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**Soil macroinvertebrates community and its temporal variation in a well-drained savannah of the Venezuelan Llanos.**

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**Abstract**

In the well-drained savannahs of Venezuelan Llanos, intensive agricultural activities could be causing damage to the soil, with negative consequences for the ecosystem. In order to avoid this problem, some agroecological alternatives are needed. Consequently, it is necessary to know the biologic dimension in this ecosystem, and within this, the soil macroinvertebrate community. The purpose of this work was to characterize this community in the natural savannah: its structure and diversity, its time variation and its relationship with the physical-chemical properties of the soil. A total of 72 samples were taken in different season along a period of time of 1405 days. The results revealed that the soil macrofauna had an average density of  $243.5 \pm 183.6 \text{ ind}\cdot\text{m}^{-2}$ , distributed in 32 families of 11 orders, with a diversity of  $N_1 = 4.5 \pm 2.8$  families. Coleoptera, Hymenoptera and Isoptera was the most dominants orders. The density, richness and diversity of families showed a temporal variation ( $r \geq -0.5$ ;  $p < 0,05$ ). Additionally, the structure of the soil macroinvertebrate community showed a vertical variation. The relationship with soil properties differed according families: Lampyridae, Aphodiidae and Formicidae had a positive correlation with soil macro-porosity (radius of the pores  $> 15 \mu\text{m}$ ); Tenthredinidae and Tenebrionidae had a

positive correlation with the micro-porosity (pores  $\leq 15 \mu\text{m}$ ). The community in general, correlated positively with soil porosity and negatively with bulk density. This suggests that these soil properties need to be considered when designing agroecological technics in this area.

Key Words: Soil macroinvertebrates; community analysis; space-time variation; tropical savannahs.

## 1. Introduction

The savannah is a tropical and subtropical ecological unit defined by the dominance of herbaceous, grass plants and sedges which can be associated to an arboreal component [1–3]. In Venezuela, the savannahs are located in the so called Llanos (plateaus) and they occupy 260000 Km<sup>2</sup>[4]. The most of the savannahs in the country centre are well-drained and have a great agricultural potential. At present, extensive cattle raising and cereals crops are normally present [5]. Due to the low quality of the soils of these savannahs [2,6], agriculture is supported by an intensive use of fertilizers, pesticides and mechanizations [5] that resulted in the gradual deterioration of the soil [7]. For this reason, the establishment of conservation plans has been brought up as a solution. Therefore, it is needed to know all the dimensions that converge into the agroecosystem [8], especially the biological dimension. In particular, the soil biota that possesses a great variety of ecological functions due to its great diversity [9].

From this biota, the edaphic macroinvertebrates (invertebrates larger than 2mm [10]), have become very important in the ecological studies of the soil [11,12]. They have an important role in the ecosystem functioning, especially in the pedogenesis and in the fertility of the soil [13–16]. Additionally, these organisms affect the ecosystem through their digestion and their role in the nutrients cycle [14,17]. Moreover, the macroinvertebrates affect the formation and stabilization of the soil structure [15,16] Likewise, their close relationship with the physicochemical and biologic characteristics of the soil [7,18,19], have been a reason for their increasing use as indicators of the soil quality [14,20].

Even though their importance in the world biodiversity is known as well as their contributions to the ecosystems and their use as quality indicators, the soil organisms have not received the same attention as the organism above the soil [21]. However, this reality is changing; its study give information of great importance for the understanding of their functions in the ecosystem and its applications in the agricultural activities which could guarantee sustainable strategies for production and at the same time for the preservation of the soil biodiversity [22,23].

For this reason, the study of soil macroinvertebrates in their natural environment regarding their structure and ecology is necessary for its scientific value and its application in the agricultural production (bio indicators, ecological restoration, pest control, etc.). Thus this study was developed in the experimental station La Iguana, in the Guárico state, Venezuela, with the following objectives: 1. Describe the community of soil macroinvertebrates in a natural savannah of Venezuelan Llanos, using their ecological attributes such as the density, richness and diversity of families; 2. Analyze the temporal variation of these ecological attributes, in general and for depth; 3. Identify the relationship between the soil properties and the edaphic macroinvertebrates which could explain these changes.

## **2. Materials and Methods**

### **2.1. Study site description:**

The study was developed in the experimental station La Iguana, geographically located in 8.3916° and 8.475° N and 65.4675° and 65.3805° W in the southeast savannahs of Guárico, Venezuela between 80-120 meters above sea level. The climate is marked by a well differentiated dry period from November to May, and a rainy period between June and October. It has an average annual precipitation of 1369mm and an average monthly temperature of 27.3 °C (isohyperthermy). The station, which occupies approximately 3000 hectares (ha), has a soft undulated with 0 - 2% slope, and a soils mosaic with a fertility between low and medium levels, slightly acidic which defines the variety of plant units dominated by the grass *Trachypogon vestitus* (Andersson) [24]. The soil where the research was conducted was classified as Ultisols: Typic Plinthustults [25] with a coarse loam texture, isohyperthermic. A previous study in this area showed that the sand content in these soils is higher than 80%, with a strong

acidic reaction, low salinity, low content of organic matter and low-nutrients-holding capacity, specially of P and Ca (Table 1) [26]. These areas have been normally used as extensive holdings of low grazing productivity [27].

## 2.2. Design of the study

Once the site inside the experimental station was selected, an analysis of the spatial variability of the soil was done in order to define the size of the study plot, its orientation and the number of samples to be taken [26]. The final selected plot was a natural savannah of 2 ha (100 m x 200 m) [28]. This plot was divided equally in three subplots where three samples were randomly taken in each one.

Trying to simulate the normal grazing conditions of these savannahs, a cattle grazing practice was done with 4 animal units per hectare. This grazing was controlled twice a year: one at the beginning of the rains and another at the end of the rains.

Each sampling was done into the different climate season during 1405 consecutive days (Table 2), with 6 sampling points per time.

