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Soil macrofauna in SE Mexican pastures and the effect of conversion from native to introduced pastures

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Abstract

A large area in the Gulf Coast region of Mexico is pastureland, generally dominated by native grass species, yet little is known of the physical, chemical and biological characteristics and limitations of soils beneath them. Furthermore, nothing is known of the effect of converting native to introduced grasses on the soil ecosystem in Mexican pastures. Over the last 30 years 60 samples were taken in 21 sites throughout SE Mexico to evaluate soil macrofauna communities. Of these, 15 samples were taken at five sites in the state of Veracruz, Mexico, taken during the dry (April–May) and/or wet (September–October) seasons of 1998 and 1999, to specifically compare soil macrofauna present in native and introduced pastures. These sites were located in a N–S transect including three biogeographic regions, separated by the transverse Neo-volcanic axis. Taking data from all sites, earthworms, ants and termites dominated in terms of density, while earthworms dominated the soil fauna biomass, commonly surpassing the weight of the grazing cattle per hectare. Of a total of 15 comparisons of soil fauna populations in native and introduced pastures, important differences in the communities were observed on nine occasions, using multivariate analyses. These differences, however, depended on the site sampled, season, and sample year, and tended to be more evident in the rainy season, when populations were at their maximum numbers. Earthworm communities were different between the two pasture types; twice as many species on average were found in native (four species) than in introduced (two species) pastures. Most species were native to Mexico, only a few exotics being found, indicating slow exotic species invasion rates or little replacement of natives by exotics. In conclusion, the present study showed that large communities of soil macrofauna are present in SE Mexican pastures and that, depending on the site's characteristics and the management practices implemented, the conversion of native to introduced pastures can significantly alter the diversity and abundance of soil-dwelling macro-invertebrates. However, further studies must be undertaken in other pastures, particularly well-managed introduced pastures with or without legume associations, to assess whether these results hold true under a wider range of management situations and sites.

Keywords: Soil macrofauna; Earthworms; Diversity; Native and introduced pastures; Veracruz

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1. Introduction

The coastal plain of the Gulf of Mexico includes the Mexican states of Tamaulipas, Veracruz, Tabasco, Campeche and Yucatan and has >5 million ha of pas-

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tures with native and introduced grasses, mainly of the C_4 photosynthetic type. In Veracruz, 64% of the total area of the state (5.74×10^6 ha) is used for agro-pastoral purposes and the cattle population of the state is the largest in the country, surpassing 4.6 million heads. Bovine meat production in Veracruz in 1996 reached 268,000 t, ranking the state in second place at national level, with 13% of total production. Milk production that year peaked at 577 million liters, contributing with 9% of the Mexican total (INEGI, 1997).

Of the grasslands in Veracruz, 70% represent native pastures, i.e. dominated by native grasses, including the genera *Paspalum*, *Sporobolus*, *Axonopus* and *Muhlenbergia* (Mejía-Saulés and Dávila, 1992). Despite the name, these pastures generally include species native to Mexico and some introduced species, mostly present as invading weeds. In introduced pastures, the same occurs, with native grasses often present as weeds. The native pastures are usually managed extensively with rotations of long duration. There is a widespread belief by the ranchers that these grasses have both low potential for forage production and poor nutrient value (Enríquez, 1996), although very few studies have actually proven this as true.

In the beginning of the 1940s, with the expansion of cattle ranching in the state and the conversion of forests into pastures (Barrera and Rodríguez, 1993), the introduction of grass species coming from Africa grew continuously (and more rapidly in the last decade), reaching 30% of the areas dedicated to grazing in 1995 (INEGI, 1997). The species most frequently introduced include: *Panicum maximum* (“Guinea” and “Tanzania” grass) before 1970; *Cynodon plectostachyus* and *Digitaria decumbens* (“Pangola”) mainly after 1970; and various *Brachiaria* spp. (especially *B. mutica*, *B. decumbens*, *B. dictyoneura*, *B. humidicola* and *B. brizantha*) in the 1980 and 1990s (Enríquez, 1996). Other species also introduced, but in more restricted areas, include *Andropogon gayanus* and *Pennisetum purpureum* (“Elephant” and “Taiwan” grass) (López, 1987). In introduced pastures, management tends to be more intensive, with frequent use of external inputs (generally absent in the native pastures) for pasture installation and weed control. Rotational grazing is also common, in areas that vary in size from <1 up to >30 ha depending on the available land, the size of the herd and grazing intensity.

Globally, it is recognized that pastures can greatly increase the populations of some soil organisms, particularly earthworms, that appear to be favored by this type of land-use (Lavelle et al., 1994). However, the diversity of groups present and the number of morphotypes or species is generally negatively affected, especially when the pastures are established over rain-forest vegetation (Barros, 1999). When the pastures are established over native savannas, the negative effect on biodiversity appears to be reduced, depending on the similarity of the native vegetation to the introduced grasses, and the diversity of taxonomic groups present may even increase (due to invading species), although total species number generally decreases (Jiménez and Thomas, 2001).

Mexico is one of the world’s mega-diversity countries, and the state of Veracruz harbors a significant proportion of the country’s biodiversity, both of plants and of animals. Furthermore, the state is divided into two main regions by the transverse Neo-volcanic axis, which serves to divide the North American biogeographic region from the South American one. Much of the state was covered by forest vegetation in the past, but this has been mostly cleared (<20% remains) for agricultural purposes, including, and probably most often, pasture establishment (Barrera and Rodríguez, 1993). In the southern part of the state, native wetlands and savannas have also been converted to pastures and, because these vegetation types originally represented a much smaller proportion of the state’s area, they are now even more vulnerable.

Practically nothing is known of the effects of changes in the grass type on the soil environment in Mexican pastures (organic matter, nutrients, microflora, fauna). It appears that (up to now) no data are available on this topic, as no references were found in an extensive bibliographical review. Therefore, the effects of pasture conversion on various soil processes, including soil fauna communities were studied at five sites in the state of Veracruz over a 2-year period. For comparative purposes, the results of various previous studies concerning soil macrofauna populations in Mexican pastures were also compiled and analyzed.

