Earthworm communities under an agricultural intensification gradient in Colombia

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Abstract

This study was carried out in the Eastern Plains of Colombia and assessed the impact of agricultural intensification on the structure of earthworm communities. Earthworms were hand-sorted in a variety of agroecosystems of increasing intensity, from natural savanna to pastures and annual crops. An agricultural intensification index was used to rank systems along an intensification gradient, i.e. from native savanna to pastures and annual crops. Earthworm biomass, specific richness and Shannon index sharply decreased along the gradient. The disappearance of some species in cultivated systems was mostly attributed to the lack of recovery of populations after major perturbations like e.g. tillage. The more resistant species were those presenting high surface mobility (i.e. high colonisation capacity) or high population growth potential (i.e. high ability of population recovering after perturbation). Sensitive species disappeared after pasture establishment but richness was recovered in a period of about 3 years. In 17 year-old pastures, the community has regained its initial diversity and present very high biomass due to the presence of abundant populations of an anecic species. On the opposite side, annual crops had deep detrimental impacts that were more accentuated in the rotations (i.e. systems that were tilled twice a year) and were still present in a 2 year-old fallow.

Introduction

The impacts of earthworms on soil properties and plant growth have been widely documented during the past 15 years. From these studies, abundant evidence has emerged that earthworms are powerful regulators of soil processes, participating in the maintenance of soil structure and the regulation of soil organic matter dynamics (Lavelle, 1997). Their positive impacts on plant growth was first recognised by Darwin (1881), and have been confirmed in most recent studies, although negative or null effects have also been described (see reviews by Brown et al., 1999; Spain et al., 1992). Consequently, earthworms have been

considered as a natural resource of agronomic interest that may be used to increase the sustainability of most production systems (Lavelle et al., 1998; Lee, 1985).

In agroecosystems, earthworm communities are generally very sensitive to land use practices which directly modify both the rate of perturbations and the availability of trophic resources for soil fauna. This has been broadly described in tropical environments, where communities can be modified greatly when forests or savannas are converted into agroecosystems (Dangerfield, 1990; Fragoso et al., 1997; Gilot et al., 1995; Lavelle and Pashanasi, 1989). These changes may occur even at a taxonomical (e.g. substitution of native by exotic species), an ecological (changes in the relative importance of ecological categories), or a quantitative (modifications of biomass or density) level. While crops generally have dramatic effects on

both the abundance and the diversity of communities, pastures enhance earthworm biomass but lead in some cases to a decrease in taxonomic richness (Fragoso et al., 1999).

Impacts of land use on earthworm communities are likely to have significant consequences on soil functioning. This can occur when populations are reduced below a critical level of biomass. Brown et al. (1999) in a recent synthesis considered 30 g m^{-2} as the minimum earthworm biomass below which significant positive impacts on plant growth are not observed. Such biomass levels are generally achieved in pastures, but not in most cropping systems (see review by Lee, 1985). On the other hand, loss of functions can also be observed when biomass is enhanced while species diversity is decreased at the same time. A spectacular example has been observed in Amazon pastures, where the shift of forest into herbaceous systems leads to the disappearance of the species-rich native community, which is replaced by abundant monospecific populations of pantropical exotic earthworms (Barros, 1999). In these systems, the regulating function of soil fauna on soil structure is not achieved, and earthworm casts accumulate at the soil surface in excess, generating severe problems of soil compaction and pasture degradation (Chauvel et al., 1999). Similar results have been reported from recent polders in The Netherlands, where enormous densities of *Aporrectodea caliginosa* was considered to be responsible for superficial compaction and problems of harvesting in potato crops (van Rozen and Ester, unpubl. data).

A great challenge for soil scientists in the near future will be to develop useful techniques for managing earthworm populations in cultivated soils. Direct techniques (i.e. breeding and inoculation of earthworms in the fields) have proven their effectiveness in increasing yields of tea production in India, but are too expensive to be used in most systems of production (Senapati et al., 1999). A possible alternative may be to manage populations indirectly, i.e. by facilitating the activity of the pre-existent native fauna. To match this objective, scientists need to understand how agricultural intensification can lead to modifications in the structure of earthworm communities. Exploring these relationships rigorously will imply the use of universal indexes of agricultural intensification, allowing effective comparisons of data from different regions of the earth, and the description of general patterns of responses not only for earthworms but also for other groups of plants or animals (Swift et al., 1996).

