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Original article

Comparative analysis of *Andiodrilus pachoensis* casts in forests and pastures of South-Eastern Amazon (Brazil)

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ABSTRACT

Soil ecosystem engineers produce biogenic structures (casts, mounds, galleries) that strongly affect soil processes. A comparative analysis of the physical characteristics of the casts produced by the earthworm *Andiodrilus pachoensis* was carried out in four pastures sowed with *Brachiaria brizantha* and four primary forests on the deforestation front of the Amazonian forest. In both systems, we recorded surface cast density and spatial patterns as well as surface cast physical properties. Cast and vegetation distributions were mapped within plots of sizes ranging from 25 to 50 m², and cast production was monitored during 2 months. Cast spatial distribution varied greatly among plots and across spatial scales ranging from regular at small spatial scales (0–20 cm) to clumped for larger distance ranges (>80 cm). Cast density was not significantly correlated with grass tuft density and their production was independent from the presence of grass tufts in pastures or litter quantity in forests. Although bulk soil properties (pH, C content, structural stability, etc) differed between pastures and forests, cast physical properties did not differ significantly among the studied ecosystem.

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1. Introduction

The current rate of deforestation in the Brazilian Amazonian plain is considered a major environmental concern with dramatic consequences for both wildlife biodiversity and human welfare. In 1978, forests covered nearly 4 millions of km² in this region, a surface that was decreased by 18% in 2006. From 2001 to 2004, an average of 25 000 km² of forest were cleared every year [29]. Family farming has been pointed as one of the main factors responsible for forest clearance [1,12,55] as deforestation is the traditional practice that precedes the set up of slash-and-burn agriculture [22,49,55]. It is well known that land-use changes and especially deforestation followed by culture settlements greatly affect soil physical and chemical properties [2,14,36] as well as the diversity and activity of soil biota [7,28]. In many cases, these changes have been reported to induce severe soil degradation with dramatic impacts on the sustainability of agricultural systems [34,50,61].

Soil functioning results from complex interactions between physical, chemical and biological factors [40]. Soil ecosystem engineers (mainly earthworms, termites, and ants) are organisms that modify the properties of their physical environment by producing organo-mineral structures called biogenic structures (e.g. casts, mounds, galleries, etc) [18,21,35,39]. As an example, earthworm casting and burrowing activities are known to affect soil profile development and soil structure dynamics and to modify soil physical properties such as porosity and aggregation [7,25,54]. By doing so, earthworms usually improve water and air circulation within the soil profile and enhance soil resistance to erosion [11,37], although opposite effects have been reported in some cases [17]. In this context, cast features and dynamics (abundance, size, production rate, spatial distribution, degradation dynamics, etc) are important parameters that mediate earthworm effects upon their environment. The study of cast physical properties such as structural stability and rainfall sensitivity allow understanding how environmental factors affect their degradation dynamics and the way they affect soil functioning.

Many studies already reported that earthworm community structure and activity are sensitive to land-use types and agricultural practices [24,31,42]. Besides, earthworm populations have often been reported to be spatially clumped [20,57]. Rossi and Nuutinen [59] also reported the presence of spatial autocorrelation in earthworm biostructures (i.e. middens) within a forest of Finland. These spatial patterns have been mainly explained by environmental heterogeneity (e.g. soil hydromorphy [13]), interspecific competition [30,33] and population self-organization [6,52]. How these patterns respond to land-use changes, and how they drive the spatial location of surface casting and its impact on soil heterogeneity are questions that have been seldom addressed in past studies.

In this study, we aimed at investigating how deforestation may affect the nature and strength of the impact on soil functioning of the anecic earthworm *Andiodrilus pachoensis* (Michaelsen, 1900). This question was explored by (i) analysing the abundance and spatial distribution of the surface casts

that *A. pachoensis* produces in primary forests and in young pastures settled after deforestation, (ii) comparing physical properties of these casts to those of the superficial bulk soil, (iii) comparing the properties of casts produced in both ecosystems, and (iii) identifying the factors responsible for the degradation of surface casts (cattle trampling and rainfall). We also assessed the relationship between cast production and litter quantity in the forest and between cast production and grass tuft density in pastures.

2. Material and methods

2.1. Study site

The study was undertaken in the locality of Benfica (5°16'S; 49°50'W) in the state of Pará, Brazil. Climate is tropical humid with a mean rainfall of 1800 mm and a dry season from July to November. The region comprises a hilly landscape covered by a mosaic of forest patches and 5–6 years old pastures. Soils are clayey-sandy ferralsol [33,65] with iron and aluminium oxides. The study plots were located on hill tops where the ferralsol permeable B horizon (with a well-developed microstructure) is deeper than 2 m. The B horizon of these soils, already described in other studies [5,62], displays a uniform microgranular structure, usually attributed to soil fauna activities, and was investigated using standard soil profile observation. Study plots were localised in two contrasted land-use systems: (i) slightly exploited primary forests where farmers hunt and export some trees for personal use; mean trees up to 15 cm diameter density was estimated at about 5400 per ha; (ii) pastures sowed just after deforestation with *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf (1919) (cultivar marandu), permanently grazed by cattle and burnt once a year during the dry season. Grass tufts were clearly separated from one another by bare ground, producing a kind of clumped vegetation cover with high spatial heterogeneity.

The bulk density of the first 30 cm soil layer was higher in pastures (1.45 g cm⁻³) than in forests (1.20 g cm⁻³). This compaction expresses a loss of 17% of the total porosity in the forest soil as a consequence of farming system establishment and management [3]. In all the selected plots, carbon content was low (less than 5%) in the 0–10 cm layer. Surface soil acidity was significantly greater in forests (pH = 4.0) than in pastures (pH = 5.27) (t test, $p = 0.003$), likely as a result of a lower Al³⁺ concentration in pastures (0.56 cmolc kg⁻¹) compared to forests (2.01 cmolc kg⁻¹) and to an increased sum of basic Ca²⁺, Mg²⁺ and K⁺ concentrations ($S = 2.59$ cmolc kg⁻¹ in pastures and $S = 0.63$ cmolc kg⁻¹ in forests). The CEC did not differ significantly between the two systems (6.0–7.2 cmolc kg⁻¹). In all studied plots a ferralsol permeable horizon was observed below 60 cm depth, which was characterised by a polyedric sub-angular structure with microaggregated sub-structure sometimes above an ironed reddish nodules layer.

