

# Deciphering earth mound origins in central Brazil

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Received: 13 October 2009 / Accepted: 15 February 2010 / Published online: 10 March 2010  
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**Abstract** Mound fields are a common landscape throughout the world and much of the evidence for their origin has been of a circumstantial nature. It has been hypothesized that earth mounds emerge over grasslands by termite activity; alternatively, they might be formed after erosion. We tested whether a mound field in central Brazil was generated by termite activity or erosion. We used soil organic matter isotopic composition, soil chemical, physical and floristic composition to determine the origin of a mound field. If the mounds emerged by termite activity in an established grassland the soil organic matter below the mound should have the isotopic signature of C<sub>4</sub> dominated grassland, which contrasts with savanna C<sub>3</sub> + C<sub>4</sub> signature. Additionally, soil

traits should resemble those of the grassland. All markers indicate that the mounds were formed by erosion. The soil isotopic composition, chemical traits and texture below the mound resembled those of the savanna and not those of the grassland. Moreover, most of the species present in the mound were typical of savanna. Concrete evidence is provided that mound fields in the studied area were produced by erosion of a savanna ecosystem and not termite activity. The use of the techniques applied here would improve the assessments of whether analogous landscapes are of a biogenic nature or not.

**Keywords** Carbon isotope · Soil · Erosion · Savanna · Termites · *murundus*

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Responsible Editor: Hans Lambers.

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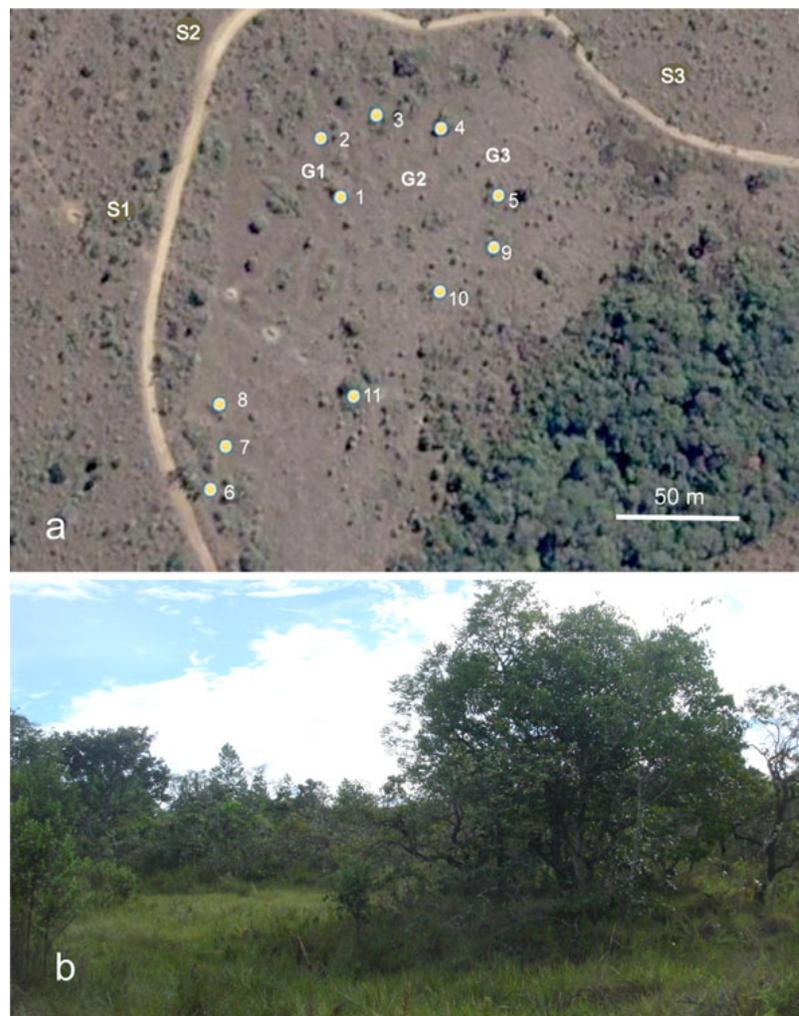
## Introduction

