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Applied Soil Ecology 27 (2004) 23–29

Applied Soil Ecology

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Soil macrofaunal communities along an abandoned rice field chronosequence in Northern Argentina

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Received 8 January 2003; received in revised form 9 March 2004; accepted 18 March 2004

Abstract

This study assessed the biodiversity of soil macrofauna along a chronosequence of abandoned rice paddy fields including situations of 2, 4, 7 and 15 years since the last rice harvest, compared to a control without agricultural disturbance. The density of soil macrofauna changed dramatically according to the chronosequence. It was maximum in the 2-year-abandoned rice field (4360 ind m^{-2}) and minimum in the natural grassland (397.3 ind m^{-2}). A total of 133 morphospecies was found, distributed among 20 main families. The highest species richness was observed in the natural grassland and in the 2-year-fallow with 53 and 59 species, respectively, whereas the lowest richness was found in the 7-year-fallow (39 species). The proportion of shared species was minimum (19.1%) when comparing the natural grassland and the 2-year-fallow and remained surprisingly low between the natural grassland and the 15-year-fallow (23.4%). The species diversity as measured by the Shannon index varied strongly along the chronosequence. It was maximum in the natural grassland (1.98), minimum in the 2-year-fallow (1.01) and increased progressively throughout the chronosequence, although, it was still lower in the fallow after 15 years of abandonment as compared to the natural grassland. The same trend was observed using the evenness index. The indicator value index (Indval) was computed for each species and showed that 14 species out of 133 were statistically associated with a given chronosequence stage. This survey showed that soil macrofauna quickly recolonized the ex-rice fields after the abandonment of rice culture and that the species richness was higher in recent ex-rice fields (2 years) as compared to the natural grassland. The pool of species that colonise the newly abandoned rice fields is substantially different from the one inhabiting the natural grassland, therefore suggesting that most of the successful colonisers probably originate from neighbouring fallow plots. This highlights the possible effects of landscape structure upon the dynamics of the soil macrofaunal biodiversity.

Keywords: Biodiversity; Soil macrofauna; Rice; Fallow; Natural grassland

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1. Introduction

The activities of soil organisms have dramatic effects on various ecosystem functions such as soil structure dynamics and decomposition of organic matter (Lavelle and Spain, 2001). Various studies have shown

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doi:10.1016/j.apsoil.2004.03.002

that an increase in the intensity of agricultural practices and the establishment of pasture cause important changes in the community structure, abundance and biomass of soil macrofauna (Lavelle and Pashanasi, 1989; Fragoso et al., 1997).

In Northern Argentina, natural grasslands have been traditionally used for cattle ranching since the last century. Nowadays in large farms, rice production is becoming a common agricultural activity and 10% of the natural grasslands of the Corrientes province have been converted into rice fields. Rice culture involves farming practices that cause great impacts on the soil physico-chemical properties and soil biota (Lavelle and Pashanasi, 1989). Besides, soil cultivation is likely to affect all the species inhabiting soil as shown by various authors in different parts of the world (Giller et al., 1997).

The goal of this study was to describe the abundance and the biological diversity of the soil macrofauna along a chronosequence including natural grassland (undisturbed is equal to control plots) and fallows (ex-rice fields) of different ages: 2, 4, 7 and 15 years. We assessed the level of species richness and diversity and investigated the community composition and how it changed throughout the chronosequence.

2. Materials and methods

2.1. Study site

This study was carried out in Mercedes Department, Province of Corrientes, Argentina (29°S, 58°W). The climate is wet sub-tropical, without a definite dry season. Rainfall mostly occurs from January to April. Mean annual precipitation is 1270 mm and mean annual temperature is 20.1 °C. Air humidity is high (>73%) throughout the year (Fernández et al., 1993). Soils are Alfisol (Soil Survey Staff, 1992) developed on a several-meters-thick clayey saprolite of calcareous sandstone. In plots after rice cultivation, a distinct “ploughing pan” appeared at a 15–25 cm depth caused by mechanised cultivation. Hydromorphy (i.e. soil moisture excess) increases in cultivated plots relative to the natural grassland (Folgarait et al., 2003). Soil texture did not change significantly between natural grassland and abandoned rice fields (Folgarait et al., 2003). The natural grassland vegetation is dominated by *Andropogon lateralis*. The abandoned rice fields are not managed and their vegetation is mainly composed of species colonising from the natural grassland (Folgarait et al., 2002).