2.2. Soil fauna and *A. pachoensis* casts

Soil macrofauna is composed by soil animals of body sizes ranging from 2 to 100 mm. Macrofaunal communities at the

study site have been previously described by Mathieu et al. [46,47], who found a higher invertebrate density in forests compared to pastures. They also described that pasture establishment significantly modify macrofaunal community composition, which species richness dropping from 76 species in primary forests to 30 species in recently sowed pastures. Ants, termites, and spiders were the more affected by agricultural disturbance, while no significant impact was observed for earthworms [47].

A. pachoensis (Glossoscolecidae) is an anecic earthworm (i.e. a species that lives in vertical burrows and consume litter at the soil surface) that is present in both forests and pastures at densities of 3 and 13 ind m⁻², respectively (Mathieu, unpublished data). It is a large species with an average adult body length of c.a. 200 mm. Its cutaneous pigmentation is dark-grey on the dorsal-side and light-grey on the ventral-side. It builds vertical galleries and deposits easily recognizable piles of cast material at the soil surface. Casts are generally produced in less than 1 week in several deposition events (Thomas, personal observation). This generates an important physical and chemical disparity between old and fresh sections of a given cast, but this heterogeneity progressively disappear sometimes after cessation of cast formation process. Casts can reach 12 cm in height and present a central canal which corresponds to the earthworm gallery. Field observations showed that these casts represent the most abundant type of surface biogenic structures and are common in all the land-use types present at the study site. *A. pachoensis* is the unique large anecic species present at the study site, and is thus the only species likely to deposit such large casts at the soil surface.

2.3. Cast sampling and experimentations

Cast sampling and experimentations were conducted during the rainy seasons of the years 2002–2003. Four independent replicated plots were randomly set in each system, and one individual study plot (referred as “study plot” hereafter) was selected in each of them (F1–F4 for forests and P1–P4 for pastures). Due to technical constraints (presence of tree, decaying trunks, etc) the surface of each study plot varied from 25 to 50 m². We selected: (1) in the forests, one area of 5 × 10 m (F1), one of 3 × 10 m (F2) and two of 5 × 5 m (F3 and F4); and (2) in the pastures, four of 5 × 10 m (P1–P4) plots that were enclosed to protect them from cattle trampling.

Within each study plot, casts were mapped just after plot enclosure by using a regular grid of 100 cm-mesh placed on the study plot to record their spatial coordinates. The same data were used to calculate cast mean density (number of casts m⁻²). Using the same grid, we also mapped grass tufts of *B. brizantha* by recording the spatial coordinates of their centre and their basal circumference. In each system, two plots were randomly selected (F1, F4, P1, P2) and all their casts were removed and weighed to obtain cast individual mean mass.

Surface cast production was assessed by observing the appearance of new casts during a total period of 65 days. In three pasture plots (P1, P3, P4) and two forest plots chosen at random (F1, F4), all surface casts were removed at an initial time (referred as t_0) and newly produced casts were counted at two successive dates ($t_1 = t_0 + 28$ days; $t_2 = t_0 + 65$ days).

Surface cast production was then expressed as the mean number of casts produced per day.

The effect of soil protection by vegetation on surface cast production was assessed in both pasture (protection by herbaceous vegetation) and forest plots (protection by litter). In three pasture plots chosen at random (P1, P3, P4), aerial parts of *B. brizantha* tufts were cut and removed to expose bare soil to rain and sun. Similarly, litter was removed from the soil surface in two forest plots (F1, F4). In all cases, the removing manipulation was done on half of the plot surfaces, the remaining being kept as control (soil with vegetation or litter). We then assessed the impact of grass or litter protection on cast production and distribution by measuring these parameters as described above in both unchanged and bare soil areas.

2.4. Spatial analyses

The spatial coordinates of earthworm casts constitute point-referenced data that were analyzed using the Ripley's $L(r)$ index. This metric averages the number of neighbours within a distance r from a randomly chosen individual [16]. The estimation of $L(r)$ is hampered by edge effects [23] and $L(r)$ estimates were thus corrected using a border correction [56]. Bias in the estimator of $L(r)$ increases with r and depends on study plot geometry. We therefore restricted the r value to a maximum of 1/4 of the smaller side length of the rectangular plots. $L(r) = 0$ indicates a random cast distribution; $L(r) > 0$ denotes an aggregated pattern, while $L(r) < 0$ corresponds to a regular distribution. In order to test the null hypothesis of complete spatial randomness (CSR) we performed a large number of simulations (999) of a Poisson process with density equal to that of the observed data set. Areas corresponding to grass tufts were excluded from the randomization process so that no point could fall within these areas devoid of any cast. For each randomized point pattern, $L(r)$ was computed for every distance lag r and upper and lower critical envelopes were computed by sorting the 999 simulated values, and taking the 25-th lowest and 25-th highest values (i.e. corresponding to 2.5 and 97.5% levels of the overall distribution). For a given distance lag r the null hypothesis is rejected when the observed $L(r)$ value lies outside the envelope. This test has exact significance level $\alpha = 2 \times 25 / (1 + 999) = 5\%$. Computations were done using the R package spatstat [4] under the R system [53].

2.5. Casts and soil physical properties

In each study plots, three to five surface casts and bulk soil samples from the 0–10 cm layer (i.e. the soil layer preferentially ingested by most earthworm species) were randomly sampled to compare their respective physical properties. For each sample (casts and soil), particle size distribution was determined using a standard gravimetry and sieving procedure which separates particles in function of the speed of their gravitational sedimentation in liquid [60]. Total organic carbon was estimated with the Walkley and Black method [51].

