Population dynamics and adaptive strategies of Martiodrilus carimaguensis (Oligochaeta, Glossoscolecidae), a native species from the well-drained savannas of Colombia.

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Abstract

Martiodrilus carimaguensis (Oligochaeta, Glossoscolecidae) is a large, dorsally dark-grey anecic native earthworm species that was found in natural and disturbed savannas in the Oxisols of the Colombian Llanos. The population dynamics of this species were studied in a native savanna and in a 17-yr old grazed grass-legume pasture from April 1994 to September 1995 (except June 1994). High values of density and biomass were obtained in the latter system compared to the former. The difference in population was reflected in the number of fresh casts deposited on the soil surface. Monthly deposition in the improved pasture system was $38.4x10^3$ fresh casts. ha^{-1}, eleven times greater than that in the native savanna. A strong relationship was found between numbers of M. carimaguensis and numbers of fresh surface casts. Different patterns of adaptation to the dry season were observed for adults and juveniles. Adults are active for 8 months whereas juveniles enter diapause 3-4 months earlier. Vertical distribution of earthworm populations also shows marked seasonal changes.

Key words: Population dynamics, Adaptive strategies, Martiodrilus carimaguensis, Oligochaeta, Glossoscolecidae, Savannas.

1. Introduction

There is a lack of information concerning the biology of tropical earthworms (Dash and Patra, 1977; Lavelle, 1978). Of the few species which have been fully studied in both temperate tropical ecosystems, most have been introduced by man, e. g., Pontoscolex corethrurus Müller, 1856 and Dichogaster bolaui (Michaelsen, 1891). In most disturbed areas local earthworm communities disappear, being displaced by introduced species (Lavelle and Pashanasi, 1989; Lavelle et al., 1987; Bohlen et al., 1995).

However, less attention has been paid to the role of those native earthworm species that are well-adapted to perturbation of natural ecosystems. In Carimagua, man-made pastures derived from natural savannas retained the in-original earthworm biodiversity and their biomass increased from 4.8 g fresh weight m^{-2} in the native savanna up to 51.1 g fresh weight m^{-2} (Decaëns et al, 1994). One species, Martiodrilus carimaguensis (Jiménez and Moreno, in press) has been greatly favoured by this land practice, increasing significantly in abundance and biomass ($P<0.001$).

M. carimaguensis. is a large anecic earthworm species belonging to the family Glossoscolecidae, with an average adult size of 9.3 mm in diameter and 194.3 mm in length and a fresh weight of 11.2 g (in 4% formaldehyde) (n = 29). Its body colour is dark-grey on the dorsal side and light-grey on its ventral side (Jiménez y Moreno, in press).

2. Material and methods

2.1. Study site

The study area is located at the CIAT-CORPOICA (Centro Internacional de Agricultura Tropical and Corporación Colombiana de Investigación Agropecuaria agreement) Carimagua Research Station, in the well-drained isohyperthermic savannas of the Eastern Plains of Colombia (4° 37' N and 71° 19' W and 175 meters altitude). Average annual rainfall and temperature are about 2280 mm and 26°C respectively, with a dry season from December to March. Soils are of two types: predominant low-fertility Oxisols in the upland (“altos”) and Ultisols in the low-lying (“bajos”) savannas. The former are characterized by their acidity (pH (H_20) 4.5), a high Al saturation (> 90%) and low values of exchangeable Ca, Mg and K. Chemical factors that contribute to acid-soil infertility and subsequent effects on plant growth are complex and include Al toxicity, low content of available P and low rates of N mineralization (Rao et al., 1993).

Two different and contrasting systems were evaluated: A native savanna (NS) without management, in which the predominant plant species are Andropogon bicornis, Gymnopogon sp., Panicum spp., Trachypogon spp. and Imperata sp., and a 17-yr old grazed improved pasture (IP) comprising an exotic african grass, Brachiaria decumbens cv. Basilisk, and a tropical forage herbaceous legume species, Pueraria phaseoloides CIAT 9900 (“kudzu”).

2.2. Earthworm sampling

One 90x90 m plot was selected in each system and divided into 10x10 m regular quadrats. Earthworms were hand-sorted monthly from five 1x1x0.5 m soil monoliths (after Lavelle, 1978) extracted at random within five randomly-chosen quadrats in each plot. The sampling depth was varied seasonally to take into account the vertical migration of this species. The sample was split into 10 cm layers and earthworms collected from each layer washed in water and fixed in 4% formalin. They were separated in the laboratory into adults (with clitellum and associated glands) and juveniles (lacking clitellum and glands), counted and weighed. The cocoons obtained were also counted and weighed.

