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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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9 Decreasing fallow duration in tropical slash-and-burn
10 agriculture alters soil macro-invertebrate diversity: A
11 case study in southern French Guiana
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30 **Abstract**
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33 In the humid tropics, slash-and-burn cultivation causes changes in the compo-
34 sition of soil biota communities. We investigated the soil macro-invertebrates
35 (body length ≥ 2 mm) in five sites, two at Maripasoula, an Aluku village
36 along the Maroni river (French Guiana), with short fallow (≈ 8 years), and
37 the other three at Elahe, a Wayana village along the same river, with long
38 fallow (≈ 25 years). We report observed species richness, the correspond-
39 ing estimates by bootstrap and its associated standard deviation. At both
40 sites the cultivation led to impoverished communities. The overall observed
41 species richness i.e. γ diversity was ca. twice as larger in Elahe than in
42 Maripasoula. The landscape at Maripasoula was dominated by highly dis-
43 turbed areas with the direct consequence that local species richness relied on
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9 colonization from an impoverished regional species pool. On the contrary,
10 in Elahe, crops formed small patches scattered across a landscape essentially
11 constituted of rich undisturbed or slightly disturbed forests hence higher γ
12 diversity. The proportion of rare species ranged from 44% to 54%. We
13 found 6 indicator species amongst which 5 were associated to the old sec-
14 ondary forest in Elahe and one, the earthworm *Pontoscolex corethrurus* was
15 associated to crop fields in Maripasoula (short fallow system). Results are
16 discussed in a landscape context in terms of conservation and management
17 of soil macrofaunal diversity in agro-ecosystems.

18
19 *Key words:* Soil macrofauna, species richness, slash-and-burn agriculture,
20 agriculture intensification, landscape, biodiversity.
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26 27 28 29 30 31 **1. Introduction**

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34 2 Soil invertebrates are key mediators of soil functions in agro-ecosystems.
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36 3 They substantially affect many important processes that take place below-
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38 4 ground like comminution and incorporation of litter into the soil, building and
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40 5 maintenance of structural porosity and aggregation in soils through burrow-
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42 6 ing, casting and nesting activities and control of microbial activities (Lavelle
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44 7 et al., 2006, and references therein). Invertebrates therefore contribute to
45
46 8 the ecosystem services provided by soils and for this reason, they are in-
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48 9 creasingly considered as a resource to be managed and protected. Amongst
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50 10 soil biota, macrofauna (animals with body length ≥ 2 mm (Anderson and
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52 11 Ingram, 1993)) are dramatically affected by cultural practices and various
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54 12 authors have discussed the utility of managing their populations to improve
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56 13 the sustainability of soil fertility especially in countries or regions where farm-

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

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

31 In French Guiana, the demographic pressure threatens the long-lasting
32 equilibrium between slash-and-burn agriculture and nature conservation, due
33 to the progressive disappearance of shifting cultivation. In southern Guiana
34 near the Suriname border, the duration of fallow in the slash-and-burn system
35 has decreased from 15 to 7-8 years in the last 30 years (Topoliantz et al.,
36 2006). The traditional shifting cultivation is still practised in that region by
37 Amerindian communities and the duration of the fallow ranges from 15 to
38 more than 100 years (Fleury, 1998). The aim of this study was to assess the

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39 impact of slash-and-burn cultivation upon the diversity of soil macrofauna in
10 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*
18
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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48 **2. Materials and methods**

