

Review

Earthworm Populations in Savannas of the Orinoco Basin. A Review of Studies in Long-Term Agricultural-Managed and Protected Ecosystems

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Abstract: Earthworm biomass and production in savannas are limited by seasonal precipitation and the lack of organic and nutrient resources; I hypothesize that after a long-term protection of savanna from fire and agricultural activities drastic changes in the physical and chemical characteristics of the soil occur with a concomitant increase in earthworm abundance and activities. Similar changes might occur after a long-term fertilization of savannas with manure. This review article considers the earthworm communities and other soil quality indices in *Trachypogon* savannas of the Orinoco Basin in an organic agricultural forestal savanna (OAFS) amended with compost over forty years in Puerto Ayacucho, Venezuela, and in an Experimental Station long-term protected (PS) from fire and cattle raising from more than four decades in Central Llanos, Venezuela, comparison is made with results from similar savannas. Long-term additions of organic manure or a long protection have induced significant changes in the soil physical and chemical properties of the natural savanna (NS) soils that induce a significant increase in the density and biomass of earthworm populations. On the other hand, the protection of the savanna promotes an improvement in the physical and chemical properties of the soil, which favors an increase in the density and biomass of earthworms in the PS compared with the NS subjected to recurrent burning and grazing. The results emphasize the importance of appropriate organic matter management and the relevance of earthworms in such agroecosystems.

Keywords: protected savanna; organic farms; soil quality; microbial biomass; enzymatic activities; Amazonia; pedofauna

1. Introduction

A very important extension of savannas in the north of South America (Llanos of Colombia and Venezuela) are located in dystrophic and well drained soils dominated by grasses such as *Trachypogon plumosus* Ness., *Andropogon* sp., and *Axonopus* sp., locally known as *Trachypogon* savannas [1]. Those savannas have been considered as one of the less productive terrestrial ecosystems since they are, in general, present on nutrient depleted soils affected by seasonal precipitations [2,3].

Although, the information regarding pedofauna communities from tropical savannas is very scarce, we know that their earthworm biomass and production are limited by the seasonal precipitation and the lack of organic and nutrient resources [4–6].

Despite their predominance on nutrient poor soils, savannas are key production areas in Venezuela, Colombia and Brazil, where agricultural activities have been established and represent a substantial income for their economies. For this reason, much research with emphasis in nutritional aspects has been done to characterize their ecological features and to assess the impact of different land uses [7,8].

A management tool strongly associated with natural savannas is the regular burning of vegetation. Fire is used to manage rangeland and protected areas maintaining a savanna environment by preventing bush encroachment and selecting for fire tolerant species. Those fire managed savannas are used for extensive cattle raising (0.1–0.2 animal unit/ha). When fire is suppressed, vegetation develops from open savannas to densely wooded ecosystems (Cerrado type), at least, in the most humid savannas [9–11]. Apart from tree densification, fire suppression induces, in turn, an increase in total soil carbon, nitrogen and available nutrients. Changes in soil fauna populations, soil enzymatic activities and microbial biomass also occur as soon as a savanna sector is protected from fire [7,12,13].

In savanna ecosystems termites and earthworms appear as the most conspicuous components of soil macrofauna. Earthworms in both temperate and tropical ecosystems, play a dominant role on the decomposition processes of organic matter inducing changes in the physicochemical and biological properties of the soil due to the construction of galleries and the excretion of mucus and casts (in a broad sense those components of soil affected by earthworm activities are known as drilosphere). There is a lack of information concerning the species composition and structure of earthworm communities in tropical savannas; until recently, studies were mainly referred in India and Ivory Coast [14,15].

Since earthworm biomass and production in savannas are limited by seasonal precipitation and the lack of organic and nutrient resources, it must be hypothesized that after a long-term protection of savanna from fire and agricultural activities a drastic change in the physical and chemical characteristics of the soil occur with a concomitant increase in biological activity, particularly in earthworm abundance and activities. Similar changes might occur after a long-term fertilization of natural savannas with organic manure.

This review article considers information on earthworm communities and other soil quality indices in *Trachypogon* savannas of the Orinoco Basin in an organic agricultural forestal savanna (OAFS)

amended with organic fertilizer (compost) over forty years located around the city of Puerto Ayacucho, Venezuela, and in an Experimental Station long-term protected (PS) from fire and cattle raising from more than four decades in Central Llanos, Venezuela, a comparison is made with results from similar savannas, particularly with the earthworm populations of Eastern Llanos in Carimagua, Colombia.

2. General Characteristics of the Studied Savannas

2.1. Soils of *Trachypogon* Savannas

Trachypogon savannas are generally associated to acid soils with high P fixation capacity and consequently low P availability, low organic matter, nitrogen and exchangeable base contents (Σ exchangeable bases < 5 cmol kg⁻¹ soil), but high aluminum saturation due to its acidity (Table 1). The dystrophic nature of soils is a consequence of parent materials with low nutrient contents and/or pedogenetic processes which favors the progressive loss of nutrients. Strong weathering associated to high temperature and also relatively high seasonally precipitation also results in the accumulation of resistant primary minerals (e.g., quartz), sesquioxides and clays with low exchange activities [16].

Table 1. Soil chemical characteristics of chosen *Trachypogon* savannas from Colombia and Venezuela. Adapted from López-Hernández and Hernández-Valencia [16].

Location	pH	Available P (mg P kg ⁻¹ soil)	Total N (mg N kg ⁻¹ soil)	Total C (mg C kg ⁻¹ soil)	Σ Exchangeable bases (cmol kg ⁻¹ soil)	Exchangeable aluminum (cmol kg ⁻¹ soil)
Calabozo	5.8	2.9	503	8,000	0.34	0.80
Puerto Ayacucho	5.5	4.8	393	6,000	1.17	-
Uverito	4.5	0.9	227	3,000	0.44	0.40
La Iguana	5.2	4.0	320	7,000	1.06	0.90
Cabruta	5.6	2.0	40	1,000	0.30	0.30
Carimagua- Colombia	4.8	6.2	1450	23,000	0.45	2.42

On the other hand, soil water regime is seasonal with periods of excessive wet and eventually anaerobic conditions, alternated with periods where the soil becomes dry and below the permanent wilting point. In those areas where groundwater fluctuation or impeded surface water drainage occurs, it is possible to find a lateritic layer or concretions which evidence the accumulation of sesquioxides due to the redox environment [16]. According to the Soil Taxonomy classification system proposed by United States Department of Agriculture [17], the soils of *Trachypogon* savannas are identified mainly as oxisols, ultisols and entisols or arenosols, ferralsols, lixisols and plinthosols in the World Reference Base for Soil Resource.