Additionally, for each of the sampling dates, samples of soil were also taken, at different depths in the soil profile, dividing it in depth strata, the A horizon (0-15 cm) and the E horizon (15-30 cm). Of the A horizon, one layer was taken, from 0 to 5 cm depth to evaluate the changes in the edaphic properties, as a result of litter and root system of the grass in those first centimetres of the soil, leaving the depths of 0-5, 5-15 and 15 to 30 cm [6].

## 2.3. Sampling of the soil macroinvertebrates

The sampling in each sampling time was random and stratified. The stratification was made by dividing the plot equitably into three subplots. Inside each subplot two sampling points were selected randomly. According to the Tropical Soil Biology and Fertility Program [29], every sample consisted of a monolith of 25x25x30cm divided in the before-mention strata from where the macroinvertebrates were with direct manual sampling techniques [30]. The macrofauna was taken and preserved in ethylic alcohol

(70%) vials. The collected invertebrates belonging to the taxonomic group of winged insects corresponded to organisms in their larvae stages.

#### 2.4. Sampling of the soil

For each sampling time, inside each subplot, four composite soil samples were taken in zigzag in the before mentioned depths. For the physical analysis, procedures described in [6,31], it was taken non altered mixed soil samples in 5x5cm cylinders. The humidity percentage of the soil was measured with the gravimetric method. The bulk density (BD) was measured using the method of the cylinder. The pores size distribution was determined with desktops of saturation voltage (TP: total porosity) in a matric potential of -10 kPa ( $P_{macro}$ : radius of the pores > 15  $\mu m$ .) The retention's porosity ( $P_{micro}$ ) was measured as a result of the difference TP -  $P_{macro}$  [32]. The saturated hydraulic conductivity (Ksat) was measured in a constant charge disc permeameter [33]. For the chemical analysis, the pH was analysed, measuring the total acidic-AT and electrical conductivity (EC) in a soil-water reaction of 1:1 [6]. The organic matter (OM) was studied with the method described in the work of Heanes [34]. The available phosphorus in the soil was extracted with the Olsen solution [35] and detected with the colorimetric method.

#### 2.5. Statistical processes and calculations

The soil macroinvertebrate diversity was calculated with the  $N_1$  (families diversity) from Hill series [36]. In order to compare the average of the density, richness and diversity values, an analysis of variance was used, with STATISTIC software, version 6 [37]. When the result of the ANOVA was significant, the differences among treatments were determined using the "Least significant difference" (LSD) Fisher test [38]. To evaluate possible relationships between soil physical and chemical variables and ecological attributes of the edaphic macroinvertebrates, we performed, on the one hand, Pearson linear correlations, using STATISTIC software; And, on the other hand, multivariate analysis, with the software CANOCO for Windows, version 4.5 [39]. For this, it was decided to use the linear method "Redundancy Analysis" (RDA), since the maximum "gradient length" was less than 3 [40]. For all RDAs, the density of families was standardized with their error of variance. The Spearman minimum correlation value [41] was used, plotting a circle of significance in the graph ( $r_s = 0.71$ ,  $n = 8$ ,  $p < 0.05$ ). In

all analyses, only those with p values less than 0.05 were considered significant. For all analysis, the assumption of normal distribution of the data was checked with the Shapiro-Wilk test [41]. To adjust the normal distribution, the density and families diversity data of the soil macroinvertebrates as well as the M, TP and P were transformed with the square root of the value ( $x^{1/2}$ ). As well for the BD and Ksat data were transformed using the logarithm of the value plus one ( $\text{Log}_{10}(x+1)$ ) and the EC data with the inverse value  $x^{-1}$ .

### 3. Results

#### 3.1. Structure of the edaphic macroinvertebrates community

The edaphic macroinvertebrates community had a total average density of 243.5  $\text{ind}\cdot\text{m}^{-2}$  with standard deviation of  $\pm 183.6 \text{ ind}\cdot\text{m}^{-2}$ , a richness of 32 families, belonging to 11 orders and an average diversity of  $N_1 = 4.5 \pm 2.8$  families. Coleoptera was the most dominant order with  $84.8 \pm 47.6 \text{ ind}\cdot\text{m}^{-2}$ , followed by Hymenoptera with  $68.5 \pm 63.1 \text{ ind}\cdot\text{m}^{-2}$  and Isoptera with  $41.4 \pm 40.0 \text{ ind}\cdot\text{m}^{-2}$ . While, the less dominant was Lepidoptera with only  $0.7 \pm 0.6 \text{ ind}\cdot\text{m}^{-2}$ , within the families, the order of significance was: Formicidae with  $56.4 \pm 50.6 \text{ ind}\cdot\text{m}^{-2}$ , Termitidae with  $41.4 \pm 40.6 \text{ ind}\cdot\text{m}^{-2}$  and Glossoscolecidae with  $22.3 \pm 18.6 \text{ ind}\cdot\text{m}^{-2}$ . On the other hand, the less dominant were the Diptera: Cecydomidae and Sciaridae, and Pieridae (Lepidoptera) with  $0.7 \pm 0.5 \text{ ind}\cdot\text{m}^{-2}$  (Table 3).

#### 3.2. Variation of the soil macroinvertebrate community.

##### 3.2.1. Vertical variation

Although, independently from the depth, the most predominant orders were Coleoptera and Hymenoptera, the soil macroinvertebrates community showed a variation in their ecological structure (Fig 1), for example, Isoptera (termites) is the third order with the largest relative density in the first and second stratum, but in the third layer, Haplotaxida (earthworms) was the third order most dominant of the community.