2.2. Sampling

The change in soil macrofauna was examined in areas differing in time since soil disturbance: rice fields where cultivation has been abandoned for 2, 4, 7 and 15 years and the natural grasslands representing the reference state. In each case, two replicate plots, a few kilometres apart, were sampled. All plots were located in a farm called “Arrocera Aguaceritos” that covers 21,000 ha mainly used for cattle ranching. The plots were randomly selected within the landscape and the replicate pairs of plots were not closer to one another than the differently aged plots. Each plot was mainly surrounded by other plots of the same type, although the diversity of the landscape increased rapidly when considering larger spatial scales.

Soil faunal sampling was carried out in January 2001. Each replicate was sampled by means of two transects separated by 10 m. Each transect included three sampling points separated by 10 m. Therefore we collected 12 samples per chronosequence stage. The soil macrofauna was sampled using the TSBF protocol (Anderson and Ingram, 1993). Soil monoliths of 25 cm × 25 cm × 30 cm were excavated and divided into three layers of 10 cm from which all organisms were recovered by hand sorting. Specimens were identified at different levels, such as families, morphospecies or species when possible.

2.3. Data analysis

The diversity was described by means of the Shannon index (computed on the Napierian logarithm) and its associated evenness index (Southwood and Henderson, 2000). Species closely associated with a given chronosequence stage were sought using the Indval method (Dufrêne and Legendre, 1997). In this approach, species mostly present in a chronosequence stage and present in the majority of the samples taken in that stage are considered to be indicator species of that stage (Dufrêne and Legendre, 1997).

The between and within stage differences in the overall macrofaunal density and the density of the main taxonomical groups were tested using a nested ANOVA (Sokal and Rohlf, 1995). The factor "plot identity" was nested within the "chronosequence stage" factor.

3. Results

3.1. Macrofaunal density

The soil macrofaunal density changed dramatically according to the chronosequence stage (Table 1) and decreased with increasing soil depth irrespective of the plots considered. More than 80% of individuals were collected from the top 10 cm in the natural grassland and 72–92% in abandoned rice fields. Below 20 cm depth, the abundance of the macrofauna always represented less than 1% of collected individuals.

The soil faunal density was maximum in the 2-year-abandoned rice field (4360 ind m^{-2}) and minimum in the natural grassland (397.3 ind m^{-2}) (Table 1). The most abundant species was the ant *Camponotus punctulatus* which reached an overall mean abundance of 640 ind m^{-2}. Its density ranged from 20 ind m^{-2} in the natural grassland to 2538.6 ind m^{-2} in the 2-year-old fallow.

The density estimates of the main taxa in the replicate plots are given in Table 2. Significant effects of either chronosequence stage or replicate plot identity were observed for earthworms, Coleoptera and Diptera larvae (nested ANOVA, Table 3). There was a significant effect of the chronosequence stage but no plot effect on total density. Considerable within-plot variability was observed for the various taxa although not always significant (Tables 2 and 3).

3.2. Species richness

A total of 133 morphospecies was found, distributed among 20 main families. The highest species richness was observed in the natural grassland and in the 2-year-fallow with 53 and 59 species, respectively. The lowest richness was found in the 7-year-fallow with 39 species (Table 4, diagonal). The number of shared species indicates the closeness of the chronosequence stages in term of species composition. It was somewhat low whatever the pair of situations considered as it ranged from 17 to 26 species (Table 4, above diagonal). Given that the species composition and richness varied strongly from one stage to another, it was interesting to express the number of common species as the proportion of the total number of species present in the pair of chronosequence stages under comparison (Table 4, below diagonal). This percentage was minimum (19.1 %) when comparing the natural grassland and the 2-year-fallow and reached its maximum value of 34.8% when the 4- and the 15-year-fallow were compared (Table 4). The proportion of common species between the natural grassland and the 15-year-fallow was low (23.4%).