2.2. Vegetation of *Trachypogon* Savannas

The *Trachypogon* savannas are dominated by grass species of the genus *Trachypogon*, particularly *Trachypogon plumosus* and *T. vestitus*. *Trachypogon* spp. is a genus well characterized by its low

productivity, digestibility and palatability values and adaptation to acid, nutrient-depleted soils, especially in nitrogen and phosphorus [18,19].

In *Trachypogon* savannas other associated species are the grasses *Axonopus canescens*, *A. anceps*, *Andropogon selloanus*, *Leptocoryphium lanatum*, *Paspalum carinatum*, *Sporobolus indicus*, *S. cubensis* and *Aristida* sp.; legumes of the genera *Mimosa*, *Cassia*, *Desmodium*, *Eriosema*, *Galactia*, *Indigofera*, *Phaseolus*, *Stylosanthes* and others, and sedges of the genera *Rhynchospora* and *Bulbostylis* [16]. Tree presence varies from absent in open savannas to dense in savanna parklands where crowns are closer, but with minimal overlapping. Trees can also be found scattered or in groups locally called “matas”. In *Trachypogon* savannas pyrophytes species are abundant such as *Byrsonima crassifolia*, *Curatella americana* and *Bodwichia virgilioides* and in a lesser proportion *Copaifera officinalis*, *Casearia silvestris*, *Genipa americana* and *Cochlospermum vitifolium*; however, in all those cases the herbaceous layer plays an important role defining structural and functional attributes of this plant community [16].

2.3. Agriculture Use in *Trachypogon* Savannas

In the last four decades, the natural herbaceous vegetation with low nutrient requirements in the well drained savannas (Llanos) of Colombia and Venezuela, as well as in the Cerrado (Brazil) has been partially replaced by introduced African pastures, particularly from the genera *Brachiaria* and *Andropogon* [7,8]. The introduction of african pastures and annual and perennial crops has been possible with important doses of fertilization (N, P, K and lime) and pesticide control. Chemical inputs have had important effects on the native populations of earthworms. In pasture managed agroecosystems earthworm biomass and density may have increased due to the increment in belowground biomass, although the population diversity may have decreased [4,5].

2.4. Role of Macrofauna in Savannas

The soil-plant interface in tropical savannas provides micro-environmental conditions ideal for the development of a prolific biological activity, particularly of invertebrates [20]. Within these communities, the macrofauna (the animals greater than or equal to 2 mm in size) has the most striking effects on the biological and physical-chemical properties of soils [21].

The effects of earthworms on soil properties differ markedly on the ecological categories of the species, e.g., epigeic, anecic or endogeic species [22]. Earthworms are not very diverse and the situation does not differ in well drained neotropical savannas where few reports are available.

In many tropical savanna soil communities' earthworms have a dominant role in shaping the soil environment due to both their abundance and effects of their activities [23]. The beneficial effects of the earthworms include: (i) improvement of soil physical properties which affect soil water retention capacity, drainage, and the formation and degradation of aggregates [24,25]; (ii) chemical and biological effects on the rate of organic matter degradation and nutrient cycling [21,26,27]; and (iii) alteration of the composition and activity of microorganisms and soil invertebrates [28]. All these processes significantly impact the soil fertility primarily through the release of available forms of nitrogen (N) and phosphorus (P) [21,27,29–32] once the soil passes through the gut of the earthworm species.

3. Supporting Case Studies

Methodological aspects concerning earthworm collection and other soil quality indices of the Case Studies of the present revision have been already presented by López-Hernández and collaborators [5,6,12,13,33].

3.1. Earthworm Populations in a Savanna Organic Agroforestral System of the Venezuelan Amazonia

Amazonia represents one-fifth of the Venezuelan territory (approximately 180,000 km²); most of this surface is covered by pristine primary forests where, due to the lack of accessible roads, human activity is of minor importance. An important piece of savanna land, however, extends in the northern and southern part of Puerto Ayacucho, the capital of Amazonas State [33]. Nonetheless, a problem of sustainability derived from the potential use of Puerto Ayacucho's savannas is that they are located on very sandy soils (over 90%) and consequently they are nutrient limited. Therefore, they need to incorporate significant rates of fertilizers to maintain yields. Moreover, in addition to their high cost, fertilizer and other agricultural items need to be imported from distant regions [34].

Organic amendments appear to be one alternative to achieve sustainable agriculture in those savannas. Therefore, despite the limitations of soil fertility and of the distribution of the water regime, in the forest-savanna ecotone around Puerto Ayacucho some producers have established, for more than 40 years, small (2–5 ha) organic agroforestry systems of production (OAFS) on sandy savanna soils by adding animal manure and/or compost as the main fertilizer inputs. As a result of the long-term organic fertilization regime, the natural savanna (NS) has been replaced by agro-forestral systems composed mainly of fruit-trees combined spatially or temporarily with agricultural crops. The amount of organic amendments used is low (around 1–2 Mg ha⁻¹) and locally disposed; in other words, the fertilizer is not widely spread but deposited in the places where trees are to be planted. The hand labor for that operation is the familiar group; therefore, little by little they have conquered the savanna ecosystem by amending new patches of savanna land. Under organic fertilization, the soil has changed in its physical and chemical qualities [35], with an associated increase in biological activities in the OAFS as compared with the natural savanna. At the end, and after long-term organic fertilization, the savanna ecosystems are replaced by agro-forestral systems.

This part of the contribution examines the effect of long-term organic (compost) fertilization on soil properties and earthworm communities in an organic agroforestry system (OAFS) established in a sandy soil located near the city of Puerto Ayacucho, Amazonas State, Venezuela.

