46 change to permanent agriculture due to demographic pressure (Aluku village)
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25 47 (Grandisson, 1997).
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28 48 **2. Materials and methods**

30 49 *2.1. Sites*

32
33 50 The present survey was carried out in southern French Guiana near
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35 51 the border between France and Suriname along the Maroni river. We in-
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37 52 vestigated soil macrofauna diversity in agricultural fields of two communi-
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39 53 ties, Wayanas (indians) and Alukus (maroons, of ancient African lineage).
40
41 54 Wayana Amerindians are still using the traditional slash-and-burn system
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43 55 where short cropping periods (ca. 2–3 yr) alternate with long fallow periods
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45 56 (≈ 25 yr). The fields (thereafter referred to as “abattis”) are settled by cut-
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47 57 ting and burning forest plots and are planted with manioc which constitutes
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49 58 the basic food. Soils are not tilled and manioc cuttings (from previous crops)
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51 59 are planted after resprouting. Neither Wayanas nor Alukus use pesticides,
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53 60 herbicides or fertilizers. Alukus are using a similar system with the difference
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55 61 that cultivation does not exceed 1 year and fallows are shorter (≈ 8 yr on
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57 62 average). The length of the cultivation period depends on the soil fertility
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and the spontaneous regrowth of vegetation (Topoliantz et al., 2006).

Ameridian village of Elahe (long fallow). We sampled soil macrofauna in the Wayana (Amerindian) village of Elahe. This small village is situated on the Tampock river which is a subsidiary of Maroni (3 ° 26'N, 53 ° 59'W). Three contrasted situations were investigated. A field that had been cut, burnt and cultivated by an Indian family 3 yrs before this study (EA). This field was located next to a secondary forest and was itself a secondary forest before its cultivation. It was sampled in July 1999. We sampled an old secondary forest (EF) located nearby EA (ca. 100 m). The old secondary forest showed woody species typical of mature forests (e.g. *Astrocaryum sciophilum* (Miq.) Pulle, and *Dicorynia guianensis* Amsh. (Poncy et al., 2001) which indicated that it had been left untouched for at least 100 years. The plot located in the secondary forest was resampled in May 2000 after it had been cut and burnt in December 1999 for cultivation (EB).

Aluku village of Maripasoula (short fallow). The second site is located along the Maroni river (3 ° 39'N, 54 ° 2'W) near the village of Maripasoula, ca. 25 km downstream of the first study site. Maripasoula is a large village (pop 1200 in 1999) mostly inhabited by Aluku people. The increase in population density during the last 3 decades led to a decrease in the surface of cultivable land and the subsequent decrease of fallow duration (Fleury, 1998). We sampled a 1-yr old abattis (MA) at the end of the crop period. It had been opened by an Aluku family by cutting and burning an 8-yr-old woody fallow referred to as MF. MF was characterized by pioneer woody species such as *Cecropia latiloba* Miq. and *Inga capitata* Desv. Both MA and MF plots were sampled in July 1999. The MF plot was intended to be burnt in December

1999 and we planned to resampled in May 2000 but unfortunately the Aluku family did not burn it as expected.

The mean annual temperature is 26 °C and the mean annual rainfall is 2000 mm. There is a main dry season from September to December and a shorter one between March and April. Sampled soils are sandy Oxisols at pH of 5 and 4.7 on average in Maripasoula and Elahe, respectively (Topoliantz et al., 2006). The average total C content was 24.6, 22.5, 25.8, 19.1 and 18.6 g kg⁻¹ while the total N content was 1.65, 1.48, 1.78, 1.39 and 1.35 g kg⁻¹ the in plots MA, MF, EA, EF and EB respectively (data from Table 1 in Topoliantz et al., 2006). Other physico-chemical features of the soils at the study sites are available in Topoliantz et al. (2006).

2.2. Sampling

We used the Tropical Soil Biology and Fertility (TSBF) procedure (Anderson and Ingram, 1993). Sampling units consisted of 25 cm × 25 cm by 30 cm deep soil monoliths. As recommended in the TSBF procedure, we used 10 monoliths per transect and carried out 3 transects per plot (i.e. 30 samples per plots). The distance separating monoliths was 5 m and transects were 20 m distant from each other. The litter was collected at each sampling point and a trench was then dug to a depth of 30 cm around the 25 × 25 cm² area to get a soil monolith. Macroinvertebrates from soil and litter were hand-sorted and preserved in 4% formalin solution. Invertebrates were later counted and identified in the laboratory. We grouped specimens in morphospecies and identified most of them with the help of different taxonomists. We excluded larvae from the statistical analyses because they were partially redundant with adults found in the same samples. Overall, our estimation

of species richness is therefore underestimated.