3.3. Species diversity

The diversity as measured by the Shannon index strongly varied along the chronosequence (Table 1). It was maximum in the natural grassland (1.98) and minimum in the 2-year-fallow (1.01). The diversity increased progressively throughout the chronosequence, although it was still lower in the fallow after 15 years of abandonment than in the natural grassland. To ensure that the differences reported above were not simply due to the observed changes in the species richness

Table 1
Changes in macrofaunal density, diversity (Shannon index) and evenness throughout a chronosequence spanning from 2 to 15-year-old fallow after rice cultivation and including the original natural grassland (reference state)

Plots	Density (ind m^{-2})	Standard error (ind m^{-2})	Shannon diversity index	Evenness	*n*
Natural grassland	397.3	84.59	1.98	0.5	12
2-year-fallow	4360.0	1901.1	1.01	0.25	12
4-year-fallow	938.67	168.55	1.34	0.35	12
7-year-fallow	1644.0	360.28	1.45	0.4	12
15-year-fallow	489.33	166.04	1.52	0.41	12

Table 2
Mean density of the main taxa of soil macrofauna throughout a chronosequence spanning 2–15-year-old fallow after rice cultivation and including the original natural grassland (reference state)

		Earthworms	Ants	Termites	Coleoptera	Arachnida	Isopoda	Chilopoda	Diplopoda	Diptera (larvae)	Other groups	Total
Natural grassland	Plot 1	29.3	360	0	96	5.3	0	2.7	0	16	40	549.3
		(9.6)	(131.7)	–	(19.4)	(3.4)	–	(2.7)	–	(7.2)	(13.5)	(145.3)
	Plot 2	26.7	34.7	0	112	8	0	0	8	29.3	26.7	245.3
		(9.8)	(16.7)	–	(18.5)	(3.6)	–	–	(5.5)	(6.4)	(3.4)	(33.5)
2-year-fallow	Plot 1	536	5565.3	2.7	101.3	10.7	2.7	0	0	10.7	61.3	6290.7
		(179.8)	(3887)	(2.7)	(25.7)	(5.3)	(2.7)	–	–	(5.3)	(18.2)	(3768.3)
	Plot 2	1658.7	413.3	0	314.7	5.3	2.7	0	2.7	2.7	29.3	2429.3
		(223.7)	(225)	–	(75.2)	(5.3)	(2.7)	–	(2.7)	(2.7)	(20.4)	(459.4)
4-year-fallow	Plot 1	360	413.3	0	144	16	0	0	0	10.7	16	960
		(48.5)	(258.8)	–	(30.1)	(5.8)	–	–	–	(3.4)	(13.1)	(268.3)
	Plot 2	208	477.3	2.7	138.7	8	0	2.7	0	0	80	917.3
		(82.6)	(202.1)	(2.7)	(24.3)	(8)	–	(2.7)	–	–	(49.7)	(229.9)
7-year-fallow	Plot 1	117.3	1077.3	2.7	69.3	8	0	0	0	21.3	66.7	1362.7
		(49.2)	(347.8)	(2.7)	(38.9)	(3.6)	–	–	–	(9.8)	(26.9)	(428.8)
	Plot 2	562.7	1080	0	245.3	5.3	0	0	0	5.3	26.7	1925.3
		(118.4)	(592.9)	–	(40.6)	(3.4)	–	–	–	(3.4)	(17.4)	(596.3)
15-year-fallow	Plot 1	80	56	432	66.7	5.3	0	0	0	32	40	712
		(12.4)	(15.9)	(321.5)	(19.1)	(3.4)	–	–	–	(13.7)	(14.8)	(315.2)
	Plot 2	77.3	56	0	45.3	8	0	0	0	69.3	10.7	266.7
		(22.4)	(18.4)	–	(23.2)	(5.5)	–	–	–	(26.3)	(5.3)	(45.8)

Mean density is given in individuals per square metre. Standard error is indicated between parenthesis.

Table 3
Results of a nested ANOVA testing the effect of chronosequence stage and the plots within stage (nested factor) on the mean density of the main taxa of the soil macrofauna

	Earthworms	Ants	Termites	Coleoptera	Arachnids	Isopoda	Chilopoda	Diplopoda	Diptera (larvae)	Other groups	Total
Stage	***	NS	NS	**	NS	NS	NS	NS	***	NS	*
Plot	***	NS	NS	***	NS	NS	NS	NS	NS	NS	NS

Levels of statistical significance are indicated by NS: non significant; $^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$.