3.1.1. Changes in Earthworm Composition, Density and Biomass

The majority of the identified individuals in OAFS belonged to Glossoscolecidae family. Three different earthworm genera were distinguished in this system (Figure 1). Individuals of the *Onychochaeta* were predominant, with a small proportion of individuals of the *Goiascolex* and *Pontoscolex*; whereas earthworm populations in the NS included individuals from the Glossoscolecidae and Megascolecidae families. The corresponding genera of the individuals found in NS could not be identified due to their immaturity [5,6].

The average earthworm density for the OAFS on the top (0–10 cm) was of 145.6 ind m⁻² (Table 2) while the estimated average biomass was 17.46 g m⁻². In the control savanna (NS) the average earthworm density and biomass on one sampling was 30.40 ind m⁻² and 0.65 g m⁻² for earthworm density and biomass, respectively. In general, it was found 1.6–4.9 times more earthworms in the OAFS than in the original savanna. Results from Table 2 clearly indicate that OAFS has a considerable higher average in earthworm density and biomass than NS, which suggests that the trophic as well as the spatial conditions in the OAFS are more favourable for earthworm populations.

Figure 1. Relative abundance of the earthworm species in the OAFS. Modified from Araujo and López-Hernández [6].

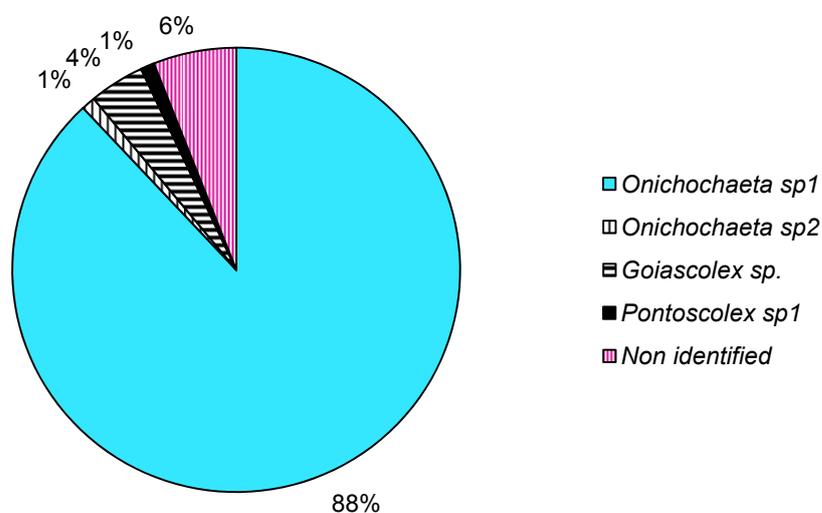


Table 2. Earthworm density (N/m²) and biomass (g/m²) at different depths in the organic agricultural forestry system (OAFS), in a protected savanna (PS) and the corresponding adjacent natural savannas (NSA, Amazonas State and NSC, Calabozo, Biological Station). Modified from Araujo and López-Hernández [6] and Hernandez *et al.* [13].

Parameter	Locality	Depth (cm)			
		0–10	10–20	20–30	0–30
Density	OAFS	145.6	8.0	1.6	155.2
	NSA	30.4	4.8	-	35.2
Biomass	OAFS	17.46	1.17	0.23	18.6
	NSA	0.65	0.44	-	1.09
Density	PS	38.4	25.6	0.0	64.0
	NSC	9.6	9.6	3.2	22.4
Biomass	PS	14.8	8.1	0.0	32.9
	NSC	2.6	1.1	1.4	5.1

Organic manure on the OAFS soil has provided appropriate food-resources for pedofauna. Since organic matter is the principal factor that determines the abundance of earthworms in agricultural soils [36], in agroecosystems, earthworms are intimately involved in the incorporation and

decomposition of plant residues and organic amendments [37]. Organic debris which is decomposed by microorganisms is the main resource commonly ingested by earthworms [38].

3.1.2. Vertical Distribution

The stratification of earthworms with depth in Puerto Ayacucho, Amazonas State, Venezuela showed a similar pattern in both localities. Table 2 shows that the majority of individuals were found in the first 10 cm of soil, thereafter, the earthworm numbers and biomass (Table 2) decreased with depth. They were almost entirely absent at 30 cm depth, and the notable difference between the top (0–10) and lower strata (10–20 and 20–30 cm) was no doubt due to the higher resource availability (organic matter, O₂ and water content) at the soil surface. Soils in organic agricultural systems present a great spatial heterogeneity, particularly due to the superficial application and non-even distribution of the manure. Consequently, in these agroecosystems earthworms are located on the superficial soil. In NS, soil conditions are less variable, but very extreme because of adverse microclimatic conditions as well as poor abundance of resources (low available nutrients and scarcity to none litter) which limits earthworms distribution to the first 10 cm of soil [6,39,40]. Furthermore, the sandy NS soils studied here are rapidly drained which favours desiccation and potential leaching of the nutrients that could be available to plants and, in turn to soil fauna. All those restrictions makes difficult the establishment and maintenance of soil organism populations, consequently earthworms in the sandy savannas near Puerto Ayacucho, Amazonas State are found aggregated in micro-sites around roots of grasses and small trees, where temperature, humidity and fertility conditions are much better than in the bare savanna [6,40,41].