2.3. Data analysis

2.3.1. Community structure

Principal Coordinate Analysis (PCoA). The first step of data analysis consisted of a Principal Coordinate Analysis (PCoA) of the raw data set (site-species abundances). This multivariate analysis is fully described in Legendre and Legendre (1998). It was first proposed by Gower (1966) and consists of the Euclidean representation of a set of objects described by any similarity or distance coefficients. We used PCoA in order to produce a general representation of our soil fauna samples and to examine to which extent they differed according to sites and land-use types. One advantage of this analysis is that the user can select the most appropriate distance or similarity index given the data at hand, which is not the case in more classical multivariate analyses e.g. PCA or CoA. We used the Bray–Curtis index (Legendre and Legendre, 1998, p. 287). The coefficient was computed using the R software (R Development Core Team, 2008) and the `labdsv` package (Roberts, 2007). The PCoA was done using the `ade4` package (Chessel et al., 2004). The significance of PCoA axes were assessed by means of a bootstrap procedure based on 1000 randomizations (Pillar, 1999).

Species indicator value: IndVal. Because the PCoA is based on the diagonalization of a distance/similarity matrix there is no direct link between factorial axes and original descriptors (i.e. macrofauna species). We thus examined the presence of species associated to one or more samples or sites by means of a specific method, the *IndVal* value (Dufrêne and Legendre, 1997). Indi-

cator species are species mostly present in one of the groups to be compared, while being mostly absent in other groups. Dufrêne and Legendre (1997) proposed to compute the *IndVal* index by combining two terms reflecting the specificity and the fidelity of a species for the samples corresponding to a certain land-use type. The specificity term is the mean abundance of a species i in the samples of the land-use j compared to all land-uses.

$$A_{ij} = N_{individuals_{ij}} / N_{individuals_{i\bullet}}$$

The fidelity term is the relative frequency of occurrence of species i in samples of land-use j .

$$B_{ij} = N_{sites_{ij}} / N_{sites_{\bullet j}}$$

The indicator value of a given species is the product of specificity and fidelity terms in percent:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

The indicator value of a species i for an array of sites is the largest value of $IndVal_{ij}$ observed over all sites j . In this paper we adopted the threshold level of 25% for the index as suggested by Dufrêne and Legendre (1997), i.e. species i is present in at least 50% of samples of land-use j and its relative abundance in land-use j is at least 50%. We assessed the statistical significance of observed *IndVal* values by means of a permutation test (1000 randomizations) as proposed by Dufrêne and Legendre (1997).

Multi Response Permutation Procedure (MRPP). We tested the significance of community dissimilarities among land-uses by means of the Multi Response Permutation Procedure (MRPP) (Quinn and Keough, 2002). MRPP

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10 153 tests whether there is a significant difference between two or more groups of
11 154 sampling units. The MRPP statistic δ is the overall weighted mean of within-
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13 155 group means of pairwise dissimilarities among sampling units. The observed
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15 156 value is statistically tested by mean of a permutation test where sampling
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17 157 units and their associated pairwise distances are permuted N times and δ is
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19 158 recalculated. The significance test is based on the proportion of permuted
20
21 159 δ s that are less than the observed δ . We used the Bray–Curtis distance to
22
23 160 quantify the dissimilarities between land-uses. MRPP was computed using
24
25 161 the **vegan** package (Oksanen et al., 2008).

26 27 162 *2.3.2. Species richness*

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29 163 Samples were pooled to compute the observed bulk species richness for
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31 164 each land-use type. We used bootstrap procedure to determine a possible bias
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33 165 in the species richness estimator and to remove it from the observed value.
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35 166 For a given land-use, a randomized sample of $n = 30$ sampling units was
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37 167 constituted by randomly sampling with replacement amongst the 30 original
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39 168 units and the observed cumulated species richness was computed. This was
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41 169 repeated N times and constituted the bootstrap sample. The bias was defined
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43 170 as the observed mean species richness minus the average of the N observed
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45 171 species richnesses (Manly, 1997). A corrected estimate of species richness
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47 172 was obtained by subtracting the bias to the observed species richness. We
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49 173 approximated the standard error of the estimated species richness by the
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51 174 standard deviation of bootstrap estimates following Manly (1997, p. 36).
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53 175 Species rarity was measured as absolute and relative frequencies of singletons,
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55 176 i.e. species with at most 1 individual per sample. We also report another
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57 177 measure of rarity based on frequency of species: the number of unique species,