2. Material and methods

2.1. Sample sites in SE Mexican pastures

Taking data available from the literature (mostly previous work of the Instituto de Ecologia researchers and students), unpublished data of the authors, and the results of the five sample sites described below, data on soil macrofauna communities [all sampled using protocols of the Tropical Soil Biology and Fertility (TSBF) Programme; Anderson and Ingram, 1993] from 21 sites and 60 pastures were obtained (Fig. 1 and Table 1). All sites had total annual rainfall >1100 mm, and only three sites were over 200 m altitude (Table 1). The climate in most places corresponded to the Aw type (Köeppen classification), while the driest sites were of the Ax type (Tuxpan and Plan de Hidalgo), the most humid were of the Am type (Tuxtlas, Huimanguillo and Chiapas), and the coldest of the C type (Cerro Buenavista and Cofre de Perote). Only six of the 21 sites were sampled in the dry season and all sites, except Huimanguillo, were sampled in the rainy season. At most of the sites (13), pastures sampled were composed predominantly of introduced grass species, including the common-most introduced species *D. decumbens*, *C. plectostachyus*, *P. maximum* and *Brachiaria* spp. Only eight sites had native grasses.

2.2. Sample locations and dates in native and introduced grass pastures

To assess the impact of pasture conversion from native to introduced grasses, sampling was performed in both native and introduced pastures next to each other or distant <1 km, and with similar soil and environmental properties, at five sites in the state of Veracruz: Tuxpan, Carranza, Isla, Martínez de la Torre and Paso del Toro (sites 1, 2, 4, 12 and 16 in Fig. 1 and Table 1). Some of the general characteristics and soil properties of these pastures are shown in Tables 2 and 3. Samples were taken in the rainy (September–October) and dry seasons (April–May) of 1998 and 1999 (except Martínez de la Torre, which was only sampled in the wet season, 1999), thus allowing the comparison of macrofauna communities present at different times of the year and/or in different years. A total of 15 pastures were sampled.

Introduced grasses studied included *D. decumbens*, *B. decumbens*, *C. plectostachyus* and *A. gayanus*. The predominant (most common) native grasses were of the *Paspalum* and *Sporobolus* genera. The age of the native pastures ranged from 20 to >100 years and of the introduced pastures, 8–36 years. The pastures at Paso del Toro and Isla (INIFAP) were used for hay production and rarely grazed. The other pastures had variable animal loads, depending on the management practices

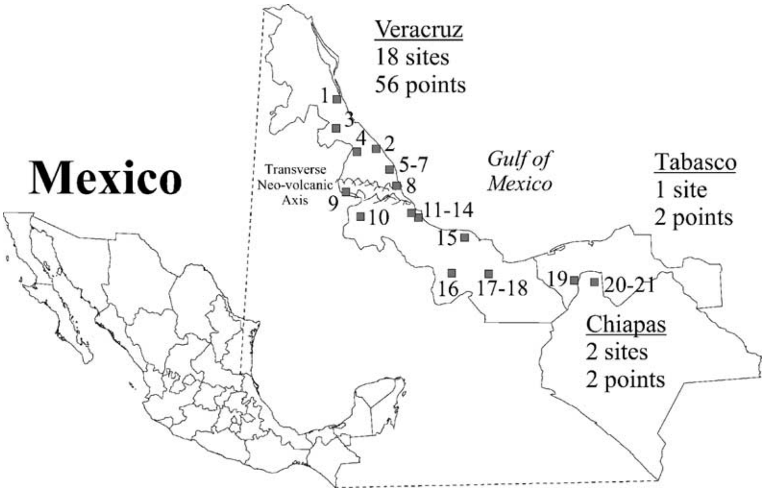

Fig. 1. Geographical location of the 21 sample sites (see numbers in Table 2) with a total of 60 sample points for soil macrofauna community characterization in Mexican humid tropical pastures.

Table 1
Sites where soil macrofauna samples have been taken in pastures in SE Mexico

State and site	Altitude (m)	Rainfall (mm)	Sample	References
Veracruz				
1. Tuxpan	75	1352	N, I, D, R	Brown et al. (this paper)
2. Carranza	35	1179	N, I, D, R	Ortiz (1999) and Brown et al. (this paper)
3. Plan de Hidalgo	200	1169	I, R	Ortiz (1999)
4. Martínez de la Torre	80	1509	N, I, R	Brown et al. (this paper)
5. Plan de las Hayas	800	1275	I, R	Lavelle et al. (1981)
6. Palma Sola	50	1235	I, R	Lavelle et al. (1981)
7. El Colorado	200	1250	I, R	Lavelle et al. (1981)
8. La Mancha	10	1300	I, R	Camacho (1995) and Rojas et al. (unpublished data)
9. Cofre de Perote	3000	1350	N, R	Rojas et al. (unpublished data)
10. Orizaba	1700	2155	I, R	Rodríguez (1998)
11. Medellín	150	1667	I, R	Ortiz (1999)
12. Paso del Toro	10	1500	N, I, D, R	Brown et al. (this paper)
13. La Víbora	35	1440	N, D, R	Brown et al. (unpublished data)
14. Tlalixcoyan	84	1418	N, R	Brown et al. (unpublished data)
15. Los Tuxtlas	180	4725	I, R	Fragoso et al. (unpublished data) and Brown et al. (1999)
16. Isla	75	1310	N, I, D, R	Brown et al. (this paper)
17. Acayucan	158	1700	I, R	Fragoso et al. (unpublished data)
18. Jaltipan	133	1890	I, R	Fragoso et al. (unpublished data)
Tabasco				
19. Huimanguillo	15	2420	I, D	Ordaz (1995) and Ordaz and Avilés (unpublished data)
Chiapas				
20. Cactus Loma	50	2250	I, R	Bueno and Barois (1997)
21. Cristo Rey	50	2250	I, R	Bueno and Barois (1997)

The numbers (1–21) correspond to those in Fig. 1. N: native pasture; I: introduced pasture; D: dry season; R: rainy season.

and the number of heads of the flock (Table 2). The livestock were mostly dual purpose (for meat and milk production).