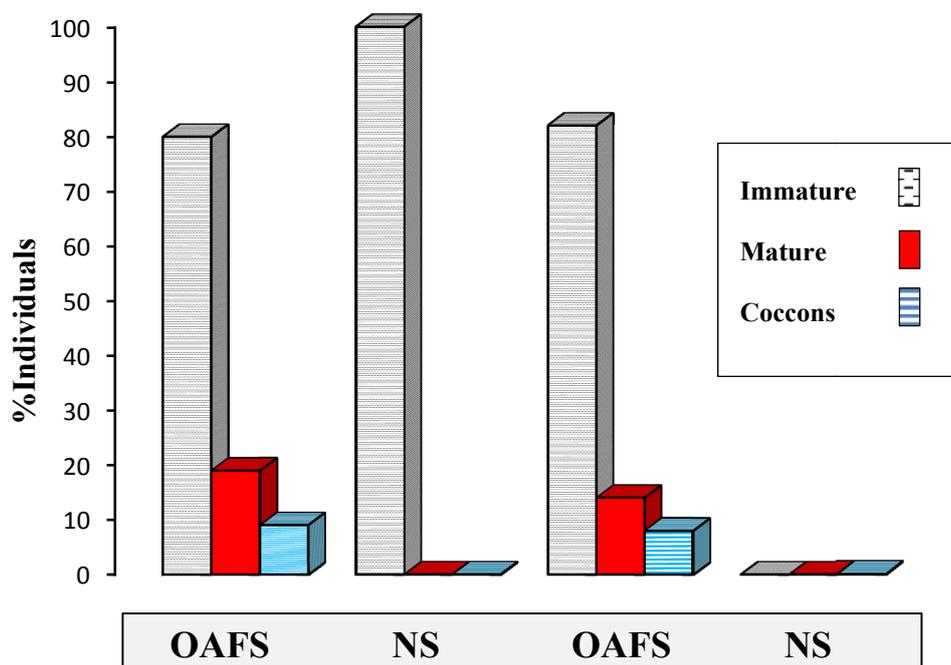
3.1.3. Horizontal Distribution

Variance/mean ratios were used to evaluate the horizontal distribution of the earthworm populations found in the two systems [42]. The results showed that the earthworm communities had an aggregated dispersion in space, since the ratios obtained were 11, particularly in the case of the members of the Glossoscolecidae located in the OAFS. The aggregated distribution pattern of earthworm populations in the studied ecosystems reflected variations in environmental factors in certain zones of the study area. In addition, the pattern reflected the low dispersion index of the collected species.

3.1.4. Age Distribution

Three age classes: Cocoon, immature and mature individuals were estimated. Figure 2 compares the frequency of individuals according to the age classes that were found in the NS and OAFS per year of sampling. In OAFS the age distribution pattern was similar in both years of sampling. Moreover, the highest numbers of individuals collected were immature (81.4% and 84.4% of the population in 1994 and 1995). A small proportion of cocoons, representing 9.3% in 1994 and 16% in 1995, with respect to the total number of collected individuals, were found. However, a certain underestimation of the number of cocoons may have occurred because of their small size and the sampling method used. In NS (1994) the age distribution was restricted to immature individuals, since cocoons were not found; it seems also likely that, at the moment of sampling, there was no deposition of eggs in this area.

Figure 2. Age distribution of earthworms in the agroforestral system (OAFS) and the natural savanna (NS). Modified from Araujo and López-Hernández [6].



Results of the age distribution indicated a pyramidal age structure similar to that presented by Dash and Patra [14], and Edwards and Bohlen [36]. These authors emphasized that most soil invertebrate populations tend to have a pyramidal age structure during most of the year, where immature individuals predominate over mature individuals. However, the proportions are not fixed and they depend upon the sampling time. Earthworms in seasonal savannas may show a high reproductive capacity, allowing the population to generate and maintain a proportion of immature individuals that guarantees the persistence of the population [36,43].

3.1.5. Changes in Soil Quality Indices Induced by Organic Fertilization

The use of a single biochemical property to estimate soil quality is a common approach, particularly when the concept of quality refers to the productive capacity. Researchers have used a general biochemical parameter such: microbial biomass, dehydrogenase activity, nitrogen mineralization or a specific parameter as phosphatase or urease activities [35]. In this part of the contribution we analyzed pedofauna abundance in association with microbial and enzymatic activities.

The addition of organic fertilizer increased the level of microbial-C, that increment matched the change in total C (Table 3). The information is partially reflected in the microbial quotients (Microbial biomass C/Organic C), where a slightly higher value was found in the case of the OAFS (0.92) respect the control (0.75, Table 3). The C and N microbial biomasses in the savanna were particularly low, López-Hernández and Hernández-Valencia [16] have emphasized that in the soils of the Orinoco savannas, in general, the contents of soil carbon biomass (C-MB) are low (about 100 mg kg^{-1}), which is in correspondence with the low soil organic matter content of the soils. In Venezuelan savannas the nitrogen microbial biomass (N-MB) followed a similar pattern to the C-MB, e.g., low values

associated with the scarce levels of organic matter (Table 3). Values of C-BM presented for Brazilian Cerrado soils are much higher (250–850 mg kg⁻¹) with a peak for microbial activity occurring at the beginning of the rainy season [44].

Table 3. Microbial and enzymatic activities in the organic agricultural forestry system (OAFS) and the natural savanna (NS) in Amazonas State, Venezuela. Modified from López-Hernández [33].

Parameter	NS	OAFS
Total C (%)	0.89 a	1.45 b
Total N (%)	0.03 a	0.12 b
Total P (%)	0.02 a	0.05 b
Microbial C (mgC kg ⁻¹)	54.0 a	106.0 b
Microbial quotient (%)	0.75	0.92
Microbial N (mgN kg ⁻¹)	11.9 a	22.1 b
Microbial C/ Microbial N (%)	4.54	4.80
Microbial P (mgP kg ⁻¹)	4.4 a	33.4 b
Phosphatase Activity (mgP-NP kg ⁻¹ h ⁻¹)	10.7 a	49.6 b
Urease Activity (mg N-NH ₄ kg ⁻¹ h ⁻¹)	9.1 a	12.1 b
N-mineralization(μgg ⁻¹ month ⁻¹)	16.2 a	23.4 b

Different letters indicate significant differences ($P < 0.05$) between ecosystems.

Microbial N-biomass also significantly increased after compost amendment, since both increment were of a similar magnitude the C-microbial biomass/N-microbial biomass was similar in NS and OAFS (Table 3). Within microbial activities (C, N and P) the most important change was registered in the case of the P-MB, in fact, the Po-MB value found in the savanna ecosystem was 4.4 mgP kg⁻¹, a value that is common in P-limited Venezuelan *Trachypogon* savannas, that value increased to 33.4 mg Po kg⁻¹ (Table 3) under organic fertilization.

The results of the enzymatic activities analyzed (Table 3) resembled the data obtained in the case of the microbial biomass, since the organic amendment increased both acid phosphatase and urease activities respect to control soil. Urease activity (Table 3) and N-mineralization (Table 3) increased due to organic fertilization. That information confirms why those parameters of the N-cycle have been widely used in the evaluation of changes in soil quality due to soil management [33,45–47]. Results support the well-known fact, that earthworm densities significantly increase enzymatic activities as well microbial biomass [32,38], although due to the abundance of organic materials in the OAFS it is difficult to separate the effect of earthworm presence from the fertility effects.