We assessed aggregate stability using the Le Bissonnais's method [41] applied to centimetric air-dried aggregates.

This method consists in exposing aggregates to water re-moistening (test 1), water immersion (test 2) and mechanical dispersion after alcohol treatment (test 3). After each test, the material was passed through a column of sieved (0.053-, 0.125-, 0.250-, 0.5-, 1-, 2-, 5- and 10-mm meshes), and each fraction was oven dried for 48 h at 105 °C and weighed. The structural stability was expressed as the mean weighed diameter (MWD) of the stable aggregates.

Cast sensitivity to rainfall impacts was evaluated with a home-made basic rain simulator. Simulated rain presented an intensity of about 25 ml min⁻¹ and a fall-height of 40 cm. Both intact and manually squashed casts (to represent the impact of cattle trampling on casts) were exposed to simulated rainfalls during three different time durations (T1 = 1 min, T2 = 3 min, T3 = 5 min). Times were chosen arbitrarily but advised from Mariani et al. [44]. We thus calculated the percentage of cast mass loss that was induced by drop impacts.

2.6. Statistical analyses

Significant differences between means were assessed using t test and analyses of variance (ANOVA). Non-parametric tests were also used to compare variables which did not conform to normal distributions or homogeneity of the variance: Mann-Whitney (MW) Rank Sum Test (two-group comparison) or Kruskal & Wallis ANOVA (several group comparisons). Tests were made with SigmaStat software (Systat Software, Inc).

3. Results

3.1. Casts abundance and production

Mean cast density was significantly higher in forests (19.0 casts m⁻²) than in pastures (4.2 casts m⁻²) (MW Rank Sum Test, $p = 0.004$), and mean total mass of air-dried casts was more than 10 folds higher in forests (2.86 kg m⁻²) than in pastures (0.26 kg m⁻²) (Table 1). Mean mass of individual cast was also significantly lower in pastures (112 g) than in forests (185 g) (t tests, $p < 0.001$; Table 1).

The production of surface casts was 0.64 and 0.68 per m⁻² per day in grasslands and forests, respectively (Table 1), with no significant differences between both systems. This corresponds to a global annual production of 15.2–26.7 Mg of dry

casts per ha in the pasture and the forest systems, respectively (calculation based on individual cast mass data and on the assumption that earthworm activity period is of 7 months per year).

In pastures, we found no correlation between the number of casts and the density of *B. brizantha* tufts in the study plots (Spearman correlation, $p > 0.05$), and cast production was not significantly modified when grass tufts were experimentally removed (t test, $p = 0.116$, Table 3). Similarly, removing the litter from the forest soil surface did not affect cast production in a significant way (Kruskal & Wallis, $p = 0.8$) (Table 1).

3.2. Cast spatial patterns

Cast spatial patterns were highly variable according to habitat type, plots and dates (Fig. 1,2). Fig. 2,3 shows the Ripley's function for four plots and illustrates the diversity of the patterns found in this study. In the forest plots, spatial patterns were regular at short spatial scales, i.e. for distances <15–20 cm (Table 2; Figs. 1 and 2) and mainly random at larger scales, except in one situation where a clumped distribution was observed (Table 2). In pastures, herb tufts represented a sizeable proportion of the plot surface (Fig. 1), and cast distribution exhibited randomness at short-scales (0–15 cm), except for one plot where they were regularly spaced for distances <15 cm. At larger scales cast distribution was mainly random, except for one plot where it was aggregated for both intermediate and long-range distances (Table 2; Fig. 2).

3.3. Cast properties

The particle size distribution of surface casts did not differ significantly from that of the control bulk soil (Table 3). Samples were mainly composed by clays, which comprised from 44.5 to 48.8% of the total sample mass in casts and from 37.6 to 48.7% of the total sample mass in control soil. Coarse sand proportion ranged from 28.9 to 32.8% in casts and from 36.1 to 45.5% in control soils. Soil of both the forest and the pasture plots showed sandy-clayey texture (Table 3), whereas casts had a slightly finer texture.

Mean diameter of stable aggregates was higher in pastures than in forests in control soils, while no difference was observed among systems for cast aggregates. In both systems, cast aggregates were very stable (more than 60% of the

Table 1 – Mean production characteristics of the surface casts produced by *Andiodrilus pachoensis* in the forest and pasture plots

System	Number of casts m ⁻²	Casts mass (kg m ⁻²)	Mean individual mass of casts (g)	Cast production in unmanipulated areas (casts m ⁻² year ⁻¹)	Cast production in cleared areas (casts m ⁻² year ⁻¹)	Global cast production (mg ha ⁻¹ year ⁻¹)
Forest	19.0 (1.9)	2.86	185	0.066a	0.089a	26.7
Pasture	4.8 (0.6)	0.26	112	0.066a	0.050a	15.2
p Values	0.004	–	<0.001	NS	NS	–

Standard errors into brackets; p values refer to the significance levels obtained for mean comparisons between systems; for the cast production data, different letters indicate significant differences between production in unmanipulated and cleared areas.