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10 i.e. species that occurred in only one sample. The observed species richnesses
11 in the different land-uses were compared by mean of a one-factor analysis
12 of variance. Because our data did not satisfy most of the assumptions of
13 ANOVA we used the randomization test described by Manly (1997, p.117).
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15 The observed F statistic was tested by comparison with corresponding values
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17 in N ANOVAS after randomization of raw data.
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22 3. Results

23 3.1. General statistics

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27 Soil macrofauna communities differed markedly amongst land-uses and
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29 between sites. The average macrofaunal density was higher in the secondary
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31 forest (EF) in Elahe followed by the abbatis in Maripasoula (MA) and it was
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33 lowest in the recently burnt secondary forest in Elahe (EB)(Table 1). The
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35 observed species richness varied accordingly with a total of 121 species in the
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37 secondary forest in Elahe (EF) and values ranging from 22 to 54 species in the
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39 other plots. Corresponding bias-corrected values estimated from bootstrap
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41 were somewhat higher (Table 1) but between-site ranking did not change at
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43 all (there is a linear relationship between original and corrected values). The
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45 number of singletons and unique species respectively ranged from 44% to 54
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47 % and 55% to 72%, respectively, and was fairly homogeneous amongst sites
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49 (Table 1). A grand total of $S = 186$ species was recorded (all sites pooled)
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51 amongst which 42 (22.6%) were common to Elahe and Maripasoula (shared
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53 species). One hundred and twelve (60.2%) species were encountered in the
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55 site of Elahe whereas 32 (17.2%) species were only recorded in Maripasoula.
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3.2. Community structure

First and second eigenvalues of PCoA significantly differed from those stemming from $N = 1000$ randomizations and accounted for 20.7% and 16% of the total inertia, respectively. Axis 1 clearly reflected changes in macro-fauna community structure according to the type of agriculture: Maripasoula plots (slash-and-burn agriculture with short fallow periods) are opposed to Elahe plots (traditional shifting agriculture) along Axis 1 (Fig. 1). EA, the abbatis from the Elahe village was intermediate. Interestingly, plots EA, EF and EB were clearly different and much more heterogeneous than MA and MF. Within-plot heterogeneity was graphically represented by the scattering of samples around each centre of inertia. Axis 2 mainly reflected within site variability and did not discriminate land-uses. MRPP (1000 randomizations) showed that community dissimilarity among the five land-uses was highly significant ($p < 0.001$).

3.3. Species richness within and between sites

A total of 145 species were found in Elahe amongst which 121 were recorded in the secondary forest (EF) i.e. 83% of the total (Table 2). The abattis (EA) hosted 45 species among which 17% were shared with EF. The recently burnt forest (EB) harboured a total of 22 species, ca. 15% of the total richness (Table 2). The number of exclusive species i.e. those species that were found in only one land-use was 93, 20 and 12 for EF, EA and EB, respectively. The proportion of shared species between EB and both EF and EA was low and ranged from 6.7% to 9.8% (Table 2). In the short fallow system (Maripasoula) the total species richness (all sites pooled) was 77. The woody fallow that served as reference hosted 54 species (70% of the total)

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10 while the abattis hosted 41 species (53% of the total) (Table 3). The propor-
11 tion of shared species was 28% (Table 3) which was higher than Elahe (Table
12 2). The observed species richness significantly differed among land-uses as
13 indicated by the ANOVA test based on 1000 randomizations ($p < 0.001$).
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18 3.4. *Indicator species*

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20 Six morphospecies showed *IndVal* values $\geq 25\%$ and significant associ-
21 ated probabilities at $\alpha = 0.05$: two earthworms, two centipedes, a termite
22 and a bristletail (Table 4). Five of these were associated to the old secondary
23 forest (traditional slash-and-burn shifting agriculture) while one earthworm
24 species, *Pontoscolex corethrurus*, was indicator of the abattis in the short
25 fallow system in the Aluku village of Maripasoula.
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33 4. Discussion