##### 3.2.2. Temporal variation

The ecological attributes of the macroinvertebrates of the soil, showed different patterns of temporal variation ( $p < 0.05$ ; supplementary material, table A) in each layer of soil depth (Table 4). In the first stratum (0-5 cm), the density of the macrofauna and families richness significantly decreased with time ( $r = -0.56$  and  $r = -0.46$ , respectively); the families diversity had another variation pattern. In the 5-15 cm depth layer, also the density diminished ( $p < 0.05$ ) with time ( $r = -0.53$ ). While the families richness and diversity had another variation pattern, registered the highest values in the start of the rainy season (T2) and in the rainy season (T6), and the lowest values were in the dry season (T8). Moreover, in the 15-30 cm layer there was a similar variation pattern in the three ecological attributes: the highest values ( $p < 0.05$ ) were registered in the start of the rainy season (T2) and the dry season (T4), while the rest of the time, the values were relatively low.

On the other hand, without discriminating on the depth, it was shown that the families density (supplementary material, table B), families richness and diversity of the soil macroinvertebrates tended to decrease with time (Fig 2), showing differences between sampling times by ecological attribute (supplementary material, table C). This was confirmed by applying the Pearson linear correlation between each ecological attribute ( $p < 0.05$ ), the families density, richness and diversity, and the time ( $r = -0.62$ ;  $r = -0.50$  and  $r = -0.50$ , respectively).

### 3.3. Interaction of the soil macroinvertebrates and the soil properties.

When analyzing the relationships of the attributes of the edaphic macroinvertebrate community with the physical-chemical properties of the soil, through Pearson's linear correlation (table 5), it was found that EC correlated negatively with density, richness and diversity of families of the macrofauna of the soil. Likewise, it was recorded that BD was negatively related to the richness of families, while TP was positively related to the density and richness of families of the edaphic macroinvertebrates.

The Redundancy Analysis (RDA) (Fig 3), presented 82% of the total variance explained for the first three axes of the RDA. The first axis, it was determined mainly by Rutelidae and Geotrupilidae, and in the opposite direction by Cerambycidae and Formicidae. The second was determined axis by Termitidae and Staphylinidae. The



third, it was established by Tenthredinidae and Tenebrionidae, and in opposite direction by Aphodiidae and Lampyridae. According to the minimal value of the Spearman correlation  $r_s = 0.71$  ( $p < 0.05$ ), the soil variables that correlates significantly with the three first axes were the  $P_{macro}$  and  $P_{micro}$  (Table 6).

Given the proximity between the vectors that constitute the RDA, Lampyridae, Aphodiidae and Formicidae had a positive correlation with  $P_{macro}$ ; Tenthredinidae and Tenebrionidae had a positive correlation with the  $P_{micro}$ . Sampling times do not present a clear clustering.

#### 4. Discussion

The results of the ecological structure of the soil macroinvertebrates community were similar to those reported for others authors [18,42–45], demonstrating that Coleoptera, Hymenoptera, Isoptera and Haplotaxida, the most preeminent orders in this study matched with the ones reported in others environments. However, the average density of the edaphic macroinvertebrates obtained in this study ( $243.5 \pm 183.6 \text{ ind}\cdot\text{m}^{-2}$ ) was inferior to the one referred to in those papers ([18]: 407; [42]:  $520.9 \pm 38.4$ ; [43]: 1870; and [44]:  $3349 \text{ ind}\cdot\text{m}^{-2}$ ), while richness (32 families) was similar or superior ([42]: 10; [43]: 33; and [44]: 20; [45]: 31 families). This could be explained by the edaphic and climatic factors, especially the high temperatures and the soils with low humidity retention [31] which could determine not only the available resources but also the conditions for the macroinvertebrates metabolism [7]. This combination of factors could be unfavourable for a great number of populations inside each family which, on the other hand, could indirectly increase the amount of niche and facilitate greater families richness.

On the other hand, the vertical variation of the ecological structure of the soil macrofauna community could be due to the existence of functional groups of macroinvertebrates (epigeous, endogenous and anecic) which could be adapted to certain conditions characteristically of each level underground [46]. But also, the result could be influenced by the type of sampling protocol used.

The variables TP and EC, could explain the decrease in time of ecological attributes, since they showed a significantly relationship with the time (TP:  $r = -0.82$ ; EC:

$r = 0.77$ ), as well as the density (TP:  $r = 0.52$  and EC:  $r = -0.37$ ), richness (TP:  $r = 0.38$  and EC:  $r = -0.41$ ) and the families diversity only related with the EC ( $r = -0.51$ ). The decrease of the TP could have a relationship with the effect of trampling due to the grazing. Although grazing was controlled, it is possible that in the dry season the cattle had a greater impact on the savannah, by the decrease of the forage, affecting negatively the T7 and T8, in dry season. The negative effect of the grazing over the soil porosity [47,48] and over the soil macroinvertebrates [49,50] has been proved. Besides, the increase of the EC over time could be associated with the decrease of TP, a factor which affects the soil water infiltration [51], and therefore the M, which according to several authors [52,53], was correlated and negatively with the EC ( $r = -0.52$ ;  $p < 0.05$ ).

The results of the RDA, regarding the correlations between the families of the macrofauna and the properties of the soil, correspond to the results obtained by other authors. The positive correlation between  $P_{macro}$  and the Lampyridae and Aphodiidae families of the order Coleoptera was explained in previous studies by the activity that these organisms develop in the soil [50]. On the other hand, the relationship between Tenthredinidae and Tenebrionidae with the  $P_{micro}$  may be associated to the fact that the higher the values of this variable, the greater the soil capacity to retain water, which is a benefit in the dry season [54].

## 5. Conclusions

This study shows that soil macroinvertebrate in this well-drained savannah of Venezuelan Llanos had a low density compared to others works cited, but also a great richness of families.

A decrease in time of the ecological attributes of the soil macroinvertebrates community with time was registered. This was associated negatively with the soil bulk density and conductivity electrical and positively with total porosity.

Thus, it was evidence this soil macroinvertebrate community of the soil and the structure of the soil are closely related, so that although this soil is sandy loam, the soil bulk density and porosity, it should be to take into account when designing agricultural practices in this area, for example, reducing grazing in the dry season.