Table 1. List of the agroecosystems studied with their corresponding codes (see text for complete descriptions), number of plots assessed for each of them and number of earthworm samples performed in each plot

Systems	Codes	N of plots	N of samples
Native savanna	NS	2	60
B. decumbens + P. phaseoloides pasture	Bd	1	100
B. humidicola + A. pintoi pasture	Bh	2	120
P. maximum + A. pintoi pasture	Pm	2	120
Rice monocrop	RM	2	60
Maize monocrop	MM	1	60
Rice/green manure rotation	R/GM	1	60
Rice/cowpea rotation	R/C	1	60
Maize/green manure rotation	M/GM	1	60
Fallow	F	1	60

This study assessed the impacts of agricultural intensification on the structure of earthworm communities in a tropical savanna environment. An intensification index is proposed to rank agroecosystems along an 'intensification gradient', i.e. from natural to extensive and intensive. Special attention was paid to changes in the density, the biomass and the structure of earthworm communities.

Materials and methods

Study site

The study was carried out at the CIAT-CORPOICA research station of Carimagua (4° 37′ N, 71° 19′ W), located in the phytogeographic unit of the well-drained isohyperthermic savannas of the 'Oriental Llanos' of Colombia. The climate is subhumid tropical with annual mean temperatures and rainfall of 26 °C and 2300 mm, respectively, and a dry season from November to March. Native vegetation is open savannas in the uplands ('altos' and 'planos'), and gallery forests or flooded savannas in the low-lying areas ('bajos'). Soils are Oxisols (Tropeptic Haplustox Isohyperthermic) in the uplands and Ultisols (Ultic Aeric Plintaquox) in the low-lying areas. Both are characterised by high aggregation, porosity and water retention, high acidity (pH$_{(H20)}$ < 5) and very low chemical fertility (Al saturation > 80%, CEC < 5 meq. 100 g^{-1}).

Experimental plots

Ten land management options were selected in an upland area to reflect the main production systems used by farmers in the study area. All agroecosystems were established after slashing and burning the native savanna vegetation. According to the land use system, from 1 to 2 independent plots were assessed (Table 1):

1. A *Trachypogon vestitus* Anders. native savanna, protected from grazing for 4 years and traditionally managed by burning of the vegetation every year during the dry season.

2. A 17 year-old permanent pasture of *Brachiaria decumbens* Stapf. and *Pueraria phaseoloides* Benth. C.V. CIAT 9900, grazed by cattle and maintained at a stocking rate of 1.0 Animal Unit (AU). ha^{-1} during the dry season and 2.0 AU. ha^{-1} during the wet season.

3. A 3 year-old temporary pasture of *Brachiaria humidicola* (Rendle), *Arachis pintoi* Krap and Greg, *Stylosanthes capitata* Vog. and *Centrosema acutifolium* Benth. (pasture B), established together with a single rice crop (*Oryza sativa* L. cv. Savanna 6 CIAT) and grazed at an average stocking rate of 2.0 AU. ha^{-1}.

4. A 2 year-old temporary pasture of *Panicum maximum* (Rendle) and *Arachis pintoi* Krap, established with a single rice crop and grazed by cattle at an average stocking rate of 2.0 AU. ha^{-1}.

5. A 3 year-old annual rice monocrop, sown at the onset of the dry season and harvested at the end of the first semester.

6. A 2 year-old annual maize monocrop (*Zea mays* L. cv. Sikuani CIAT) managed in the same way as the rice monocrop.

7. A 3 year-old annual rotation of rice and cowpea (*Vigna unguiculata*), harvested at the end of the first and second semesters, respectively.

8. A 3 year-old annual rotation of rice and cowpea, where rice is harvested at the end of the second semester and cowpea is used as green manure and incorporated into the soil through tillage at the end of the rainy season.

9. A 2 year-old annual rotation of maize and soybean (*Glycine max*) L. used as green manure in the same way as for the rice/green manure rotation.

10. A 2 year-old fallow, initially cropped during one year with maize and soybean in rotation.

The low number of plot replicates that were selected for the study was due to logistical issues, i.e. the absence of more than 1 or 2 plots in an homogeneous
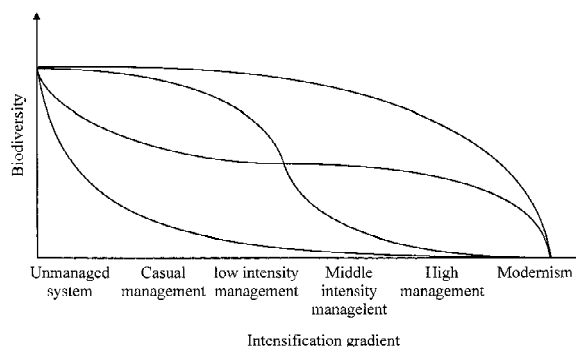

Figure 1. Hypothetical relationships between agricultural intensification and biodiversity (according to Swift et al., 1997).

area at the study site (especially regarding topographic position and water constraints). This lack was assumed to be partially compensated by the large number of pseudo-replicates that were sampled in each plot (from 60 to 120).