34 4.1. *Forest logging and fire*

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36 Forest clearing and burning had a strong impact upon soil macrofauna
37 species richness in Elahe. Soil macrofauna communities were dramatically
38 impoverished soon after fire (plot AB) and remained strongly affected three
39 years after crop establishment (plot EA). Tree harvesting is known to affect
40 the composition of soil faunal communities as well as food web structure in
41 various ways (Bengtsson et al., 1997). One direct and strong impact is the
42 change in soil climatic conditions (temperature, moisture) that is associated
43 to the direct exposure of soil to solar radiation (Matlack, 1993). These effects
44 are magnified by fire associated with forest logging. During fire, the temper-
45 ature of the surface soil can exceed 400 ° C (Gimeno-García et al., 2004) with
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important consequences upon soil dwelling organisms and most notably non-mobile species that inhabit litter layers and/or upper soil strata (Mathieu et al., 2005; Abbott et al., 2003). Fire also indirectly affects soil fauna by destroying epigeic microhabitats like decaying wood, fine twigs, dead plant stems and leaves that serve as trophic resources or habitat for numerous species (Mathieu et al., 2005).

Not surprisingly, the species pool observed in the recently burnt plot EB was constituted either by species that withstand forest logging and burning or by colonisers originating from adjacent areas.

After a few years of cropping, the species richness had increased but remained low (plot EA) and ca. half the species richness of the abattis was constituted by species also present in the forest (Table 2). One may hypothesize that these species are eurytopic (species with large niche breadth) that can withstand the environmental conditions that prevail in crop plots. These results are fully in accordance with data collected in eastern Amazonia (Brazil) (Mathieu et al., 2005).

Interestingly, forest clearing and the set up of manioc crop has a lower impact on the observed richness in the region of Maripasoula where crop rotation is more rapid. The abattis (MA) and the woody fallow (MF) share more species than corresponding plots in Elahe (EA and EF): one reason for this is that the plots that are logged and burnt in Maripasoula are woody fallows ca. 7–8 yr-old and by no means old growth forests as in Elahe. The species richness of such plots is low and roughly comparable to what is observed in the abattis in the traditional slash-and-burn system in the native Amerindian area of Elahe. These results indicate that agricultural intensi-

274 fication leads to impoverishment of species richness and homogenization of
 275 soil macrofaunal communities.

276 All but one species that were found to be indicators were associated to the
 277 old secondary forest in Elahe (EF). Given huge environmental differences that
 278 exist between the forest and other land-uses, forest specialists could be ex-
 279 pected to have high *IndVal* values. This index encapsulates two contrasted
 280 and complementary information, specificity and fidelity. Soil macroorgan-
 281 isms generally display a highly aggregated spatial distribution (Ettema and
 282 Wardle, 2002) and this is even more marked in the case of social insects
 283 like termites or ants. This leads to high variance of abundance data and
 284 may cause low values of the fidelity term B_{ij} and subsequently low and/or
 285 not-significant *IndVal* index (Nahmani et al., 2006). Apart from specialist
 286 species from the secondary forest, only one species was associated to crops
 287 with short fallow periods, the pantropical endogeic earthworm *P. corethrurus*
 288 (Oligochaeta, Glossoscolecidae). This peregrine species has been dispersed
 289 worldwide by man and is probably indigenous to the Guianas plateau in
 290 South America (Righi, 1984). This species exhibits a very good aptitude to
 291 withstand soil disturbance and scarcity of organic matter and is abundant
 292 in open areas over a wide range of tropical regions (Lavelle et al., 1987).
 293 *P. corethrurus* has been shown to have the capacity to invade Amazonian
 294 pastures and to cause soil degradation through physical compaction of the
 295 soil surface (Chauvel et al., 1999). However, other studies showed that it
 296 can incorporate charcoal to the topsoil thereby increasing its humus content
 297 of the topsoil by adding finely powdered black carbon (Ponge et al., 2006;
 298 Topoliantz and Ponge, 2003, 2005).

4.2. Landscape context and species diversity

Our sampled soils differed in terms of physico-chemical parameters (e.g. total C content) and these differences can be explained by land management practices among which fallow duration. Land management can have direct effects upon soil biodiversity as well as indirect effects through changes in soil parameters like C or N content. Both direct and indirect effects convey land-use impacts on soil biodiversity. In that context, our plots can be compared although our data do not allow unravelling such direct and indirect effects.