2.3. *Soil macrofauna sampling (field) and processing (laboratory)*

To sample the soil and litter macrofauna in the native and introduced grasses, the standard TSBF methodology (above) was slightly modified, so that four samples of 50 cm × 25 cm up to 40–50 cm depth were taken in each pasture, in a linear transect of 20 m (one sample for every 5 m). In the dry season at some locations, the soil was excessively compact and difficult to dig, so only 25 cm × 25 cm squared samples were taken on these occasions. The traditional TSBF method consists in 5–10 samples of 25 cm × 25 cm square up to 30 cm depth, with manual revision of the soil and separation of the macrofauna in the field.

All fauna encountered in the surface litter and in each soil layer of 10 cm were separated and preserved in plastic vials with 4% formalin (earthworms) and ethyl alcohol at 70% (the remaining organisms). In the laboratory, >18 main taxonomic groups of organisms were counted, including: Oligochaeta, Isoptera, Formicidae, Hemiptera, Araneæ, Homoptera, Orthoptera, Diplopoda, Chilopoda, Lepidoptera, Isopoda, Gastropoda, Blattodea, Pseudoscorpionida, Coleoptera, Diptera, Dermaptera, Mermithidæ.[1] Identification of taxa was performed up to the minimum level of order, except for the earthworms, which were identified up to the level of family, genera or species (at all sites sampled in 1999). Each macrofauna order was then combined within each sample, so that all ants, termites, earthworms, etc. were weighed together in each sample, and the alcohol- or formalin-preserved weight taken (to 0.0001 g).

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[1] The Nematomorph mermithids (mainly entomopathogens) can reach several centimeters in length and could be considered as macrofauna using some of the definitions found in the literature.

Table 2
General characteristics of the native and introduced pastures at the five sites used for comparing soil macrofauna communities

Location	Owner	Pasture	Area (ha)	Age (years)	Animals	Inputs
Carranza	Private	Native: *Paspalum* and *Sporobolus* spp.	1.5	>100	60 (1 night) or 40 (1–2 days), Zebu × Swiss	Herbicides and burns
		Introduced: *D. decumbens*	1.5	36	60 (1 night) or 40 (1–2 days), Zebu × Swiss	K_2SO_4, lime, urea $(NH_4)_2SO_4$
Tuxpan	Private	Natives 1 and 2: various species	>20	20	1.5–2.5 heads ha^{-1}, Holstein Swiss	None (maize previously)
		Introduced 1 and 2: *D. decumbens* and *C. plectostachyus*	20	28	1.5–2.5 heads ha^{-1}, Holstein Swiss	Herbicides
Isla	INIFAP	Native: *Paspalum* and *Sporobolus* spp.	1.5	>20	None	None (probably previously pineapple)
		Introduced 1 and 2: *Brachiaria decumbens* and *A. gayanus*	0.8	19	None	Herbicides, fertilizers NPK
Martínez de la Torre	UNAM (CIEEGT)	Native: *Paspalum* and *Sporobolus* spp.	∼0.5	>20	35 heifers for 2–3 days	Urea, protein for the animals
	UNAM (CIEEGT)	Introduced: *C. plectostachyus*	∼1	8	35 heifers for 2–3 days	Urea, protein for the animals
Paso del Toro	Private	Native: *Paspalum* and *Sporobolus* spp.	∼1	>15	Some horses and cows (maximum 5)	None
	INIFAP	Introduced: *D. decumbens*	2.5	20	None	Fertilizers, herbicides

Table 3
Selected properties of the surface soil (A horizon) of the 15 (native and introduced) pastures studied at five sites in Veracruz state

Site (soil type)	Sand (%)	Silt (%)	Clay (%)	C (%)	N (%)	C/N	pH (H_2O)	Ca ($\mathrm{cmol_c\,kg^{-1}}$)	Mg ($\mathrm{cmol_c\,kg^{-1}}$)	Na ($\mathrm{cmol_c\,kg^{-1}}$)	K ($\mathrm{cmol_c\,kg^{-1}}$)	P ($\mathrm{mg\,kg^{-1}}$)
Tuxpan (Entisol)												
Native 1	16	30	54	2.4	0.26	9.5	7.3	37.5	1.0	0.17	0.57	2.5
Native 2	16	30	54	3.3	0.32	10.0	7.4	34.8	3.7	0.16	0.86	0.1
D. decumbens	4	40	56	2.5	0.27	8.7	7.3	35.1	1.1	0.22	0.62	1.8
C. plectostachyus	14	36	50	3.5	0.39	9.3	7.6	28.4	2.9	0.16	0.86	0.1
Carranza (Vertisol)												
Native 1	14	34	52	3.0	0.24	13.0	5.3	10.2	6.8	1.04	0.37	9.3
Native 2	32	30	38	3.6	0.32	11.1	5.7	10.5	8.8	1.66	0.38	6.1
D. decumbens	22	28	50	2.9	0.26	11.6	5.4	8.6	6.1	1.39	0.24	6.3
Paso del Toro (Alfisol)												
Native	71	4	25	1.8	0.17	10.8	5.6	5.9	3.4	0.19	0.79	5.2
D. decumbens	61	14	25	2.1	0.19	11.0	5.4	7.8	4.4	0.40	0.23	2.3
Isla (Ultisol)												
Native 1	54	30	16	0.9	0.10	9.7	5.1	0.9	0.4	0.04	0.07	4.8
Native 2	66	26	8	1.4	0.11	14.4	5.2	1.3	1.1	0.16	0.13	5.8
B. decumbens	60	27	13	1.2	0.11	10.5	4.9	1.0	0.5	0.09	0.04	6.5
A. gayanus	72	21	7	1.1	0.11	10.2	4.9	0.8	0.9	0.11	0.06	4.0
Martínez de la Torre (Alfisol)												
Native	33	31	36	3.0	0.24	12.2	4.7	4.5	1.0	0.50	0.34	5.9
C. plectostachyus	38	26	36	3.3	0.32	10.6	4.6	10.2	2.3	0.45	0.32	13.5

Values shown are the means of samples taken in the wet (September–October) and dry (April) seasons of 1998 and/or 1999.

