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Soil properties and the macrofauna community in abandoned irrigated rice fields of northeastern Argentina

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Abstract This study compared soil physical, chemical, and biological characteristics between natural grassland and recently abandoned rice fields in order to identify those variables that might explain the observed increase of *Camponotus punctulatus* anthills in abandoned rice paddy fields from Northern Argentina. Mainly due to a reduction of macropores and mesopores, overall porosity decreased by around 6% and bulk density was about 7% greater, in the 0- to 10- and 10- to 20-cm layers of the abandoned rice fields. Carbon and nitrogen content from organic matter increased (29% and 41% respectively for the 0- to 20-cm horizon) during cultivation but decreased (38% and 24%) 2 years after the last rice harvest. Forty percent of natural grassland-organic matter and 30% of abandoned rice-organic matter mineralized in less than 2 years. There was a different community structure between the abandoned rice fields and the undisturbed natural grassland and only a 20.6% (i.e. only 19 species from a total of 92) overlap in species composition. The abundance of macrofauna was greater in abandoned rice fields (2,208 individuals m^{-2}) in comparison to natural grasslands (288 ind m^{-2}) due to higher densities of small earthworms and *Camponotus punctulatus* ants; however, the Shannon index showed lower values in comparison to natural grasslands. Earthworms and *C. punctulatus* in the abandoned rice fields showed a change in their $\delta^{13}C$ signature indicating a switch in diet from natural grassland organic matter (C4) to organic matter from rice (C3). Our results indicate that the effects of rice cultivation practices did not seem to produce any physical or trophic limitations to recolonization by the macrofauna. It seems that changes in overall soil conditions have favored a change in the construction behavior of *C. punctulatus* which, in combination with population increases, could explain the explosion in number of anthills.

Keywords Biodiversity · Natural ^{13}C abundance · Natural grassland · Physical properties · Soil organic matter

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Introduction

Within the Espinal phytogeographical region of Argentina in Corrientes Province, natural grasslands have been used for traditional cattle ranching since the last century (Carnevalli 1994). However, on large farms, with the increasing availability of artificial water reservoirs, rice production has recently become a common agricultural activity. Consequently, 10% of the natural grasslands of this province have been converted into rice fields. In these new agroecosystems, the density of anthills of the ant *Camponotus punctulatus* Mayr has unexpectedly and conspicuously increased (Folgarait et al. 2002), the highest densities occurring in those agricultural fields that have the greater soil disturbance. For example, less disturbed sown pastures attain densities of 180 anthills ha^{-1} (Folgarait and Gorosito 2001) whereas more disturbed soils such as those in rice fields exhibit 2,400 anthills ha^{-1} 3 years after being abandoned (Folgarait et al. 2002). Natural grasslands never show more than 20–50 anthills ha^{-1}. This native ant species has a broad geographical distribution in Argentina (Kusnezov 1951) and can either build aboveground nests (anthills) or can develop nests underground at the base of tussocks, rosettes, or under rocks (Kusnezov 1951; Folgarait et al. 2002). The presence of flooded areas (Lewis et al. 1991) and an increase in agricultural activities (Folgarait et al. 1996) have been correlated with aboveground nest building. Although the anthills themselves represent a fertile microsite (Folgarait et al. 2002) and these ants do not represent a direct hazard to crops as they are neither herbivores nor granivores (Gorosito et al. 1997), local people consider them unsightly. Moreover, farmers incur high economic costs destroying the hard-packed, large mounds built by *C. punctulatus* when they want to restart agricultural activities after land has lain fallow.

The causes for the spectacular increase in anthill density of this species are unknown but are most probably related to a soil ecosystem disequilibrium. Rice paddy fields are intensive farming systems that greatly impact the soil, and likely affect fundamental soil properties such as soil porosity and aggregation, soil organic matter content and quality, and soil fauna communities especially the bioturbators termed “ecosystem engineers” (Roger et al. 1995; Brussaard et al.1997; Neue et al. 1997). The use of machines to plough the rice field and to level the soil in order to maintain the surface water level may exacerbate problems of soil compaction, and therefore change soil structure, aeration, and water holding capacity (Lal 2000). Soil organic matter dynamics may also be affected since irrigation for rice cultivation induces anaerobic conditions and in general produces an accumulation of organic matter and a reduction in mineralization (Tate 1979). Finally, rice fields also affect soil microflora, microfauna and macrofauna during rice cultivation (Lavelle and Pashanasi 1989; Roger et al. 1995; Gijsman et al. 1997; Settle et al. 1996) and the anoxia imposed by irrigated rice cultivation as well as the application of chemicals are expected to reduce drastically the overall abundance and diversity of soil organisms (Roger 1996).