2.3. Surface cast deposition

Part of the soil ingested by earthworms is ejected on the soil surface. As an anecic species M. carimaguensis has the ability to deposit large tower-like casts, up to 15 cm in height, on the soil surface. In both systems these surface casts, which are easily recognised, from other depositions were counted in two monthly randomly-chosen 1m^2 samples and classified into two broad categories, fresh and dry. Casts were oven-dried at 60 ºC for 72 hours and weighed.

3. Results

3.1. Density and biomass

Monthly fluctuations in the abundance and biomass of M. carimaguensis are shown in Figure 1. Average population of 17.9 m^{-2} and 0.2 m^{-2} were observed in the improved pasture and native savanna, respectively (Table 1).

In the natural savanna values of density ranged from 0 in November 94 to 0.6 m^{-2} in September 95. Under the improved pasture density ranged from 11 m^{-2} (September 94) to 23.2 m^{-2} (May 95). The highest values of density were recorded at the beginning of the rainy season and the increase in numbers in October 94 was due to the hatching of new juveniles.

Eathworm biomass ranged from 0.24 g m^{-2} (March 94) to 8.76 g m^{-2} (September 95) in the native savanna. In the improved pasture values of biomass ranged from 26.5 g m^{-2} (January 95) to 94.8 g m^{-2} (May 94). A significant correlation was found between monthly values of biomass and precipitation in the improved pasture ($r = 0.821$; $P < 0.01$), but not in the native savanna. The highest values of biomass appeared at the onset of the wet season when all the population was active. In July-August there was a reduction in biomass due to the inactivation of juveniles. At the end of the rainy season values of biomass declined 50% as adults went deeper into the soil to become inactive after emptying their guts.

In the native savanna, M. carimaguensis comprised up the 15.1% of the total earthworm biomass whereas in the improved pasture this value rose to 85.1%. The 84.9 % of earthworm biomass in native savanna and the 14.9% in improved pasture was apported by other native species found along with M. carimaguensis, four endogeics and one epigeic.

No relationship was found between average monthly numbers of individuals and soil moisture, but significant correlations were observed between soil moisture and biomass ($r = 0.651$; $P < 0.01$) and the percentage activity of the overall population ($r = 0.673$; $P < 0.01$).

3.2. Surface cast production

On average, fresh cast production in the improved pasture was eleven times greater than in the native savanna (Table 2). The total dry weight of earthworm casts collected during one year in the native savanna was 31.3 Mg ha^{-1}, whereas in the improved pasture it was 37.7 Mg ha^{-1}.

Both average monthly fresh cast and total cast production were significantly higher ($P < 0.01$, t-test) in improved pasture than in native savanna, reflecting the differences in abundance of M. carimaguensis (Figure 2). Fresh cast production declined during July 94 and July 95 when all the juveniles had already descended some tens of centimetres to enter diapause and only adults remained active. A positive correlation between numbers of fresh casts and the density of individuals in the first 10 cm was observed in the improved pasture ($r = 0.907$; $P < 0.01$).

3.3. Vertical distribution

Data on the vertical distribution of M. carimaguensis are only available for the improved pasture, since abundance in the native savanna was too low to establish patterns of vertical distribution throughout the soil profile. M. carimaguensis ocurred at an average depth of 30.1 cm, with a minimum in May (13.5 cm) and a maximum during the summer (47.6 cm). More than 50% of the total population was located in the top 30 cm and in the wet season more than 80% of individuals were close to the surface where the organic matter content is higher. Cocoons were layed at a depth of 20 to 50 cm. In Figure 3 the vertical distribution of the overall population in some periods is shown.

3.4. Adaptation to the dry season

M. carimaguensis showed interesting behaviour, with a true diapause, although different patterns were found between adults and juveniles. The latter were only active for four months, from April to July, so they entered diapause much earlier than adults which remained active until December (for 8 months). Inactivation occurred after the individuals went down to 60-110 cm depth. Each individual built an aestivating chamber at the end of its semi-permanent burrow in which it coiled itself up, after emptying its gut, and ceased activity until the onset of the wet season. The end of the burrow was usually sealed with several septae to avoid loss of tegumental moisture, which is vital to support a minimal rate of respiration. The degree of activity during the whole study period is shown in Figure 4. In the second year of study there seemed to be a delay in resumption of activity as the rainfall in April 95 (155.7 mm) was very similar to that in March 94 and approximately 60% of the population was active. By May 95 the entire population was active again.

3.5. Reproductive strategy

In August, after juveniles became inactive, adults started the reproductive period and one month later the first cocoons were deposited at 20-50 cm depth. Cocoons collected in the field, nearly always from pasture sites and incubated under laboratory conditions were found to have a maximum incubation period of 48 days. The incubation time was long compared to other tropical earthworms since they are exposed to minimal environmental fluctuations at that depth.