3.1.6. Correlations between Density and Biomass of Earthworms and Soil Parameters

Results of Pearson's correlation coefficients (r) for the agroforestral system (Table 4) showed positive, significant correlation ($P \sim 0.05$) between density and biomass of earthworms and moisture ($r = 0.62$ and $r = 0.73$, respectively), organic matter ($r = 0.52$ and $r = 0.63$) and pH ($r = 0.43$ and $r = 0.45$). In addition, some soil parameters were significantly correlated to each other, for example, moisture and organic matter ($r = 0.57$), and pH and organic matter ($r = 0.45$).

Table 4. Pearson's correlation coefficients between density and biomass of earthworms and soil variables in the OAFS (above the diagonal) and NS (below the diagonal). Modified from Araujo and López-Hernández [6].

	Density	Biomass	Humidity	Temp	Sand	Clay	Silt	O. M.	pH
Density	-	0.81 *	0.62 *	-0.16	0.33	-0.36	0.01	0.52 *	0.43 *
Biomass	0.69 *	-	0.73 *	-0.03	0.35	-0.35	-0.04	0.63 *	0.45 *
Humidity	0.65 *	0.21	-	-0.01	0.36 *	-0.47 *	0.12	0.57 *	0.31
Temp	0.64 *	0.21	0.99 *	-	-0.36	0.17	0.31	0.09	-0.03
Sand	0.54 *	0.26	0.71 *	0.68 *	-	-0.79 *	-0.41 *	0.05	-0.01
Clay	-0.41 *	-0.16	-0.63 *	-0.62 *	-0.89 *	-	-0.23	-0.29	-0.03
Silt	-0.48 *	-0.28	-0.48 *	-0.42 *	-0.64 *	0.23	-	0.35	0.07
O.M.	-0.22	-0.06	-0.35	-0.33	0.08	-0.09	-0.01	-	0.45 *
pH	-0.07	-0.11	-0.07	-0.05	0.06	-0.12	0.06	-0.06	-

* $p < 0.05$; Temp = Temperature.

Contrary to the results obtained for the OAFS, the biomass of earthworms in the natural savanna did not show significant correlations with any soil parameter (Table 4), whereas earthworm density showed positive correlations with moisture ($r = 0.65$), temperature ($r = 0.64$) and sand content ($r = 0.54$).

Due to the high number of significant correlations between soil variables, it was hard to identify the factors that were really related to density and biomass of earthworms. Nevertheless, a stepwise regression analysis can be a useful tool in such cases [48]. Based on the r s, a regression analysis was applied. The results of these analyses showed that the most important regressor for density and biomass was soil moisture. In the OAFS, soil moisture accounted for 41% of the variation in earthworm density distribution, and 58% of the variation corresponded to biomass. In the NS, soil moisture represented 42% of the variation in the density distribution of earthworms (Table 5).

Table 5. Multiple regression for all variables studied in the OAFS and NS. Modified from Araujo and López-Hernández [6].

Locality	Dependent variable	Intercept	B	Adjusted R^2
OAFS	Density	-452.71	13.88	0.41
	Biomass	-46.47	1.64	0.58
NS	Density	-10.13	5.44	0.42

Independent variable in all cases is soil moisture.

The correlations among earthworm populations and soil parameters suggested that earthworms in OAFS can be limited by the amount of food (organic matter) present in the soil. The availability of organic matter mainly depends upon factors such as moisture and pH which, in turn, affect the activity of soil microorganisms and macrofauna. Meanwhile, earthworm distribution in the NS is mainly influenced by soil physical parameters, such as texture, temperature and moisture content. According to the regression analysis applied, soil moisture is the principal factor limiting earthworm distribution.

Moisture, in turn, affects other parameters that are important for earthworm distribution. Soil moisture content is not only important in terms of water availability for fauna, but also affects earthworm movement, soil resistance, thermic properties and gas transfer. Moreover, soil strength and

adhesion between particles depends upon water content and water potential, factors which can affect earthworm's ability to penetrate soil. Guerra [49], working on earthworm communities in a secondary forest and a grassland in Brazil, concluded that soil moisture regulated the increase in abundance and the rhythm of vital activities of the species *Chibui bari* and *Rhinodrilus curiosus*. The author asserted that the increase in abundance was not only a result of the higher soil moisture content during the rainy season, but also a result of a rapid decomposition of litter during this season. Similarly, Buckerfield *et al.* [50], working on Australian paddocks, reported that density and biomass of earthworms were significantly positively correlated with an increase in annual rainfall, and inversely correlated with increasing levels of coarse sand. As we have shown, earthworm populations in sandy savannas can be determined by a variety of factors, including edaphic and other environmental parameters. The dynamics are complex and the factor-effects interactive.

3.2. Earthworm Populations in a Long-Term Protected Savanna of Central Venezuela

The Estación Biológica de los Llanos (EBLL), located in Calabozo, Guárico State, has been protected from fire, grazing and cultivation since 1961. However, in recent years, despite management efforts occasional fires have occurred. The extended period of protection has resulted in an increased woody component [9] and improved physical-chemical and biological properties of the soil [12,13] that may, in turn have a strong influence in the establishment in the earthworm communities in this protected savanna. The existing knowledge of the biology and ecology of earthworms in this region is limited. Work in similar savanna ecosystems has suggested that marked climatic seasonality can limit the activity of earthworms to the wet season [4–6,51,52]. The main objectives of this part of the contribution are: (1) to examine the general aspects of the biology and ecology of earthworm populations in a protected savanna (PS) of the EBLL compared to a natural savanna (NS) adjacent to EBLL under frequent burning and grazing; (2) to analyze the effect, that the long period of protection from fire and agricultural activities, has had on generating conditions for the establishment of oligochaeta communities.