The general hypothesis of this study is that the increased number of *C. punctulatus* aboveground could be related to physical, organic matter, and biological changes that result from a type of rice farming which favors their establishment. In particular, we have three hypotheses. The physical one assumes that a compacted soil could delay the invasion of macrofauna species but not of *C. punctulatus* which has a great capacity for digging. The chemical-trophic hypothesis considers that rice practices deplete the stocks of organic matter affecting negatively the establishment of detritivores but not of other organisms like *C. punctulatus* which does not feed directly from detritus. Finally, the biological hypothesis assumes that most macrofauna are slow at recolonization whereas *C. punctulatus* is comparably faster. To prove these hypotheses, natural grasslands, which represent the dominant plant community of the region (Carnevalli 1994), were compared with abandoned rice fields, which had been cultivated for three-four cropping cycles (common practice in the region) and then abandoned for 2 years. In the recently abandoned rice field we expected to observe a greater soil compaction due to ploughing and soil flooding, decreased stocks and a slower organic matter turnover and poor return of crop residues to the soil due to anaerobic conditions generated during flooding, and a different macrofauna community with lower richness representing a sub-set of species that were able to re-invade the system after flooding ceased. To test these predictions we measured bulk density and porosity to infer compaction, used C stable isotope analyses for soil organic matter dynamics (Cerri et al. 1985; Mariotti 1991) and feeding habits of earthworms and *C. punctulatus* (Spain and Le Feuvre 1997) and we studied the abundance and richness of macrofauna under both types of land uses.

Materials and methods

Study site

The study was conducted in Mercedes Department, Province of Corrientes, Argentina (29°S, 58°W). The climate is wet sub-tropical, without a definite dry season; autumns (March and April) are rainy, winters and springs (July and August, October and November) humid, and summers (December, January, and February) are hot and frequently wet; mean annual precipitation is 1,270 mm and mean annual temperature is 20.1°C (Fernández et al. 1993).

This study was performed on the farm “Aguaceritos”, which is located north of Mercedes and covers 21,000 ha mainly used for cattle ranching on natural grassland vegetation dominated by *Andropogon lateralis.* Around 1,500 ha have been cultivated with rice and are now at different stages of abandonment because the cost/benefit balance becomes unfavorable after four cropping cycles. Two plots of natural grasslands separated at least by 1 km (to prevent autocorrelation) and two plots of 2-year-old abandoned rice fields separated by 5 km were chosen for data collection (the only exception was for measurements of soil organic matter for which we chose one plot of each but added an additional plot of 0.5 years of abandonment to evaluate the organic matter dynamics more closely). Recolonization by soil macrofauna in abandoned rice fields is a highly dynamic process. In this paper we compared data from second year plots in order to minimize the time from the last rice harvest and yet maximize the time for ant mound density increase.

A preliminary pedological survey was performed on several plots in this farm and the soil was characterized as Albaqualf (Soil Survey Staff 1992). These soils are developed on a several-meters-thick clayey saprolite of calcareous sandstone. In plots after rice cultivation, large compact clods occurred in the ploughed layer and a distinct plough pan appeared at a 15- to 25-cm depth caused by mechanical farming. The following year, the whole topsoil appeared homogeneously compacted by cattle trampling and the plough pan could no longer be morphologically distinguished. Hydromorphy increased in cultivated plots relative to the natural grassland. The texture of natural grassland and abandoned rice field plots was similar (Table 1).

Soil physical measurements

Samples were collected in January 2001 at both plots of each land-use type. We used two transects, 10 m apart, with three sampling stations each separated by 10 m. At each sampling station, samples for bulk density measurements were taken using 250-cm^3 cylinders (McIntyre and Loveday 1974). We gathered two samples per depth on the first replicate plot and one on the second, the samples centered at 2.5-, 10-, 20-, and 30-cm depth. From bulk density data

Table 1 Texture (%) at different depths in natural grassland and 2-year-old abandoned rice soils at the study site

	Natural grassland				Abandoned rice field			
Depth (cm)	0–5	5–10	10–20	20–30	0–5	5–10	10–20	20–30
Clay	16.9	17.3	16.8	19.2	14.4	15.1	15.6	18.6
Fine silt	47.9	46.5	42.8	41.4	48.9	49.3	49.6	42.5
Coarse silt	12.5	11.8	17.8	14.7	14.4	11.8	14.3	18.9
Fine sand	16.0	18.0	16.2	16.3	16.3	17.1	14.6	14.2
Coarse sand	6.8	6.5	6.5	8.4	5.9	6.7	5.9	5.8

(γd) and particle density data (γs) determined with a water pycnometer, we calculated porosity (n) following $n = 1-(\gamma d/\gamma s)$ (Hillel 1998). Additional soil samples were taken at three depths (10, 20 and 30 cm) in one of the holes (at each land-use type) to make a more detailed characterization of the soil structure. Bulk density of small clods (1 cm^3) was measured after kerosene saturation (McIntyre and Loveday 1974). Pore size distribution was determined by mercury porosimetry (porosimeter CARLO-ERBA-2000) on soil clods. The volume of mercury introduced in each 1-cm^3 clod, dehydrated (at 105°C) and degassed, was measured at an increasing applied pressure, which was inversely proportional to the size of the penetrated pores (Lawrence 1977; Vachier et al. 1979):

$$PHg = -\frac{2\mu \cos\theta}{r\ eq}$$

where P_{Hg} is the pressure of mercury (Pa), μ is the surface tension of mercury (0.480 Nm^{-1}), θ is the contact angle of mercury with the soil particles, and r_{eq} is the equivalent pore radius (m). The porosimeter used allows analysis of an equivalent pore radius between 0.0035 and 100 µm.