The *campos de murundus* (literally ‘mound fields’) represent one of the several types of savanna vegetation typical of the cerrado region in central Brazil. Savannas in this region, consisting of a mixture of woody plants (trees and shrubs) in a grassland matrix, are the predominant vegetation type. However, the *campos de murundus* formation differs from the typical savannas by its small, round, earth mounds, usually found in areas where seasonal flooding limits the establishment of woody plants to these mounds (Resende et al. 2004). This landscape type, with tree-covered mounds in a matrix of flood-tolerant grasses, occurs extensively throughout the cerrado (Fig. 1; Oliveira-Filho and Furley 1990), but there are analogous formations elsewhere in the Neotropics (Cox et al. 1989; Ellery et al. 1998;

McCarthy et al. 1998; Brossard et al. 2007) in Africa and Australia (Picker et al. 2007; Midgley et al. 2002; Rahlao et al. 2008) and also in north America, where mound fields (prairie mounds) occur from Saskatchewan to Minnesota and south through Iowa and Missouri to Arkansas, eastern Oklahoma, and the coastal plain of Louisiana and Texas (Ross et al. 1968; Mollard 1982).

Several authors have shown that in Brazil these mound fields frequently occur within ecotone zones, towards forest/savanna boundaries (Eiten 1972, 1984; Furley 1986; Araújo Neto et al. 1986; Oliveira-Filho and Furley 1990). This makes the investigation of this ecosystem especially relevant to the understanding of past and present vegetation dynamics such as the riparian forest expansion recently shown in this region (Silva et al. 2008). There are previous descriptions of the vegetation that typically occur in

**Fig. 1 a** Locations of grassland (campo) (G), savanna (cerrado *sensu stricto*) (S), soil cores at the University of Brasilia Experimental Station, Federal District, Brazil. The earth mounds sampled for soil cores are numbered from 1 to 5 and for floristic composition from 1 to 11. The lower panel **b** shows a close up of a typical earth mound at the site



the *campos de murundus*, where the mounds were found mostly populated by savanna tree species, even though forest species also occur (Eiten 1984; Furley and Ratter 1988; Oliveira-Filho and Furley 1990; Resende et al. 2004). However, the question of which processes created this landscape is not yet settled. The lack of quantitative evidence in support to previous circumstantial explanations for the origins of this ecosystem hinders comparisons both within the cerrado and with analogous vegetation elsewhere. Deciphering earth mounds origins would allow such comparisons, serving the interests of ecologists and soil scientists.

There are two main hypotheses that attempt to explain the genesis of earth mounds in central Brazil. The first proposes that termite nests, often associated with the mounds, were responsible for raising the microtopography above the grassland vegetation (Eiten 1984, 1990; Oliveira-Filho 1992; Ponce and Cunha 1993). These termite nests, being above the flood levels of the surrounding grassland during the wet season, then became populated by flood-intolerant woody vegetation. The second hypothesis proposes that differential erosive processes produced the microtopography typical of the *campos de murundus* (Araújo Neto et al. 1986; Furley 1986). Specifically, this hypothesis proposes that the locations where the *campos de murundus* formed were once typical savannas and that erosion left behind the mounds on which savanna vegetation persisted. The surrounding areas where erosion occurred became increasingly flooded and only sustained flood-tolerant grasses. This last hypothesis does not exclude the possibility that the presence of termite mounds in the slightly sloping savanna created the initial microtopography, which in turn led to differential erosion and mound formation.

The two hypothetical processes leading to mound formation would, however, leave distinct traces in the soil chemistry and the floristic composition of the mound. For example, a grassland origin of the mounds by termite activity would be reflected by soil organic matter (SOM) having the carbon isotopic signature typical of the C<sub>4</sub>-rich grassland at depths below the mound (Fig. 2). However, if the mounds originated in a savanna, the stable carbon isotopic signature of SOM typical of savanna previously measured in this area (Silva et al. 2008) would persist in soil layers below the mounds (Martinelli et al. 1996; Silva et al. 2008; Victoria et al. 1995). Traces of the mounds' origin would also be found in chemical

substances within the soil, including organic carbon, cations and anions, as well as in the soil physical properties. Chemical traces could, however, be subject to change because some of these components are highly mobile. In addition to leaving traces in the soil chemistry and texture, these hypothetical processes would also leave different floristic traces. We would expect that the differential erosion of the savanna would leave the mounds mostly occupied by species already present in the mounds and vicinity, i.e. species commonly found in the savanna. These species would persist through time, since they provide the most abundant seed rain by their proximity. On the other hand, if the mounds originated in grasslands bordering forests, they would be open to establishment by new species. Therefore, one could expect that the abundance of forest species occupying the mounds may be related to the distance from the forest and its seed rain. We investigate here soil isotopic, chemical and physical markers, and floristic evidence, in a typical *campos de murundus* located in the Federal District in Central Brazil in an attempt resolve the question of its origin. Specifically we test the following hypotheses.