Intensification index

Agricultural intensification can be defined as a set of patterns of land use change of increasing intensity that aim at increasing agricultural production (Giller et al., 1997). It is generally associated with a specialisation in a few crop or livestock species, an increased mechanisation of management practices, and a generalised use of inputs and pesticides.

Agroecosystems can be arranged according to their degree of intensification, i.e. the temporal intensity of land use and the range of practices applied to the system. Swift et al. (1996) hypothesised that plotting biodiversity against agriculture intensification will result in a monotonic and decreasing relationship. They also specified that the exact shape of the curve remains uncertain and proposed some hypothetical response patterns (Figure 1). Curve I hypothesises a substantial loss in biodiversity as soon as any management is brought to bear on the ecosystem, and probably represents the most commonly held prediction of the relationship; curve II, in which diversity is only significantly affected by high intensity systems, would in contrast be considered as less likely; curves II and III are intermediate scenarios proposed by the authors. Each pattern may have differing implications for biodiversity conservation.

Ordering agroecosystems along an intensification gradient can be done empirically by classifying land use practices subjectively from the 'less' (e.g. burning and grazing of the vegetation) to the 'more' (e.g. tilling of the soil, use of chemicals, etc) intensive

ones. Alternatively, agricultural intensification of a given system may be assessed quantitatively by calculating an index that takes into account the frequency of human interventions and the duration of the periods during which land is productive. This index, modified from Giller et al. (1997), is given by the equation:

$$AI = \frac{LUI + FF + TF + MPF + SR + FR + PCR}{N},$$

where AI is the agricultural intensification index, LUI the mean land use intensity (proportion of the year the system is cropped), FF the mean fire frequency (number of burning per years), TF the mean tillage frequency (per year), MPF the mean frequency of motorised practices (per year), SR the mean annual stocking rate (International Animal Units ha^{-1}), FR the mean fertilisation rate (kg of fertilisers used per year), PCR the mean pest control rate (kg of chemicals used per year), N the number of factors or 'sub-indices' used for the calculation of the AI index. Each sub index is an annual mean use of a given agricultural practice, which takes into account all the years since the establishment of the system. Their respective maximum values are brought back to 1 by dividing each individual value by the corresponding higher value. As a consequence, all sub-indices are weighted equally for the calculation of AI, which range from 0 to 1 for all systems. Details about the calculation are given in the Appendix together with individual values of the index for each agroecosystem.

Earthworm sampling

Earthworms were sampled during the rainy season (June 1996), which is known to be the period of maximum activity of earthworm populations (Jiménez et al., 1998a). Most of the species and one genus at the study site are probably new for science and still undescribed, so there were no species name for each of them (Jiménez, 1999). However, identifications were done according to the differences in the external morphology of each taxa that were pointed out by Jiménez (1999).

In each plot, from 60 to 120 soil monoliths (25 × 25 × 25 cm) were dug out with a spade and hand sorted in the field. Sampling design was initially drawn to allow further assessments of the spatial distribution of earthworm species assemblages (not shown in this paper), and points were consequently located every 5 m along a regular grid. Collected earthworms were identified at species level, counted and released.

Prior to the monolith extraction, the density of the large anecic species *Martiodrilus carimaguensis* Jiménez and Moreno was estimated by counting the fresh casts it produced at the surface of a 1 m^2 square that was centred on the monolith. The direct positive correlation between the number of individuals and the number of fresh casts present at the soil surface was considered as the more efficient method for assessing the populations of this species (Jiménez et al., 1998b). In fact, *M. carimaguensis* easily escapes into deep soil horizons when using classic hand sorting or formaldehyde methods, due to its large size and the deep semi-vertical burrows it digs.

The sampling procedure above described was only one sampling date of a long-term study of earthworm community in agricultural systems. For this reason, earthworms were released in the sorted soil to avoid excessive removal of individuals that would have been prejudicial for further samplings in the same plots. Hence, biomass was estimated using available data of the average individual weights of each species at the period of sampling (Table 2; Jiménez, 1999).