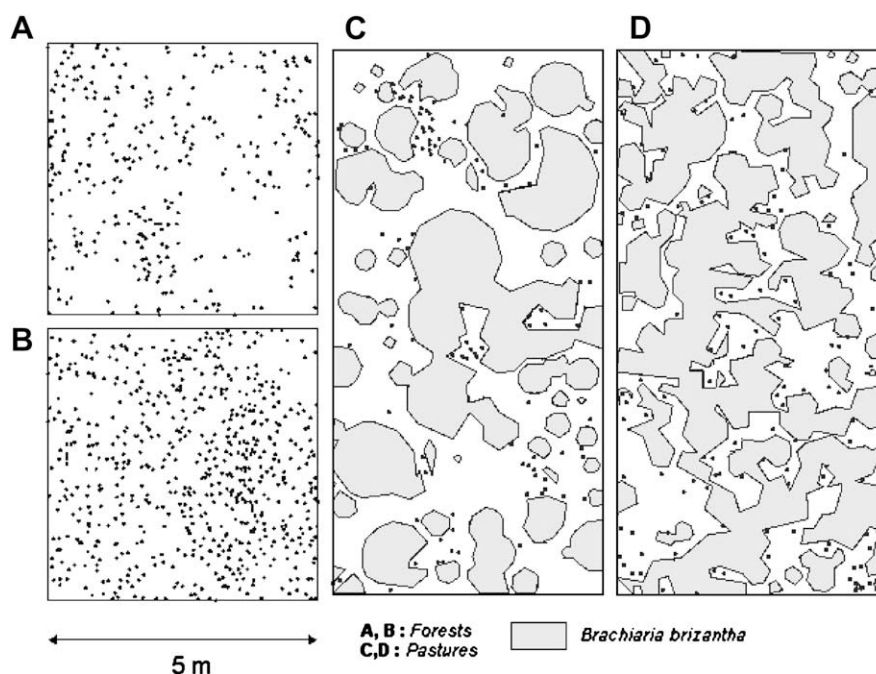


Fig. 1 – Locations of surface casts of *Andiodrilus pachoensis* and *Brachiaria brizantha* tufts in forest and pasture plots. One point = one cast. A and B: Forest plots (F1 and F4, respectively); C and D: Pasture plots (P1 and P2, respectively). Grey areas = *Brachiaria brizantha* tufts.

aggregates corresponded to the superior 2 mm class) when compared to control bulk soil, indicating that classical stability tests did not succeed to disperse cast particles (Fig. 3).

In both systems, control soil was very sensitive to the effect of simulated rains, while dried casts presented a great

cohesion and resistance (Fig. 4). Neither a higher intensity nor a longer simulation time induced significantly higher erosion. Only squashed casts appeared to be more sensitive to simulated rainfalls (32% of mass loss after 3 min of rain exposure).

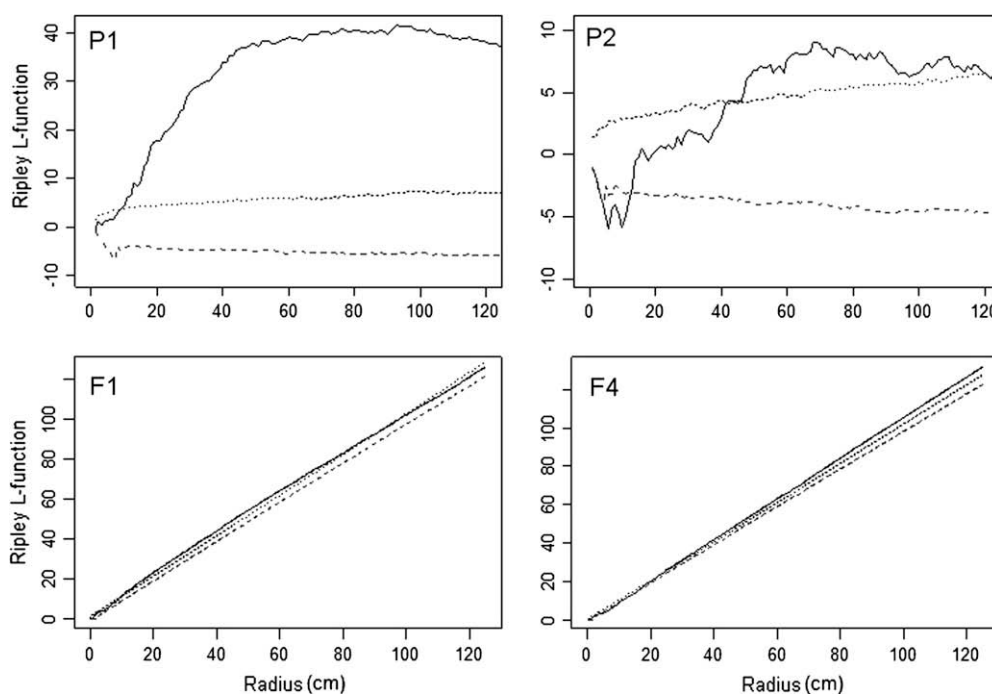


Fig. 2 – Spatial pattern of *Andiodrilus pachoensis* surface casts distribution in two pasture and two forest plots illustrated by the corrected edge effect Ripley's L function in its 95% confidence interval. Plain line = Ripley's L function of cast distribution; dashed line = lower bound of the 95% envelope; dotted line = upper bound of the 95% envelope.

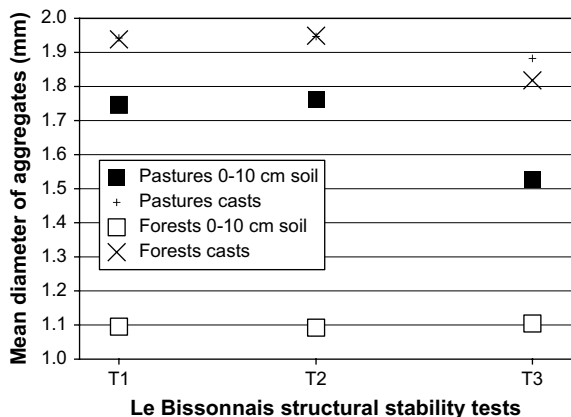


Fig. 3 – Mean weighed diameter of *Andiodrilus pachoensis* surface casts and control soil (0–5 cm) aggregates after the three Le Bissonnais & Souder tests of aggregate stability. T1 = water immersion test; T2 = water re-moistening test; T3 = dispersion test after alcohol treatment.

Organic carbon content ranged from 51 mg g^{-1} in forest casts to near 60 mg g^{-1} in pasture ones (t test, $p < 0.001$). In both systems, observed values were also significantly higher in casts when compared to control soil (about 21.6 mg g^{-1} in forests and 18.7 in pastures in the first 10 cm of soil) (t test, $p < 0.001$) (Table 3). As a result, based on our estimation of cast production, the total amount of carbon deposited in surface casts of *A. pachoensis* may range between $0.91 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in pastures and $1.47 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in forests.