- 1) The carbon isotopic composition of SOM below the earth mounds, at the level of the surrounding grassland, shows an isotopic signature similar to that of the surrounding grassland.
- 2) The soil physical and chemical properties below the mound resemble those in soils of the surrounding grassland.
- 3) Mounds that are closer to the neighbouring forest have a greater number of species from the forest compared to those farther from the forest.

Confirmation of the above would support the hypothesis that mounds were formed in grasslands by the build-up of the microtopography via termite activity. On the other hand, rejection of the above hypotheses and the presence of isotopic, chemical and floristic signatures typical of the savanna would support the erosive origin of the mounds.

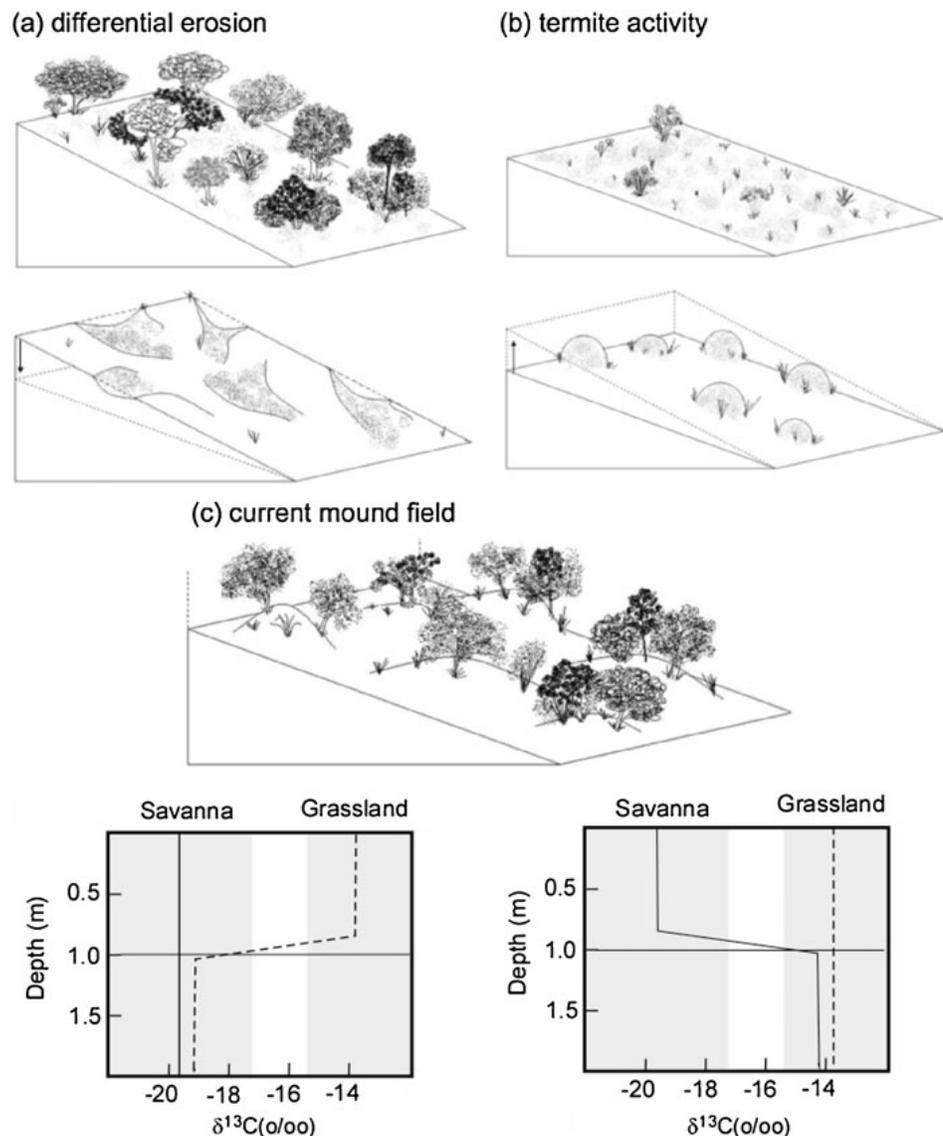
## Materials and methods

### Site description

Measurements were taken in an undisturbed *campos de murundus* site on a grassy slope, having lower than