3.2.1. Earthworm Composition, Density and Biomass

The improvement of the physical and chemical conditions under protection induces better microclimatic and nutritional conditions for the proliferation of earthworms, which is reflected in a higher density and biomass of earthworms in the PS compared with SN (Table 2). In the case of the PS, the biomass of earthworms registered exceeded the values reported by Decaëns *et al.* [53], Jiménez *et al.* (1998) [4] and Araujo & López-Hernández [5,6] in neotropical savannas, whereas the density of earthworms had a maximum value greater than the results reported by Jiménez *et al.* [4] and Araujo and López-Hernández [6], but lower than the presented by Decaëns *et al.* [53] in a savanna of Carimagua, Colombia. Lavelle [15] and Dash and Patra [14], also registered higher values of density and biomass of earthworms than the values here presented for tropical savannas in Ivory Coast and India, respectively.

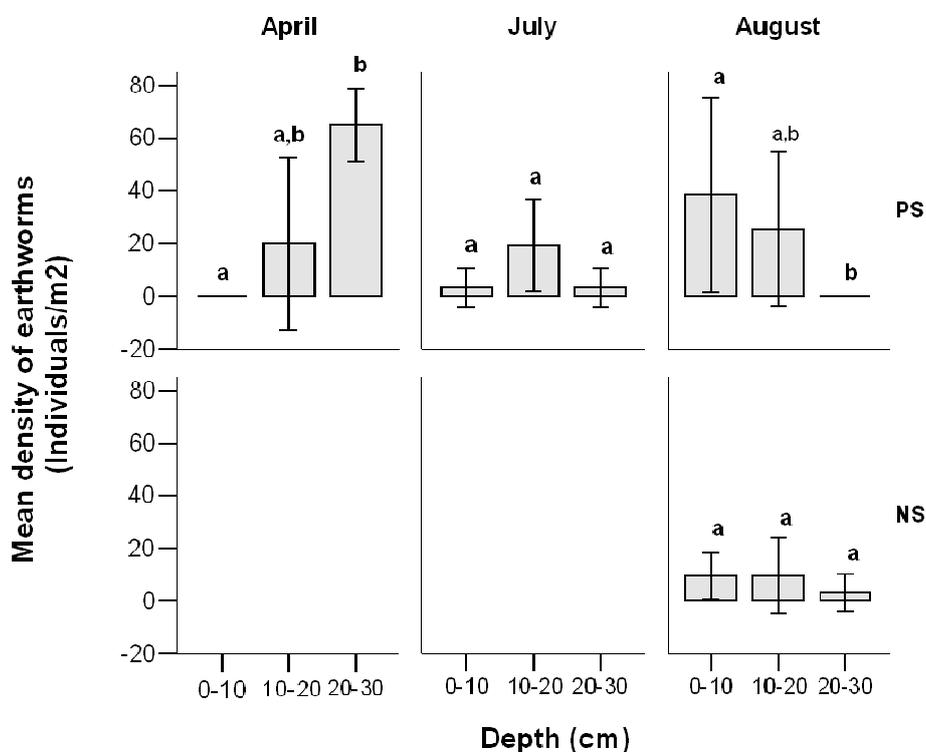
All collected individuals belong to the Glossoscolecidae family. Total average for the density and biomass of earthworms differed greatly between the two systems, showing higher values in the PS. The average density of earthworms in the PS reached 64.0 individuals/m², and average biomass was

32.9 g/m². In the NS earthworms only were found in the month of August, with a mean density of 22.4 individuals/m² and a mean biomass of 5.1 g/m² (Table 2).

3.2.2. Vertical Distribution of Earthworms

The vertical distribution pattern could only be analyzed for the PS, as in the NS we found no earthworms in the dry season. In the PS we noted a migration of earthworms to deeper horizons in the dry season. In the rainy season (July–August) individuals moved into the upper soil layers to feed (Figure 3). In contrast in the NS there were no differences among soil depths with respect to abundance and biomass of earthworms in August which was the only collection in which earthworms were found (Figure 3). It was noted that the marked climatic seasonality determines a migratory process of earthworms in the dry season into deeper areas in the profile. Once earthworms sense a critical level of humidity in the surrounding soil individuals enter a stage of aestivation, which is a biological mechanism that allows them to survive unfavorable environmental conditions. This pattern of diapause already has been described previously by Jiménez & Decaëns [54] in individuals belonging to *Martiodrilus n. sp.*

Figure 3. Mean biomass of earthworms (g/m²) and standard deviation in Protected Savanna (PS) and Natural Savanna (SN) at different depths. Different letters indicate significant difference ($p < 0.05$). Modified from Hernández *et al.* [13].



In the rainy season the earthworms migrate to feed, in the upper layer of soil, much richer in organic matter content than the subsoil [32]. Similar values for the pattern of vertical distribution of earthworms in different seasons or periods of the year have been registered by Jiménez &

Decaëns [54] in Colombian llanos, while Araujo & López-Hernández [6] in savannas of Puerto Ayacucho, Venezuela, recorded a similar distribution during the rainy season.

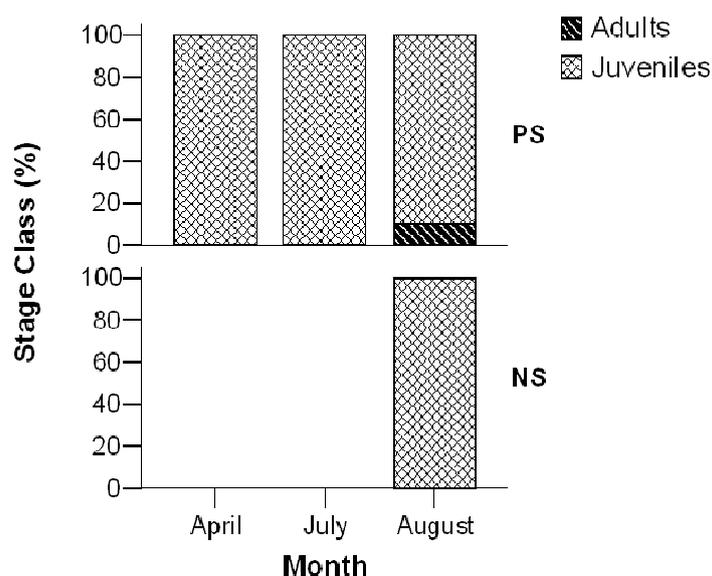
Biomass and density of earthworms could have a different contribution to the vertical distribution due to the great variability of worm sizes found, thus it was observed that while the density varied significantly with the vertical distribution, biomass showed no significant variation.