2.4. Statistical analyses

Means of the biomass and density values for each taxonomic group from all the SE Mexican pastures sampled using TSBF methodology were obtained only for the rainy season. All soil, plant and macrofauna data (abundance and biomass of each of the 18+ taxonomic groups) from the native and introduced pastures sampled were entered into a database and the means for each parameter calculated by site (e.g., Tuxpan), pasture type (e.g., native Tuxpan) and season (dry versus rainy season). The means were submitted to ANOVA using Superanova (Abacus Concepts) and Statistica (StatSoft) software programs and the significant differences revealed using Tukey's honest LSD. Given the large and frequently non-uniform variances usually associated with macrofauna samples using the TSBF method, multivariate analysis were performed on the data. Thus, a principal components analysis (PCA) was undertaken using mean values of macrofauna abundance (of main taxonomic groups) in native and introduced pastures at each of the five sites, to determine the patterns of distribution of the soil macrofauna in each site, pasture type and sample dates.

3. Results

3.1. Soil macrofauna in SE Mexican pastures

Using the data for the rainy season in 20 of the 21 sites sampled, an average of 812 individuals m^{-2} (Fig. 2A) and a biomass of 32.1 g m^{-2} fresh (preserved) weight (Fig. 2B) of soil macrofauna was obtained. Termites, earthworms and ants dominated in terms of abundance with 28, 27 and 24% of the total, respectively. Beetles represented 7% of the total density (5% adults, 2% larvae) and the other organisms represented 9% of the total. These values were closer to the proportions obtained for the introduced pastures in Veracruz, than those of the native pastures, where earthworms were proportionally less abundant, and termites, more abundant (Table 4). As for the biomass, earthworms predominated, representing 84% of the total. The beetles represented 9% (larvae 5%, adults 4%) and the other organisms, 4% of the total. The remaining taxa had a low contribution to the total biomass. Compared with native and introduced pastures, these proportions were smaller for earthworms and larger for beetles and other organisms. The proportion of earthworms in the wet season

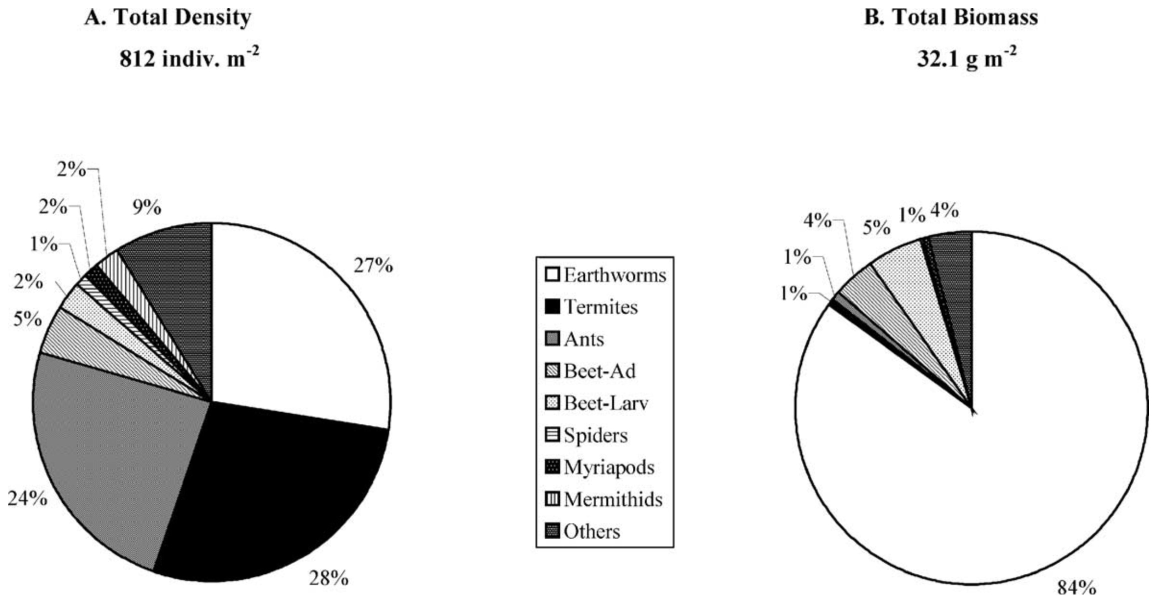

Fig. 2. Proportion of the total density (A) and biomass (B) of the different organisms representing the soil macrofauna in Mexican pastures. Samples were taken in the rainy season. Means calculated from 39 sample points in 20 sites. Beet-Ad: beetle adults; Beet-Larv: beetle larvae. Values for the percentage biomass of Mermithids and Spiders are not shown as they represented <1% of the total.

Table 4
Average density and biomass of the soil macrofauna in native and introduced (Intro) pastures, in the dry and wet season in five sites of the state of Veracruz ($n = 30$ samples)

	Density (individuals m^{-2})				Biomass ($g\,m^{-2}$)			
	Intro (wet)	Native (wet)	Intro (dry)	Native (dry)	Intro (wet)	Native (wet)	Intro (dry)	Native (dry)
Earthworms	246 ab	277 a	116 ab	92 b	37.37 a	44.09 a	6.19 b	4.70 b
Termites	253 ab	750 a	55 b	49 b	0.29 a	0.69 a	0.05 b	0.06 b
Ants	301	603	417	502	0.13	0.45	0.21	0.34
Beetle adults	33	58	29	25	0.51	1.16	0.82	1.54
Beetle larvae	7 ab	15 a	0 b	2 b	0.21 b	1.51 a	0.00 b	0.06 b
Spiders	9	13	9	13	0.02	0.04	0.03	0.05
Myriapods	11	8	5	5	0.11	0.03	0.53	0.10
Mermithids	26 ab	31 a	0 b	1 b	0.06 a	0.06 a	0 b	<0.01 b
Others	24	8	4	11	0.37	0.34	0.03	0.30
Total	908 b	1763 a	635 b	699 b	39.09 a	48.36 a	7.86 b	7.16 b

When shown, different lower- or upper-case letters indicate significant differences ($P < 0.05$) in abundance and/or biomass of different organisms and total values, as determined by ANOVA (Tukey's LSD).

reached as high as 96% in the introduced pastures (see Table 4).