4. Discussion

Our results highlight the impact of deforestation on surface casting activities performed by the earthworm *A. pachoensis* and provide information about the potential consequences forest conversion into pastures may have on earthworm engineering activities and soil functioning.

The total dry masses of earthworm casts observed in our study (28.6 Mg ha^{-1} in forests and 2.6 Mg ha^{-1} in pastures) are in the range or lower to what has been reported by Jiménez et al. [32] in savannas and pastures of Eastern Colombia

(values of $31.3\text{--}37.7 \text{ Mg}$ of dry casts per ha, respectively). Our estimations of cast production ($15.2\text{--}26.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in pastures and forests, respectively) also correspond to what is usually found in tropical ecosystems, e.g. $21.8\text{--}27.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in savannas of Côte d'Ivoire [38], $24.5 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in forests of North Eastern Thailand [66], and $14\text{--}114 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in Colombian savannas and pastures, respectively [19].

That earthworm cast density and global mass production were higher in forests than in pastures is surprising since the observed population density of *A. pachoensis* was lower in the former system (Mathieu, unpublished data). Global mass production was strongly correlated with the individual mass of casts, which was in fact higher in forests than in grasslands. Intraspecific differences in cast size and mass may reflect the quality of the available food substrate [32]. To fulfil their energetic requirements, earthworms feeding on low quality substrate will in fact ingest more soil and thus deposit more casts than others feeding on a high quality resource. This was illustrated by Curry and Schmidt [15] who compared soil ingestion rates of different species feeding on soils with different organic matter contents. These authors also pointed that some species can compensate for inadequate soil organic matter content to an extent by increasing soil consumption rates. This is for example the case for the large anecic *Martiodrilus* sp. in the Eastern Plains of Colombia, which is known to present a high diet variability [43] and to produce larger casts in soils with low organic content [32]. Although we found no significant differences in soil C content between pastures and forests, a higher quality and palatability of pasture litter may have accounted for differences in cast individual mass and may thus partly explain the higher global mass production found in forests.

On the other hand, cast density at the soil surface may also reflect cast life expectancy (half-life time), which is known to be strongly affected by environmental factors that differ between both systems [17]. By comparing cast production levels to their density at the soil surface, we estimated that cast life expectancy may range from 2 months in pastures to more than 1 year in forests. This is similar to the results found by Decaëns [17] who reported half-life of surface casts ranging from 2 months in grazed pastures to 11 months in natural savannas protected from animal trampling. They suggested that cast production and longevity may be strongly influenced

Table 2 – Spatial distribution of the surface casts of *Andiodrilus pachoensis* in the forest and pasture plots (results are derived from analyses of Ripley's L function)

System	Spatial scales		
	Short-range	Intermediate	Long-range
Forest	Regular (4; $d < 10\text{--}20 \text{ cm}$)	Random (3; $d = 20\text{--}90 \text{ cm}$) Clustered (1; $d = 20\text{--}120 \text{ cm}$)	Random (3; $d > 90 \text{ cm}$) Clustered (1; $d > 120 \text{ cm}$)
Pasture	Regular (1; $d < 15 \text{ cm}$) Random (3; $d < 10\text{--}15 \text{ cm}$)	Random (3; $d = 15\text{--}45 \text{ cm}$) Clustered (1; $d = 20\text{--}120 \text{ cm}$)	Random (3; $d > 45 \text{ cm}$) Clustered (1; $d > 120 \text{ cm}$)

The nature of the spatial distribution (random, clustered or regular) is indicated at three spatial scales. The number into parentheses corresponds to the number of plots that corresponded to the specified distribution. The distance (d) ranges at which each type of distribution was observed are also specified.

Table 3 – Particle size distribution and carbon content (in g per 100 g) of *Andiodrilus pachoensis* surface casts and control soil (0–10 cm layer) in forests and pastures (S.E. in brackets)

	Forests		Pastures	
	Casts	0–10 cm layer	Casts	0–10 cm layer
Clay	48.8 (±1.3)	48.7 (±3.6)	44.5 (±5.9)	45.9 (±5)
Fine silt	4.0 (±0.1)	3.7 (±0.4)	13.2 (±5.8)	2.6 (±1.3)
Coarse silt	2.6 (±0.1)	1.8 (±0.1)	2.6 (±0.1)	1.7 (±0.2)
Fine sand	11.8 (±0.6)	9.7 (±0.1)	10.8 (±0.4)	9.8 (±0.7)
Coarse sand	32.8 (±2.1)	36.1 (±4.2)	28.9 (±2.8)	40.0 (±5.9)
Carbon content	51.1 (±2.0)	21.4 (±1.2)	59.9 (±4.0)	15.1 (±3.5)

by different factors including: (1) the protection of casts by litter and vegetation, which prevents cast destruction due to raindrop impacts; (2) the intensity of cattle trampling; (3) the activity of small soil invertebrates that dig burrows into large earthworm casts and accelerate their degradation dynamics. In our study, the same mechanisms may operate to reduce half-life and density of surface casts in grasslands when compared to forests.

The higher structural stability of surface casts of *A. pachoensis* compared to the bulk soil broadly supports the

idea that dry earthworm casts are stable and impermeable biogenic structures [10,26,64]. Although surface casts are known to be sensitive to dispersion by rainfall when fresh, they progressively acquire a high stability when experiencing successive dry/humid events during their ageing process [27,44,63,67]. Intact casts did not appear to be sensitive to structure stability tests and rainfall simulations. When their structure was lost by crushing, they were significantly more sensitive to simulated rainfall events. Although intact casts presented a higher resistance to rainfall, casts previously destroyed by animal trampling were more intensively dispersed during simulations, suggesting that a significant proportion of these casts may be dispersed by rainy events in field conditions.

An interesting result of our study is that despite we found significant differences in soil structural stability between forests and pastures, cast stability was the same in both systems. The specific properties of the aggregates produced by *A. pachoensis* thus seem to be relatively independent from the nature of the initial soil substrate. This concord with the work of Decaëns [17] who found that the casts produced by *Martiodrilus* sp. presented a similar structural stability whatever the system considered. It suggests that engineering activities by earthworms may operate as a buffering factor on the soil structure submitted to different land-use practices.