49 *2.1. Sites*

50 The present survey was carried out in southern French Guiana near
51 the border between France and Suriname along the Maroni river. We in-
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53 52 vestigated soil macrofauna diversity in agricultural fields of two communi-
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55 53 ties, Wayanas (indians) and Alukus (maroons, of ancient African lineage).
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57 54 Wayana Amerindians are still using the traditional slash-and-burn system
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59 55 where short cropping periods (ca. 2–3 yr) alternate with long fallow periods
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61 56 (≈ 25 yr). The fields (thereafter referred to as “abattis”) are settled by cut-
62
63 57 ting and burning forest plots and are planted with manioc which constitutes
64
65 58 the basic food. Soils are not tilled and manioc cuttings (from previous crops)
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67 59 are planted after resprouting. Neither Wayanas nor Alukus use pesticides,
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69 60 herbicides or fertilizers. Alukus are using a similar system with the difference
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71 61 that cultivation does not exceed 1 year and fallows are shorter (≈ 8 yr on
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73 62 average). The length of the cultivation period depends on the soil fertility
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63 and the spontaneous regrowth of vegetation (Topoliantz et al., 2006).
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64 *Ameridian village of Elahe (long fallow)*. We sampled soil macrofauna in the
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65 Wayana (Amerindian) village of Elahe. This small village is situated on the
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66 Tampock river which is a subsidiary of Maroni (3 ° 26'N, 53 ° 59'W). Three
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67 contrasted situations were investigated. A field that had been cut, burnt and
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68 cultivated by an Indian family 3 yrs before this study (EA). This field was
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69 located next to a secondary forest and was itself a secondary forest before
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70 its cultivation. It was sampled in July 1999. We sampled an old secondary
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71 forest (EF) located nearby EA (ca. 100 m). The old secondary forest showed
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72 woody species typical of mature forests (e.g. *Astrocaryum sciophilum* (Miq.)
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73 Pulle, and *Dicorynia guianensis* Amsh. (Poncy et al., 2001) which indicated
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74 that it had been left untouched for at least 100 years. The plot located in
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75 the secondary forest was resampled in May 2000 after it had been cut and
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76 burnt in December 1999 for cultivation (EB).

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77 *Aluku village of Maripasoula (short fallow)*. The second site is located along
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78 the Maroni river (3 ° 39'N, 54 ° 2'W) near the village of Maripasoula, ca. 25
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79 km downstream of the first study site. Maripasoula is a large village (pop
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80 1200 in 1999) mostly inhabited by Aluku people. The increase in population
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81 density during the last 3 decades led to a decrease in the surface of cultivable
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82 land and the subsequent decrease of fallow duration (Fleury, 1998). We
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83 sampled a 1-yr old abattis (MA) at the end of the crop period. It had been
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84 opened by an Aluku family by cutting and burning an 8-yr-old woody fallow
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85 referred to as MF. MF was characterized by pioneer woody species such as
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86 *Cecropia latiloba* Miq. and *Inga capitata* Desv. Both MA and MF plots were
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87 sampled in July 1999. The MF plot was intended to be burnt in December

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88 1999 and we planned to resampled in May 2000 but unfortunately the Aluku
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11 89 family did not burn it as expected.

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13 90 The mean annual temperature is 26 ° C and the mean annual rainfall is
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15 91 2000 mm. There is a main dry season from September to December and a
16
17 92 shorter one between March and April. Sampled soils are sandy Oxisols at pH
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19 93 of 5 and 4.7 on average in Maripasoula and Elahe, respectively (Topoliantz
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21 94 et al., 2006). The average total C content was 24.6, 22.5, 25.8, 19.1 and 18.6
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23 95 g kg⁻¹ while the total N content was 1.65, 1.48, 1.78, 1.39 and 1.35 g kg⁻¹
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25 96 the in plots MA, MF, EA, EF and EB respectively (data from Table 1 in
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27 97 Topoliantz et al., 2006). Other physico-chemical features of the soils at the
28
29 98 study sites are available in Topoliantz et al. (2006).

30 31 99 *2.2. Sampling*

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33 100 We used the Tropical Soil Biology and Fertility (TSBF) procedure (An-
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35 101 derson and Ingram, 1993). Sampling units consisted of 25 cm × 25 cm by
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37 102 30 cm deep soil monoliths. As recommended in the TSBF procedure, we
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39 103 used 10 monoliths per transect and carried out 3 transects per plot (i.e. 30
40
41 104 samples per plots). The distance separating monoliths was 5 m and transects
42
43 105 were 20 m distant from each other. The litter was collected at each sampling
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45 106 point and a trench was then dug to a depth of 30 cm around the 25 × 25
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47 107 cm² area to get a soil monolith. Macroinvertebrates from soil and litter were
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49 108 hand-sorted and preserved in 4% formalin solution. Invertebrates were later
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51 109 counted and identified in the laboratory. We grouped specimens in morphos-
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53 110 pecies and identified most of them with the help of different taxonomists.
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55 111 We excluded larvae from the statistical analyses because they were partially
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57 112 redundant with adults found in the same samples. Overall, our estimation

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9 of species richness is therefore underestimated.