**Fig. 2** Two possible ways of mound formation:

**a** erosion and **b** termite activity that would lead to **c** current mound field, and the expected soil profiles of soil organic matter (SOM) carbon isotope ratios. The *solid* and *stippled* lines represent the expected carbon isotope profile with depth in the mound and in the grassland, respectively, for each hypothetical mound formation process. Carbon isotope ratio values below the horizontal solid line for the mound profile represents hypothetical SOM values below the mound (~100 cm depth). Slope has been exaggerated to illustrate the possible processes of mound formation



5° inclination and bordering a savanna/gallery forest ecotone, at the University of Brasilia Experimental Station (FAL-UnB), Federal District, Brazil (Fig. 1; 15° 56' 40.17" S and 47° 54' 36.35" W). This mound field contained mounds averaging  $1.1 \pm 0.14$  m in height above the grassland and an average perimeter of  $32 \pm 11$  m. These mounds often had termite colonies of the species *Armitermes cerradoensis* (Mathews). The average annual temperature for this region is 22.5°C and average annual rainfall 1,426 mm (1993–2002). Rainfall is seasonally distributed, with more than 80% falling during the months of November to April. Soils in this savanna can be generally characterized as deep, well drained oxisols, with low organic matter and nutrient contents. Soils in the

seasonally flooded grassy areas can have higher fertility and organic matter content (Eiten 1990). The area of each mound was estimated by using perimeter measurements, taken by metric tape from the intersection between the bases of the mounds with the grassy area level, considering their shapes as perfect circles. The distance from the forest was also determined for each mound, by measuring the shortest straight-line distance from each of them to the forest border.

#### Soil cores

During the dry season of 2007 we sampled the soil profile with a soil auger to a depth of 2.5 m or less if the water table was reached or the presence of gravel

impeded further sampling. Three soil profiles were acquired in three savanna sites (Fig. 1; S1, 2 and 3), three in the *campos de murundus* grassland area (Fig. 1; G1, 2 and 3) and five in the mounds (Fig. 1; mounds 1 to 5). At the savanna profile S2 a gravel layer at 90 cm depth impeded the ongoing sampling. The water table was reached at approximately 75 cm depth in the grassland area, preventing the sampling of soil at lower depths. Soil samples were collected every 10 cm of depth and dried at room temperature after which the fine roots were removed by sieving through a 2 mm mesh. The sieved soil was used for analyses of isotopic abundance as well as chemical and physical properties.

#### Soil stable isotope analysis

Carbon isotope ratios of soil samples were determined after a new sieving through a 0.8 mm mesh at the Laboratory of Stable Isotope Ecology in Tropical Ecosystems at the University of Miami. Soil samples (10 mg) were loaded in tin cups (3 mm diameter and 8 mm height; Elementar Americas Inc, NJ, USA), which were placed in an automated elemental analyser (Eurovector, Milan, Italy) connected to a continuous flow Isoprime isotope ratio mass spectrometer (Elementar, Hanau, Germany). Soil samples were not pretreated with acid to remove carbonates since these soils were acidic and do not contain inorganic carbon.  $^{13}\text{C}$  abundances are expressed as  $\delta^{13}\text{C}$  values:

$$\delta^{13}\text{C}(\text{‰}) = \left( \frac{R_{\text{SAMPLE}}}{R_{\text{PDB}}} - 1 \right) * 1000 \quad (1)$$

where  $R_{\text{SAMPLE}}$  and  $R_{\text{PDB}}$  represent the  $^{13}\text{C}/^{12}\text{C}$  ratios of the sample and PeeDee standard, respectively. The precision of analysis was  $\pm 0.1\text{‰}$  ( $\pm\sigma$ ).

#### Soil chemical and textural characterization

The soil pH was determined in a water suspension (2:1, v.v.). Total nitrogen was determined by the Kjeldahl method (Bremner and Mulvaney 1982). Available phosphorus and potassium concentrations were determined by the method of Mehlich (1953).

Exchangeable aluminum, calcium and magnesium were extracted by 1M KCl solution and their concentrations determined by titulation and atomic absorption. Organic carbon content was determined by wet oxidation (Walkley and Black 1934). Soil texture was determined by the international pipette method (Day 1965).