3.2. The influence of the pasture type on soil macrofauna: native versus introduced

Comparing the means of total density of macrofaunal taxonomic groups in native and introduced pastures (Table 4; for complete data see Appendices A and B), a significantly higher number of individuals (two-fold higher) was found in the wet season. No significant differences were observed in the total density in the dry season, or in the total biomass of organisms in both seasons. The soil macrofauna communities were dominated by termites, earthworms and ants in terms of numbers and by earthworms in terms of their biomass. In terms of the different taxonomic groups identified, significant differences between native and introduced pastures were only observed for beetle larvae biomass in the wet season (higher in native pastures; Table 4). The comparison of the proportion of different groups present in each pasture type revealed different patterns. In the native pastures in the wet season, the contribution of termites and earthworms to total abundance and biomass was higher and lower, respectively, than in introduced pastures. In the dry season, contribution of ants and earthworms to the total density and biomass of soil fauna tended to be higher and lower, respectively, in native than introduced pastures.

Likewise, the principal components analysis showed important differences in the community structure of the macrofauna populations of native and introduced pastures, depending on the site and the sample date (year and season) (Fig. 3A and B). The first two factors of the analysis explained more than 80% of the variance in both cases (dry and rainy season) (Table 5).

In the rainy season (Fig. 3A) two main groups of points were observed on the PCA plot (of factors 1 and 2), representing the upper and lower parts of the graph. This separation is due to the vertical axis (factor 2) that represents places with high or low density of social insects (ants and termites). In the horizontal axis (factor 1), three to four different groups can be seen, representing sites with decreasing abundance of ecosystem "engineers" (ants + termites + earthworms).

Table 5
Weight (percentage of the explained variance) of the first two factors of the principal component analysis, using mean density of different macrofauna groups (individuals m^{-2}) in native and introduced pastures in the state of Veracruz

Attribute	Time of the year	
	Rainy season	Dry season
Percentage of the explained variance		
Factor 1	54.3	66.9
Factor 2	26.7	17.9
Cumulative total	81.0	84.8

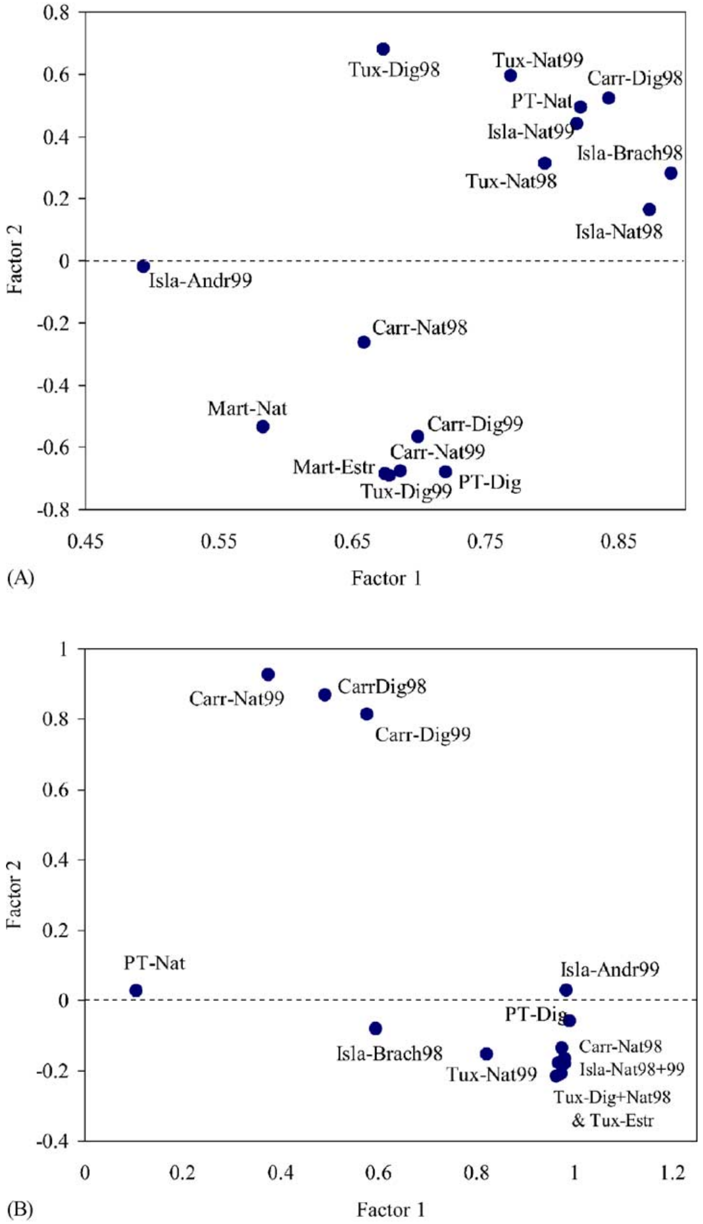

Fig. 3. Location of the different native and introduced pastures in relation to the first two factors of the principal components analysis in the rainy (A) and dry seasons (B). Carr: Carranza; Mart: Martínez de la Torre; Tux: Tuxpan; PT: Paso del Toro; 98: 1998 samples; 99: 1999 samples; Nat: native; Dig: *D. decumbens*; Brach: *B. decumbens*; Estr: *C. plectostachyus*; Andr: *A. gayanus*.

Regarding sampling dates, it can be seen that in 1999 the difference among the communities of the macrofauna in Tuxpan and Isla were much larger than in 1998, with the opposite observed in Carranza. As for the pasture types, large differences between the communities of the native and introduced pastures were seen at Paso del Toro, while at Martínez de la Torre, these were smaller. At Tuxpan and Isla, the differences between the pasture types varied according to the sample date (year); in 1998 they were small, but in 1999 they were much larger. At Carranza the contrary was seen with marked difference in 1998, and smaller in 1999.