Comparing Elahe and Maripasoula sites allows us to discuss the effects of the reduction of fallow duration upon γ , i.e. regional diversity. The impact of reduced fallow on the pooled richness was huge (145 versus 77 species in Elahe and Maripasoula, respectively). The main difference between these species pools is due to the low richness of the woody fallow (MF) in Maripasoula as compared to the old secondary forest (EF) in Elahe. The woody fallow is the typical habitat that is cut and burnt before crop settlement in the reduced fallow system. There is no secondary forest nor older fallow left in the region of Maripasoula where all areas accessible by foot or by canoe have been and are still used for cultivation (Topoliantz et al., 2006). On the other hand, abattis are similar in Elahe and Maripasoula in terms of richness (roughly 40 to 45 species) although the proportion of shared species is low ($\approx 21\%$).

Various mechanisms contribute to link α diversity to neighbouring landscape configuration (Dunning et al., 1992; Rossi and van Halder, in press). Species richness in the abattis could be affected by the neighbouring species-rich secondary forest or by woody fallows through the so-called “vicinism” or

“mass” effect (Zonneveld, 1995) whereby a flow of individuals originates from species rich habitat and allows the presence of species in neighbouring habitats where they are not self-maintaining (Shmida and Wilson, 1985). This corresponds to the “spillover effect” by which species can be maintained in unsuitable habitat patches in the framework of source-sink dynamics (Holt, 1997). In the context of accelerated crop rotation, the amount of land covered by pristine habitats is very low if not zero. In the site of Elahe, the situation is inverse, crops constituting a habitat distributed as small patches scattered across a landscape essentially constituted of rich undisturbed or slightly disturbed forests. In highly anthropised landscapes, the overall proportion of species with high capacity to colonize abattis is larger and the landscape context tends to favour a rapid colonization of newly settled fields. This is not the case in the Amerindian region where abattis are hardly spatially connected.

4.3. The importance of rare species

We defined rare species as species collected as single individuals, singletons. All studied sites exhibited roughly 50% of singletons and an even larger proportion of unique species. Such high values were reported e.g. for insect communities associated to tropical trees (Novotný and Basset, 2000) and soil macrofauna in Amazonian pastures (Rossi et al., 2006). Rarity can be a problem during data analysis and various indices have been proposed to correct estimates of species richness and shared species (Colwell and Coddington, 1994; Chao et al., 2005). In this study we used a bootstrap correction of species richness estimates which led to corrected estimates that were linearly correlated to observed species richnesses. This indicated that our perception of between-site similarity in terms of species richness were correct even when

solely based on raw data.

Statistics aside, rare species raise the question why are they so numerous. First, rare species could be species that were inadequately sampled and this must be considered with caution. Indeed, soils are highly variable habitats with various nested sources of spatial heterogeneity that affected species distribution and hence short-scale diversity patterns (Mathieu et al., 2009). The problem of sampling deficiency in estimating biodiversity in soils is discussed elsewhere (Rossi et al., 2006) and could possibly be responsible for a certain proportion of our rare species. It must be also noted that the TSBF sampling protocol may not be optimal for certain type of organisms and notably litter inhabiting species. Other sampling methods like Winkler bags may also be used (Smith et al., 2008) while specific strategies have been developed for social insects (termites) (Jones and Eggleton, 2000). On the other hand, the “spillover effect” could lead to the presence of rare species simply because they are transient species i.e. species that cannot maintain in one habitat but originates from a neighbouring habitat that acts as a permanent source. Distinguishing transient species is a very difficult task (Novotný and Basset, 2000) that would require a huge amount of additional field data (and directional activity traps) in our case. However, this is the only way to refine our estimates of species richness while controlling for close neighbourhood effects and therefore assessing landscape effects upon crop field species richness.

4.4. Conservation and management of soil macrofaunal diversity in agroecosystems

It is broadly acknowledged that the conservation of soil macrofauna in agroecosystems is an important aspect of sustainable agriculture (Brussaard

et al., 2007) but the spatial facet of that question have not yet received the attention it requires (but see Tschardt et al., 2005). The landscape at Maripasoula is dominated by highly disturbed areas and the direct consequence is an erosion of γ diversity. Local species richness thus rely on colonization from impoverished regional species pool. Swift et al. (2004) argue that the management of biodiversity in agricultural context is more effective at the landscape scale than at the local plot scale where strictly utilitarian options prevail. Following this line of reasoning, and given that most forest species are unlikely to maintain themselves within abattis, the management of γ diversity may be based on the maintenance of fallow plots of a large range of age and not only of pristine ecosystems. It is additionally important to consider the spatial arrangement of these plots across the landscape. They act as source of colonisers for newly abandoned field crops and as such their spatial location may be of prime importance. The dispersal abilities of most soil invertebrates are not very well documented but are certainly limited for many species and this reinforces the importance of the distribution of the source of colonisers within agricultural landscapes.