Soil organic matter

Soils for organic matter measurements were sampled in July 2000 at one of the two replicates of each land-use type, plus at a rice field abandoned for 6 months after the last harvest. Five composite samples of approximately 500 g corresponding to the 0- to 10-cm and the 10- to 20-cm layers were collected manually. These samples were homogenized, per layer, air-dried and sieved at 2 mm.

Organic carbon and total nitrogen concentration

Total soil organic carbon (C) and total nitrogen (N) concentrations were determined by dry combustion of an aliquot of the samples ground at 100 μm, using a Fisons NA 1500CHN autoanalyser. Results are shown in $mg.g^{-1}$.

Stable carbon isotopic analyses

Natural grasslands in sub-tropical Corrientes Province are characterized by C4 plants whereas rice plants (*Oryza sativa*) have a C3 photosynthetic pathway. The change in vegetation due to the new agricultural activity offers a good opportunity to trace the dynamics of organic matter of different origins (Boutton et al. 1998).

The ^{13}C natural abundance of the CO_2 released by the CHN autoanalyser was measured with a mass spectrometer Fisons SIRA 10 Isotope Ratio MS (Girardin and Mariotti 1991). Precision of the on-line procedure was better than ±0.2‰ for C isotope ratios. ^{13}C natural abundance on each sample was expressed in δ units, by reference to the international standard PDB (Craig 1957), according to the following equation:

$$\delta^{13}C^{0/00} = 10^3 \times \left[\left(^{13}C/^{12}C\right)_{sample} - \left(^{13}C/^{12}C\right)_{PDB}\right] / \left(^{13}C/^{12}C\right)_{PDB}$$

The total C concentration derived from C3 rice plants (Cr), and from C4 vegetation (natural grassland and invading grass from ex-rice field as Cng) was calculated as follows for each soil layer or fraction:

$$Cr = [(\delta-\delta_0)/(\delta_R-\delta_0)] \times Ct \qquad Cng = Ct - Cr$$

where δ is the $\delta^{13}C$ of the soil sample in abandoned rice field, δ_0 the $\delta^{13}C$ of the soil sample under natural savanna and δ_R is the $\delta^{13}C$ of the rice grass. The $\delta^{13}C$ of the rice is not the ideal estimator of δ_R because it represents the signature of the plant and not of the soil organic matter. However, it is commonly used because at our field site there were no soils that had been cultivated with rice for a long time (Balesdent 1991).

Soil macrofauna

Macrofauna samples were gathered using the standard Tropical Soil Biology and Fertility (TSBF) method (Lavelle 1988; Anderson and Ingram 1993), which consists of excavating monoliths of 25×25×30 cm of soil from which the organisms are manually removed in the field. Each monolith corresponded to a sampling point used to measure physical properties. Specimens were later identified at the level of morphospecies (as a surrogate for real species; Oliver and Beattie 1996), families and orders by a trained parataxonomist, and the abundance of each morphotype was also recorded in order to calculate the Shannon index of diversity (H), the equitability (J), and richness (S); (Magurran 1988; Gotelli and Colwell 2001).

Studies of feeding habits of earthworms and *C. punctulatus* ants were performed at each of the two plots of each type of land use in January 2001. Besides our interest in *C. punctulatus*, we also chose to study earthworms because they are soil feeders and we were interested in exploring whether there were feeding limitations for soil feeders after rice cultivation. A 10×10 m quadrat was placed close to the TSBF macrofauna sampling site (see above). All *C. punctulatus* nests were identified and 20–30 individual ants were sampled from each colony. At each corner of the quadrat, a 25×25×20 cm monolith was excavated in order to collect earthworms. Specimens were dried at 60°C for more than 24 h, ground into a fine powder, and finally used for C isotopic analyses. Samples were analyzed as described for soil organic matter.

Statistical analyses

Results have been statistically analyzed using non-parametric statistics because data were not normally distributed and did not show homoscedasticity due to small sample sizes. When more than one treatment was compared we used the Kruskal Wallis test. In the case of two comparisons we used Mann-Whitney tests (Siegel 1974; Sherrer 1984). Results are reported as medians with 25% and 75% percentiles.