114 2.3. Data analysis

115 2.3.1. Community structure

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

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

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10 137 cator species are species mostly present in one of the groups to be compared,
11 138 while being mostly absent in other groups. Dufrêne and Legendre (1997)
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13 139 proposed to compute the *IndVal* index by combining two terms reflecting
14
15 140 the specificity and the fidelity of a species for the samples corresponding to
16
17 141 a certain land-use type. The specificity term is the mean abundance of a
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19 142 species i in the samples of the land-use j compared to all land-uses.

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

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

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

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

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

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37 143 The indicator value of a species i for an array of sites is the largest value of
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39 144 $IndVal_{ij}$ observed over all sites j . In this paper we adopted the threshold
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41 145 level of 25% for the index as suggested by Dufrêne and Legendre (1997),
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43 146 i.e. species i is present in at least 50% of samples of land-use j and its
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45 147 relative abundance in land-use j is at least 50%. We assessed the statistical
46
47 148 significance of observed *IndVal* values by means of a permutation test (1000
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49 149 randomizations) as proposed by Dufrêne and Legendre (1997).

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52 150 *Multi Response Permutation Procedure (MRPP)*. We tested the significance
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54 151 of community dissimilarities among land-uses by means of the Multi Re-
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56 152 sponse Permutation Procedure (MRPP) (Quinn and Keough, 2002). MRPP

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9 153 tests whether there is a significant difference between two or more groups of
10 154 sampling units. The MRPP statistic δ is the overall weighted mean of within-
11 155 group means of pairwise dissimilarities among sampling units. The observed
12 156 value is statistically tested by mean of a permutation test where sampling
13 157 units and their associated pairwise distances are permuted N times and δ is
14 158 recalculated. The significance test is based on the proportion of permuted
15 159 δ s that are less than the observed δ . We used the Bray–Curtis distance to
16 160 quantify the dissimilarities between land-uses. MRPP was computed using
17 161 the `vegan` package (Oksanen et al., 2008).

162 2.3.2. *Species richness*

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

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10 178 i.e. species that occurred in only one sample. The observed species richnesses
11 179 in the different land-uses were compared by mean of a one-factor analysis
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13 180 of variance. Because our data did not satisfy most of the assumptions of
14
15 181 ANOVA we used the randomization test described by Manly (1997, p.117).
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17 182 The observed F statistic was tested by comparison with corresponding values
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19 183 in N ANOVAS after randomization of raw data.
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22 184 **3. Results**

23 24 25 185 *3.1. General statistics*

26
27 186 Soil macrofauna communities differed markedly amongst land-uses and
28
29 187 between sites. The average macrofaunal density was higher in the secondary
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31 188 forest (EF) in Elahe followed by the abbatis in Maripasoula (MA) and it was
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33 189 lowest in the recently burnt secondary forest in Elahe (EB)(Table 1). The
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35 190 observed species richness varied accordingly with a total of 121 species in the
36
37 191 secondary forest in Elahe (EF) and values ranging from 22 to 54 species in the
38
39 192 other plots. Corresponding bias-corrected values estimated from bootstrap
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41 193 were somewhat higher (Table 1) but between-site ranking did not change at
42
43 194 all (there is a linear relationship between original and corrected values). The
44
45 195 number of singletons and unique species respectively ranged from 44% to 54
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47 196 % and 55% to 72%, respectively, and was fairly homogeneous amongst sites
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49 197 (Table 1). A grand total of $S = 186$ species was recorded (all sites pooled)
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51 198 amongst which 42 (22.6%) were common to Elahe and Maripasoula (shared
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53 199 species). One hundred and twelve (60.2%) species were encountered in the
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55 200 site of Elahe whereas 32 (17.2%) species were only recorded in Maripasoula.
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201 *3.2. Community structure*