#### Floristic composition

Following the Botany Classification System Angiosperm Phylogeny Group II (Apg II 2003; Souza and Lorenzi 2005) the floristic census of trees, shrubs and herbs was made in 11 mounds, which were at various distances from the neighbouring gallery forest (Fig. 1). A species/area curve was generated for the woody vegetation (>5 cm circumference at breast height) by adding the new species found on each randomly selected mound in relation to the cumulative area. Also, following standard methodology (Magurran 1988; Kent and Coker 1995), we determined total basal area, density and diversity for the woody vegetation over all the 11 inventoried mounds. Diversity was determined by Shannon's index ( $H'$ ) based on the total number of individuals and relative abundance of woody species, as:

$$H' = - \sum_{i=1}^S p_i \ln p_i \quad (2)$$

where  $S$  is the number of species and  $p_i$  is the relative abundance of each species, calculated as the proportion of individuals of a given species to the total number of individuals.

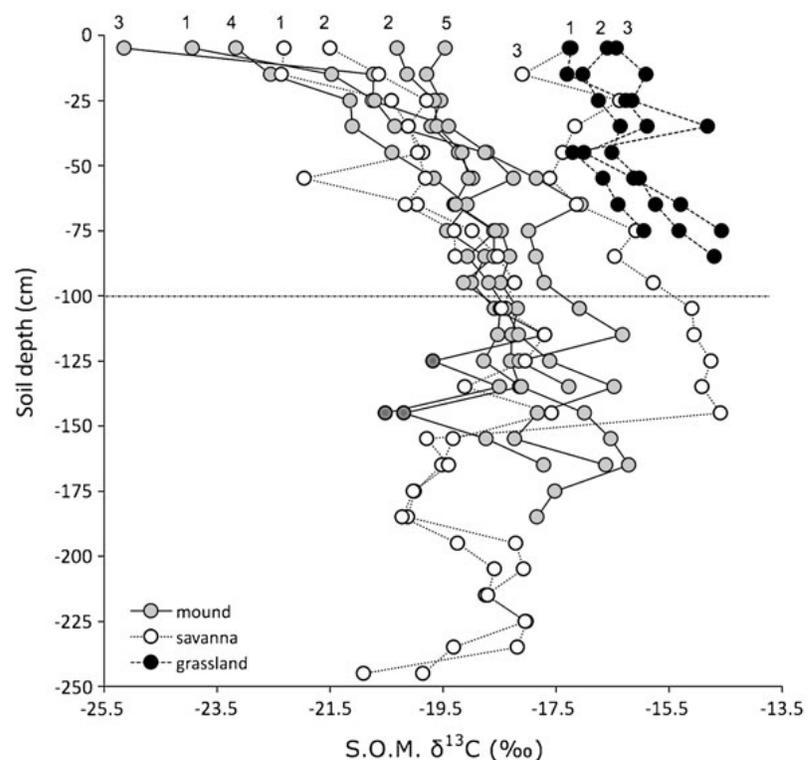
The floristic composition of the nearby savanna and forest areas were gathered from previous studies (Felfili and Silva Júnior 1992, 1993; Felfili et al. 1993; Felfili 1995; Andrade et al. 2002; Silva Júnior 2004; Ribeiro and Tabarelli 2002; Guarino and Walter 2005). A detailed floristic composition inventory was not done for surrounding grassland, as it was mostly dominated by grasses of the genera *Axonopus* and *Andropogon*.

## Results

### Carbon isotope ratios

Carbon isotope ratios of soil organic matter (SOM) of the surface layer (0–10 cm) from three of the mounds

**Fig. 3** Soil organic matter (SOM) carbon isotope composition ( $\delta^{13}\text{C}$ ) for five earth mounds, three savanna and grassland profiles at the University of Brasilia Experimental Station, Federal District, Brazil. Numbers above the curves represent location of the profiles as shown on Fig. 1. The dashed line represents the average depth of the mounds