Diversity indices

Species richness (S) was defined as the total number of species found in one plot. Diversity (H) and evenness (H') were calculated with density data using the Shannon-Wiener index of diversity (Pielou, 1966):

$$H = -\sum_{i=l}^{n} p_i \log_2 p_i,$$

where pi is the frequency of the i species:

$$H' = H/\log_2 S$$

Statistics

Data normality was tested using a Wilk–Shapirov test performed with the 'Statistix' software (Statistix, 1998). The sets of data for which normality was not initially reached were successfully transformed by a simple ln transformation. Mean comparisons were performed using Fisher PLSD tests at the probability level of 0.05. Interactions between agricultural intensification and community structure was tested by plotting biomass, density and diversity indices against AI index and performing linear regressions using the 'S+' Software (S+, 2000). Additionally, non-linear models were fitted to the results to identify which

Table 2. List of the earthworm species present at the study site and mean individual weights of each of them for the month of June (based on Jiménez, 1999)

Species	Ecological category[a]	Mean individual weight (g ind^{-1})
Glossodrilus sp.	Polyhumic endogeic	0.07
Andiodrilus sp.	Polyhumic endogeic	0.42
Aymara sp.	Epigeic	0.03
Martiodrilus carimaguensis	Anecic	2.57
Ocnerodrilidae sp.	Polyhumic endogeic	0.01
Andiorrhinus sp.	Endo-anecic	2.97

[a]*Sensu* Bouché (1977) and Lavelle (1979).

of the four hypothetical response models shown in Figure 1 corresponds the best to the observed patterns.

Results

Agricultural intensification index

The values obtained with the index of agricultural intensification (AI) reveal the existence of a continuum of intensification rather than discrete categories of agroecosystems (Appendix). Nonetheless, three distinct levels of intensification were identified to increase the effectiveness of data interpretation: (1) semi-natural systems (AI index < 0.2) were represented by the native savanna plots; (2) pastures and fallow were considered as medium-intensification systems (AI index ranging from 0.2 to 0.4); (3) monocrops and crop rotations were identified as high-intensification systems (AI > 0.4).

Interestingly, pastures were ordered along this gradient according to their age. More recently implanted pastures had a greater index and were consequently located near crops, while old pastures had a low index not so different to that of the native savanna.

Earthworm density and biomass

Earthworm density and biomass in the native savanna ranged from 16 to 25 ind m^{-2} and 1.7 to 4.2 g m^{-2}, respectively. Six earthworm species were collected during the sampling period with a wide variety of morphological and ecological attributes (Table 2). Agricultural intensification affected earthworm communities in different ways according to the land use system (Figure 2a, b).
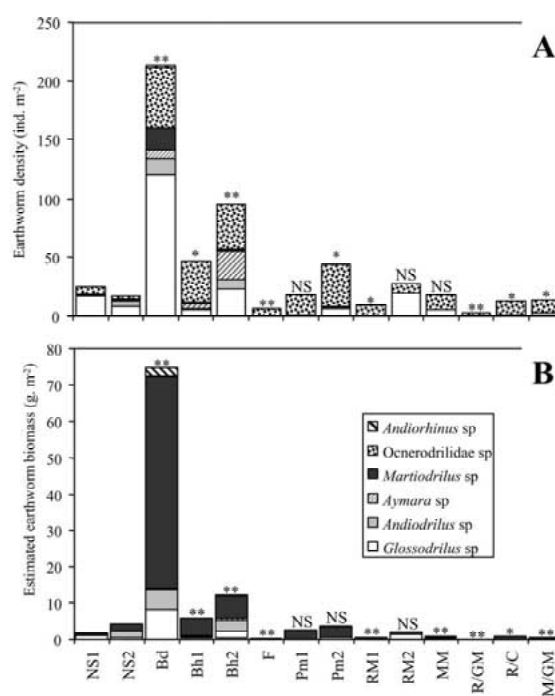

Figure 2. Earthworm density and estimated biomass in the native savanna and derived agroecosystems (codes as in Table 1). NS=not significant; *=significantly different from one savanna plot; **=significantly different from both savanna plots.