The cocoons were yellowish, becoming slightly brown just before hatching, oval in shape (25x15 mm) and weighing on average 1804 mg. Two individuals (1.91 ± 0.3; n = 46), with an average weight of 760 mg, hatched out from each cocoon and rapidly burrowed down to enter diapause.

The fecundity (number of cocoons per adult per year) was somewhat low (c. 0.49) though the cocoon weight: adult weight ratio was 0.19, the highest ever recorded in temperate or tropical ecosystems . A single cocoon peak was observed in August 94 just after juveniles descended into the deeper soil layers and adults started the reproductive period (Figure 5).

4. Discussion

To date no studies have considered the population dynamics of anecic species in tropical soils and their response to changes in natural environments. Most references deal with exotic species that have been introduced by man, e.g. P. corethrurus (Lavelle et al., 1987) or D. bolaui (Senapati, 1980; Sahu et al., 1988).

M. carimaguensis is an endemic species in the well-drained savannas of Carimagua. It may be considered as an anecic species, as defined by Bouché (1972) and Lavelle (1981), being of large size, dorsally pigmented, and litter feeding and surface-casting through opened semi-permanent burrows. After heavy rains they are normally observed on the soil surface.

There is little information on the population dynamics of anecic species in other comparable sites. Data from Lavelle (1978) in the savannas of Lamto, Ivory Coast, show that the anecic species Millsonia lamtoiana (Omodeo et Vaillaud, 1967) ranged in density from 0.02 ind. m^{-2} to 1.43 ind. m^{-2} and from 0.01 g. fresh weight. m^{-2} to 8.43 g. fresh weight. m^{-2} in biomass, very similar values to those obtained in the present study.

Soil moisture is the most important of all environmental variables for earthworms in tropical soils (Lavelle, 1983**)**. Garnsey (1994) also reported a correlation between earthworm biomass and soil moisture in the Midlands of Tasmania. A relationship between soil moisture content at different depths and numbers of individuals must be sought since no relationship was obtained between average monthly abundances and soil moisture.

M. carimaguensis has a patchy distribution pattern with high density spots alternating with low density areas (Jiménez, unpubl.). There is strong evidence for vertical migration of this species during unfavourable conditions, with the population as a whole reaching 80 cm depth before the onset of the summer. Both juveniles and adults obtain the enough energy for their metabolic processes; the former to enter a facultative diapause mainly in August and the latter to initiate the reproductive period followed by cocoon deposition. The ability to aestivate before the onset of summer and to construct deep semi-permanent burrows explain why the population is less affected by drought and is able to maintain its density during the dry season.

Earthworm aestivation has been observed throughout in temperate regions (Evans and Guild, 1948; Nordstrom, 1975; Anderson, 1980), in Africa (Madge, 1969) and in Australia (Garnsey, 1994), but this is the first time it has been studied in SouthAmerican glossoscolecid earthworms.

Soil surface casting activities have been reported by Madge (1969) and Lavelle (1978), although there are few reports dealing with cast production by earthworms in agroecosystems (Bhadauria and Ramakrishnan, 1989). Watanabe and Ruaysoongnern (1984) reported 24.5 Mg ha^{-1}. $year^{-1}$ of cast material, less than obtained here in both systems, and 15.7 to 40 Mg ha^{-1}. $year^{-1}$ in 5 and 15-year old fallows, respectively (Bhadauria and Ramakrishnan, 1989).

Despite no data on carbon and nutrient dynamics are presented here, the anecic effect of this earthworm must be taken into account since it is of the utmost importance in regard to cycling of carbon and nutrients. Grass-legume pastures need the nitrogen input provided by the legume. When the N content is high the C/N ratio is reduced and in soils with low C/N earthworm densities decline (Kale and Krishnamoorthy, 1981). But pastures at Carimagua are also introducing C into the soil (Fisher et al., 1994) so the C/N ratio becomes higher and this may, subsequently, be related to an earthworm increase. The C/N ratio in the savannas is 25, three times greater than in temperate soils, and the C/N ratios for tropical pastures with and without legumes are 30 and 35 respectively (Fisher, pers. comm.). Further studies must be focused on the role of earthworm activities in carbon and nutrient cycling.

It has been also observed that grass and legume roots colonize the casts that are in the burrows, and that a small Ocnerodrilidae oligohumic earthworm feeds upon these casts (Jiménez et al., 1994). To date no data are available on the interrelations among earthworms, casts in burrows and roots located very close to these casts in the soil profile. We consider this task of great relevance if *M. carimaguensis* is proved to be, in part, responsible on the growth of these roots, and so contributing to incorporate Carbon into the soil.