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Table 1. Initial physicochemical characteristics of soil under study at the experimental station La Iguana.

Parameter	Depth (cm)		
	0-5	5-15	15-30
Clay [ < 2 $\mu\text{m}$ ] <sup>†</sup> (%)	2,50 (0,38) <sup>‡</sup>	2,94 (0,09)	10,00 (1,20)
Silt [2-5 $\mu\text{m}$ ] (%)	12,51 (1,15)	11,00 (0,98)	12,00 (1,02)
Very fine sand [50 - 100 $\mu\text{m}$ ] (%)	6,99 (0,32)	3,17 (0,89)	10,00 (1,92)
Fine sand [100 - 250 $\mu\text{m}$ ] (%)	48,91 (5,15)	29,05 (2,13)	36,00 (3,16)
Medium sand [250 - 500 $\mu\text{m}$ ] (%)	25,29 (1,12)	44,59 (3,32)	22,93 (2,16)
Coarse sand [500 - 1000 $\mu\text{m}$ ] (%)	3,29 (0,78)	7,98 (1,12)	8,20 (0,32)
Very coarse sand [1000-2000 $\mu\text{m}$ ] (%)	0,51 (0,11)	1,27 (0,08)	0,78 (0,10)
Textural class	Loamy Sand	Loamy Sand	Sandy Loam
Reaction of the soil (pH)	5,01 (0,18)	4,81 (0,25)	4,75 (0,24)
Total acidity ( $\text{cmol}^+ \cdot \text{kg}^{-1}$ )	0,46 (0,21)	0,83 (0,58)	1,18 (0,73)
Interchangeable aluminum ( $\text{cmol}^+ \cdot \text{kg}^{-1}$ )	0,16 (0,09)	0,34 (0,23)	0,50 (0,31)
Interchangeable hydrogen ( $\text{cmol}^+ \cdot \text{kg}^{-1}$ )	0,30 (0,18)	0,49 (0,42)	0,67 (0,53)
Electrical conductivity ( $\mu\text{S} \cdot \text{cm}^{-1}$ )	27,53 (1,32)	23,62 (3,26)	22,77 (3,62)
CIC ( $\text{cmol}^+ \cdot \text{kg}^{-1}$ )	2,21 (0,54)	1,94 (0,66)	1,90 (0,82)
Organic matter (%)	1,33 (0,30)	1,23 (0,26)	1,04 (0,27)
Total nitrogen (%)	0,039 (0,007)	0,032 (0,007)	0,028 (0,007)
Inorganic nitrogen ( $\text{mg} \cdot \text{kg}^{-1}$ )	21,34 (11,18)	17,23 (8,45)	15,73 (9,54)
Phosphorus ( $\text{mg} \cdot \text{kg}^{-1}$ )	11,30 (0,30)	10,01 (3,62)	8,67 (3,26)
Potassium ( $\text{mg} \cdot \text{kg}^{-1}$ )	29,94 (14,10)	19,51 (7,31)	11,53 (4,40)
Calcium ( $\text{mg} \cdot \text{kg}^{-1}$ )	89,64 (25,21)	63,15 (27,87)	38,11 (14,76)
Magnesium ( $\text{mg} \cdot \text{kg}^{-1}$ )	51,35 (16,94)	47,19 (12,07)	39,11 (14,66)
Sodium ( $\text{mg} \cdot \text{kg}^{-1}$ )	2,09 (1,33)	2,40 (1,65)	3,11 (1,86)
Iron ( $\text{mg} \cdot \text{kg}^{-1}$ )	44,61 (22,07)	53,36 (25,03)	54,38 (24,96)
Copper ( $\text{mg} \cdot \text{kg}^{-1}$ )	0,71 (0,44)	0,90 (0,60)	1,07 (0,57)
Manganese ( $\text{mg} \cdot \text{kg}^{-1}$ )	7,76 (3,60)	3,52 (2,64)	2,63 (1,73)
Zinc ( $\text{mg} \cdot \text{kg}^{-1}$ )	1,07 (0,57)	0,86 (0,37)	0,79 (0,39)

<sup>†</sup> Size of the aggregates.

Source: [28]

<sup>‡</sup> Values in parentheses are Standard deviation.

511 Table 2. Distribution of sampling times for the study of soil macroinvertebrates and soil  
 512 of a well-drained savannah in the Venezuelan Llanos.

Descriptor		Sampling times						
Days after initiation	0	370	446	558	733	831	1048	1405
Climate season	Start of rainy season	Start of rainy season	Rainy season	Dry season	Start of rainy season	Rainy season	Dry season	Dry season
Chronological order	T1	T2	T3	T4	T5	T6	T7	T8
Number of samples	6	6	6	6	6	6	6	6

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516 Table 3. Orders and families' density (ind·m<sup>-2</sup>) and their standard deviation of the soil  
 517 macroinvertebrates community in a well-drained savannah of the Venezuelan Llanos.

