Enregistrement scientifique: 1977
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Seedlings and invertebrates in the casts of an anecic earthworm from Colombian savannas (Glossoscolecidae, Oligochaeta)
Plantules et invertébrés dans les turricules d'un ver de terre anécique des savanes colombiennes (Glossoscolecidae, Oligochaeta)

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Large soil invertebrates, the ecosystem engineers, are able to dig the soil, produce organo-mineral structures and biopores, and hence influence the abundance and diversity of other soil organisms. This study aimed to assess changes in communities of macroinvertebrates and plant seeds that are induced by casting activity of the large anecic worm *Martiodrilus carimaguensis* Jiménez and Moreno. Experiments were carried out in natural savanna and introduced pasture of the Eastern Plains of Colombia. Macroinvertebrates and seeds were sampled in both surface casts and soil, using hand sorting and laboratory germination respectively.

Results revealed important effects of earthworms on seed and macroinvertebrate communities:

(1) The number of germinable seeds excreted each year in surface casts was important. Seedling richness and diversity were different in soil and casts. In the savanna, the composition of the seedlings emerging from casts was closer to the vegetation than the one of the seedlings emerging from soil.

(2) The presence of surface casts positively affected macrofaunal density, richness and diversity, and modified the relative dominance of each ecological categories.

These results are largely attributed to the modulation by earthworms of resource availability through: (i) concentration of organic matter and nutrients for humivorous invertebrates and seedlings, (ii) creation of suitable microhabitats for epigeic arthropods species, and (iii) proximity of the soil surface for viable seeds transported from deeper soil strata. The ecological significance of such processes is discussed.

Keywords: anecic earthworm, casts, soil biodiversity, ecosystem engineers, soil macrofauna, seed banks, land management, savanna, Colombia
Mots clés : ver de terre, turricules, biodiversité du sol, ingénieurs des écosystèmes, macrofaune du sol, banques de graines, gestion des sols, savanes, Colombie

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The distribution and abundance of species living in soil is largely determined by their. These interactions are not restricted to inter-specific competition for abiotic and biotic resources, predation, parasitism or mutualism (Jones et al., 1994). In fact, some functional key species, the physical ecosystem engineers (*sensu* Jones et al., 1994; Lavelle, 1997), are able to modulate resource availability for other organisms and thereby influence the abundance and diversity of their communities. In the soil, these species are generally large (earthworms) or social invertebrates (termites and ants) that produce physical "biogenic" structures (e.g. galleries, chambers, casts, mounds, nests), thus influencing soil properties and life conditions for other smaller and less mobile soil organisms (Hypothesis of Nested Biodiversities, Lavelle, 1996).

Earthworm effects on soil microflora have been largely investigated (Brown, 1995), and have been refered to as the "Sleeping Beauty Paradox" (Lavelle 1996). Studies also commonly refer to the positive or negative effects of earthworms on micro- and mesoinvertebrates communities (Brown, 1995; Loranger et al., 1997). Conversely, only a few isolated studies deal with the impacts of earthworm activities on macrofaunal communities (Kirk, 1981; Szlavecz, 1985; Thompson et al., 1993). An other little known aspect of earthworm impact on soil biodiversity is the influence they have on the soil seed banks (Thompson et al. 1994, Willems and Huijsmans 1994).

As different invertebrate or plant species will have different impacts and therefore different functions in the soil (Lavelle, 1996), it is now important to reach a good comprehension of the role of biodiversity in soils, and of the condition for its maintenance. For this purpose, it is essential to (i) clearly identify the links existing among species and (ii) test to which extent the presence of a given species may influence the presence of others.

The aim of this study was to evaluate the effects of the large anecic earthworm *Martiodrilus carimaguensis* Jiménez and Moreno (Oligochaeta: Glossoscolecidae) on the soil biodiversity of a natural savanna and an associated pasture of the eastern plains of Colombia. Special attention was paid to the impact of the big surface casts produced by this species on the diversity and abundance of soil macrofaunal communities and soil seed banks.