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

215 *3.3. Species richness within and between sites*

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

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9 226 while the abattis hosted 41 species (53% of the total) (Table 3). The propor-
10 tion of shared species was 28% (Table 3) which was higher than Elahe (Table
11 227 tion of shared species was 28% (Table 3) which was higher than Elahe (Table
12 228 2). The observed species richness significantly differed among land-uses as
13 229 indicated by the ANOVA test based on 1000 randomizations ($p < 0.001$).
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18 230 3.4. *Indicator species*

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20 231 Six morphospecies showed *IndVal* values $\geq 25\%$ and significant associ-
21 232 ated probabilities at $\alpha = 0.05$: two earthworms, two centipedes, a termite
22 233 and a bristletail (Table 4). Five of these were associated to the old secondary
23 234 forest (traditional slash-and-burn shifting agriculture) while one earthworm
24 235 species, *Pontoscolex corethrurus*, was indicator of the abattis in the short
25 236 fallow system in the Aluku village of Maripasoula.
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33 237 4. Discussion

34 238 4.1. *Forest logging and fire*

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36 239 Forest clearing and burning had a strong impact upon soil macrofauna
37 240 species richness in Elahe. Soil macrofauna communities were dramatically
38 241 impoverished soon after fire (plot AB) and remained strongly affected three
39 242 years after crop establishment (plot EA). Tree harvesting is known to affect
40 243 the composition of soil faunal communities as well as food web structure in
41 244 various ways (Bengtsson et al., 1997). One direct and strong impact is the
42 245 change in soil climatic conditions (temperature, moisture) that is associated
43 246 to the direct exposure of soil to solar radiation (Matlack, 1993). These effects
44 247 are magnified by fire associated with forest logging. During fire, the temper-
45 248 ature of the surface soil can exceed 400°C (Gimeno-García et al., 2004) with
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9 249 important consequences upon soil dwelling organisms and most notably non-
10 250 mobile species that inhabit litter layers and/or upper soil strata (Mathieu
11 251 et al., 2005; Abbott et al., 2003). Fire also indirectly affects soil fauna by
12 252 destroying epigeic microhabitats like decaying wood, fine twigs, dead plant
13 253 stems and leaves that serve as trophic resources or habitat for numerous
14 254 species (Mathieu et al., 2005).

20 255 Not surprisingly, the species pool observed in the recently burnt plot EB
21 256 was constituted either by species that withstand forest logging and burning
22 257 or by colonisers originating from adjacent areas.

26 258 After a few years of cropping, the species richness had increased but re-
27 259 mained low (plot EA) and ca. half the species richness of the abattis was
28 260 constituted by species also present in the forest (Table 2). One may hy-
29 261 pothesize that these species are eurytopic (species with large niche breadth)
30 262 that can withstand the environmental conditions that prevail in crop plots.
31 263 These results are fully in accordance with data collected in eastern Amazonia
32 264 (Brazil) (Mathieu et al., 2005).

39 265 Interestingly, forest clearing and the set up of manioc crop has a lower
40 266 impact on the observed richness in the region of Maripasoula where crop
41 267 rotation is more rapid. The abattis (MA) and the woody fallow (MF) share
42 268 more species than corresponding plots in Elahe (EA and EF): one reason for
43 269 this is that the plots that are logged and burnt in Maripasoula are woody
44 270 fallows ca. 7–8 yr-old and by no means old growth forests as in Elahe. The
45 271 species richness of such plots is low and roughly comparable to what is ob-
46 272 served in the abattis in the traditional slash-and-burn system in the native
47 273 Amerindian area of Elahe. These results indicate that agricultural intensi-

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9 274 fication leads to impoverishment of species richness and homogenization of
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11 275 soil macrofaunal communities.