Grasslands are known to support high earthworm populations and biomass (Lee, 1985; Syers and Springett, 1983). Litter composition is the first factor determining these high values (Cuendet, 1984; Mishra and Ramakrishnan, 1988). Differences in the litter quality and a great amount of cow dung, which is rapidly incorporated into the soil by this species and dung beetles, may also be factors responsible for the enhancement of *M. carimaguensis* activity in improved pastures.

Despite the low density of this species and the low number of fresh casts in the native savanna, the weight of total casts collected during one year does not differ much from that in improved pasture. Perhaps in the latter system the high activity of earthworms leads to a reingestion of their own casts, after a microbial incubation has ocurred (Swift et al., 1979).

Finally, improved pastures have greatly enhanced soil micro- and macrobiological activity which in turn improves chemical and physical properties, i.e., soil quality parameters. Recent studies at Carimagua are considering the possibilities of management in agricultural plots where zones of great earthworm activity, i. e. improved pastures, are placed adjacent to annual crops in order to facilitate the spread of populations and colonization of those systems. Since Lavelle et al. (1994) have provided a better understanding of local soil faunal activities and the potential use of native species in tropical agroecosystems, we suggest that further studies should take into account the influence of such activities on both physical and chemical soil properties.

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Table captions

Table 1. Average values of density and biomass of M. carimaguensis in g m^{-2} in the two systems studied.

Table 2. Monthly average production of casts by M. carimaguensis per m^2 (numbers ± Std. dev.) in the two systems.

Figure captions

Figure 1. Abundance and biomass of M. carimaguensis in the native savanna and improved pasture.

Figure 2. Monthly average number of fresh casts per m^2 of M. carimaguensis.

Figure 3. Vertical distribution of M. carimaguensis in improved pasture in May 1994 (a), July 1994 (b), November 1994 (c) and January 1995 (d).

Figure 4. Activity of the total population of M carimaguensis in improved pasture (Arrows indicate months with subestimated values).

Figure 5. Monthly total number of cocoons obtained in improved pasture during the whole study period.

Table 1

Average values of density and biomass of M. carimaguensis in g m^{-2} in the two systems studied.

	Native savanna	Improved pasture
Density	0.22 ± 0.3	17.89 ± 4.3
Biomass	0.64 ± 1.0	52.56 ± 20.33

Table 2

Monthly average production of casts by M. carimaguensis per m^2 (numbers ± std. dev.) in the two systems.

Condition	Native savanna		Improved pasture	
	Wet season	Study period	Wet season	Study period
Dry casts	7.15 ± 3.5	6.38 ± 3.4	20.38 ± 7.9	17.35 ± 8.9
Recent fresh casts	0.31 ± 0.5	0.23 ± 0.5	3.25 ± 3.8	2.48 ± 3.6
Non recent fresh casts[1]	0.12 ± 0.2	0.09 ± 0.21	1.77 ± 2.1	1.39 ± 2.0
Total	7.58 ± 3.6	6.72 ± 3.6	25.43 ± 10.3	21.21 ± 11.9

[1] Fresh cast with a dry basis.