There is scarce knowledge about the relationship between the pattern of vertical distribution of earthworms, the soil physical parameters and the physiological responses of each species. Jiménez & Decaëns [54] pointed out that environmental factors influence the vertical distribution pattern of the species of earthworms; however, occasionally the physiological response may be responsible for that action. For example, they found that juvenile individuals of *M. carimaguensis* tend to migrate to deeper areas in the middle of the rainy season to enter into aestivation, while the adults remain in the upper layer of soil to deposit their cocoons.

3.2.3. Distribution by Classes of Stages of Development

Earthworms collected were separated into two developmental stages: juveniles and adults, cocoons were not found. Figure 4 shows the distribution of relative frequencies for the classes of stages of development found in the different systems, the absence of individuals in the NS in April and July is highlighted. The stage of development dominant in both systems is the juvenile. In the PS, only in the month of maximum rainfall, were worms in adult stage found, representing 10% of the total number of collected individuals (Figure 4).

Figure 4. Distribution of earthworms by age classes in Protected Savanna (PS) and Natural Savanna (NS). Modified from Hernández *et al.* [13].



During the dry season the earthworm population in the PS was dominated by juveniles, which could be a result of their better adaptability to those stress conditions. At the peak of the rainy season a pyramidal structural class was observed with a low percentage of adults in the population. Similar

results to those presented in this study, were found in Colombian and Venezuelan savannas by Jiménez & Decaëns [54,55] and Araujo & López-Hernández [6], respectively.

The structure by classes of stages of development can vary for different taxa, the highest proportion in one of the classes depend on certain phases of the life cycle, the nature of the individual and its response to the environment at specific time of the year. The absence of cocoons in both systems in the sampled periods could be due to deposition of ootecas in specific months, as reported by Jiménez & Decaëns [54] with individuals belonging to *Martiodrilus carimaguensis*, species which deposited its cocoons just before the dry season. In addition, it is notable that in environments where there is a well-defined dry season, as in this study, the deposition of cocoons could be limited to certain months, although more observations must be done in this respect.

3.2.4. Changes in Soil Quality Indices Induced by Long-Term Protection

3.2.4.1. Soil Physical Changes in Protected and Natural Savanna

As a result of the protection of the savanna (PS) in the EBLL some physical parameters were modified in relation to NS (Table 6). As expected, soil moisture showed strong seasonal variations, with greater values during the rainy season. The PS soils had higher soil moisture with differences between sites significant in July (0–10 cm) and August ($p < 0.05$, Table 6). Soil moisture varied with depth only during the dry season since, after the start of the rainy season, the soil was saturated with water. Field capacity in the PS was greater than that in the NS (Table 6). The apparent bulk density for the surface layer of soil (0–10 cm) was lower in the PS than in the NS reflecting a lower soil compaction in the PS. The soils in the two sites were similar in terms of texture; however, a trend of increased proportion of fine particles with depth ($p < 0.05$) was measured in the NS but not in the PS. The predominant textural class was the sandy type (FA), except the layer (0–10 cm) in the NS which was sandy-loam (SL), possibly associated with the type of management.

3.2.4.2. Soil Chemical Changes in Protected and Natural Savanna

Soil chemical parameters (pH, organic matter, nitrogen and phosphorus) in each locality are presented in Table 7. As expected, there was an important increment in soil fertility parameters due to the protection of the savanna. The total contents of organic carbon (OC) and nitrogen in the first 10 cm, tend to be significantly higher in the PS (9900 mg OC kg⁻¹ and 529 mg N kg⁻¹, respectively) than the NS (7660 mg OC kg⁻¹ and 458 mg N kg⁻¹, respectively), that increment decrease with soil depth (data no presented). The natural acidity of the soil (5.75) was slightly neutralized in PS (6.00). Protection also introduced an important increment in other parameters of soil fertility (exchangeable K, Ca and Mg) (Table 7) and microbial biomass (C and N), whereas acid phosphatase activities were not affected by protection.

Table 6. Soil physical characteristics. Modified from Hernández *et al.* [13].

Parameter	Month	PS			NS		
		Depth (cm)			Depth (cm)		
		0–10	10–20	20–30	0–10	10–20	20–30
Temperature (°C)	April	29.2 (±0.57) a, D	29.3 (±0.67) a, D	30.3 (±1.48) b, D	29.4 (±0.42) a, D	29.4 (±0.55) a, D	30.4 (±0.55) b, D
	July	25.30 (±0.27) a, D	25.90 (±0.22) b, D	26.30 (±0.27) b, D	27.00 (±0.35) a, F	27.60 (±0.55) ab, F	28.00 (±0.35) b, F
	August	25.90 (±0.65) a, D	25.80 (±0.57) a, D	26.50 (±0.27) a, D	24.54 (±0.35) a, F	24.50 (±0.50) a, F	25.10 (±0.22) b, F
Soil water content (%)	April	2.31 (±1.77) a, D	4.35 (±1.92) b, D	5.29 (±1.16) b, D	1.79 (±1.66) a, D	4.56 (±1.08) b, D	5.80 (±0.66) b, D
	July	14.35 (±1.77) a, D	11.36 (±0.91) a, D	10.01 (±2.66) b, D	10.27 (±1.09) a, F	9.04 (±1.77) a, D	11.09 (±1.42) a, D
	August	17.58 (±2.34) a, D	15.80 (±1.11) a, D	15.29 (±1.18) a, D	13.14 (±1.94) a, F	12.21 (±2.05) a, F	11.97 (±1.02) a, F
Sand (%)	April	76.6 (±4.96) a, D	71.7 (±4.70) a, D	72.4 (±5.23) a, D	79.6 (±2.24) a, D	74.5 (±3.35) b, D	71.6 (±4.00) b, D
Clay (%)		12.1 (±4.61) a, D	14.6 (±3.73) a, D	14.6 (±3.36) a, D	8.9 (±1.66) a, D	13.6 (±2.25) b, D	15.0 (±3.26) b, D
Silt (%)		11.3 (±6.43) a, D	13.8 (±2.61) a, D	13.0 (±3.18) a, D	11.5 (±0.61) a, D	11.9 (±1.24) a, D	13.4 (±0.96) b, D
Texture		FA	FA	FA	AF	FA	FA

PS = Protected Savanna, NS = Natural Savanna; Different letters indicate significant differences ($p < 0.05$); Small letters indicate significant difference between depth and capital letters indicate significant difference between systems. Standard deviation in brackets.