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13 276 All but one species that were found to be indicators were associated to the
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15 277 old secondary forest in Elahe (EF). Given huge environmental differences that
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17 278 exist between the forest and other land-uses, forest specialists could be ex-
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19 279 pected to have high *IndVal* values. This index encapsulates two contrasted
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21 280 and complementary information, specificity and fidelity. Soil macroorgan-
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23 281 isms generally display a highly aggregated spatial distribution (Ettema and
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25 282 Wardle, 2002) and this is even more marked in the case of social insects
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27 283 like termites or ants. This leads to high variance of abundance data and
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29 284 may cause low values of the fidelity term B_{ij} and subsequently low and/or
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31 285 not-significant *IndVal* index (Nahmani et al., 2006). Apart from specialist
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33 286 species from the secondary forest, only one species was associated to crops
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35 287 with short fallow periods, the pantropical endogeic earthworm *P. corethrurus*
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37 288 (*Oligochaeta*, *Glossoscolecidae*). This peregrine species has been dispersed
38
39 289 worldwide by man and is probably indigenous to the Guianas plateau in
40
41 290 South America (Righi, 1984). This species exhibits a very good aptitude to
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43 291 withstand soil disturbance and scarcity of organic matter and is abundant
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45 292 in open areas over a wide range of tropical regions (Lavelle et al., 1987).
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47 293 *P. corethrurus* has been shown to have the capacity to invade Amazonian
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49 294 pastures and to cause soil degradation through physical compaction of the
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51 295 soil surface (Chauvel et al., 1999). However, other studies showed that it
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53 296 can incorporate charcoal to the topsoil thereby increasing its humus content
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55 297 of the topsoil by adding finely powdered black carbon (Ponge et al., 2006;
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57 298 Topoliantz and Ponge, 2003, 2005).

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9 299 *4.2. Landscape context and species diversity*

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11 300 Our sampled soils differed in terms of physico-chemical parameters (e.g.
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13 301 total C content) and these differences can be explained by land management
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15 302 practices among which fallow duration. Land management can have direct
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17 303 effects upon soil biodiversity as well as indirect effects through changes in
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19 304 soil parameters like or C or N content. Both direct and indirect effects
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21 305 convey land-use impacts on soil biodiversity. In that context, our plots can
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23 306 be compared although our data do not allow unravelling such direct and
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25 307 indirect effects.

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27 308 Comparing Elahe and Maripasoula sites allows us to discuss the effects of
28
29 309 the reduction of fallow duration upon γ , i.e. regional diversity. The impact of
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31 310 reduced fallow on the pooled richness was huge (145 versus 77 species in Elahe
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33 311 and Maripasoula, respectively). The main difference between these species
34
35 312 pools is due to the low richness of the woody fallow (MF) in Maripasoula as
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37 313 compared to the old secondary forest (EF) in Elahe. The woody fallow is the
38
39 314 typical habitat that is cut and burnt before crop settlement in the reduced
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41 315 fallow system. There is no secondary forest nor older fallow left in the region
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43 316 of Maripasoula where all areas accessible by foot or by canoe have been and
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45 317 are still used for cultivation (Topoliantz et al., 2006). On the other hand,
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47 318 abattis are similar in Elahe and Maripasoula in terms of richness (roughly
48
49 319 40 to 45 species) although the proportion of shared species is low ($\approx 21\%$).

50 320 Various mechanisms contribute to link α diversity to neighbouring land-
51
52 321 scape configuration (Dunning et al., 1992; Rossi and van Halder, in press).
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54 322 Species richness in the abattis could be affected by the neighbouring species-
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56 323 rich secondary forest or by woody fallows through the so-called “vicinism” or

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9 324 “mass” effect (Zonneveld, 1995) whereby a flow of individuals originates from
10 325 species rich habitat and allows the presence of species in neighbouring habi-
11 326 tats where they are not self-maintaining (Shmida and Wilson, 1985). This
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13 327 corresponds to the “spillover effect” by which species can be maintained in
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15 328 unsuitable habitat patches in the framework of source-sink dynamics (Holt,
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17 329 1997). In the context of accelerated crop rotation, the amount of land covered
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19 330 by pristine habitats is very low if not zero. In the site of Elahe, the situation
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21 331 is inverse, crops constituting a habitat distributed as small patches scattered
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23 332 across a landscape essentially constituted of rich undisturbed or slightly dis-
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25 333 turbed forests. In highly anthropised landscapes, the overall proportion of
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27 334 species with high capacity to colonize abattis is larger and the landscape con-
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29 335 text tends to favour a rapid colonization of newly settled fields. This is not the
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31 336 case in the Amerindian region where abattis are hardly spatially connected.
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337 4.3. *The importance of rare species*