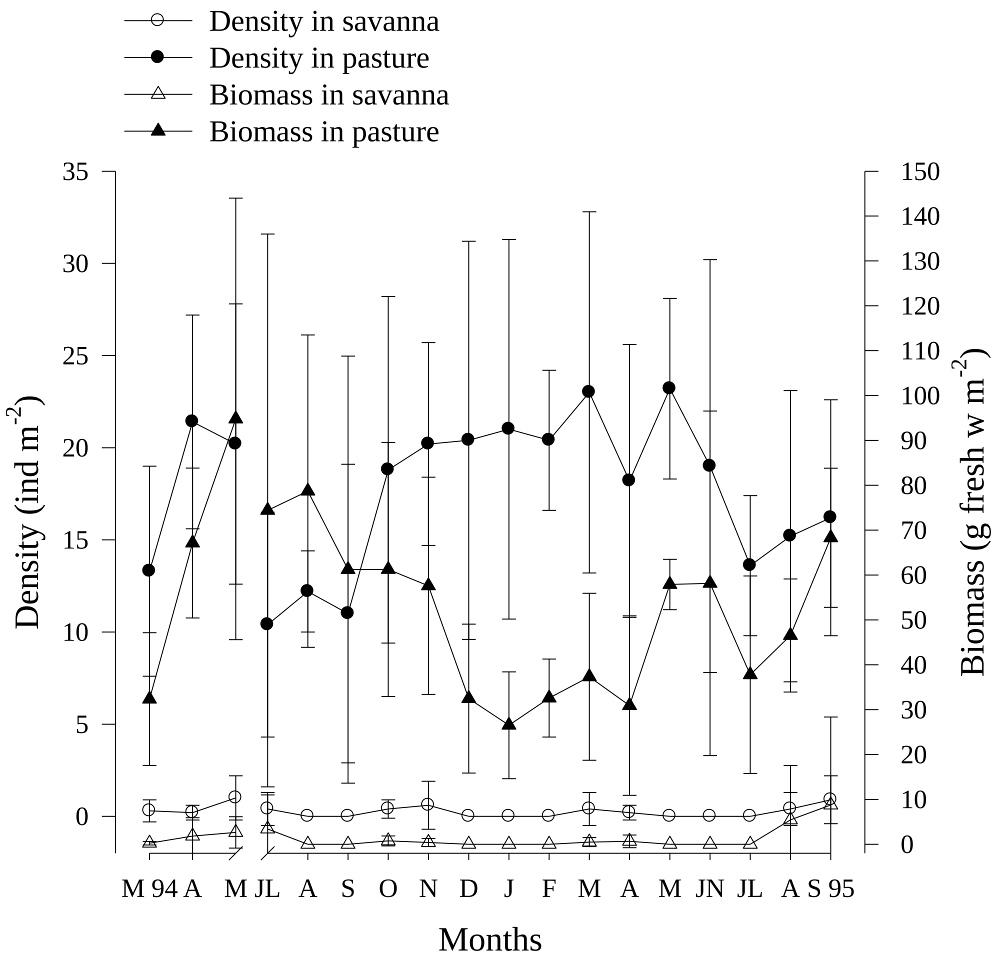
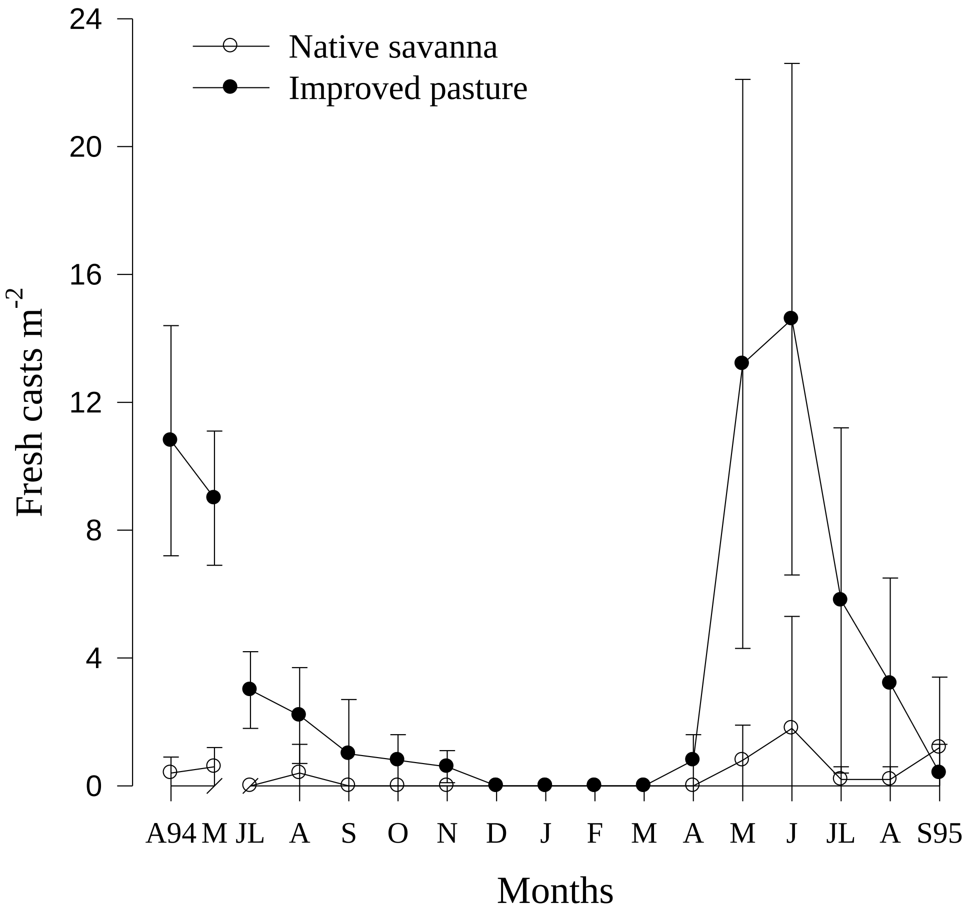