Spatial analyses clearly showed that cast distribution at the soil surface is scale dependent and highly variable between and within management systems. Variability among systems was probably linked to significant differences in local factors such as the soil compactness, food distribution at the soil surface, or the presence of grass tufts. As an example, the degree of soil compaction, which creates local physical heterogeneity, may explain differences between pasture plots as reported for cultivated soils in temperate areas [8].

In all our forest plots, cast spatial distribution was regular at a short spatial scale (i.e. for distances <20 cm) and random to aggregated at both intermediate and long-range scales. This kind of distributional pattern partially agrees with the prediction of Moody et al. [48] that most animals should exhibit regularity at small and aggregation at large scales. We hypothesise that regular patterns at small spatial scales reflect intraspecific competition for food resource that imposes a minimal distance between burrow entries (and thus between casts). Intraspecific competition may for example occur when a single individual forages in the immediate vicinity of its burrow opening, thus depleting litter resource for other conspecific individuals. This has been reported for e.g. territorial spiders, which maintain a certain distance to neighbours, leading to a regular spatial pattern through social spacing [9,45]. In pastures, the predominantly random short-range distribution of surface casts suggests that earthworm density was too low to observe significant intraspecific interactions. The fact that we detected aggregation only in a reduced number of plots for intermediate to long-range distances may be easily explained by the overall short scale of our study. In fact, the well known aggregated structure of earthworm communities, at distance ranges of a few 10 m [20,58,59], was probably above the spatial resolution of our study. This highlights the fundamentally scale dependent nature of earthworm distributional patterns.

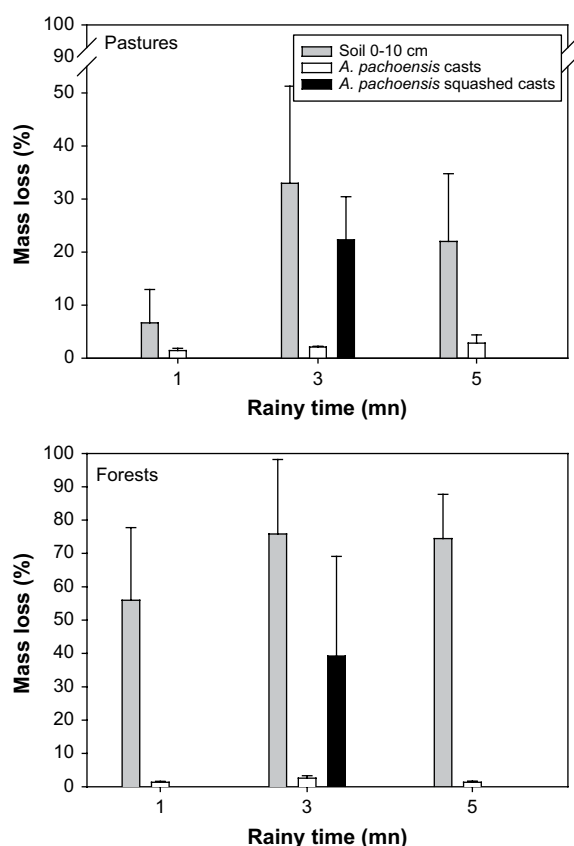


Fig. 4 – Mean mass loss of *Andiodrilus pachoensis* surface casts (normal or squashed) and soil aggregates (0–10 cm layer) from pastures and forests after rainfall simulations. Error bars correspond to standard errors.