Results

Physical measurements

Bulk density data did not differ significantly across replicate plots (for each comparison $p > 0.05$); therefore, data were grouped for analyses of relationships related to the type of land use. Total bulk density was significantly lower in the natural grassland in comparison to the abandoned rice field at each soil depth (each comparison $p < 0.05$) and it increased with depth for both land-use types (Table 2). Porosity showed a 3–4% overall reduction with rice cultivation in comparison to natural grassland (Table 2). Similar results were found with bulk density of small clods, although greater differences were measured at 10- and 30-cm depth (6–7%). The pore size distribution obtained from mercury porosimetry was dominated for both land-use types by mesopores of 0.014 μm $< r_{eq} <$ 12 μm (Fig. 1). The modal mesopore class size was marginally smaller in the 0- to 10-cm soil layer in the abandoned rice field (0.6 μm) than in the natural grassland (1.0 μm). Similarly, the percentage of mesopores from the total accounted for by mercury porosimetry was less in the rice fields (26.5%) in comparison to the natural grassland (29.0%). The other size categories, microporosity (0.0035 μm $< r_{eq} <$ 0.014 μm) and macroporosity ($r_{eq} >$ 12 μm) were less represented. This analysis, however, did not take into account macropores with $r_{eq} >$ 100 μm. Despite this limitation, we observed a reduction in the macroporosity of the abandoned rice field soil, especially at 10- and 30-cm depth (macropores at 10 cm 1.7%, at 30 cm 1.3%, mesopores at 10 cm 26.5% at 30 cm 23.1%) in comparison to the natural grassland (Thomas 2000).

Soil organic matter

Organic C and total N concentrations

Organic C and total N concentrations were significantly greater (in each case $p < 0.05$, except for total C at 0–10 cm) in the rice field abandoned for 6 months than in the natural grassland (Fig. 2). In the field abandoned for 2 years, organic C and total N were similar to those found in the natural grassland (each comparison $p < 0.05$), except for organic C concentration at 0–10 cm which was significantly smaller in the former (Fig. 2). Carbon concentrations were similar between depths within each age of abandoned rice field ($p > 0.05$) but in the natural grassland the C concentration was marginally smaller ($p = 0.09$) at 10–20 cm than at 0–10 cm. Total N concentration either increased or remained similar with depth, although not significantly ($p > 0.05$ in each ex rice stage), in the abandoned rice fields while it was significantly smaller ($p = 0.008$) at greater depths in the natural grassland (Fig. 2).

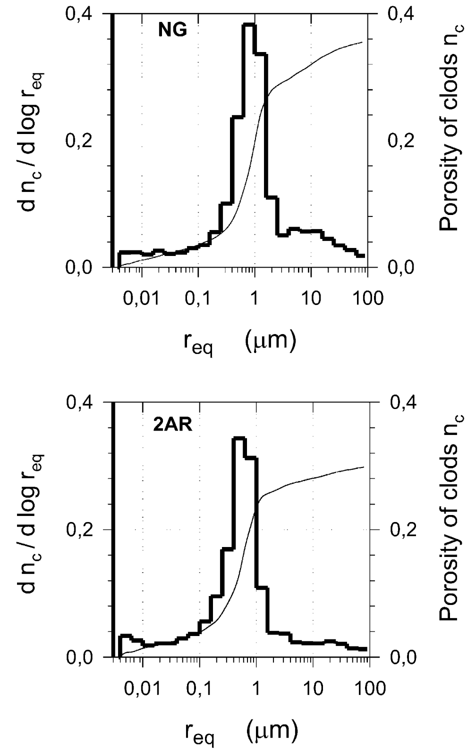

Fig. 1 Pore size distribution determined by mercury porosimetry on soil clods from natural grassland (*NG*) and a rice field abandoned for 2 years (*2AR*). The *left axis* is the derivation of the cumulative pore volume curve (on the *right axis*); n_c refers to the porosity of clods

Table 2 Soil particle density and bulk density measured in 250-cm^3 cylinders and on 1-cm^3 clods [soil porosity registered as percentage of sample volume (cylinders or clods); *10*, *20*, and *30 cm* refers to the 0- to 10-, 10- to 20-, and the 20- to 30-cm horizons]

Land use/Depth	Particle density mean Mg m^{-3}	Total bulk density[a] Mg m^{-3}	Total porosity (%)	Clods bulk density[b] Mg m^{-3}	Clods porosity (%)
Natural grassland: 10 cm	2.60	1.21 (0.042)	53.2	1.47 (0.022)	43.4
20 cm	2.61	1.25 (0.035)	52.1	1.55 (0.029)	40.8
30 cm	2.63	1.26 (0.044)	52.2	1.57 (0.043)	40.4
Abandoned rice field: 10 cm	2.59	1.30 (0.052)	49.8	1.63 (0.020)	37.1
20 cm	2.60	1.34 (0.058)	48.5	1.51 (0.075)	41.7
30 cm	2.63	1.35 (0.040)	48.5	1.73 (0.011)	34.4