Study site

The study was carried out at the CIAT-CORPOICA research station of Carimagua (4°37' N, 71°19W). The climate is subhumid tropical (annual mean temperature and rainfall of 26°C and 1300 mm respectively). Soils (Oxisols and Ulisols) are characterised by favourable physical properties, high acidity and very low chemical fertility (CIAT data).

Material and Methods

Experimental plots

Soil macrofauna was sampled in two different treatments on a well drained upland Oxisol: (1) a recently burned native savanna, protected from grazing for four years and managed traditionally by burning each year during the dry season, and (2) a 3 year-old associated *Brachiaria humidicola*-legume pasture grazed by cattle (2.0 animal units. ha^{-1} on average).

Seed banks and aboveground vegetation

In each experimental plot, 20 soil cores (8 cm diameter, 6 cm deep) and 300 fresh casts were taken randomly. Soil and casts were put on to a layer of sand in germination trays and displayed in a greenhouse, kept moist and exposed to natural light and temperature. Once a week, seedlings were identified at the species level and removed. After three months, casts were broken in small fragments (< 5 mm of diameter) before being placed in the trays to continue the evaluation.

Above ground vegetation composition was determined in each plot by three transects (100 punctual records).

Soil Macrofauna

In each treatment, a total of 88 samples were randomly taken during one year. Each sample consisted of: (i) the cast, (ii) the underlying soil, and (iii) the control soil, located 20 cm apart from the cast. Samples were taken using a 10 cm diameter and 10 cm deep cylinder, and were hand-sorted in a plastic tray. Macroinvertebrates were killed and kept in 70% alcohol.

Invertebrates were separated according to morphotype, *viz.* morphologically distinct taxa. Then, density and biomass were calculated for three ecological categories (*i.e.* endogeic, anecic and epigeic) (Lavelle, 1979).

Data processing

Sorensen's index of similarity (*Cs*) was used to compare the composition of soil seed banks, cast seed banks and above ground vegetation within and between each experimental plot (Sorensen 1948). Species richness (*R*) was defined as the total number of species or morphotypes found in one situation (*i.e.* treatment, sample location). Diversity (*H*) and evenness (*H'*) were calculated using the Shannon index of diversity (Pielou 1966).

Results

Earthworm effects on soil seed banks

Seedlings were observed on casts of both treatments. The mean number of seedlings contained in casts and soil, and the number of seeds able to germinate excreted in surface casts is presented in Fig. 1. Only 41% of the seeds were able to emerge on intact casts, the remaining (i.e. the part contained in the deeper cast layers) needed cast destruction to germinate.

The taxonomic richness and diversity of soil seedlings were higher in the pasture than in the savanna, while those of casts seedlings were similar in the two treatments (Table 1). Seedling diversity and richness were highest in casts than in soil for both treatments.

In the pasture, similarity indices revealed an important difference between species composition of the vegetation and both the soil and cast seedlings (Fig. 2). In the native savanna, this disparity was observed with soil seeds, but the species composition of cast seedlings was closer to that of the standing vegetation.