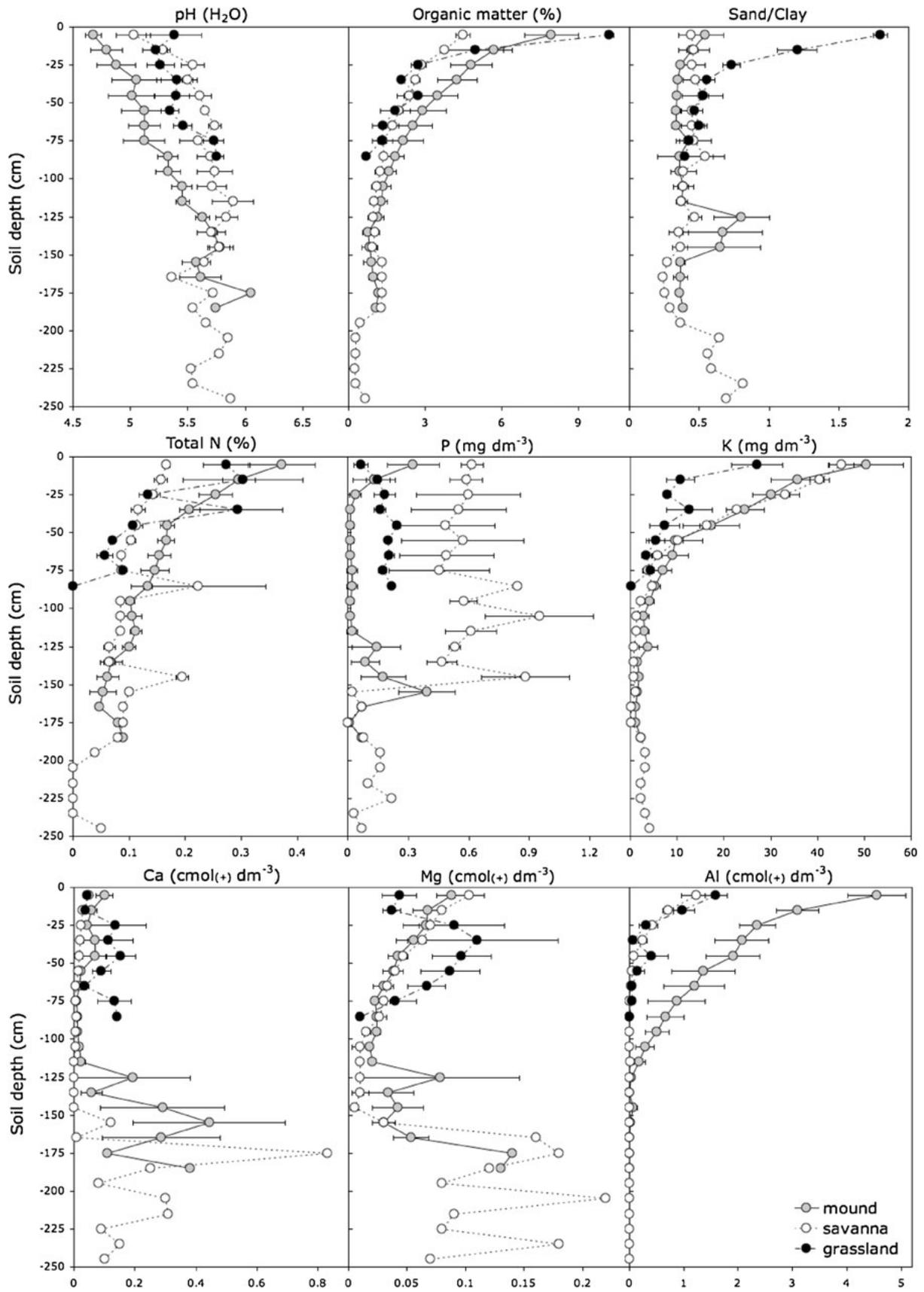


(mound 1, 3 and 4) were distinctly more negative than those of the other two mounds (Fig. 3; mound 2 and 5). Carbon isotope ratios of the SOM profile at depths below 25 cm from all mounds, however, increased to values between  $-22\text{‰}$  to  $-17\text{‰}$ , typical of savanna SOM at these depths (Victoria et al. 1995; Martinelli et al. 1996; Pessenda et al. 1998; Sanaiotti et al. 2002; Silva et al. 2008). With the exception of the S3 savanna profile,  $\delta^{13}\text{C}$  values of SOM for the mound and savanna profile represent a strong  $\text{C}_3$  contribution to the SOM isotopic signature. The  $\delta^{13}\text{C}$  values of the top 100 cm of the S3 savanna profile are clearly distinct from those observed at the mounds and other savanna profiles (S1 and 2), but similar to the values registered in the soil profiles from the grassland area (G1, 2 and 3), in which we found  $\delta^{13}\text{C}$  values above  $-17\text{‰}$ . This isotopic signature represents a greater contribution of  $\text{C}_4$  plants to SOM compared to the other savanna profiles and to those reported in previous savanna studies (Victoria et al. 1995; Martinelli et al. 1996; Pessenda et al. 1998; Sanaiotti et al. 2002; Silva et al. 2008). However,  $\delta^{13}\text{C}$  values of the S3 savanna profile abruptly changed to those typical of the savanna vegetation at depths below 150 cm (Fig. 3).