Orden (density)	Family	Density
ind·m <sup>-2</sup>		ind·m <sup>-2</sup>
Coleoptera (84.8 ± 47.6)	Carabidae	16.3 ± 8.9
	Scarabaeidae	14.0 ± 13.5
	Staphylinidae	13.2 ± 11.1
	Tenebrionidae	6.1 ± 3.6
	Aphodiidae	5.8 ± 5.2
	Miridae	5.4 ± 4.1
	Chrysomelidae	4.3 ± 3.7
	Cerambycidae	3.6 ± 3.4
	Elateridae	3.5 ± 2.5
	Rutelidae	3.2 ± 2.8
	Geotrupidae	2.5 ± 1.5
	Lampyridae	2.2 ± 1.8
	Coccinellidae	2.0 ± 1.0
	Hydroscaphidae	1.5 ± 1.5
	Dynastidae	1.3 ± 1.0
Hymenoptera (68.5 ± 63.1)	Formicidae	56.4 ± 50.6
	Tenthredinidae	8.8 ± 8.2
	Tenthredinidae	2.0 ± 1.0
	Hym (NI)	1.3 ± 1.0
Isoptera	Termitidae	41.4 ± 40.6
Haplotaxida	Glossoscolecidae	22.3 ± 18.6
Diptera (10.7 ± 10.0)	Muscidae	8.0 ± 7.0
	Dip (NI)	1.3 ± 1.0
	Cecydomidae	0.7 ± 0.5
	Sciaridae	0.7 ± 0.5
Araneae (6.9 ± 6.0)	Paratropididae	4.9 ± 4.9
	Dipluridae	2.0 ± 1.0
Solifugae	Ammotrechidae	1.5 ± 1.5
Chilopoda	Cryptopidae	1.3 ± 1.0
Hemiptera	Lygaeidae	1.3 ± 1.0
Homoptera	Cercopidae	1.0 ± 1.0
Lepidoptera	Pieridae	0.7 ± 0.5

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Table 4. Density (ind·m<sup>-2</sup>), richness and diversity of families of soil macroinvertebrates of a well-drained savannah in the Venezuelan Llanos. Values in parentheses are standard deviation.

Depth <sup>†</sup>	Attribute <sup>‡</sup>	Time							
		Start of rainy season <sup>§</sup>	Start of rainy season	Rainy season	Dry season	Start of rainy season	Rainy season	Dry season	Dry season
		0 <sup>#</sup>	370	446	558	733	831	1048	1405
		T1 <sup>††</sup>	T2	T3	T4	T5	T6	T7	T8
0-5	Density	156.0 <sup>a††</sup>	136.0 <sup>a</sup>	10.6 <sup>b</sup>	0 <sup>b</sup>	21.3 <sup>b</sup>	42.6 <sup>b</sup>	26.7 <sup>b</sup>	16.0 <sup>b</sup>
		(95.5)	(30.6)	(9.2)		(20.0)	(40.0)	(22.0)	(0)
	Richness	3.6 <sup>ab</sup>	5.5 <sup>b</sup>	0.7 <sup>c</sup>	0 <sup>c</sup>	1.3 <sup>ac</sup>	2.3 <sup>ac</sup>	1.3 <sup>ac</sup>	1.0 <sup>c</sup>
		(1.6)	(1.2)	(0.4)		(1.0)	(2.1)	(0.4)	(0)
	Diversity	2.9 <sup>a</sup>	5.2 <sup>b</sup>	0.7 <sup>ac</sup>	0 <sup>c</sup>	1.3 <sup>ac</sup>	2.2 <sup>ac</sup>	1.3 <sup>ac</sup>	1.0 <sup>c</sup>
		(1.4)	(1.2)	(0.4)		(1.1)	(2.0)	(0.4)	(0.0)
5-15	Density	144.0 <sup>ab</sup>	228.0 <sup>b</sup>	53.3 <sup>ac</sup>	165.3 <sup>ab</sup>	101.3 <sup>abc</sup>	128.0 <sup>abc</sup>	10.6 <sup>c</sup>	21.3 <sup>c</sup>
		(100.8)	(45.9)	(24.4)	(148.6)	(100.0)	(82.0)	(9.2)	(20.0)
	Richness	3.1 <sup>b</sup>	7.5 <sup>a</sup>	2.7 <sup>bc</sup>	3.7 <sup>b</sup>	2.3 <sup>bc</sup>	6.0 <sup>a</sup>	1.7 <sup>bc</sup>	1.0 <sup>c</sup>
		(0.6)	(1.0)	(0.8)	(2.0)	(1.1)	(0.6)	(0.8)	(0.6)
	Diversity	2.6 <sup>b</sup>	6.2 <sup>a</sup>	2.6 <sup>bc</sup>	2.2 <sup>bc</sup>	1.6 <sup>bc</sup>	5.4 <sup>a</sup>	1.5 <sup>bc</sup>	1.0 <sup>c</sup>
		(0.5)	(1.0)	(0.8)	(1.6)	(0.4)	(0.5)	(0.7)	(0.6)
15-30	Density	40.0 <sup>b</sup>	236.0 <sup>a</sup>	26.6 <sup>b</sup>	288.0 <sup>a</sup>	16 <sup>b</sup>	42.7 <sup>b</sup>	5.3 <sup>b</sup>	32.0 <sup>b</sup>
		(39.9)	(61.7)	(25.2)	(150.0)	(15.3)	(40.0)	(5.0)	(27.7)
	Richness	1.1 <sup>b</sup>	7.0 <sup>a</sup>	1.7 <sup>b</sup>	5.6 <sup>a</sup>	0.3 <sup>b</sup>	1.7 <sup>b</sup>	0.3 <sup>b</sup>	1.0 <sup>b</sup>
		(0.6)	(1.0)	(1.5)	(4.7)	(0.2)	(1.2)	(0.2)	(0.6)
	Diversity	1.1 <sup>b</sup>	5.6 <sup>a</sup>	1.7 <sup>b</sup>	4.4 <sup>a</sup>	0.3 <sup>b</sup>	1.6 <sup>b</sup>	0.3 <sup>b</sup>	1.0 <sup>b</sup>
		(0.6)	(1.2)	(1.5)	(1.7)	(0.4)	(1.0)	(0.4)	(0.6)

<sup>†</sup> Depth in centimeters.

<sup>‡</sup> Ecological Attribute: Density (ind·m<sup>-2</sup>); Richness of families; Diversity of families

<sup>§</sup> Climate season

<sup>#</sup> Days after the initiation of the study

<sup>††</sup> Chronological order of the samplings

<sup>‡‡</sup> Unequal letters indicate differences (p < 0.05) between times for a same depth. summarizing the effects

530 Table 5. Pearson linear correlations ( $r$ ) among the ecological attributes: density,  
 531 richness and diversity of families of soils macroinvertebrates and edaphic variables in a  
 532 well - drained savanna of the Llanos Venezuelan. N = 48.