In general, medium intensified systems increased both the density and the biomass of native earthworm species (e.g. up to 213 ind m^{-2} and 74.8 g m^{-2} in the *B. decumbens* pasture) or, on the contrary, had no significant effects on them (e.g. in the recently established pastures). This pattern was not observed in the fallow where both the density and the biomass of earthworms were reduced (6 ind m^{-2} and 0.3 g m^{-2}, respectively). All earthworm species were enhanced in the old pastures, but they did not exhibit the same
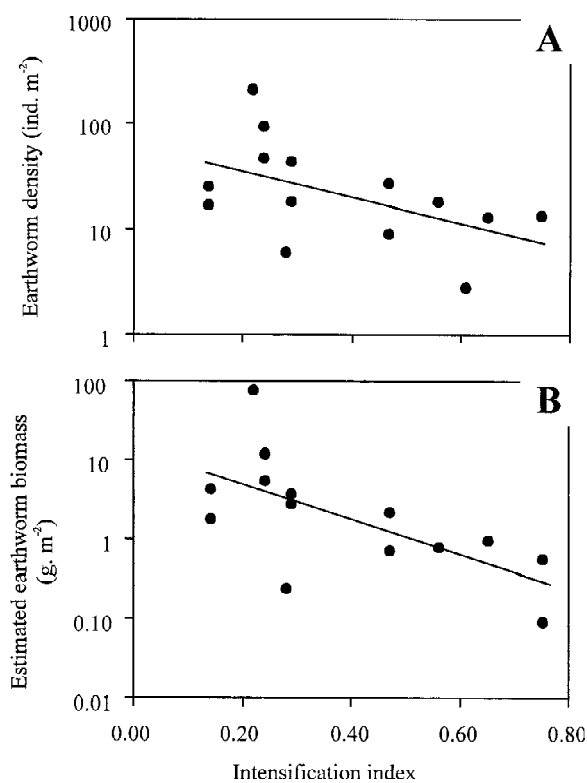
Figure 3. Earthworm density (a) and estimated biomass (b) along an intensification gradient (regression curves).

patterns. In the *B. decumbens* system, 80% of the total earthworm biomass was made up by the anecic *M. carimaguensis*, which only represented 15–40% in the native savanna. Conversely, the two dominant populations of the native community (i.e. *Glossodrilus* sp. and *Andiodrilus* sp.) did not respond within the same range and their relative contribution to the total biomass decreased in the pastures.

Highly intensified systems were generally detrimental for most earthworm species. In most cases, both the total density and biomass were significantly reduced in these systems when compared with the native savanna (down to 3 ind m^{-2} and 0.1 g m^{-2} in the rice/green manure rotation, Figure 2). One plot of rice monocrop, however, did not show any significant differences. Only one species, the small endogeic Ocnerodrilidae sp., seemed to be enhanced by the conversion of the savanna into annual crops.

A linear and significant relationship was found between the AI index values and the ln of earthworm biomass (Figure 3, $R^2 = 0.43$, $p < 0.05$), while the similar pattern observed for density was not supported by statistical tests ($R^2 = 0.26$, not significant).

Earthworm diversity

All the species collected during the sampling period belong to the local pool of native species. *Andiorrhinus* sp. was only found in the *B. decumbens* pasture, probably because of its relative rarity in natural ecosystems. Apart from this species, the species composition in the pasture was the same as in the savanna. Conversely, annual monocrops and rotations led to a drastic reduction of the number of species. *Andiodrilus* sp., *Aymara* sp. and in some cases *Glossodrilus* sp. often disappeared from the soil of these agroecosystems. A reduced number of species was also observed in recently established pastures.

Linear regressions between AI index and diversity indices were significant for specific richness ($R^2 = 0.44$, $p < 0.05$) and Shannon index ($R^2 = 0.34$, $p < 0.05$) but not for evenness ($R^2 = 0.21$, not significant). Figure 4, however, demonstrates that the relationships between agricultural intensification and earthworm diversity should be non-linear rather than linear. Hence, the best fitted models for the data sets were polynomial equations of third order ($R^2 = 0.69$, 0.45 and 0.30 for richness, Shannon and evenness, respectively), which showed systematically a higher correlation index than linear models (Figure 4).

Discussion

General patterns

Two main types of agroecosystems can be identified on the basis of their AI index and their impacts on soil communities: (i) pastures are moderately intensified and, on average, led to a spectacular increase of earthworm biomass (Figure 5a) and a slight decrease of specific richness (Figure 5b); (ii) annual crops and crop rotations are highly intensive systems, with detrimental effects on both the biomass (Figure 5a) and the specific richness (Figure 5a). Recently sown pastures may be considered as intermediate systems, since they are characterised by a relatively high IA index and have crop-like impacts on earthworm populations.