[a] 12 measures wet soil; mean (STD) $N = 12$
[b] 3 measures – dry soil; mean (STD) $N = 3$

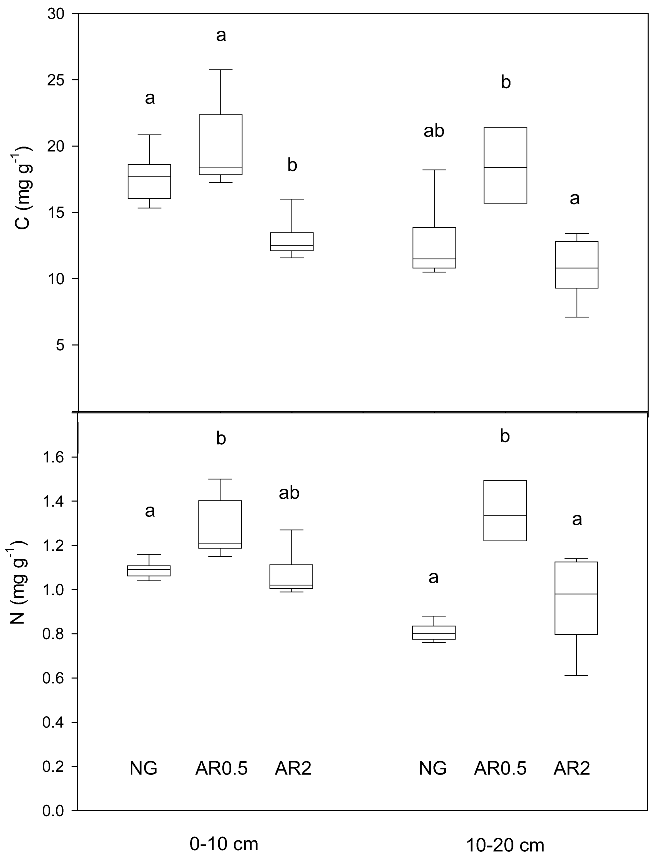

Fig. 2 Median organic C and total N concentrations (with the 25% and 75% percentiles), expressed in mg g^{-1}, in the natural grassland (*NG*), the 6-months-old abandoned rice field (*AR0.5*) and a 2-years-abandoned rice field (*AR2*). *Different letters* indicate that C and N contents differed statistically (p <0.05) between land uses whereas *same letters* indicate no differences (p >0.05)

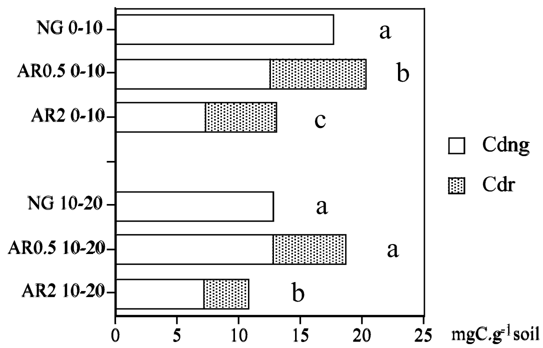

Fig. 3 Organic C derived from natural grassland (*Cdng*) and from rice (*Cdr*) in the natural grassland (*NG*), the 6-month-old abandoned rice field (*AR0.5*) and the 2-year-old abandoned rice field (*AR2*) calculated from ^{13}C isotopic values. *Different letters* indicate that Cdng differed statistically (p <0.01) between land-uses whereas *same letters* indicate no differences (p >0.05). Cdr did not differ significantly (p >0.05) between rice fields either at the 0- to 10-cm or at the 10- to 20-cm levels

Stable isotopic analyses

δ^{13}C decreased significantly (p <0.05) in the 0- to 10-cm horizon of rice fields abandoned for 6 months (Me =−19.40; 25% =−20.21; 75% =−19.27) or for 2 years (Me =−20.5; 25% =−19.7; 75% =−21.3) in comparison to values of the corresponding horizon of the natural grassland (Me =−14.8; 25% =−14.5; 75% =−15.0). The same pattern was observed in the 10- to 20-cm layer (Me for natural grassland −14.3, for 6-month-old −18.4, and for 2-years-old −18.5).

The amount of organic C derived from the 0- to 10-cm layer of natural grassland (Cng) was significantly different among the three land-use types (p <0.05), being smaller in the rice fields (Fig. 3). An overall 58% of Cng had been lost during rice cultivation and abandonment. This meant that 6 months after the last rice harvest, Cng had decreased by 5 mg g^{-1}, which represented a 29% C reduction, whereas 42% of the C had mineralized in the soil sampled from the field 2 years after the last rice harvest. The pattern was different in the 10- to 20-cm horizon. We did not find differences (p >0.05) in the Cng between the natural grassland and the rice field abandoned 6 months earlier. However, in this layer, Cng was significantly smaller (p <0.05) in the rice field abandoned 2 years ago in comparison to the natural grassland with a Cng reduction of 44%. Therefore, 2 years after the last rice harvest, a similar percentage of C of natural grassland origin had mineralized in both horizons.