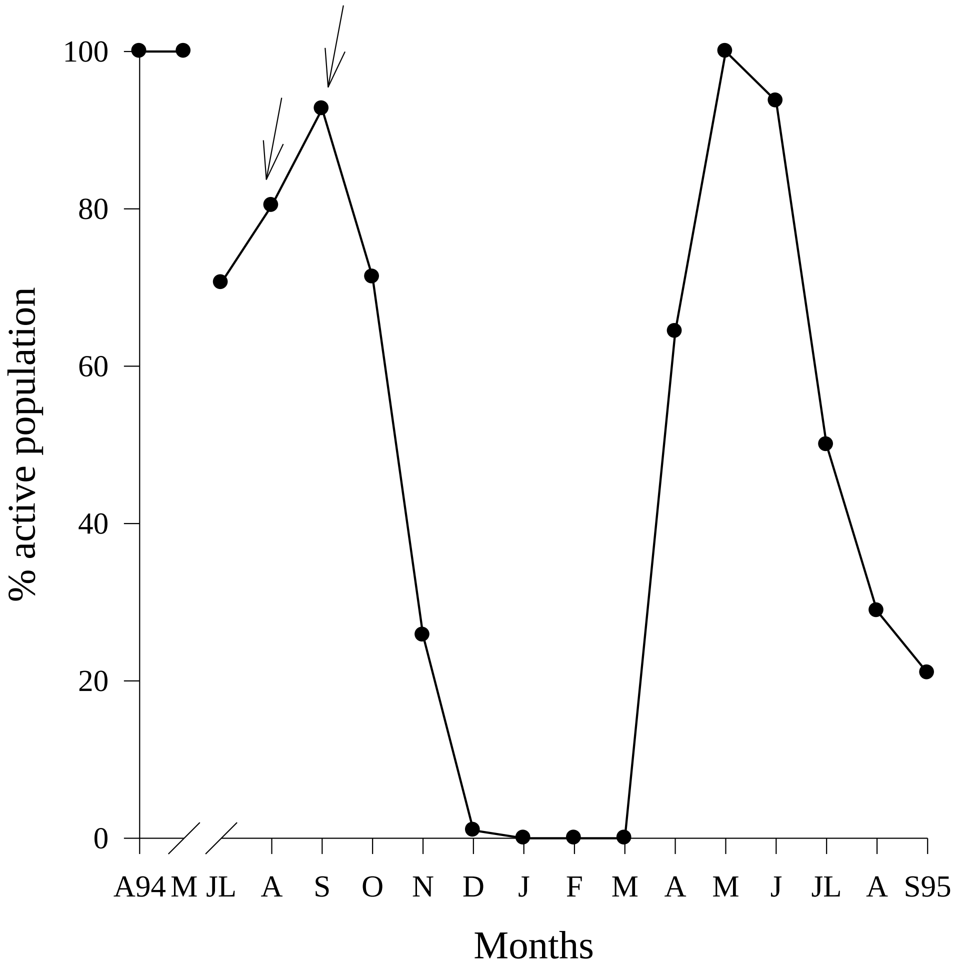