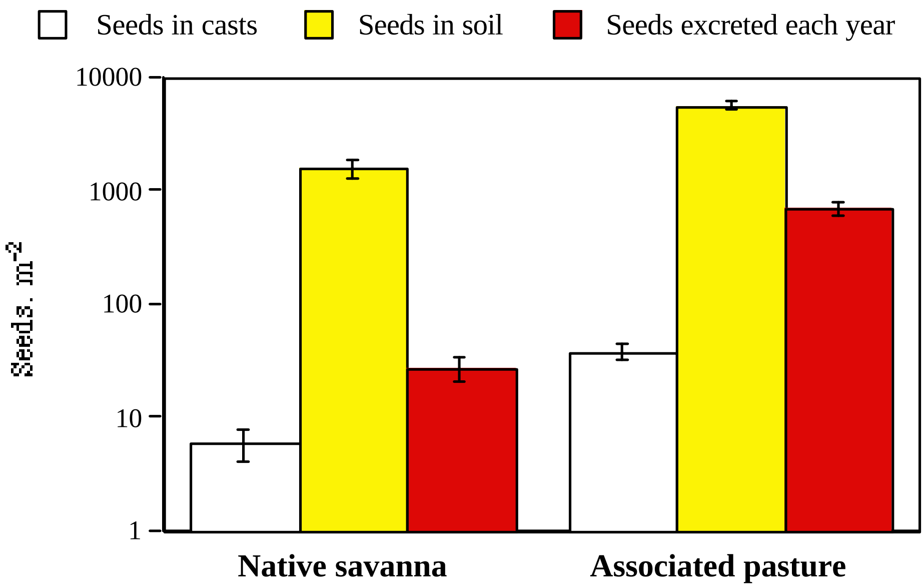

Figure 1. Seeds in soil and earthworm casts.

	Native savanna		Associated pasture	
	Casts	Soil	Casts	Soil
Richness (R)	21	9	22	18
Diversity (H)	2.78	1.83	3.33	2.99
Evenness (H')	0.63	0.58	0.75	0.72

Table 1. Richness, diversity and evenness of seeds in soil and earthworm casts

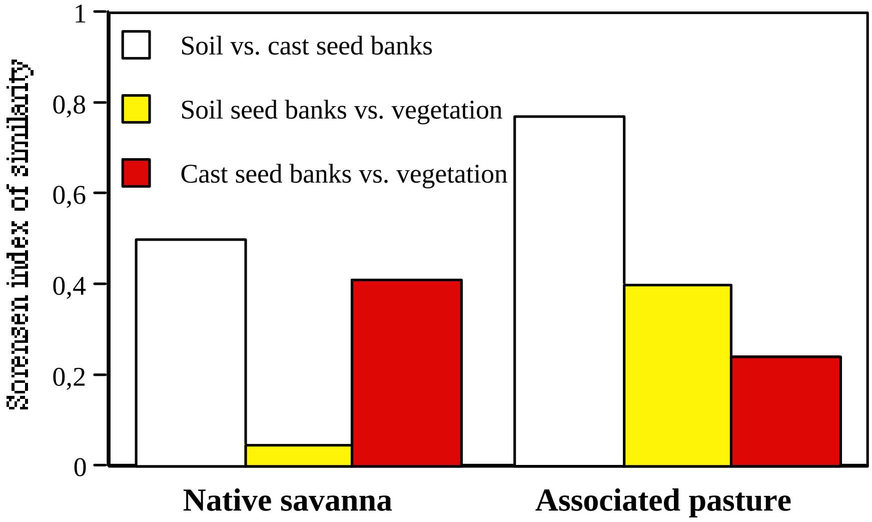

Figure 2. Similarity between species composition of the cast seed banks, the soil seed banks and the standing vegetation.

Macrofauna

The density of invertebrates found inside casts was insignificant when compared with those found in soil (Fig. 3). In the two treatments, the overall macrofaunal density was significantly higher bellow casts than in the test soil, while the overall biomass was unchanged.