		Edaphic variables									
Attribute <sup>†</sup>	Est <sup>‡</sup>	BD <sup>#</sup>	TP	P <sub>macro</sub>	P <sub>micro</sub>	Ksat	M	OM	pH	EC	P
DEN	$r$	-0.240	0.524 <sup>§</sup>	0.014	0.290	0.239	-0.145	0.012	-0.061	-0.373	-0.322
	$p$	0.202	0.003	0.944	0.120	0.203	0.445	0.951	0.750	0.042	0.082
RIC	$r$	-0.383	0.366	-0.005	0.220	0.329	-0.140	-0.127	-0.159	-0.411	-0.321
	$p$	0.037	0.047	0.981	0.242	0.076	0.461	0.502	0.400	0.024	0.079
DIV	$r$	-0.294	0.307	-0.142	0.315	0.299	-0.008	-0.170	-0.138	-0.505	-0.329
	$p$	0.114	0.099	0.453	0.090	0.108	0.967	0.369	0.466	0.004	0.088

533 <sup>†</sup> Den: Density; RIC: families richness; DIV: families diversity.

534 <sup>‡</sup> Statistic:  $r$ , value of Pearson linear correlation;  $p$  value

535 <sup>§</sup> Numbers in red indicate significate correlation.

536 <sup>#</sup> BD: Bulk density; TP: Total porosity; P<sub>macro</sub>: macro-porosity; P<sub>micro</sub>: micro-porosity; Ksat:  
 537 hydraulic conductivity; M: % moisture; OM: soil organic matter; EC: Electric conductivity; P:  
 538 available phosphorus

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Table 6. Correlation ( $r$ ) of the soil physical-chemical variables with the axes of the redundancy analysis, formed through the density of macrofauna families of the soil of a natural savanna in the Venezuelan plains. Values in bold indicate significant correlation ( $p < 0.05$ ) for  $n = 8$ .

Soil variable	Value $r$		
	Axis 1	Axis 2	Axis 3
Bulk density (BD)	-0.38	-0.48	-0.18
Total porosity (TP)	-0.30	0.52	0.13
Macro-porosity ( $P_{\text{macro}}$ )	-0.18	-0.20	<b>-0.82</b>
Micro-Porosity ( $P_{\text{micro}}$ )	0.00	0.38	<b>0.71</b>
Hydraulic Conductivity (Ksat)	0.46	0.08	0.10
% Moisture (M)	-0.23	-0.24	0.65
Soil Organic Matter (OM)	-0.38	-0.33	-0.58
pH	-0.34	0.06	0.10
Electric Conductivity (EC)	-0.21	-0.17	-0.61
Available Phosphorus (P)	-0.44	-0.22	-0.43

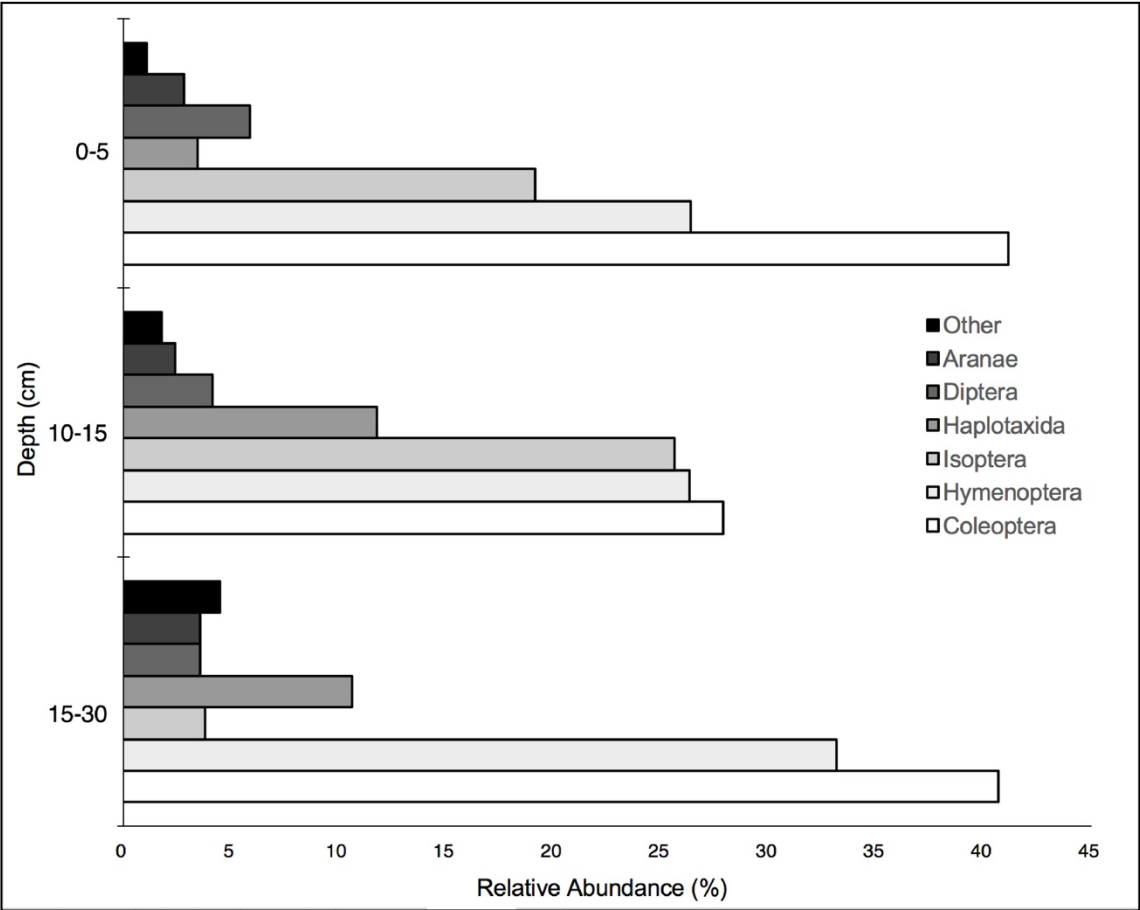
## Caption figures

Fig 1. Relative abundance (%) of the soil macroinvertebrates of a well-drained savannah in the Venezuelan Llanos according to profundity (0-5, 5-15 y 15-30 cm). Every gray tone indicates a different taxon. Other: Solifugae, Chilopoda, Hemiptera, Homoptera, Lepidoptera with less or equal to 1.5 ind·m<sup>-2</sup>.