Density in savanna
Density in pasture
Biomass in savanna
Biomass in pasture
Density (ind m-2)
Biomass (g fresh w m-2)
0
5
10
15
20
25
30
35
0
10
20
30
40
50
60
70
80
90
100
110
120
130
140
150
M 94 A M JL A S O N D J F M A M JN JL A S 95
Months

Figure 1



Native savanna
Improved pasture
24
20
16
12
8
4
0
Fresh casts m-2
A94
M
JL
A
S
O
N
D
J
F
M
A
M
J
JL
A
S95
Months

Figure 2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80
60
40
20
0
% active population
A94 M JL A S O N D J F M A M J JL A S95
Months

Figure 3

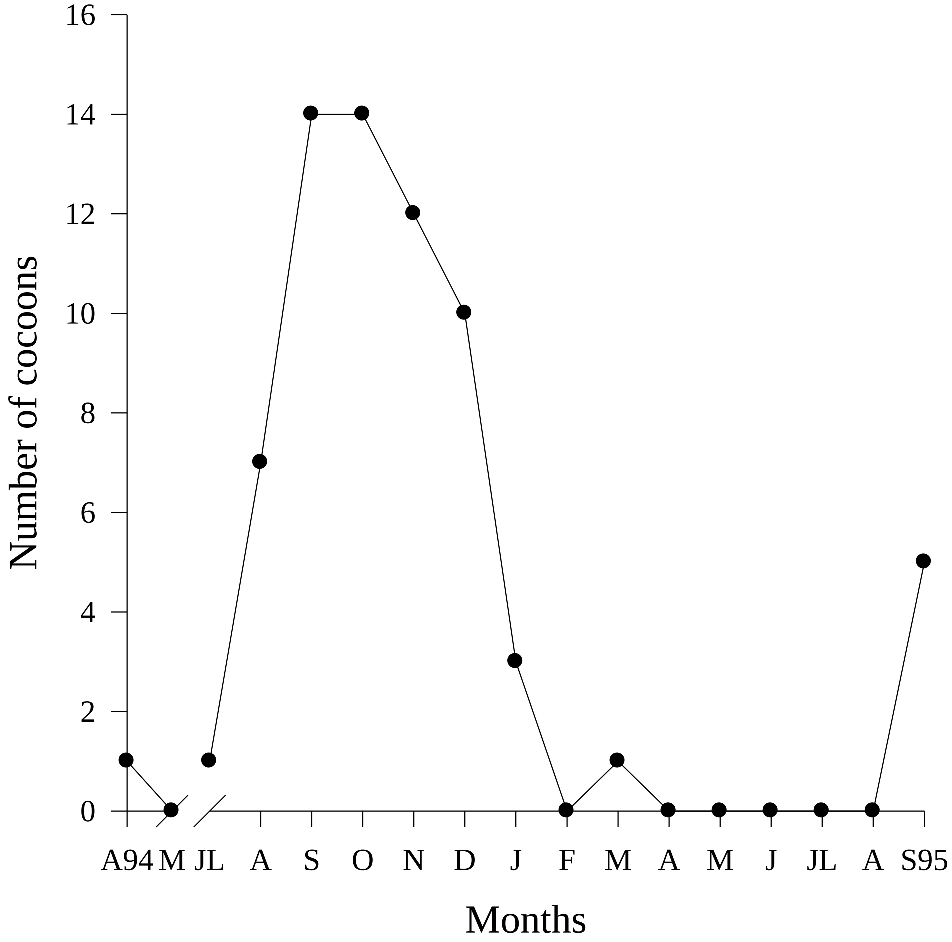

16
14
12
10
8
6
4
2
0
Number of cocoons
A94
M
JL
A
S
O
N
D
J
F
M
A
M
J
JL
A
S95
Months