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REFERENCES

- [1] C. Albadalejo, J.-C. Tuleu, Les Fronts pionniers de l'Amazonie brésilienne: la formation de nouveaux territoires, L'Harmattan, Paris, 1996.
- [2] E.A. Araujo, J.L. Lani, E.F. Amaral, A. Guerra, Land use and physical and chemical properties of a dystrophic yellow argisol in the western Amazon region, *Rev. Bras. Cienc. Solo* 28 (2004) 307–315.
- [3] X. Arnaud de Sartre, C. Albadalejo, P. Martins, I. Veiga, M. Grimaldi, Identification et évaluation de la diversité des modes d'exploitation des milieux en Amazonie Orientale, *Cah. Agric.* 14 (2005) 85–89.
- [4] A. Baddeley, R. Turner, Spatstat: an R package for analyzing spatial point patterns, *J. Stat. Softw.* 12 (2005) 1–42.
- [5] L.C. Balbino, A. Bruand, M. Brossard, M. Grimaldi, M. Hajnos, M.F. Guimaraes, Changes in porosity and microaggregation in clayey Ferrasols of the Brazilian Cerrado on clearing for pasture, *Eur. J. Soil Sci.* 53 (2002) 219–230.
- [6] S. Barot, J.P. Rossi, P. Lavelle, Self-organization in a simple consumer-resource system, the example of earthworms, *Soil Biol. Biochem.* 39 (2007) 2230–2240.
- [7] E. Barros, P. Curmi, V. Hallaire, A. Chauvel, P. Lavelle, The role of macrofauna in the transformation and reversibility of soil structure of an oxisol in the process of forest to pasture conversion, *Geoderma* 100 (2001) 193–213.
- [8] F. Binet, R.C. Le Bayon, Space-time dynamics in situ of earthworm casts under temperate cultivated soils, *Soil Biol. Biochem.* 31 (1998) 85–93.
- [9] K. Birkhofer, J. Henschel, S. Scheu, Spatial-pattern analysis in a territorial spider: evidence for multi-scale effects, *Ecography* 29 (2006) 641–648.
- [10] E. Blanchart, A. Bruand, P. Lavelle, The physical structure of casts of *Millsonia anomala* (Oligochaeta: Megascolecidae) in shrub savanna soils (Cote d'Ivoire), *Geoderma* 56 (1993) 119–132.
- [11] E. Blanchart, A. Albrecht, G. Brown, T. Decaëns, A. Duboisset, P. Lavelle, L. Mariani, E. Roose, Effects of tropical endogeic earthworms on soil erosion, *Agric. Ecosyst. Environ.* 104 (2004) 303–315.
- [12] M.B. Bush, M.R. Silman, Amazonian exploitation revisited: ecological asymmetry and the policy pendulum, *Front. Ecol. Environ.* 5 (2007) 457–465.
- [13] M. Cannavacciuolo, A. Bellido, D. Cluzeau, C. Gascuel, P. Trehen, A geostatistical approach to the study of earthworm distribution in grassland, *Appl. Soil Ecol.* 9 (1998) 345–349.
- [14] C.E.P. Cerri, K. Paustian, M. Bernoux, R.L. Victoria, J.M. Melillo, C.C. Cerri, Modeling changes in soil organic matter in Amazon forest to pasture conversion with the Century model, *Glob. Change Biol.* 10 (2004) 815–832.
- [15] J.P. Curry, O. Schmidt, The feeding ecology of earthworms – a review, *Pedobiologia* 50 (2007) 463–477.
- [16] M.R.T. Dale, *Spatial Pattern Analysis in Plant Ecology*, Cambridge University Press, Cambridge, 1999.
- [17] T. Decaëns, Degradation dynamics of surface earthworm casts in grasslands of the eastern plains of Colombia, *Biol. Fertil. Soils* 32 (2000) 149–156.
- [18] T. Decaëns, J.H. Galvis, E. Amezcuita, Properties of the structures created by ecological engineers at the soil surface of a Colombian savanna, *C. R. Acad. Sci. III, Sci. Vie* 324 (2001) 465–478.
- [19] T. Decaëns, A.F. Rangel, N. Asakawa, R.J. Thomas, Carbon and nitrogen dynamics in ageing earthworm casts in grasslands of the eastern plains of Colombia, *Biol. Fertil. Soils* 30 (1999) 20–28.
- [20] T. Decaëns, J.P. Rossi, Spatio-temporal structure of earthworm community and soil heterogeneity in a tropical pasture, *Ecography* 24 (2001) 671–682.
- [21] C.A. Edwards, *Earthworm Ecology*, CRC Press, London, 2004.
- [22] P.M. Fearnside, Causes of deforestation in the Brazilian Amazonia, in: R.E. Dickinson (Ed.), *The Geophysiology of Amazonia: Vegetation and Climate Interactions*, John Wiley and Sons, New York, 1987, pp. 37–62.
- [23] M.J. Fortin, M.R.T. Dale, *Spatial Analysis: a Guide for Ecologists*, Cambridge University Press, Cambridge, 2005.
- [24] C. Fragoso, G.G. Brown, J.C. Patron, E. Blanchart, P. Lavelle, B. Pashanasi, B. Senapati, T. Kumar, Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms, *Appl. Soil Ecol.* 6 (1997) 17–35.
- [25] C. Gilot, Effects of a tropical geophageous earthworm, *M. anomala* (megascolecidae), on soil characteristics and production of a Yam crop in Ivory Coast, *Soil Biol. Biochem.* 29 (1997) 353–359.
- [26] G. Guggenberger, R.J. Thomas, W. Zech, Soil organic matter within earthworm casts of an anecic-endogeic tropical pasture community, Colombia, *Appl. Soil Ecol.* 3 (1996) 263–274.
- [27] R.P. Hindell, B.M. McKenzie, J.M. Tisdall, Influence of drying and ageing on the stabilization of earthworm (Lumbricidae) casts, *Biol. Fertil. Soils* 25 (1997) 27–35.
- [28] H. Höfer, W. Hanagarth, M. Garcia, C. Martius, E. Franklin, J. Römbke, L. Beck, Structure and function of soil fauna communities in Amazonian anthropogenic and natural ecosystems, *Eur. J. Soil Biol.* 37 (2001) 229–235.
- [29] INPE, Projeto PRODES, monitoramento da floresta amazônica brasileira por satélite. <<http://www.obt.inpe.br/prodes/index.html>> (accessed 09/2008).
- [30] J.J. Jimenez, T. Decaëns, J.-P. Rossi, Stability of the spatio-temporal distribution and niche overlap in neotropical earthworm assemblages, *Acta Oecol.* 30 (2006) 299–311.
- [31] J.J. Jiménez, A.G. Moreno, T. Decaëns, P. Lavelle, M. Fisher, R.J. Thomas, Earthworm communities in natural savannas and a man-made pastures of the Eastern Plains of Colombia, *Biol. Fertil. Soils* 28 (1998) 101–110.
- [32] J.J. Jiménez, A.G. Moreno, P. Lavelle, T. Decaëns, Population dynamics and adaptive strategies of *Martiodrilus carimaguensis* (Oligochaeta, Glossoscolecidae), a native species from the well-drained savannas of Colombia, *Appl. Soil Ecol.* 9 (1998) 153–160.
- [33] J.J. Jimenez, J.P. Rossi, Spatial dissociation between two endogeic earthworms in the Colombian "Llanos", *Eur. J. Soil Biol.* 42 (2006) S218–S224.
- [34] M.S. Johnson, J. Lehmann, T.S. Steenhuis, L.V. de Oliveira, E.C.M. Fernandes, Spatial and temporal variability of soil water repellency of Amazonian pastures, *Aust. J. Soil Res.* 43 (2005) 319–326.
- [35] C.G. Jones, J.H. Lawton, M. Shachak, Organisms as ecosystem engineers, *Oikos* 69 (1994) 373–386.
- [36] A.S.R. Juo, A. Manu, Chemicals dynamics in slash and burn agriculture, *Agric. Ecosyst. Environ.* 58 (1996) 49–60.
- [37] R. Lal, Effects of macrofauna on soil properties in tropical ecosystems, *Agric. Ecosyst. Environ.* 24 (1988) 101–116.