Fig 2. Density, richness and diversity of families of the soil macroinvertebrates of a well-drained savannah of the Venezuelan Llanos for every time sample starting in 0 to 1405 days of study. Unequal lowercase letters bold indicate significant differences ( $p < 0.05$ ) for the density, uppercase letters for the families richness of and lowercase letters italic for the families diversity. It indicates the climate season (start of rainy season, rainy season, dry season).

Fig 3. Ordering of the sampling sites (times) according to average density of the families of the soil macroinvertebrates (*italic writing*) and their correlation with soil properties (**bold writing**) of a well-drained Savannah of the Venezuelan Llanos, through a Redundancy Analysis. First and second axes are on the left side and the third on the right side. The size of the central circle indicates the minimum value of significance of the correlation coefficient ( $r = 0.071$ ;  $p < 0.05$ ;  $n = 8$ ). EC: electric conductivity; P: available phosphorus; P<sub>macro</sub>: macroporosity; P<sub>micro</sub>: microporosity; TP: total porosity; BD: bulk density; M: percentage of humidity; Ksat: hydraulic conductivity.

571 Figure 1



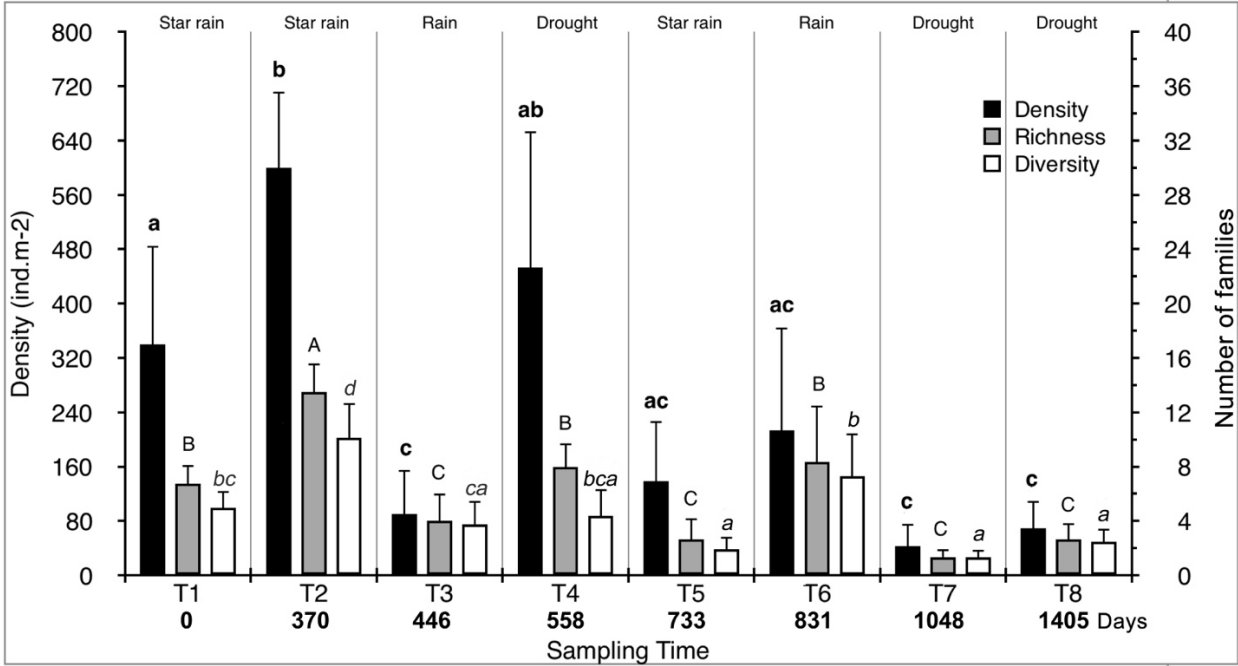
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575 Figure 2



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582 Table A. Summary of the effects of ANOVA for the comparison between times of  
 583 sampling by depth layers, using the average density of the macrofauna of the soil, its  
 584 richness and diversity of families

Attribute		Degree of				
Depth	Ecology	SS	Freedom	MS	F	<i>p</i>
cm						
0-5	Density	126000.000	7.000	17900.000	4.858	0.002
	Richness	89.430	7.000	12.780	3.625	0.009
	Diversity	70.050	7.000	10.010	3.410	0.013
05-15	Density	137000.000	7.000	19500.000	2.761	0.032
	Richness	118.800	7.000	16.970	7.108	0.000
	Diversity	87.240	7.000	12.460	9.973	0.000
15-30	Density	288000.000	7.000	41200.000	4.870	0.002
	Richness	164.100	7.000	23.440	11.670	0.000
	Diversity	97.600	7.000	13.940	5.978	0.001

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588 Table B. Orders and families' density (ind·m<sup>-2</sup>) and their standard deviation of the soil macroinvertebrates community by time sampling  
589 and average in a well-drained savannah of the Venezuelan Llanos.