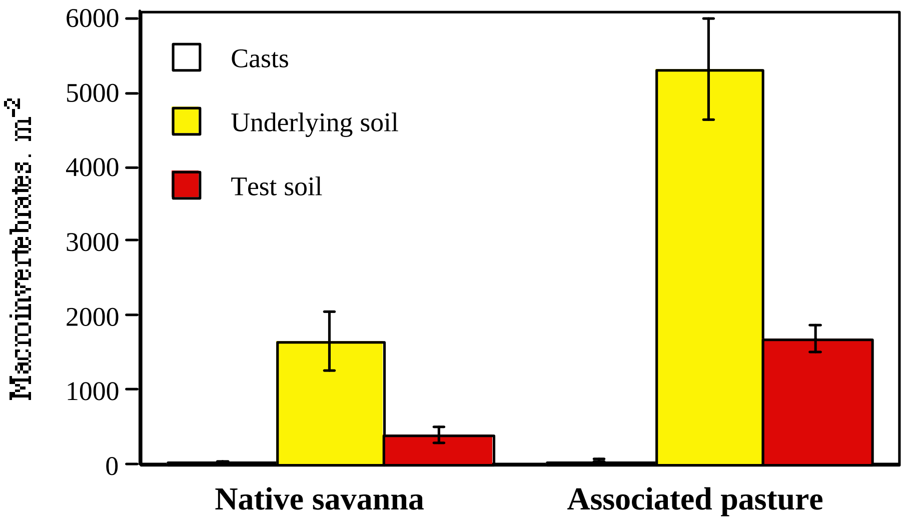

Figure 3. Macrofaunal density in the casts, the underlying soil and the test soil.

The contribution to density and biomass of the three ecological categories was dramatically affected by surface casting earthworm activity (Fig. 4). The contributions to density and biomass of epigeic and anecic species were higher when communities were located inside or bellow casts than in the test soil. Inversely, endogeic community was depressed by the presence of surface casts of *M. carimaguensis*.

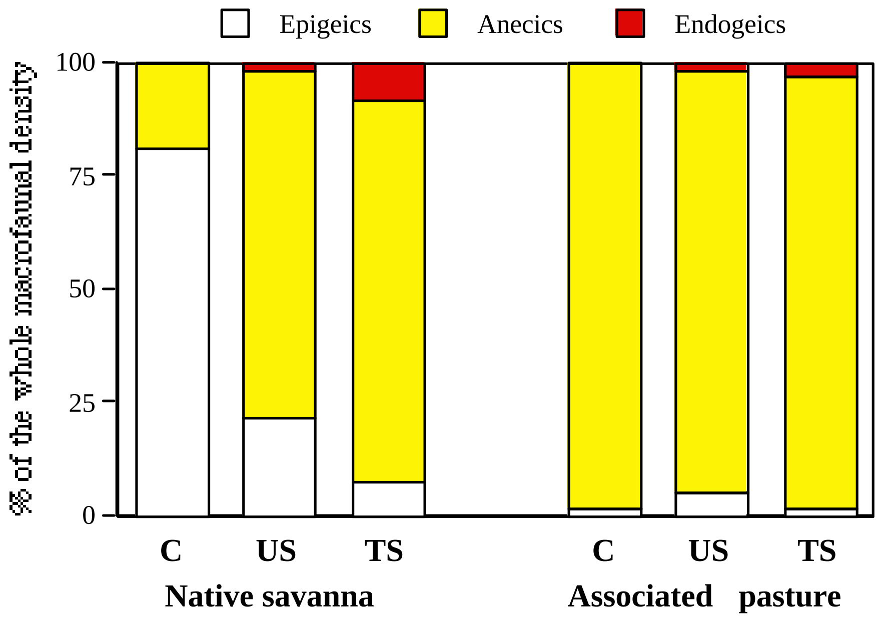

Figure 4. Contributaion of each ecological categories to the overall macrofauna density in the casts (C), the underlying soil (US) and the control soil (TS).

Taxonomic richness was lower in casts than in soil. In the soil, it was higher bellow than beside casts (Table. 2). Diversity and evenness were higher in casts in the pasture, while they were inversely higher in the control soil than in casts in the savanna.

	Native savanna			Associated pasture		
	Casts	U soil	T soil	Casts	U soil	T soil
Richness (R)	12	38	31	17	53	39
Diversity (H)	1.43	2.75	3.20	2.57	1.95	2.09
Evenness (H')	0.40	0.53	0.65	0.63	0.34	0.40

Table 2. Richness, diversity and evenness of macrofauna in the casts, the underlying (U) soil and the test (T) soil.