Organic C content derived from rice (Cr) did not differ significantly (each comparison p >0.05) between the two types of rice fields at either of the two depths (Fig. 3). During the 2 years of abandonment, the Cr losses were slightly greater in the 10- to 20-cm layer (36%) than in the 0- to 10-cm horizon (26%).

Soil macrofauna

Density and diversity

The total density of individuals per m^2 in natural grassland (median =288; 25% percentile =240; 75% percentile =496) was significantly lower (p <0.001) than in the abandoned rice fields (median =2,208; 25% percentile =1,424; 75% percentile =2,616) and did not differ between replicate plots (for natural grasslands p >0.93; for rice field p >0.07).

After excluding a young nest of *C. punctulatus* (as an outlier), we still found a higher density of total macrofauna in the abandoned rice field (p <0.001) than in the natural grassland. This difference was explained mainly by a greater number of earthworms (p <0.02). The abundance of other groups such as ant species, besides *C. punctulatus*, was lower (p <0.049) in the abandoned rice fields than in the natural grassland, whereas the number of Coleoptera larvae (p >0.38) did not differ between different land-use plots (Fig. 4). Interestingly, after removing the data from the young nest, there were no differences (p >0.05) in *C. punctulatus* abundance between land-use types.

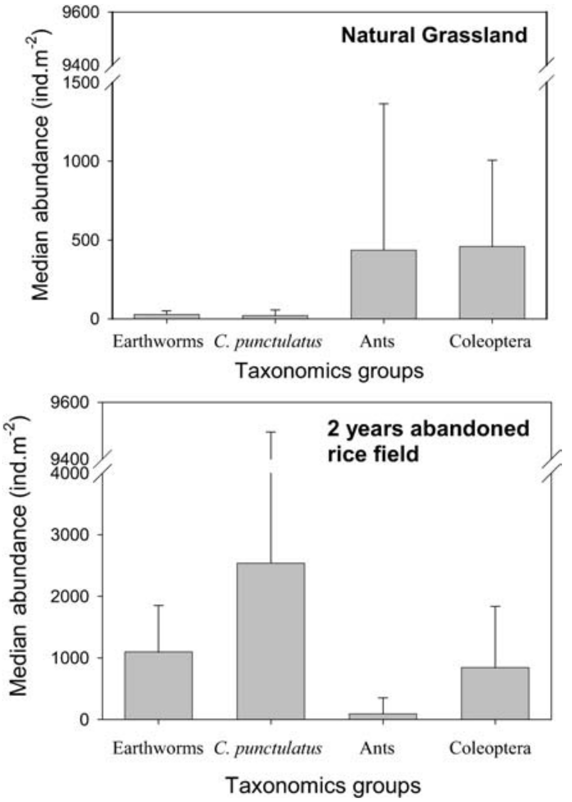

Fig. 4 Median abundance of organisms (with the 25% and 75% percentile) from the main taxonomic groups in natural grassland and 2-years-abandoned rice field. Data from the nest of *Camponotus punctulatus* found in the abandoned rice field has been removed. Ants refer to all ant species except *C. punctulatus*

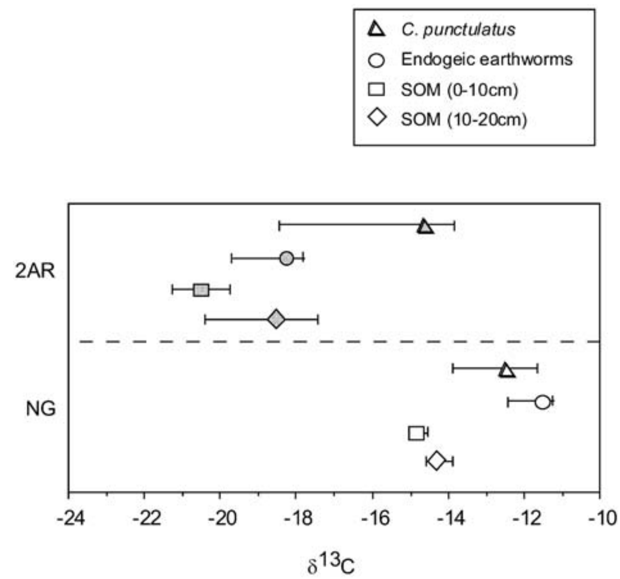

Fig. 5 δ^{13}C values for the ant *C. punctulatus*, endogeic earthworms (sp. A and sp. B) and soil organic matter (0–10 cm and 10–20 cm) in the 2-year-old abandoned rice field (*2AR*; *hatched marks*) and in the natural grassland (*NG*; *open marks*)

Macrofauna density was concentrated in the upper 10 cm of soil in both types of land-use plots; between 80% and 98% of organisms were found at 0–10 cm and less than 1% at 20–30 cm from the total number of individuals sampled at each site.