Pasture establishment shows a progressive decrease of IA index followed by a reconstitution of community biomass and specific richness over time. Tillage and pesticides used for the system establishment may explain the observed short-term negative impact in the recent plots. Afterwards, stable and suitable conditions lead to a progressive reconstitution of the populations with the recolonisation of the soil by
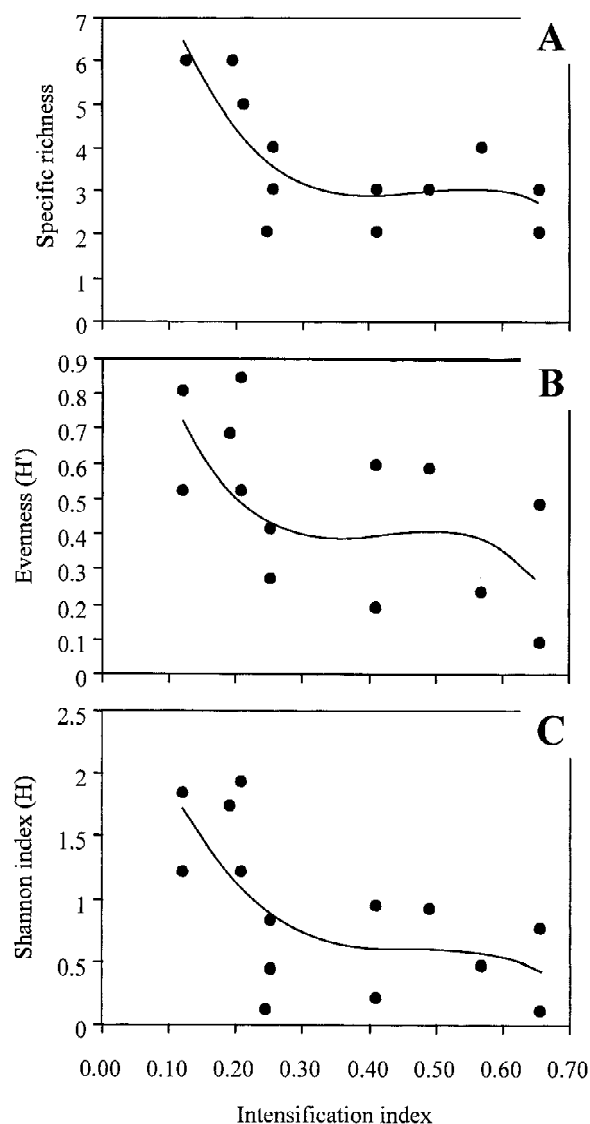
Figure 4. Earthworm diversity along an intensification gradient (regression curves): species richness (a), evenness (b) and Shannon's index (c).

Figure 5. Models of response of earthworm biomass (a) and species richness (b) to the conversion of native savanna agroecosystems.

species that were initially extinct (e.g. *Aymara* sp. and *Andiodrilus* sp.). In the older pasture, the total biomass is more than a 10-fold of the native savanna, with a high dominance of *M. carimaguensis,* whose adaptive potential in pastured systems was described in other studies (Decaëns et al., 1994; Jiménez et al., 1998a, b). Hence, the initial deleterious effects of pasture establishment on earthworm communities are progressively attenuated with time, and the global long-term impact of these moderately intensified systems is broadly positive.
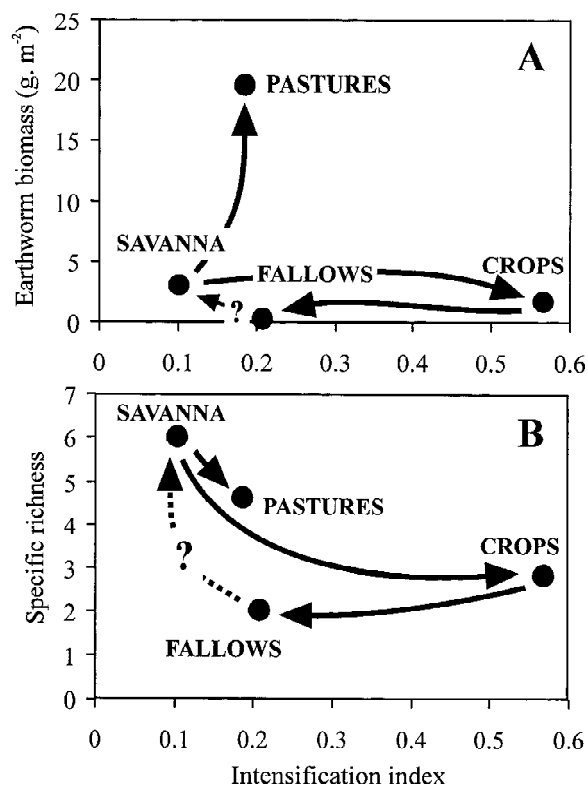
These findings support previous studies where the suitability of the pasture environment for earthworm activity has been demonstrated (Decaëns et al., 1994; Fragoso et al., 1997, 1999; Lavelle and Pashanasi, 1989). This pattern is mainly attributed to the production of litter of high nutritive quality, important amounts of dead roots for geophagous species and the protection of the soil by a permanent vegetation layer (Fragoso et al., 1999; Syers and Springett, 1983). In most cases, however, the increase of earthworm biomass is linked to a reduction of the number of native species with the predominance of a few exotic species (Fragoso and Lavelle, 1992; Lavelle and Pashanasi, 1989). This has been principally observed when environmental conditions provided by pastures are highly different from those of the initial native vegetation (e.g. when a pasture is established after slashing and burning a tropical rain forest). At Carimagua, functional differences between pastures and native savanna are not really sharp (Swift et al., 1996). Hence, native species are all represented in pastoral systems, and take advantage of suitable trophic and microclimatic conditions, even if some of them adapt better or faster than others.