338 We defined rare species as species collected as single individuals, single-
339 tons. All studied sites exhibited roughly 50% of singletons and an even larger
340 proportion of unique species. Such high values were reported e.g. for insect
341 communities associated to tropical trees (Novotný and Basset, 2000) and soil
342 macrofauna in Amazonian pastures (Rossi et al., 2006). Rarity can be a prob-
343 lem during data analysis and various indices have been proposed to correct
344 estimates of species richness and shared species (Colwell and Coddington,
345 1994; Chao et al., 2005). In this study we used a bootstrap correction of
346 species richness estimates which led to corrected estimates that were linearly
347 correlated to observed species richnesses. This indicated that our perception
348 of between-site similarity in terms of species richness were correct even when

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9 349 solely based on raw data.

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11 350 Statistics aside, rare species raise the question why are they so numerous.
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13 351 First, rare species could be species that were inadequately sampled and this
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15 352 must be considered with caution. Indeed, soils are highly variable habitats
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17 353 with various nested sources of spatial heterogeneity that affected species dis-
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19 354 tribution and hence short-scale diversity patterns (Mathieu et al., 2009). The
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21 355 problem of sampling deficiency in estimating biodiversity in soils is discussed
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23 356 elsewhere (Rossi et al., 2006) and could possibly be responsible for a certain
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25 357 proportion of our rare species. It must be also noted that the TSBF sampling
26
27 358 protocol may not be optimal for certain type of organisms and notably litter
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29 359 inhabiting species. Other sampling methods like Winkler bags may also be
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31 360 used (Smith et al., 2008) while specific strategies have been developped for
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33 361 social insects (termites) (Jones and Eggleton, 2000). On the other hand, the
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35 362 “spillover effect” could lead to the presence of rare species simply because
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37 363 they are transient species i.e. species that cannot maintain in one habitat
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39 364 but originates from a neighbouring habitat that acts as a permanent source.
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41 365 Distinguishing transient species is a very difficult task (Novotný and Basset,
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43 366 2000) that would require a huge amount of additional field data (and direc-
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45 367 tional activity traps) in our case. However, this is the only way to refine our
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47 368 estimates of species richness while controlling for close neighbourhood effects
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49 369 and therefore assessing landscape effects upon crop field species richness.

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51 370 *4.4. Conservation and management of soil macrofaunal diversity in agro-*
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53 371 *ecosystems*

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55 372 It is broadly acknowledged that the conservation of soil macrofauna in
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57 373 agroecosystems is an important aspect of sustainable agriculture (Brussaard

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9 374 et al., 2007) but the spatial facet of that question have not yet received the
10 attention it requires (but see Tschardt et al., 2005). The landscape at Mari-
11 375 pasoula is dominated by highly disturbed areas and the direct consequence
12 376 is an erosion of γ diversity. Local species richness thus rely on colonization
13 377 from impoverished regional species pool. Swift et al. (2004) argue that the
14 378 management of biodiversity in agricultural context is more effective at the
15 379 landscape scale than at the local plot scale where strictly utilitarian options
16 380 prevail. Following this line of reasoning, and given that most forest species
17 381 are unlikely to maintain themselves within abattis, the management of γ
18 382 diversity may be based on the maintenance of fallow plots of a large range
19 383 of age and not only of pristine ecosystems. It is additionally important to
20 384 consider the spatial arrangement of these plots across the landscape. They
21 385 act as source of colonisers for newly abandoned field crops and as such their
22 386 spatial location may be of prime importance. The dispersal abilities of most
23 387 soil invertebrates are not very well documented but are certainly limited for
24 388 many species and this reinforces the importance of the distribution of the
25 389 source of colonisers within agricultural landscapes.
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25 406 **References**

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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.

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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%)

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

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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.

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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

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551 **Figure captions**

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13 553 **Figure 1**

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15 554 Principal Coordinates Analysis (PCoA) of soil macrofaunal communities in
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17 555 different land-uses in southern French Guiana. Projection of site scores in
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19 556 the plane defined by Axes 1 (horizontal) and 2 (vertical). Labels are placed
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21 557 at the centre of gravity of each site and are linked to each sample of the
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23 558 corresponding site. See Table 1 for site codes.

Figure
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