In the dry season, the vertical axis (factor 2) separated two main groups of points (Fig. 3B), representing sites with high (Carranza) or low (all other sites) earthworm density. The horizontal axis (factor 1) represented mainly the density of ants and also separated two main groups: those with high ant density to the right, and those with smaller density to the left. As for the sample date, an important effect was only found in 1998 at Carranza. As for the pasture types, important differences were only seen at Paso del Toro and Carranza in 1998.

The earthworm fauna found at each site in 1999 was greatly different (Table 6). Species of the family (Megascolecidae) typical of N America were found in the sites N of the transverse Neo-volcanic axis (Fig. 1), i.e. Tuxpan and Carranza, while those typical of S America (Glossoscolecidae) were found in the southern sites, i.e. Paso del Toro and Isla. At Martinez de la Torre (on the axis), only exotic earthworm species were found (*P. corethrurus* and *O. occidentalis*), while at Tuxpan only native species were observed. At Isla and Paso del Toro, two exotic earthworm species were found and at Carranza only one species was found. The total number of exotics found was low (three species), compared with the natives (10 species).

Highest earthworm species diversity was observed at Paso del Toro (seven species) and Isla (six species), S of the transverse Neo-volcanic axis, and lowest was seen at Martínez de la Torre (two species) on the axis, although further sampling efforts may reveal more species at these sites. The conversion of native to introduced pastures tends to have a negative effect on the number of earthworm species (except at Martínez de la Torre, where equal number was found in both pasture types). In native pastures a mean of four species was found, while in the introduced pastures only half the number of species (two species) was observed (significant difference at $P < 0.07$). At Isla and Tuxpan, the differences were larger (four to five species in the native pastures and one to two species in the introduced), while at Carranza and Paso del Toro, the differences were less marked.

Table 6
Earthworm families and genera/species found in native and introduced pastures at five sites in Veracruz, in the rainy and/or dry season of 1999

Earthworm family	Tuxpan		Carranza		Martínez de la Torre		Paso del Toro		Isla	
	Intro	Native	Intro	Native	Intro	Native	Intro	Native	Intro	Native
Megascolecidae										
Balanteodrilus pearsei (n)		+ (l)						+ (1)		+ (s, l)
Diplocardia sp. (n)				+						
Diplotrema murchei (n)							+	+		+
Diplotrema sp. (n)		+								
Larsonidrilus microscolecinus (n)			+	+			+			
Zapatadrilus sp. nov. (n)		+								
Zapotecia sp. (n)	+	+								
Dichogaster saliens (e)								+		+
Dichogaster sp. (?)								+		
Ocnerodrilidae										
Ocnerodrilus occidentalis (e)			+	+	+	+	+			
Glossoscolecidae										
sp. nov. 1 (n)									+	
sp. nov. 2 (n)							+	+		
Pontoscolex sp. 1 (?)										+
Pontoscolex corethrurus (e)					+	+			+	+
Total species number	1	4	2	3	2	2	4	5	2	5

s: small morphotype; l: large morphotype; n: native species; e: exotic species; ?: unknown species origin.

3.3. The influence of the time of year (rainy versus dry seasons)

When macrofauna biomass and abundance were grouped according to seasons (irrespective of pasture type), total macrofauna density was >2 times higher and biomass >5 times higher in the rainy than the dry season. The difference in biomass was due mostly to earthworms while the differences in abundance were due mostly to earthworms and termites. In the rainy season significantly higher numbers and biomass of earthworms, termites, beetle larvae and mermithids were observed, compared to the dry season.

4. Discussion

It is important to study soil macrofauna communities and their composition in pastures because each organism can have different effects (positive and/or negative) on soil processes and plant and animal productivity. Populations of a particular organism may reach abundance and/or biomass thresholds that result in positive or negative effects on the system or one of its component parts. For example, when very abundant, the rhizophagous scarab beetles can cause considerable decreases in root biomass (Morón, 1997), compromising plant nutrient and water absorption (Villalobos, 1994). On the other hand, high geophagous earthworm populations may help increase plant production, due to their ameliorating effects on soil physical and chemical properties (faster mineralization rates and nutrient and water availability) (Brown et al., 2001). It is through the study of the whole macrofauna community and its changes throughout the year or due to ecosystem management practices that a proper understanding can be reached of its role in ecosystem function (e.g., soil processes and productivity) and the impact of human activities on these communities. This is particularly important to prevent the occurrence of disequilibria that can have “catastrophic” effects on the ecosystem, such as that observed in a site N of Manaus, Brazil, where the conversion of the Amazonian rainforest to pastures eliminated most of the native forest macrofauna and facilitated the invasion of the “compacting” earthworm *P. corethrurus*, leading to soil structural collapse and pasture degradation (Barros, 1999; Chauvel et al., 1999).

The present work constitutes the first study in Mexico comparing the soil fauna communities of native and introduced grass pastures. Combining all the results for each site (Appendices 1 and 2), the modification of the pasture plant communities from native to introduced was not accompanied by significant changes in the biomass of soil macrofauna, although the density was significantly higher in the rainy season. Soil macrofauna populations are often aggregated and/or sparsely distributed, hence monolith samples using the TSBF method often lead to high and uneven mean variance, thus limiting the use of ANOVA tests. Therefore, multivariate analysis are generally preferred for these type of data. Thus, whereas ANOVA tests often reveal few differences between the fauna community at different sites, PCA is more successful at showing these differences (e.g., Carranza, 1998; Tuxpan, 1999; Isla, 1999 and Paso del Toro). In the present case, differences between native and introduced pastures are probably related to site history (previous uses and soil preparation when introducing new grass species), differences in soil characteristics (quantity and quality of OM produced, soil C stocks, some nutrients), or to different grass species’ spatial–temporal resource utilization. Many native pastures (e.g., *Muhlenbergia*, *Sporobolus*) tend to have bunch grasses with tussocks that intensively occupy discrete surface areas and root volumes of the soil, while most introduced grasses generally tend to spread their roots and shoots more evenly over the soil surface (except *A. gayanus*). Furthermore, native pastures tend to have a conglomeration of grass species and weeds with different life cycles and phenologies. These phenomena all combine to create a more diverse micro-environment that ultimately reflects itself on the soil community.