Orden	Family	Sampling Time								Average	
		T1	T2	T3	T4	T5	T6	T7	T8		
	ind·m <sup>-2</sup>					ind·m <sup>-2</sup>					
Coleoptera	84.8 ± 47.6	Carabidae	14.0 ± 14.0	36.0 ± 20.2	10.7 ± 9.2	16.0 ± 10.7	5.3 ± 4.1	32.0 ± 21.3	10.7 ± 9.2	5.3 ± 4.1	16.3 ± 8.9
		Scarabaeidae	16.0 ± 12.0	0	5.3 ± 4.1	0	48.0 ± 21.3	10.7 ± 7.1	0	32.0 ± 21.3	14.0 ± 13.5
		Staphylinidae	20.0 ± 16.0	64.0 ± 40.0	10.7 ± 7.1	10.7 ± 9.2	0	16.0 ± 11.3	0	0	13.2 ± 11.1
		Tenebrionidae	10.0 ± 10.0	12.0 ± 12.0	5.3 ± 4.1	5.3 ± 4.1	0	10.7 ± 7.1	0	5.3 ± 4.1	6.1 ± 3.6
		Aphodiidae	0	36.0 ± 14.0	0	10.7 ± 9.2	0	0	0	0	5.8 ± 5.2
		Miridae	10.0 ± 10.0	12.0 ± 12.0	0	10.7 ± 9.2	5.3 ± 4.1	5.3 ± 5.3	0	0	5.4 ± 4.1
		Chrysomelidae	0	24.0 ± 16.0	0	0	0	5.3 ± 4.1	0	5.3 ± 4.1	4.3 ± 3.7
		Cerambycidae	14.0 ± 14.0	4.0 ± 4.0	0	10.7 ± 9.2	0	0	0	0	3.6 ± 3.4
		Elateridae	0	12.0 ± 12.0	0	0	0	10.7 ± 7.1	5.3 ± 4.1	0	3.5 ± 2.5
		Rutelidae	0	20.0 ± 12.0	0	0	0	5.3 ± 4.1	0	0	3.2 ± 2.8
		Geotrupidae	0	20.0 ± 20.0	0	0	0	0	0	0	2.5 ± 1.5
		Lampyridae	0	12.0 ± 6.0	0	5.3 ± 4.1	0	0	0	0	2.2 ± 1.8
		Coccinellidae	0	0	5.3 ± 4.1	0	0	10.7 ± 9.2	0	0	2.0 ± 1.0
		Hydroscaphidae	0	12.0 ± 12.0	0	0	0	0	0	0	1.5 ± 1.5
		Dynastidae	0	0	5.3 ± 4.1	0	0	5.3 ± 4.1	0	0	1.3 ± 1.0
Hymenoptera	68.5 ± 63.1	Formicidae	50.4 ± 38.1	44.0 ± 6.0	0	298.7 ± 206.2	0	21.3 ± 17.8	26.7 ± 17.8	10.7 ± 7.1	56.4 ± 50.6
		Tenthredinidae	14.0 ± 14.0	24.0 ± 12.0	26.7 ± 17.8	0	0	5.3 ± 4.1	0	0	8.8 ± 8.2
		Tenthredinidae	16.5 ± 14.9	0	0	0	0	0	0	0	2.0 ± 1.0
		Hym (NI)	0	0	0	10.7 ± 7.1	0	0	0	0	1.3 ± 1.0
Isoptera		Termitidae	126.0 ± 106.0	128.0 ± 112.0	0	0	74.7 ± 68.2	0	0	10.7 ± 9.2	41.4 ± 40.6
Haplotaxida		Glossoscolecidae	40.4 ± 18.1	64.0 ± 16.0	16.0 ± 10.7	21.3 ± 14.2	0	37.3 ± 24.9	0	0	22.3 ± 18.6
Diptera	10.7 ± 10.0	Muscidae	0	48.0 ± 24.0	5.3 ± 4.1	0	5.3 ± 4.1	5.3 ± 4.1	0	0	8.0 ± 7.0
		Dip (NI)	0	0	0	10.7 ± 7.1	0	0	0	0	1.3 ± 1.0
		Cecydomidae	0	0	0	0	0	5.3 ± 4.1	0	0	0.7 ± 0.5
		Sciaridae	0	0	0	0	0	5.3 ± 4.1	0	0	0.7 ± 0.5
Araneae	6.9 ± 6.0	Paratropididae	10.0 ± 10.0	8.0 ± 8.0	0	10.7 ± 7.1	0	10.7 ± 9.2	0	0	4.9 ± 4.9
		Dipluridae	0	0	0	16.0 ± 10.7	0	0	0	0	2.0 ± 1.0
Solifugae		Ammotrechidae	0	12.0 ± 12.0	0	0	0	0	0	0	1.5 ± 1.5
Chilopoda		Cryptopidae	0	0	0	5.3 ± 4.1	0	5.3 ± 4.1	0	0	1.3 ± 1.0
Hemiptera		Lygaeidae	0	0	0	10.7 ± 7.1	0	0	0	0	1.3 ± 1.0
Homoptera		Cercopidae	0	8.0 ± 8.0	0	0	0	0	0	0	1.0 ± 1.0
Lepidoptera		Pieridae	0	0	0	0	0	5.3 ± 4.1	0	0	0.7 ± 0.5
		Total	340.2 ± 117.1	600.0 ± 88.0	90.7 ± 46.2	384.0 ± 213.3	138.7 ± 67.6	160.0 ± 85.3	42.7 ± 24.9	69.3 ± 28.4	243.5 ±183.6

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592 Table C. Summary of the effects of ANOVA for the comparison between times of  
 593 sampling, using the average density of the macrofauna of the soil, its richness and  
 594 diversity of families.

Attribute Ecology	SS	Degree of Freedom	MS	F	p
Density	1010000.000	7	144000.000	6.762	< 0.0001
Richness	399.1	7	57.020	15.080	< 0.0001
Diversity	214.2	7	30.600	9.883	< 0.0001

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