Figure 4

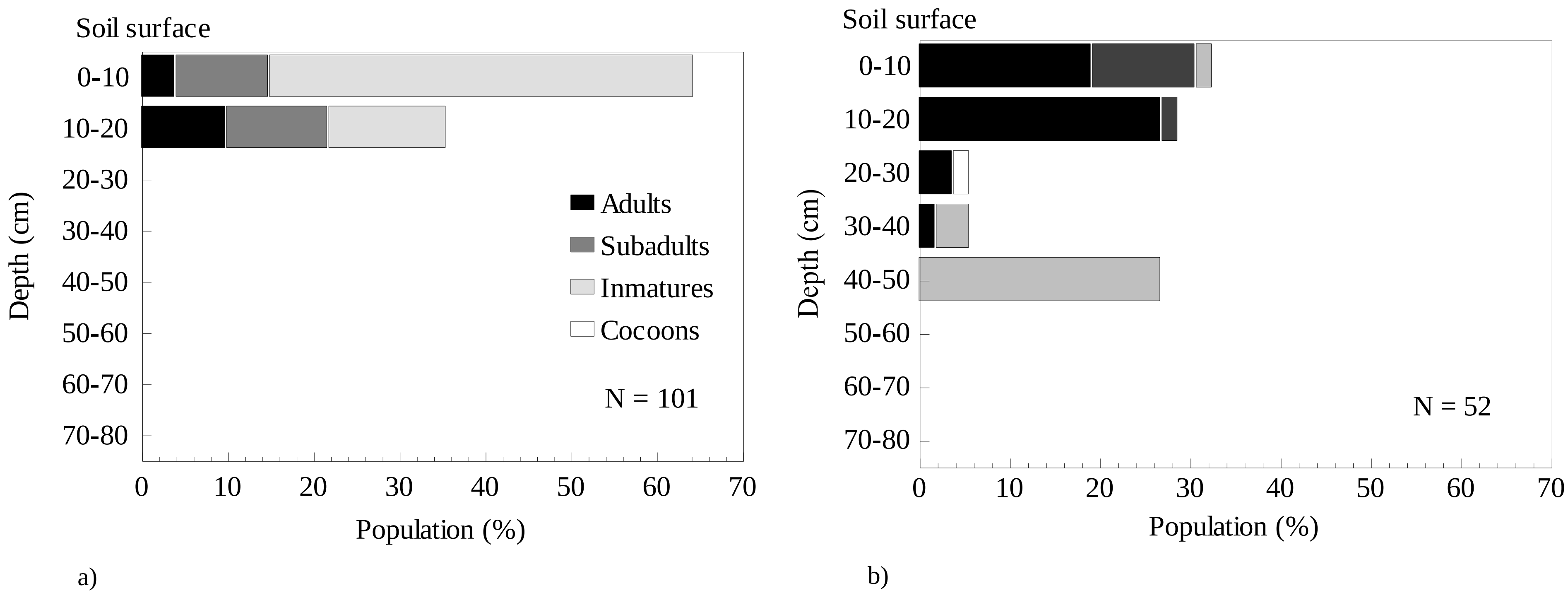
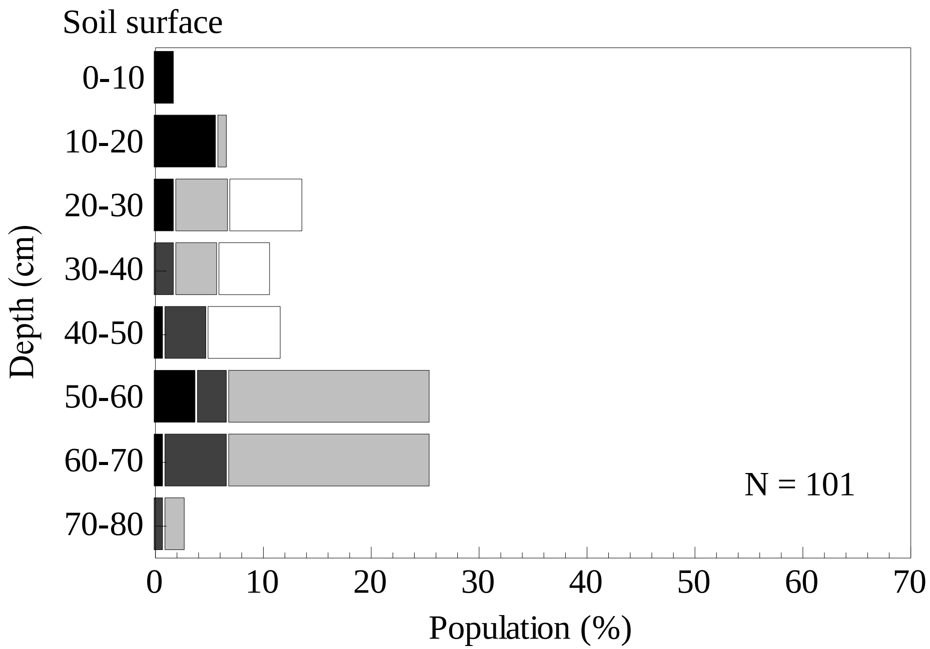
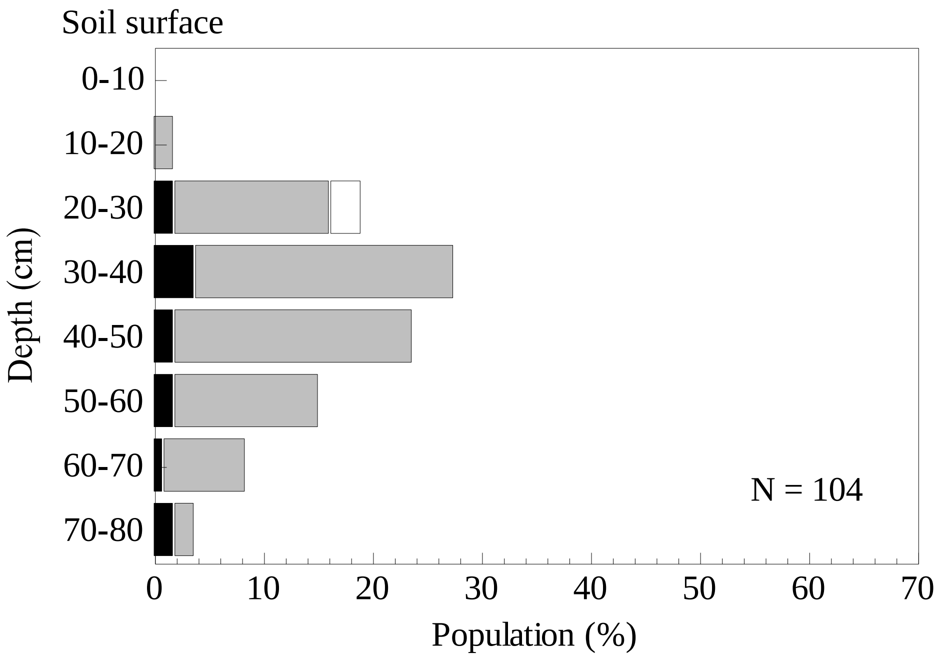

Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
Adults
Subadults
Inmatures
Cocoons
N = 101
0
10
20
30
40
50
60
70
Population (%)
a)
Soil surface
Depth (cm)
N = 52
Population (%)
b)

Figure 5


Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
N = 101
0
10
20
30
40
50
60
70
Population (%)

c)


Soil surface
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Depth (cm)
N = 104
0
10
20
30
40
50
60
70
Population (%)

d)

Figure 5