Annual monocrops and crop rotations are the more intensified systems in this study. Earthworm responses to both systems are relatively similar and characterised by a spectacular decrease of both the biomass and the specific richness of populations. This supports previous studies in which negative impacts of cropping on earthworms is attributed to tillage, pesticides and the reduction of the amount of available trophic resources (Bohlen et al., 1995; Jordan et al., 1997; Lee, 1985; Reddy et al., 1995; Rovira, 1994).

In comparison, the two-year old fallow presented a lower AI index, although no reconstitution of earthworm populations was observed. On the contrary, both the biomass and the specific richness of earthworm were slightly lower in this system when compared to monocrops and rotations. Hence, cropping systems seem to have much more resilient negative effects than those observed after the establishment of pastures. Synchronic or diachronic studies of secondary successions (following abandonment of cropping) will now be necessary to determine if long term fallows may lead to a recovery of the initial earthworm populations and what should be the minimal time to achieve this.

Individual species responses

Obviously, the patterns of response to agricultural intensification are not the same for all earthworm species, with significant differences in the shape of the density variations along the gradient. These divergent results may be interpreted in light of the ecological attributes of individual species (see Jiménez, 1999), which drives to a certain extent their ability to reconstitute their population densities after perturbations.

The anecic *M. carimaguensis* is a large anecic species (*sensu* Bouché, 1977), characterised by a reduced reproduction potential ('K-selected' species, *sensu* Southwood, 1977), and a high individual mobility at the soil surface. In consequence, it is well established in stable environments (pastures), but highly affected in crops where it is not able to maintain its populations under a high perturbation regime.

The largest endogeic species (*sensu* Bouché, 1977) are broadly affected by land use in the same way as *M. carimaguensis*. Conversely, the small Ocnerodrilidae sp. that exhibits a high population growth potential ('r-selected' species, *sensu* Southwood, 1977) increases its populations in all the agroecosystems where it takes immediate advantage of trophic conditions enhancement (e.g. legume litter availability in crop rotations and pastures).

The epigeic *Aymara* sp. present a similar adaptive strategy as the *Ocnerodrilidae* sp. and a higher mobility capacity (Jiménez, 1999), but is critically dependent of its litter habitat to persist in a given place. This explains why this species was only found in the savanna and the older pasture.

Earthworm diversity

The decrease of earthworm diversity along the agriculture intensification gradient is as expected. In fact, it is widely acknowledged that biological diversity is negatively affected when natural ecosystems are substituted by agroecosystems of increasing intensity (Holloway and Stork, 1991; Pimentel et al., 1992). In the present study, the shape of the decreasing curve is less dramatic than what ecologists intuitively might expect (type I of Figure 1). It rather corresponds to the thirst hypothetical model proposed by Swift et al. (1996): the immediate loss of species is sharp when converting the native savanna into pastures, even if richness is recovered in the older plots. Afterwards, the decrease of diversity as land management intensifies is relatively slight until it reaches the extreme values of the AI index.