#### Soil chemical and physical properties

All profiles studied here showed acid soils (pH 4 to 6), with high Al concentration and low nutrient content (Fig. 4). They can thus be classified as dystrophic soils according to the Brazilian Soil Classification System (Embrapa 1999). The soils had less than  $1 \text{ cmol (+) dm}^{-3}$  of exchangeable Ca, and general low K and Mg concentrations, leading to base saturation values below 50%. The mound profiles had the lowest pH values as well as the greatest Al concentration; but layers deeper than 125 cm showed acidity and Al content equal or very similar to savanna profiles. The savanna profiles had the greatest P and the lowest N content at depths between 0 cm and 75 cm. While mounds had slightly higher P than grassland for the surface soil, there was a complete absence of available P in the mound profile until 125 cm depth,

**Fig. 4** Soil chemical and textural characteristics for five earth mounds, three savanna and grassland profiles at the University of Brasilia Experimental Station, Federal District, Brazil. There were three replicates for the grassland and savanna profile and five replicates for the mound profile. Error bars represent  $\pm 1$  standard deviation



below which it increased, reaching values higher than those encountered at the surface. The grassland surface soil had the highest organic matter percentage (9%), which quickly decreased to values similar to those of savanna, but lower than those of the mound soil at 30 cm depth (<3%). The organic matter content in soils of mounds remained greater than that in savanna soil until 80 cm depth and it was similar to values of the savanna soil below this depth (Fig. 4).

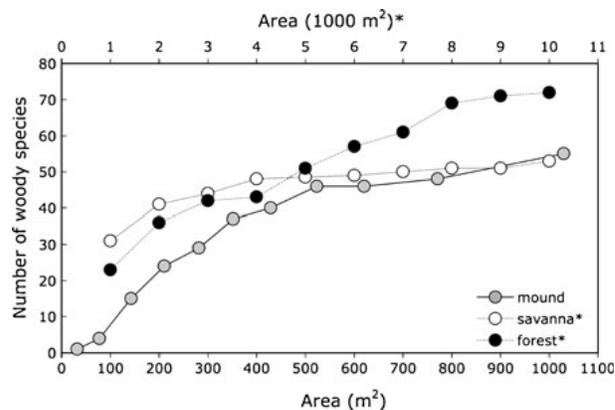
Fertility and organic matter content tended to be higher on the surface soil, decreasing at lower depths of the soil profile (Fig. 4). However, Ca, Mg and P were the exception. The concentration of these elements either increased at a lower depth or oscillated in concentration throughout the profile.

Soil particle size properties show strong and consistent differences between profiles. Soil texture was sandier on grassland soils compared to mounds and savanna (Fig. 4). At the surface layers (0–10 cm) sand/clay ratios are on average four times higher in grassland soils than in the savanna or mounds.

#### Floristic composition

The floristic composition of the eleven *mounds* inventoried included 37 families, 64 genera and 83 species, of which 59% were tree species, 24.1% shrubs and 14.5% herbs. The six most frequent families were the Melastomataceae (14 species), Poaceae (six species), Fabaceae (six species), Myrtaaceae (five species), Lauraceae and Euphorbiaceae (four species each). Of the species recorded, 61.4% are usually encountered in open savanna vegetation, while 18.1% are characteristic of forests (mostly gallery forests) and 19.3% can be found in both ecosystems. There was no correlation between relative abundance of forest species present in the mound and distance of the mound from the forest ( $R^2=0.11$ ,  $P>0.05$ ). No trees or shrubs were encountered out of the mounds on the surrounding grassland, where *Andropogon* sp. and *Axonopus* sp. ( $C_4$  grasses) were dominant.