The total number of taxa was slightly greater in the ex-rice field, (64 morphotypes) than in the natural grassland (56 morphotypes). However, the Shannon diversity index, which considers not only the number of morphotypes (species richness) but also their relative abundance, showed that diversity was significantly lower (p <0.001) for the abandoned rice field (Me =0.48, 25% =0.30–0.56) than in the natural grassland (Me =0.87, 25% =0.70, 75% =0.92). This result was due to a greater evenness (p <0.001), but not richness (p >0.05) in the natural grassland in comparison to the rice field. The percentage of shared species between both land-use types was 20.6%, i.e. 19 species only from a total of 92.

Differences in the structure of the communities were found when the mean abundance of taxa was ranked. The natural grassland community (N =12) was characterized by 2 highly abundant taxa of ants (46–50 ind m^{-2}), 6 taxa with high (20–25 ind m^{-2}) abundance, 5 taxa with intermediate (10–16 ind m^{-2}) abundance, 16 with low (2–8 ind m^{-2}) abundance and, 25 taxa that were found only once (1.33 ind m^{-2}). In the abandoned rice field (N =11), there were 2 (1 morphospecies of earthworm and *C. punctulatus*) very abundant taxa (500–1,200 ind m^{-2}), 2 with high (100–400 ind m^{-2}) abundance, 7 with intermediate (10–50 ind m^{-2}) abundance, 4 with low (1–4 ind m^{-2}) abundance, 23 with very low abundance (<1 ind m^{-2}) and, 25 found only once (0.19 ind m^{-2}). *C. punctulatus* and 1 earthworm species were the most abundant taxa in the abandoned rice field whereas 2 other ant species had the greatest abundance in the natural grassland.

Stable isotopic analyses of earthworms and C. punctulatus

δ^{13}C values were significantly smaller in the rice field abandoned for 2 years in comparison to the natural grassland for earthworms, *C. punctulatus*, and SOM at both depths (in each case p <0.05).

δ^{13}C values of the endogeic earthworms in the natural grassland were 3–4‰ higher than those found in the soil organic matter (SOM) in the 0- to 10-cm (p <0.05) and 10- to 20-cm (p <0.05) layers. δ^{13}C values of *C. punctulatus* were not significantly different from those of earthworms (p =0.056; Fig. 5).

In the 2-year-abandoned rice plots, δ^{13}C values of the endogeic earthworms were also 2–3‰ higher than those of SOM at the 0- to 10-cm depth (p <0.05), but were not significantly different from those of SOM at the 10- to 20-cm depth (p >0.05). In contrast to the natural grassland, δ^{13}C values of the *C. punctulatus* were significantly higher than those of the endogeic earthworms (p <0.05; Fig. 5).

Discussion

Rice is one of the main food crops for the human world population and sustainability of its production has come into question (Cassman and Pingalli 1995). The long-term effects of this intensive and peculiar practice have recently been studied (Olk et al. 1998). The anoxia produced during rice germination, when fields are flooded, drastically reduces the diversity of soil organisms (Roger 1996) and changes the composition of the microflora because not all microbial species can survive in those conditions (Neue et al. 1997; Liesack et al. 2000; Reichardt et al. 2001). Yet our results show that despite the presumably adverse conditions imposed by rice cultivation, the fields we studied showed a great capacity for recovering after being abandoned. For example, the organic matter mineralized at normal rates after a short period of time. Soil macrofauna was able to recolonize in spite of its absence during rice cultivation. The abandoned rice field showed relatively little soil compaction, although this was possibly in a class or pore size that may have an important function in water drainage (Hillel 1998). Overall, our results allow us to reject the three hypotheses proposed to explain the dramatic increase of anthills of *C. punctulatus* in abandoned rice fields.

The macrofauna community established in abandoned rice fields was substantially different from the macrofauna community found in natural grasslands. The abandoned rice community may represent the initial stages of the succession of the grassland macrofauna community. Macroinvertebrates were more abundant in the abandoned rice field (on average 2,727 ind m^{-2}) than in the natural grassland (on average 406 ind m^{-2}), mainly due to a great increase in earthworm numbers and *Camponotus*. Earthworms depend on their own locomotion through the soil for their dispersion whereas *Camponotus* rely on alates, although nuptial flights have never been registered for this species. In spite of a larger number of taxa (64 as opposed to 56 in the original grassland), the abandoned rice field community was less diverse as indicated by the Shannon index. We found a smaller proportion of singletons (25 singletons out of 64 morphospecies) in the abandoned rice field and a low number of shared taxa (19 species of a total pool of 92) were found at both land-use sites.