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References

- Abbott, I., Burbidge, T., Strehlow, K., Mellican, A., Wills, A., 2003. Logging and burning impacts on cockroaches, crickets and grasshoppers, and spiders in Jarrah forest, Western Australia. *Forest. Ecol. Manage.* 174, 383–399.
- Anderson, J., Ingram, J., 1993. *Tropical Soil Biology and Fertility: a Handbook of Methods*. CAB International, Oxford.
- Bengtsson, J., Persson, T., Lundkvist, H., 1997. Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. *J. Appl. Ecol.* 34, 1014–1022.
- Brussaard, L., de Ruiter, P. C., Brown, G. G., 2007. Soil biodiversity for agricultural sustainability. *Agric. Ecosyst. Environ.* 121, 233–244.
- Chao, A., Chazdon, R. L., Colwell, R. K., Shen, T.-J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159.

- Chauvel, A., Grimaldi, M., Barros, E., Blanchart, E., Desjardins, T., Sarrazin, M., Lavelle, P., 1999. Pasture damage by an Amazonian earthworm. *Nature* 398, 32–33.
- Chessel, D., Dufour, A.-B., Thioulouse, J., 2004. The ade4 package-I: One-table methods. *R News* 4, 5–10.
- Colwell, R. K., Coddington, J. A., 1994. Estimating terrestrial biodiversity through extrapolation. *Philos. Trans. R. Soc. Lond. B* 345, 101–118.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Dunning, J. B., Danielson, B. J., Pulliam, H. R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169–175.
- Ettema, C., Wardle, D., 2002. Spatial soil ecology. *Trend. Ecol. Evol.* 17, 177–183.
- Fleury, M., 1998. Les populations du Haut-Maroni et le projet du Parc National de la Guyane. *JATBA* 40, 577–610.
- Gimeno-García, E., Andreu, V., Rubio, J., 2004. Spatial patterns of soil temperatures during experimental fires. *Geoderma* 118, 17–38.
- Gower, J., 1966. Some distance properties of latent root and vector methods used in multivariate analysis. *Biometrika* 53, 325–338.
- Grandisson, M., 1997. Diagnostic de la reproductibilité de la fertilité dans les abattis de la région ouest-Guyane: étude des stratégies de gestion et analyse des trajectoires d'évolution des composantes de la fertilité en fonction

- 443 du milieu et des modes de mise en valeur. Ph. thesis, Université Antilles-
444 Guyane, Cayenne, France.
- 445 Holt, R. D., 1997. From metapopulation dynamics to community structure
446 - some consequences of spatial heterogeneity In: Hanski, I. A., Gilpin,
447 M. E. (Eds.), Metapopulation Biology - Ecology, Genetics, and Evolution.
448 Academic Press, San Diego, pp. 149–164.
- 449 Jones, D. T., Eggleton, P., 2000. Sampling termite assemblages in tropical
450 forests: testing a rapid biodiversity assessment protocol. J. Appl. Ecol. 37,
451 191–203.
- 452 Lavelle, P., Barois, I., Cruz, C., Hernandez, A., Pineda, A., Rangel, P.,
453 1987. Adaptative strategies of *Pontoscolex corethrurus* (Glossoscolecidae,
454 Oligochæta), a peregrine geophagous earthworm of the humid tropics. Biol.
455 Fert. Soils 5, 188–194.
- 456 Lavelle, P., Decaëns, T., Aubert, M., Barot, S., Blouin, M., Bureau, F.,
457 Margerie, P., Mora, P., Rossi, J.-P., 2006. Soil invertebrates and ecosystem
458 services. Eur. J. Soil Biol. 42, S3–S15.
- 459 Legendre, P., Legendre, L., 1998. Numerical Ecology, Second English Edition.
460 Elsevier, Amsterdam.
- 461 Manly, B., 1997. Randomization and Monte Carlo methods in Biology. Chap-
462 man & Hall, London.
- 463 Mathieu, J., Grimaldi, M., Rouland, C., Lavelle, P., Desjardin, T., Rossi, J.-