- [38] P. Lavelle, Les vers de terre de la savane de Lamto (Côte d'Ivoire): peuplements, populations et fonctions dans l'écosystème, Laboratoire de zoologie de l'ENS de Paris 6, Paris, 1978.
- [39] P. Lavelle, T. Decaëns, A. Aubert, S. Barot, M. Blouin, F. Bureau, P. Margerie, P. Mora, J.-P. Rossi, Soil invertebrates and ecosystem services, *Eur. J. Soil Biol.* 42 (2006) S3–S15.
- [40] P. Lavelle, A.V. Spain, *Soil Ecology*, Kluwer Scientific Publications, Amsterdam, 2001.
- [41] Y. Le Bissonnais, Aggregate stability and assessment of soil crustability and erodibility. Theory and methodology, *Eur. J. Soil Sci.* 47 (1996) 425–437.
- [42] K.E. Lee, *Physical Effects on Soils I. Casts, Earthworms, their Ecology and Relationships with Soils and Land Use*. Sydney, 1985, pp. 173–200.
- [43] L. Mariani, N. Bernier, J.J. Jiménez, T. Decaëns, Diet of an anecic earthworm from the Colombian savannas: questioning ecological groups, *C. R. Acad. Sci. III, Sci. Vie* 324 (2001) 733–742.
- [44] L. Mariani, J.J. Jiménez, E.A. Torres, E. Amézquita, T. Decaëns, Rainfall impact on ageing casts of a tropical anecic earthworm, *Eur. J. Soil Sci.* 58 (2007) 1525–1534.
- [45] S.D. Marshall, The ecological determinants of space use by a burrowing wolf spider in a xeric shrubland ecosystem, *J. Arid Environ.* 37 (1997) 379–393.
- [46] J. Mathieu, Etude de la macrofaune du sol dans une zone de déforestation en Amazonie du Sud-Est, au Brésil, dans le contexte de l'agriculture familiale, University Pierre et Marie Curie (Paris VI), Paris, 2004.
- [47] J. Mathieu, J.P. Rossi, P. Mora, P. Lavelle, P.F.D.S. Martins, C. Rouland, M. Grimaldi, Recovery of soil macrofauna communities after forest clearance in eastern Amazonia, Brazil, *Conserv. Biol.* 19 (2005) 1598–1605.
- [48] A.L. Moody, W.A. Thompson, B. De Bruijn, A.I. Houston, J.D. Goss-Custard, The analysis of the spacing of animals, with an example based on oystercatchers during the tidal cycle, *J. Anim. Ecol.* 66 (1997) 615–628.
- [49] M. Muchagata, K. Brown, Cows, colonists and trees: rethinking cattle and environmental degradation in Brazilian Amazonia, *Agric. Syst.* 76 (2003) 797–816.
- [50] I. Numata, D.A. Roberts, Y. Sawada, O.A. Chadwick, J.P. Schimel, J.V. Soares, Regional characterization of pasture changes through time and space in Rondonia, Brazil, *Earth Interact.* 11 (2007) 1–25.
- [51] M. Pansu, J. Gautheyrou, *L'Analyse du sol: minéralogique, organique et minérale*, Springer-Verlag, Paris, 2003.
- [52] D.A. Perry, Self-organizing systems across scales, *Trends Ecol. Evol.* 10 (1995) 241–245.
- [53] R Development Core Team, *R: a Language and Environment for Statistical Computing*, R.F.F.S. Computing, Vienna, Austria, 2005.
- [54] M.V. Reddy, V.R. Reddy, P. Balashouri, V.P.K. Kumar, A.L. Cogle, D.F. Yule, M. Babu, Responses of earthworm abundance and production of surface casts and their physico-chemical properties to soil management in relation to those of an undisturbed area on a semi-arid tropical alfisol, *Soil Biol. Biochem.* 29 (1997) 617–620.
- [55] V.d Reynal, M.G. Muchagata, O. Topall, J. Hebette, Des paysans en Amazonie: agriculture familiale de développement du front pionnier amazonien, in: H. Théry (Ed.), *Environnement et Développement en Amazonie Brésilienne*, Belin, Paris, 1997, pp. 76–123.
- [56] B.D. Ripley, *Statistical Inference for Spatial Processes*, Cambridge University Press, 1988.
- [57] J.P. Rossi, Clusters in earthworm spatial distribution, *Pedobiologia* 47 (2003) 490–496.
- [58] J.P. Rossi, The spatiotemporal pattern of a tropical earthworm species assemblage and its relationship with soil structure, *Pedobiologia* 47 (2003) 497–503.
- [59] J.P. Rossi, V. Nuutinen, The effect of sampling unit size on the perception of the spatial pattern of earthworm (*Lumbricus terrestris* L.) middens, *Appl. Soil Ecol.* 27 (2004) 189–196.
- [60] D.L. Rowell, *Soil Science: Methods and Application*, British Library, Harlow (England), 1994.
- [61] H. Schack-Kirchner, P.T. Fenner, E.E. Hildebrand, Different responses in bulk density and saturated hydraulic conductivity to soil deformation by logging machinery on a Ferralsol under native forest, *Soil Use Manage.* 23 (2007) 286–293.
- [62] C.E.R. Schaefer, Brazilian latosols and their B horizon microstructure as long-term biotic constructs, *Aust. J. Soil Res.* 39 (2001) 909–926.
- [63] M.J. Shipitalo, R. Protz, Factors influencing the dispersibility of clay in worm casts, *Soil Sci. Soc. Am. J.* 52 (1988) 764–769.
- [64] M.J. Shipitalo, R. Protz, Chemistry and micromorphology of aggregation in earthworm casts, *Geoderma* 45 (1989) 357–374.
- [65] Soil Survey Staff, *Soil Taxonomy: a Basic System of Soil Classification for Making and Interpreting Soil Surveys*, Natural Resources Conservation Service, 1999.
- [66] H. Watanabe, S. Ruaysoongnern, Cast production by the megascolecid earthworm *Pheretima* sp. in North-Eastern Thailand, *Pedobiologia* 26 (1984) 37–44.
- [67] H. Zhang, S. Schrader, Earthworm effects on selected physical and chemical properties of soil aggregates, *Biol. Fertil. Soils* 15 (1993) 229–234.