Among the most abundant colonizers of the abandoned rice fields were a small endogeic earthworm and *Camponotus* ants. Clearly, the high densities of earthworms found in abandoned rice fields suggested that there were no trophic limitations for these species. The colonizing earthworm species in the agricultural site was not the same species that dominated in the natural grassland. The increase of *Camponotus* ants in recently abandoned rice fields was due to an increase in anthill density but not in the number of ants per colony (Folgarait, unpublished). These results allow us to consider that there were no restrictions for invasion by the macrofauna community, especially for earthworms.

Despite the great abundance of *C. punctulatus* anthills and small earthworms in abandoned rice fields, we still found a smaller total porosity and modal pore size in the rice fields, indicating that the macrofauna was not yet able to overcome the compaction produced by ploughing and other related farming activities. At this point it is impossible to predict if through time bulk density will return to the higher levels typical of natural grasslands because the structure and composition of the macrofauna communities in the rice fields were different from those in natural grasslands. However, since we found high levels of colonization in rice fields we interpret that compaction did not pose a differential restriction for different types of macrofauna.

There was an increase in the SOM concentration during rice cultivation and immediately after land abandonment and losses of SOM also increased as time proceeded. Increased organic C and total N concentrations measured in the soil of the rice field abandoned for 6 months were a likely result of the higher inputs due to higher rice yields and the lower plant residue mineralization rates under flooding conditions in the rice field. However, the isotopic data showed that in the 0- to 10-cm layer there was a high C turnover, and C derived from natural grassland decreased significantly during rice cultivation and during the first 6 months of abandonment. In this surface layer, the decomposition did not stop during rice cropping despite the anaerobic conditions imposed during part of the year. Agricultural practices may have provided some oxygen influx in the soil after water was removed before harvesting, and between cultivation periods (Gijsman et al. 1997). However, in the 10- to 20-cm layer, there was no decomposition of the C derived from natural grassland during rice cultivation and the total organic matter was increased by the rice inputs. Probably, in this soil layer the O_2 inputs by rice and agricultural management of the crop was negligible. Our results are in agreement with what it is known about the decomposition of C substrates under anaerobic conditions (Tate 1979), and suggest that the 10- to 20-cm horizon remains anaerobic for a longer time than the surface layer. However, as time proceeded, the 10- to 20-cm layer of the rice field abandoned 2 years ago behaved as dynamically as the 0- to 10-cm layer, showing greater outputs of C derived from natural grassland than outputs of C derived from rice.

$\delta^{13}C$ values of earthworms were higher than those of SOM for both land-use types, which was consistent with previous reports (Martin and Lavelle 1992; Spain and Le Feuvre 1997). In the 2-year-old abandoned rice plots, ^{13}C signals suggested that the endogeic earthworms were more dependent on SOM from rice (C3 plant) than *C. punctulatus*, which seemed to be more opportunistic in its diet. The large variation in $\delta^{13}C$ values for *C. punctulatus* could be related to their omnivorous diet, which could include honeydew from sap feeders (Homoptera) present either on invading C4 plants or rice root tissues, or ingestion of prey from the natural grasslands and rice fields due to their large foraging range. Part of the variation, especially that observed in the abandoned rice fields, also could be related to inter colony differences in diet since intra colony variation among individual ants was negligible (Tayasu, personal observation).

The increased availability of organic matter recorded immediately after rice abandonment may have been utilized by small earthworms, which were very abundant in the abandoned rice field; isotopic data actually showed that these macroinvertebrates were feeding on SOM originating from natural grassland and abandoned rice field. This result indicates that probably there were no trophic limitations for these organic matter feeders. High rates of consumption may be one explanation for the decrease in C and N concentration in the rice fields abandoned for 2 years (Yoshikawa and Inubushi 1995; Villenave et al. 1999)

Our study of the dynamics of organic matter, in concert with changes in physical parameters of the soil, as well as biological characterizations, suggests that rice cultivation may have less of an effect than previously hypothesized because mineralization of organic matter proceeded rapidly, soil compaction was not too drastic, and there were no obvious trophic limitations for invading macrofauna. A successional process was rapidly initiated with a different macroinvertebrate community dominated by small endogeic earthworms and ant communities dominated by *Camponotus punctulatus*, besides Coleoptera. Moreover, changes in porosity observed in specific pore size ranges may have altered the hydraulic properties of soil in a way that could lead ants to build a much larger proportion of their nests aboveground than in the natural grassland. We can say that despite not knowing for sure the reasons for the spectacular increase of anthills in abandoned rice fields, at least this change does not seem to be related to a soil physical restriction nor to a trophic limitation as macrofauna, other than *Camponotus* ants, were able to successfully invade the system.

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