In general, the observed modification of earthworm diversity along this intensification gradient fits well within the Huston's dynamic equilibrium model, according to which the diversity of a given community is mostly driven by the balance between perturbations and productivity of the system. The maximum diversity is observed in systems where an equilibrium exists between both factors, e.g. in the native savanna with slight perturbation rates and intensities (annual fires) and relatively low potential in earthworm productivity (low quality of organic resources). In crops and recent pastures, species may be removed by the intensive and frequent perturbations generated by tillage and the decrease of potential population growth (low quantity of organic inputs). In old pastures, the potential productivity (availability and quality of organic resources) is increased while perturbations are reduced (no tillage, no fire, no pesticides) so an exclusion of less competitive species would be expected. Hence, the anecic *M. carimaguensis* dominates in pasture, but no species losses were observed, suggesting a high niche partitioning within the community.

An outstanding result of this study is that, despite the important impacts of agriculture intensification on earthworm biomass and diversity, no invasion of the community by exotic species was observed. The

maintenance of assemblages exclusively composed of autochthonous species has been observed in other tropical areas, while in other regions the conversion of native vegetation into agroecosystems leads to a partial or complete replacement of the native soil fauna by a few exotic species (Fragoso et al., 1997). Research is now necessary to accurately identify the processes implicated in the depletion or maintenance of native species and the proliferation of exotic ones.

Conclusions

The maintenance of species under high perturbation rates seems to be driven by (i) their mobility potential (e.g. *M. carimaguensis*), and (ii) their adaptive strategies which determines their potential of population growth (e.g. Ocnerodrilidae). According to these two attributes, species will respond in different ways to agricultural intensification, and be able or not to support high rates of perturbations in the more intensive systems. Hence, two management options should be developed according to one of these two results. First, the spatial arrangement of contrasting agroecosystems should facilitate the recolonisation of cropped soils through surface displacements of earthworm populations from 'source' plots such as savanna or pastures to 'sink' ones. Alternatively, the most aggressive land management practices should be either reduced, avoided or used sparingly, and the ecological attributes of earthworm species should be considered in order to allow population maintenance.

In conclusion and within the context of the Orinoco savannas, an hypothetical conservative agricultural production system for soil fauna should integrate: (i) native vegetation plots that may be used as extensive pastures and should represent a reserve of biodiversity; (ii) permanent pastures that constitute protein banks for livestock production systems (as proposed by Rippstein et al., 1996) and that allow the establishment of important earthworm biomass; (c) agro-pastoral systems, i.e. annual crops, which should be managed in rotation with temporary pastures and should be located contiguously to permanent pastures to maximise migration of populations.

Acknowledgements

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Appendix . Calculation of the Index of Agricultural Intensification (AI) for each agroecosystem. Codes for systems are given in Table 1. LUI = mean land use intensity; FF = mean fire frequency; TF = mean tillage frequency; MPF = mean motorised practice frequency; SR = mean annual stocking rate; FR = mean fertilisation rate; PCR = mean pest control rate. Italic codes correspond to the value after bringing them back to 1 (see text for more details)

Systems	LUI		FF		TF		MPF		SR		FR		PCR		Index
	% of y	LUI	y^{-1}	FF	y^{-1}	TF	y^{-1}	ML	IAU ha^{-1}	SR	kg y^{-1}	FR	kg y^{-1}	PCR	of AI
NS	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0	0.00	0.00	0.00	**0.14**
Bd	0.07	0.10	0.00	0.00	0.13	0.04	0.27	0.02	1.75	0.88	61	0.09	0.5	0.43	**0.22**
Bh	0.08	0.12	0.25	0.25	0.25	0.08	1.50	0.11	2.00	1.00	86	0.12	0.00	0.00	**0.24**
Pm	0.11	0.17	0.33	0.33	0.33	0.11	2.33	0.17	2.00	1.00	185	0.26	0.00	0.00	**0.29**
RM	0.33	0.49	0.25	0.25	2.00	0.67	8.75	0.64	0.00	0.00	325	0.46	0.88	0.75	**0.47**
MM	0.33	0.49	0.33	0.33	2.00	0.67	9.00	0.66	0.00	0.00	555	0.78	1.17	1.00	**0.56**
R/GM	0.67	1.00	0.25	0.25	2.00	0.67	13.75	1.00	0.00	0.00	418	0.59	0.88	0.75	**0.61**
R/C	0.67	1.00	0.25	0.25	3.00	1.00	12.75	0.93	0.00	0.00	418	0.59	0.88	0.75	**0.65**
M/GM	0.67	1.00	0.33	0.33	3.00	1.00	13.00	0.95	0.00	0.00	708	1.00	1.17	1.00	**0.75**
F	0.33	0.49	0.00	0.00	0.33	0.11	2.33	0.17	0.00	0.00	325	0.46	0.88	0.75	**0.28**