- P., 2009. Variations in soil macrofauna biodiversity with spatial patterns of grasses in Amazonian pastures. *Soil Biol. Biochem.* 41, 586–593.
- Mathieu, J., Rossi, J.-P., Grimaldi, M., P., M., Lavelle, P., Rouland, C., 2004. A multi-scale study of soil macrofauna biodiversity in Amazonian pastures. *Biol. Fert. Soils* 40, 300–305.
- Mathieu, J., Rossi, J.-P., Mora, P., Lavelle, P., Martins, P. F. D. S., Rouland, C., Grimaldi, M., 2005. Recovery of soil macrofauna communities after forest clearance in Eastern Amazonia, Brazil. *Conserv. Biol.* 19, 1598–1605.
- Matlack, G. R., 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Conserv.* 66, 185–194.
- Matson, P. A., Parton, W. J., Power, A. G., Swift, M. J., 1997. Agricultural intensification and ecosystem properties. *Science* 277, 504–509.
- Nahmani, J., Lavelle, P., Rossi, J.-P., 2006. Does changing the taxonomical resolution alter the value of soil macroinvertebrate as bioindicators of metal pollution? *Soil Biol. Biochem.* 38, 385–396.
- Novotný, V., Basset, Y., 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89, 564–572.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G., Stevens, M., Wagner, H., 2008. *vegan: Community Ecology Package*. R package version 1.13-1. <http://vegan.r-forge.r-project.org/>

- Pillar, V. D., 1999. The bootstrapped ordination re-examined. *J. Veg. Sci.* 10, 895–902.
- Poncy, O., Sabatier, D., Prévost, M.F., Hardy, I., 2001. The lowland high rainforest: structure and tree species diversity. In: Bongers, F., Charles-Dominique, P., Forget, P.M., Théry, M. (Eds.), *Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest*. Academic Press, San Diego, pp. 149–164.
- Ponge, J., Topoliantz, S., Ballof, S., Rossi, J.-P., Lavelle, P., Betsch, J., Gaucher, P., 2006. Ingestion of charcoal by the amazonian earthworm *Pontoscolex corethrurus*: a potential for tropical soil fertility. *Soil Biol. Biochem.* 38, 2008–2009.
- Quinn, G., Keough, M., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- R Development Core Team, 2008. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Righi, G., 1984. *Pontoscolex* (Oligochæta, Glossoscolecidae): a new evaluation. *Stud. Neotrop. Fauna Environ.* 19, 159–177.
- Roberts, D., 2007. *labdsv: Ordination and Multivariate Analysis for Ecology*. R package version 1.3-1. <http://ecology.msu.montana.edu/labdsv/R>
- Rossi, J.-P., Blanchart, E., 2005. Seasonal and land-use induced variations

- of soil macrofauna composition in the Western Ghats (South India). *Soil Biol. Biochem.* 37, 1093–1104.
- Rossi, J.-P., van Halder, I., in press. Towards indicators of butterfly biodiversity based on a multiscale landscape description. *Ecol. Indic.*, DOI: 10.1016/j.ecolind.2009.07.016.
- Rossi, J.-P., Mathieu, J., Cooper, M., Grimaldi, M., 2006. Soil macrofaunal biodiversity in Amazonian pastures: matching sampling with patterns. *Soil Biol. Biochem.* 38, 2178–2187.
- Shmida, A., Wilson, M. V., 1985. Biological determinants of species diversity. *J. Biogeogr.* 12, 1–20.
- Smith, J., Potts, S., Eggleton, P., 2008. Evaluating the efficiency of sampling methods in assessing soil macrofauna communities in arable systems. *Eur. J. Soil Biol.* 44, 271–276.
- Swift, M. J., Izac, A. M. N., van Noordwijk, M., 2004. Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? *Agric. Ecosyst. Environ.* 104, 113–134.
- Topoliantz, S., Ponge, J. F., 2003. Burrowing activity of the geophagous earthworm *Pontoscolex corethrurus* (Oligochaeta : Glossoscolecidae) in the presence of charcoal. *Appl. Soil Ecol.* 23, 267–271.
- Topoliantz, S., Ponge, J. F., 2005. Charcoal consumption and casting activity by *Pontoscolex corethrurus* (Glossoscolecidae). *Appl. Soil Ecol.* 28, 217–224.