Differences in the soil communities in each pasture type were especially evident when comparing the earthworm fauna present at each site that were more diverse in native than introduced pastures. The opening of new niches with disturbance of the native pastures creates favorable conditions for exotic species invasion. These species are often transported by humans are well adapted to disturbed conditions, and may displace the (generally) less adaptable native species. In the present study, however, this displacement was not evident, as many more native than exotic species were found, confirming previous observations of Fragoso

(2001). The proportion of native to introduced species depended on the site in question, and is probably influenced by differences in the extent of perturbation, previous site management, vegetation and soil types.

The multivariate analysis also revealed differences among the macrofauna communities of native and introduced pastures depending on the sample date. These could be due to macro- and micro-climatic differences between the pastures in different years; 1998 was exceptionally dry (el niño effect) and 1999, exceptionally wet (la niña effect). Differences between the communities present in each pasture type were more pronounced in the rainy than in the dry seasons, and observed more often in 1999 than in 1998. The low abundance and biomass of the fauna in the dry season (exacerbated by the exceptional dry season of 1998) may be the main factor responsible for these differences. Therefore, the best estimates of the effects of pasture grass species conversion on the soil macrofauna community, appear to be when samples are taken in the wet rather than the dry season.

The different responses of the fauna community to climatic factors that change from year to year and with seasons, highlight the importance of choosing the adequate season for sampling, and the need to sample in different years. This process will help guarantee adequate representation of the samples and proper indication of patterns of differences or similarities between different sites, ecosystems, soils and plant and animal communities and the possible short and/or long term effect of agricultural practices on these biological parameters.

It has been said that pastures can, in many cases, preserve a certain level of soil macrofauna biodiversity that is greater than that found in cultivated agroecosystems (Lavelle et al., 1997). However, this biodiversity tends to be reduced if the pasture was derived from a forest or another ecosystem including trees (Decäns et al., 1994). If the pasture is transformed from a native savanna with predominance of grasses, it is likely that the diversity will not be greatly affected, due to the small change induced in the soil's niches and their characteristics. In the case of the present study, the earthworm fauna of sites derived from savanna vegetation (at Paso del Toro and Isla) were the richest in number of species (seven and six species, respectively, two of which were exotic to Mexico). However, when the native pastures, probably functionally closer to the native savanna, were converted to introduced pastures (monospecific introductions), there was a negative effect on the number of earthworm species present, particularly at Isla. Compared with the savanna-derived sites, the other three sites derived from forest vegetation, were rather species-poor, with only two to four species, and at Martinez de la Torre, both species present were exotic. An interesting case was observed in Tuxpan, where all four species present were native (no exotic invaders were found), reaching very high biomass values (up to 975 kg ha^{-1}), and were responsible for intensive bioturbation, as well as selection of soil particles higher in OM (Brown et al., unpublished data). Large volumes of dark-colored nutrient-rich castings (pedo-tubules) were observed penetrating into the light-yellow colored AB and B horizons. The present results, together with those of the total macrofauna community, seem to indicate that if nutrient-poor savannas are converted to native pastures, these can maintain higher soil macrofauna populations and earthworm diversity compared with introduced pastures. On the other hand, when native forests are converted to pastures, the native fauna community diversity may be greatly impoverished, and that this may be exacerbated by planting introduced grass species.

When all the available data on soil macrofauna communities in Mexican pastures were combined, it was found that, on average, their populations could surpass 1000 individuals m^{-2} (mean = 8 million ha^{-1}), and represent a biomass of more than 300 kg ha^{-1}. Although this value is lower than that reported by Lavelle et al. (1994) (73.2 g m^{-2}), in some pastures (with low animal loads) it surpasses that of the grazing livestock per hectare. It was also seen that the macrofauna communities are dominated by termites, earthworms and ants in terms of numbers and by earthworms (>80%) in terms of their biomass. It is known that when found in biomass of above about 30 g m^{-2}, earthworm activities can result in important positive effects on plant productivity, particularly of perennial plants (Brown et al., 2001). This means that in many Mexican pastures, earthworms may be providing important benefits gratuitously to the producers, which often go unnoticed.

In conclusion, the results of the present work provide evidence that changes in pasture types, i.e., from native to introduced pastures, can lead to important changes in the soil macrofauna community. Future research should explore these communities in greater detail, determining the presence or absence of changes in the number of species and the possible impacts on soil function.

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Appendix A

Biomass ($g\,m^{-2}$) of different taxonomic groups and total biomass of soil macrofauna during the wet and dry seasons of 1998 and 1999 in native and introduced pastures in the state of Veracruz. Data used to calculate means for Fig. 3B. Beet-Ad: beetle adults; Beet-Larv: beetle larvae; Carr: Carranza; Mart: Martínez de la Torre; Tux: Tuxpan; PT: Paso del Toro; Nat: Native; Dig: *D. decumbens*; Brach: *B. decumbens*; Estr: *C. plectostachyus*; Andr: *A. gayanus*