Table 4
Species richness and community similarity throughout a chronosequence spanning 2–15-year-old fallow after rice cultivation and including the original natural grassland (reference state)

	Natural grassland	2-year-fallow	4-year-fallow	7-year-fallow	15-year-fallow
Natural grassland	53	18 (94)	17 (83)	18 (74)	18 (77)
2-year-fallow	19.1	59	26 (80)	22 (76)	21 (80)
4-year-fallow	20.5	32.5	47	21 (65)	23 (66)
7-year-fallow	24.3	28.9	32.3	39	20 (61)
15-year-fallow	23.4	26.3	34.8	32.8	42

On the diagonal: species richness. Above the diagonal: absolute number of species shared by site pairs and total number of species collected in pairs of site (between parenthesis). Below the diagonal: percentage of shared species expressed as the ratio of the number of common species to the total number of species in site pairs.

we estimated the evenness, i.e. the relative Shannon index. It showed exactly the same pattern as the Shannon diversity index. The diversity was remarkably low, even in the natural grassland where it represented only 50% of its maximum possible value (evenness, 0.5).

3.4. *Indicator species*

For each species, the Indval index value was statistically tested using 9999 random permutations (Dufrêne and Legendre, 1997) and a statistical level $\alpha = 5\%$. The natural grassland had three associated species, and the 2-, 4-, 7- and 15-year-old fallows 4, 1, 4 and 2 indicator species, respectively. Nine of these species were larvae (seven Coleoptera and two Diptera).

4. Discussion

Soil macrofauna quickly recolonized the ex-rice fields after the abandonment of cultivation. After 2 years, the faunal density had recovered up to 4360 ind m^{-2}, whereas the density in the natural grassland was 397 ind m^{-2} (Table 1). Surprisingly, the 2-year-ex-rice field hosted a higher species richness than the reference habitat, the natural grassland (Table 4). The observed species richness decreased when older ex-rice fields were compared, with the lowest number of species being found in the 15-year-fallow (Table 4). Therefore, not only did soil macrofauna quickly recolonize recent fallows but more were found in recent ex-rice fields (2 years).

The examination of the community structure raises a very interesting point. The pool of species that colonised the newly abandoned rice fields appears to be substantially different from the one inhabiting the natural grassland (Table 4). The proportion of shared species was remarkably low, i.e. 18 species out of a total of 94, if we compare the 2-year-old fallow and the natural grassland (Table 4). Thus, it is likely that most of the successful colonisers did not come from the natural grassland sites and probably originate from neighbouring fallow plots. This indicates that surveys should ideally be extended far beyond the spatial scale used in this study to explicitly cover different landscape units. At least, immediate neighbours shall be sampled or the type of habitat recorded so that possible relationships between local biodiversity and landscape structure could be examined.

Surprisingly, after 15 years of fallow, the community composition was still different from the original natural grassland with only 23.4% of shared species (Table 4). The proportion as well as the absolute number of shared species was unexpectedly low whatever the pair of chronosequence stages under comparison and was no larger than roughly 1:3. The indicator species index indicates that each stage of the chronosequence hosted at least one significantly associated species. This reinforces the idea that the community dynamics behaves more like recruiting new species while losing others rather that simply recruiting more and more species through time. As a consequence, the community was still unlike the natural grassland after 15 years of fallow. We are therefore dealing with a secondary succession that seemingly takes place at the time scale of more than 15 year. This is a time scale relevant to the vegetation dynamics and to some soil processes such as soil organic matter dynamics (Folgarait et al., 2003). These processes control some very important habitat attributes for soil macrofauna like, e.g. food resource quality and quantity and as such may exert strong influence upon the presence and abundance of certain species (Lavelle and Spain, 2001).

Another factor affecting the observed species richness at a given stage in the succession is the dispersal ability of the species (King and With, 2002). Although some species are undoubtedly good dispersers (e.g. certain Coleoptera, Diptera), most of the species inhabiting the soil or the litter are probably medium to very poor dispersers (e.g. earthworms). However, it is very difficult to determine whether habitat quality or dispersal limitations constitute the main constraint upon soil recolonisation after culture. The structure and composition of the landscape may also play an important role (With and King, 1999; Berggren et al., 2001). Very few data are available on soil macrofaunal dispersal ability and strategy, and we believe that in addition to these important factors, the landscape structure itself needs to be more precisely understood. This would in turn allow a better grasp of the diversity dynamics at least in the present situation where the landscape is fragmented.

Acknowledgements

We are indebted to M. Grimaldi who helped us all along this work, N. Gorosito, C. Garbagnoli and J. Benítez who helped in the field with data collection. We would like to thank the staff of the Agricultural Experimental Station of INTA-Mercedes and the owners of the establishments “Aguaceritos” for their continuous help. We also thank two anonymous referees for their thoughtful comments and editorial help which greatly improved the manuscript. This work was funded by ECOS-SECyT (France–Argentina, grant no. 99B01).

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