Table 7. Soil chemical and biochemical characteristics. Adapted from López-Hernández *et al.* [12].

Parameter	PS	NS
pH	6.00 a	5.75 b
Total C (mg kg ⁻¹)	9450 a	7660 b
Total N (mg kg ⁻¹)	529 a	458 b
Total P (µg g ⁻¹)	165 a	145 b
Available P (µg g ⁻¹)	3.2 a	3.5 a
Exchangeable Ca (cmol kg ⁻¹ suelo)	0.21 a	0.18 b
Exchangeable Mg (cmol kg ⁻¹ suelo)	0.16 a	0.07 b
Exchangeable K (cmol kg ⁻¹ suelo)	0.10 a	0.04 b
Exchangeable Na (cmol kg ⁻¹ suelo)	0.10 a	0.05 b
Total exchangeable bases (cmol kg ⁻¹ suelo)	0.57 a	0.34 b
Exchangeable Aluminium (cmol kg ⁻¹ suelo)	0.62 a	0.72 b
Microbial C (µg g ⁻¹)	153 a	113 b
Microbial N (µg g ⁻¹)	17.3 a	10.2 b
Microbial P (µg g ⁻¹)	8.9 a	9.0 a
Acid phosphatase activity (µg PNP g ⁻¹ ·h ⁻¹)	2.4 a	2.2 a

PS = Protected Savanna, NS = Natural Savanna; Means followed by different letters are significantly different. (Student's *t*, $p < 0.05$).

4. Conclusions

This review article has considered information on the changes in earthworm communities and other soil quality indices in *Trachypogon* savannas of the Orinoco Basin managed under long-term fertilization and/or protection. The number and biomass of earthworms found in the Venezuelan and Colombian well drained *Trachypogon* savannas were low compared with other tropical sites (Table 8 and references [56–60]). A significant increase in earthworm density and biomass occurred after the long-term organic amendment in Puerto Ayacucho site, and also at the Estación Biológica Los Llanos, Calabozo after long-term protection from fire and cattle raising activities. Results similar to those were reported in the Eastern Llanos of Carimagua, Colombia by Jiménez *et al.* [4], where they found a yearly average of both earthworm density and biomass, of 57.8 individuals (ind) m⁻² and 5.00 g m⁻², respectively (Table 8). Those values significantly increased when the natural savanna [4] was replaced by pasture species corresponding to a 17-year-grazed association between an exotic African grass, *Brachiaria decumbens* cv. Basilisk, and a tropical forage legume species, *Pueraria phaseoloides*. This association produces a high belowground production, resulting in an increased availability of superficial litter residues and concomitant soil organic matter.

Long-term additions of organic manure or a long protection have induced significant changes in the soil physical and chemical properties of the savanna soils that induce a significant increase in the density and biomass of earthworm populations. In the case of the presence of a tree canopy in the agro-forestry farm, that tree canopy has influenced some environmental parameters, causing in particular a decrease in air-temperature, concomitantly soil-moisture contents have increased due to the lower rate of evapotranspiration and higher organic matter contents. The bulk density of the OAFS at the 0–10 cm depth was lower than that of the NS without doubt; this result is a consequence of the

long-term addition of organic matter to the OAFS. As expected, there was an important increment in soil chemical fertility due to the presence of the amendment and it was related to the quality and amount of the organic fertilizer.

Table 8. Abundance and biomass of earthworms in several grassland and savannas.

Habitat	Locality	Depth (cm)	Density (n/m ²)	Biomass (g/m ²)	Reference
Grassland	Laguna Verde, México	-	1000	49.2	Lavelle <i>et al.</i> [56]
Humid grassland	Yurimaguas, Perú	30	573	116.4	Lavelle and Pashanasi [57]
Dry grassland	Yurimaguas, Perú	30	474	78	Lavelle and Pashanasi [57]
Grassland	Río Branco, Brasil	-	20	13.4	Guerra [49]
Grassland	Carimagua, Colombia	60	96.9	62.1	Jiménez <i>et al.</i> [49]
Tropical savanna	Costa de Marfil, África	60	91–400	13–54	Lavelle [58]
Tropical savanna	México	-	236	44.1	Fragoso [59]
Tropical savanna	Carimagua, Colombia	60	57.8	5.00	Jiménez <i>et al.</i> [4]
Tropical savanna	Puerto Ayacucho, Venezuela	30	35.2	1.09	Araujo and López-Hernández [5,6]
Agroforestral system	Puerto Ayacucho, Venezuela	30	155.2	18.6	Araujo and López-Hernández [5,6]
Tropical savanna	Guarico, Venezuela	30	22.40	5.17	Hernández [60]
Protected savanna	Guarico, Venezuela	30	64.0	32.9	Hernández [60]

On the other hand, the protection of the savanna in the EBLL promotes an improvement in the physical and chemical properties of the soil, which favors an increase in the density and biomass of earthworms in the PS compared with the SN that is subjected to recurrent burning and grazing. Therefore, it can be emphasized the potential use of the density and biomass of earthworms as bioindicators of soil fertility as already presented by Paoletti *et al.* [61]. In both ecosystems there was registered a pattern of vertical migration of earthworms due to a marked climatic seasonality. The information corroborated the role of earthworms as key species for soil functioning.

It has been emphasized that there is a lack of information concerning the species composition and structure of earthworm communities in tropical savannas, although Brown and Fragoso [62] have recorded over 900 species of earthworms in Latin America (LA), confirming that the most diverse countries are Brazil, Ecuador, Mexico and Colombia. They finally conclude that the knowledge of earthworm diversity and ecology in most countries must still be considered poor.

The results emphasize the importance of appropriate organic matter management and the relevance of earthworms in agroecosystems and protected savannas. By promoting the use of an earthworm population as an agroecological practice linked to the low-input schemes, it is possible to promote the major sustainability of agricultural systems. In this way, the use of inorganic fertilizer and its environmental impact may be reduced, and biodiversity and biomass of soil macro fauna, on the other hand, can be promoted.

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