Site code	Pasture type	Taxonomic groups									Total
		Earthworms	Termites	Ants	Beet-Ad	Beet-Larv	Spiders	Myriapods	Mermithids	Others	
Wet season											
Isla Brach	Introduced	50.69	0.67	0.15	0.41	0.00	0.01	0.00	0.18	5.95	58.06
Isla Nat1	Native	24.59	1.34	1.13	0.71	0.00	0.12	0.00	0.02	1.34	29.24
Isla Andr	Introduced	97.56	0.02	0.01	1.59	0.56	0.06	0.79	0.00	3.40	103.99
Isla Nat2	Native	53.17	0.38	0.04	0.05	1.06	0.00	0.08	0.12	7.99	62.88
Carr Dig	Introduced	23.58	0.83	0.08	0.00	0.00	0.00	0.00	0.00	0.40	24.90
Carr Nat1	Native	36.85	0.00	0.02	0.00	0.00	0.01	0.00	0.01	1.68	38.56
Carr Dig	Introduced	6.96	0.25	0.17	0.38	0.01	0.01	0.00	0.09	1.42	9.30
Carr Nat2	Native	26.14	0.01	0.31	0.77	1.68	0.02	0.00	0.02	2.31	31.26
Mart Estr	Introduced	2.74	0.00	0.12	1.37	1.12	0.00	0.10	0.08	0.44	5.96
Mart Nat	Native	15.41	0.00	0.43	4.04	3.00	0.00	0.02	0.08	1.22	24.21
PT Dig	Introduced	10.93	0.00	0.31	0.16	0.00	0.04	0.01	0.08	1.36	12.88
PT Nat	Native	35.41	0.53	0.01	0.80	1.05	0.18	0.05	0.20	2.29	40.52
Tux Dig	Introduced	56.89	0.52	0.03	0.07	0.00	0.03	0.00	0.01	0.81	58.35
Tux Nat1	Native	83.15	2.85	1.55	2.88	0.00	0.01	0.00	0.01	1.74	92.19
Tux Dig	Introduced	49.62	0.00	0.17	0.14	0.02	0.03	0.01	0.04	1.18	51.21
Tux Nat1	Native	77.99	0.41	0.14	0.01	5.30	0.00	0.07	0.02	0.15	84.08
Dry season											
Isla Brach	Introduced	2.96	0.02	0.84	4.39	0.00	0.01	0.20	0.00	0.22	8.64
Isla Nat1	Native	3.07	0.22	0.15	1.48	0.44	0.02	0.71	0.00	1.66	7.77
Carr Dig	Introduced	1.08	0.02	0.30	0.24	0.00	0.07	0.00	0.00	0.45	2.16
Carr Nat2	Native	1.38	0.00	0.80	0.98	0.00	0.23	0.00	0.00	1.89	5.28
Carr Dig	Introduced	0.27	0.04	0.05	0.55	0.01	0.11	0.01	0.00	2.03	3.08
Carr Nat1	Native	0.45	0.10	0.00	0.63	0.00	0.06	0.01	0.01	1.30	2.56
Tux Dig	Introduced	7.71	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.06	7.81
Tux Nat1	Native	4.60	0.00	0.34	4.16	0.01	0.00	0.00	0.00	1.39	10.50
PT Dig	Introduced	27.72	0.02	0.07	0.01	0.00	0.00	0.00	0.00	0.27	28.09
PT Nat	Native	20.86	0.00	0.04	0.00	0.00	0.00	0.00	0.00	0.36	21.26

Appendix A (*Continued*)

Site code	Pasture type	Taxonomic groups									Total
		Earthworms	Termites	Ants	Beet-Ad	Beet-Larv	Spiders	Myriapods	Mermithids	Others	
Isla Andr	Introduced	2.40	0.00	0.06	0.00	0.00	0.02	3.47	0.00	0.39	6.34
Isla Nat2	Native	0.50	0.05	0.20	2.58	0.00	0.00	0.00	0.00	0.22	3.54
Tux Estr	Introduced	1.21	0.28	0.09	0.52	0.00	0.00	0.00	0.00	2.95	5.06
Tux Nat2	Native	2.04	0.05	0.84	0.96	0.00	0.05	0.00	0.00	1.30	5.24

Appendix B

Density (number of individuals m^{-2}) of different taxonomic groups and total abundance of soil macrofauna during the wet and dry seasons of 1998 and 1999 in native and introduced pastures in the state of Veracruz. Data used to calculate means for Fig. 3A. Beet-Ad: beetle adults; Beet-Larv: beetle larvae; Carr: Carranza; Mart: Martínez de la Torre; Tux: Tuxpan; PT: Paso del Toro; Nat: Native; Dig: *D. decumbens*; Brach: *B. decumbens*; Estr: *C. plectostachyus*; Andr: *A. gayanus*

Site code	Pasture type	Taxonomic groups									Total
		Earthworms	Termites	Ants	Beet-Ad	Beet-Larv	Spiders	Myriapods	Mermithids	Others	
Wet season											
Isla Brach	Introduced	698	692	258	40	0	10	0	92	430	2220
Isla Nat1	Native	236	1584	1208	120	0	24	0	12	136	3320
Isla Andr	Introduced	448	14	14	44	12	10	64	0	88	694
Isla Nat2	Native	452	472	64	4	16	2	16	90	226	1342
Carr Dig	Introduced	244	442	98	0	0	0	0	0	16	800
Carr Nat1	Native	296	0	114	0	0	5	0	8	19	442
Carr Dig	Introduced	110	178	1000	20	16	6	2	46	88	1464
Carr Nat2	Native	314	6	1008	10	34	30	0	6	38	1446
Mart Estr	Introduced	76	0	206	74	22	2	14	8	86	488
Mart Nat	Native	274	0	592	114	20	4	10	18	734	1766
PT Dig	Introduced	234	4	612	40	0	12	2	52	98	1054
PT Nat	Native	438	522	70	70	12	22	22	104	126	1386
Tux Dig	Introduced	92	690	58	18	0	16	0	2	46	922
Tux Nat1	Native	100	3026	1696	134	0	8	0	6	42	5012
Tux Dig	Introduced	68	0	162	24	4	14	2	6	102	380
Tux Nat1	Native	104	388	74	12	38	8	18	4	50	678
Dry season											
Isla Brach	Introduced	46	304	176	24	0	2	0	0	70	622
Isla Nat1	Native	36	52	694	42	0	6	0	0	60	890
Carr Dig	Introduced	136	0	48	0	0	0	0	0	20	204
Carr Nat2	Native	112	0	1339	11	5	0	0	0	59	1525
Carr Dig	Introduced	440	16	206	2	0	4	0	0	8	676
Carr Nat1	Native	434	0	94	0	0	0	0	0	26	554
Tux Dig	Introduced	46	40	704	48	0	22	0	0	42	902
Tux Nat1	Native	8	6	812	40	0	40	0	0	110	1016
PT Dig	Introduced	26	14	142	10	2	12	2	0	32	240
PT Nat	Native	12	76	0	12	2	6	2	2	18	130
Isla Andr	Introduced	44	0	172	0	0	8	12	0	24	260
Isla Nat2	Native	8	32	364	8	0	4	0	0	20	436
Tux Estr	Introduced	72	12	1472	116	0	16	24	0	48	1760
Tux Nat2	Native	36	176	208	60	8	32	32	4	104	660

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