- 1
2
3
4
5
6
7
8
9
10 528 Topoliantz, S., Ponge, J. F., Lavelle, P., 2006. Humus components and bio-
11 529 genic structures under tropical slash-and-burn agriculture. *Eur. J. Soil Sci.*
12
13 530 57, 269–278.
14
15
16 531 Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., Thies, C.,
17
18 532 2005. Landscape perspectives on agricultural intensification and biodiver-
19
20 533 sity – ecosystem service management. *Ecol. Lett.* 8, 857–874.
21
22
23 534 Zonneveld, I. S., 1995. Vicinism and mass effect. *J. Veg. Sci.* 6, 441–444.
24
25
26
27
28
29
30
31
32
33
34
35
36
37
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Table 1: Soil macrofaunal diversity in southern French Guiana. EF and EB correspond to the same plot sampled in 1999 and 2000 was burnt in between.

Sites	Acronym	n	date	mean density (ind.m ⁻²)	S_{obs}	S_{corr}	singleton	unique
Elahe (traditional slash-and-burn)								
Secondary forest (≥ 100 -yr)	EF	30	July 1999	1781.9 (289.8)	121 (8.3)	151.2	56 (46.3%)	76 (62.8%)
Abbatis (3-yr)	EA	30	July 1999	541.3 (92)	45 (4.2)	56.8	20 (44.4%)	29 (64.4%)
Recently burnt forest	EB	30	May 2000	224.5 (60.8)	22 (2.1)	27	11 (50%)	12 (54.5%)
Maripasoula								
Woody fallow (8-yr)	MF	30	May 2000	645.3 (76.5)	41 (3.7)	51.6	21 (51.2%)	26 (63.4%)
Abbatis (1-yr)	MA	30	July 1999	1109.9 (271.2)	54 (4.6)	69.4	29 (53.7%)	39 (72.2%)

S_{obs} : observed species richness, S_{corr} : bias-corrected species richness, singleton: species with at most one individual, unique: species encountered in only one sample. Percentages for singletons and uniques are computed with reference to the total species richness in the site. Standard errors for mean density and S_{obs} are indicated in parentheses.

Table 2: Observed species richness and shared species of soil macrofauna in different land-uses in a traditional Amerindian slash-and-burn system (region of Elahe, southern French Guiana).

$S_{\bullet} = 145$	EF	EA	EB
EF	121 (83.4%)	24 (142)	9 (134)
EA	17%	45 (31%)	6 (61)
EB	6.7%	9.8%	22 (15.2%)

EF: Secondary forest, EA: Abbatis, EB: recently burnt forest, S_{\bullet} : total species richness (all sites pooled). On diagonal: observed species richness and corresponding ratio to the total number of species (in parentheses). Above diagonal: absolute number of species shared by site pairs and total number of species collected in site pairs. Below diagonal: ratio of the number of shared species to the total number of species in site pairs.

Table 3: Observed species richness and shared species of soil macrofauna in different land-uses in a short-fallow system (region of Maripasoula, southern French Guiana).

$S_{\bullet}=77$	MF	MA
MF	54 (70.1%)	21 (74)
MA	28.4%	41 (53.2%)

MF: Secondary forest, MA: Abbatis, S_{\bullet} : total species richness (all sites pooled). On diagonal: observed species richness and corresponding ratio to the total number of species (in parentheses). Above diagonal: absolute number of species shared by site pairs and total number of species collected in site pairs. Below diagonal: ratio of the number of shared species to the total number of species in site pairs.

Table 4: Soil macrofaunal indicator species in agricultural landscapes in southern French Guiana. IndVal values were tested using permutation tests ($n = 1000$). See text for definitions and Table 1 for land-use acronyms.

Species	group	Specificity	Fidelity	<i>IndVal</i>	<i>p</i>	Land-use
<i>Pontoscolex corethrurus</i>	Oligochaeta	0.38	0.97	36.9	0.001	MA
morphospecies 1	Diplura	0.92	0.33	30.4	0.001	EF
morphospecies 2	Isoptera	0.84	0.57	47.9	0.001	EF
morphospecies 3	Chilopoda	0.79	0.43	34	0.001	EF
morphospecies 4	Chilopoda	0.68	0.43	29.2	0.001	EF
morphospecies 1	Lumbricida	0.51	0.67	34.2	0.001	EF

Figure captions

Figure 1

Principal Coordinates Analysis (PCoA) of soil macrofaunal communities in different land-uses in southern French Guiana. Projection of site scores in the plane defined by Axes 1 (horizontal) and 2 (vertical). Labels are placed at the centre of gravity of each site and are linked to each sample of the corresponding site. See Table 1 for site codes.

Figure
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