Discussion

Large earthworm species may have determinant effects on the abundance and diversity of other communities. This is largely due to the production of physical structures (casts and burrows) that efficiently modulate resource for other species. Epigeic macroinvertebrates, for example, take advantage of the creation of new specific microhabitats (e.g. galleries and under-casts cracks). On the other hand, humivorous species benefit from the high organic matter content of casts or the accumulation of fresh litter in the galleries. Finally, viable seeds found suitable conditions to germinate (e.g. high nutrient content, increased light intensity, temperature fluctuations) when excreted in casts at the soil surface.

Influence of earthworm casting activity on soil organisms is operated in a specific way. For example, epigeic and anecic macrofaunal species take more advantages than endogeics of the creation of surface living spaces and the concentration of aboveground organic resource. Enhanced conditions for germination in casts increased evenness and promoted the germination of exigent species that are probably unable to germinate in soil with high chemical constraints (e.g. savanna soil). This may explain the important difference observed in the savanna between the composition of seedlings in casts and in soil.

In the light of the present results, earthworm engineering activities seem to have mostly positive effects on the diversity of the organisms they control. In general, both soil macrofaunal communities and viable seed banks had a higher taxonomic richness and diversity in casts and/or in soil influenced by casts than a soil without casts. In some situations, however, casting activity may have a contrary effect, whether some species will respond negatively to changes or will not respond and then will face competition with favoured species. As an example, earthworm casts were colonised by only a few species, because not all macrofauna is able to live in such structures. Surface casting activity in the savanna also led to a decrease in macrofaunal diversity. This can be explained by the dominance of a few highly specialised species able to withstand adverse post-fire conditions occurring near soil surface.

Impacts of ecosystem engineers on other organisms largely depend on the formation rate of the physical structures they produce, and on the durability of these structures (Jones et al., 1997). Populations of *M. carimaguensis* may produce considerable amounts of surface casts (from 1 to 12 tons. year^{-1}. ha^{-1} respectively in the savanna and the pasture). These may persist at the soil surface for periods of months to years (Jiménez et al., 1997; Decaëns, unpublished data). In the savanna protected from fire, casts may remain at the soil surface for a long time and form a pool of seeds potentially able to germinate. Burning of the vegetation destroys a large part of these casts, thus dispersing the seeds on the surrounding soil. Suitable conditions that occur at this moment (bare ground, higher light intensity, available nutrients in ashes) will enhance germination and increase chances for seedlings to participate in the standing vegetation. As fire also leads to the destruction of natural protection for surface living invertebrates by plant cover, the part of casts which has not been destroyed may form a suitable refuge habitat for epigeic fauna.

The range of earthworm control on biodiversity and/or biological activity may be considerable. Even if the number of seeds present in surface casts is negligible in comparison with that of soil seeds, the vertical transfers induced by casting activity are considerable: from 3 and 14% of the overall seeds able to germinate are excreted each year at the soil surface, respectively in the savanna and the pasture. Macrofaunal populations are locally increased from 3 to 4 times in the presence of casts. Additionally, these results only consider surface effects of casting activity, but earthworm activity is not restricted to the topsoil, and underground structures are likely to have other effects on other groups of organisms.

The present study supports and specifies the hypothesis of nested biodiversity formulated by Lavelle (1996), according to which (i) the diversity of plant community determines the diversity of soil fauna and (ii) soil ecosystem engineers determine the structure of smaller organisms communities. Effects of anecic earthworms on other macroinvertebrate groups confirm the second point of Lavelle's hypothesis. On the other hand, impacts on soil seed banks demonstrate that soil ecosystem engineers may operate an indirect feedback on vegetation structure via the germinating conditions that they influence in their biogenic structures.

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