Over the mounds we found 642 individual woody plants representing 54 species in a total area of 1,029  $m^2$  (Fig. 5). The cumulative species/area curve shows a high local species richness, where 46 species were found in the first 500  $m^2$  inventoried. After that, the curve stabilized, with an increase of just 8 more species in the next 500  $m^2$  (Fig. 5). These results



**Fig. 5** Cumulative number of woody species per cumulative area in 11 earth mounds studied and in ten 1,000  $m^2$  plots on savanna physiognomy of *cerrado sensu stricto* and gallery forest in undisturbed gallery forests in the Federal District of Brazil (Felfili 1995)

represent a total species richness similar to that previously reported for 10,000  $m^2$  of surrounding savanna *cerrado sensu stricto* vegetation, and lower than that found in gallery forests of the same watershed (Fig. 5; Felfili 1995; Guarino and Walter 2005). The total density of 6,239 individuals  $ha^{-1}$  is much higher than that observed in either surrounding savanna or gallery forest (data not shown). The total basal area of 14  $m^2 ha^{-1}$  is twice that observed in savanna and three times lower than that in gallery forest, while the diversity of 3.11, estimated by Shannon's index, is lower than for either of the two other ecosystems (data not shown).

#### Discussion

Carbon isotope ratios of the SOM profile below the mound ( $\sim 1$  m) averaging  $-18.5 \pm 1.1\%$  ( $\pm \sigma$ ) could not be distinguished from those in two of the three savanna cores taken here and were also similar to those of savanna SOM found in a previous study in the same region (Silva et al. 2008). These values are lower than the average  $\delta^{13}C$  value of SOM from the  $C_4$ -dominated grassland area surrounding the mound ( $-15 \pm 0.7\%$ ). The savanna isotopic signal below the mound indicates that this site was a savanna and not grassland before mound formation. Therefore, the isotopic data supports the erosion hypothesis. Unfortunately we could not collect samples from the surrounding grassland to

depths below 1 m. However, the interpretation of the carbon isotope ratios of SOM deeper in the grassland soil profile may be equivocal since savanna isotopic signatures could have eroded away during the formation of the mound field. The slight increase in carbon isotope ratios with depth at the top 25 cm in all soil profiles is caused by isotope fractionation during diagenetic processes in SOM (Martinelli et al. 1996; Silva et al. 2008). One particular SOM isotope profile in the savanna (S3) was unusual in that it had  $\delta^{13}\text{C}$  values typical of the grassland area and showing a stronger  $\text{C}_4$  component than the other savanna samples at depths between 0 cm and 150 cm depth. We propose that this profile is showing the process we hypothesize: differential erosion will cause some savanna areas to become grasslands. At depths greater than 150 cm, representing the older vegetation, SOM from this core has the isotopic signature typical of a savanna. After the erosion, however, this site became more populated with  $\text{C}_4$  grasses as evidenced by the shift in the carbon isotope ratios in SOM at depths shallower than 150 cm. We also note that this savanna soil profile is the closest to the gallery forest (Fig. 1) and probably more susceptible to erosion from runoff. Accordingly, this area may eventually undergo a transition to a *campos de murundus*.

Soil chemical and physical profiles for the most part matched the savanna profile. Discrepancies between savanna and mound profiles were observed in soil pH, organic matter, total nitrogen, phosphorus and aluminum. The differences, however, did not indicate that mound profiles were more similar to those of grassland than the savanna profile. Rather, they indicated that savanna and grassland were similar and the mound profiles were unusual. To some extent this is expected because, with the exception of phosphorus, nutrients can be highly mobile and their profile may not be conserved during the erosive process that left the mounds behind. Phosphorus, however, can easily bind to organic matter. The near absence of available phosphorus in the mound profile up to a depth of 100 cm might be explained by its binding to organic matter observed at higher concentration in the mounds compared to savanna and grassland (Fig. 4). In addition, fauna activity can affect these nutrient concentrations (Oliveira-Filho 1992). Differential nutrient input through termites, birds and mammals may have increased productivity in the mounds over savanna and grassland, also

explaining low P and high N, organic matter and plant density.

In contrast, there was a close match between savanna and mound soil profiles for potassium, calcium and magnesium, with the grassland showing a different profile. The soil texture, which may be a more permanent feature of the soil profile and therefore more faithfully record the mound genesis, showed a close agreement between mound and savanna profile, with the grassland showing a much greater proportion of sand compared to the mound and savanna soil profiles (Fig. 4). The sandiness of the grassland soil compared to those of the mounds is further evidence that erosion processes were important in the formation of the *campos de murundus*. We propose that erosion carried away the smaller and lighter clay particles leaving the remaining soil, where erosion occurred, rich in the larger and heavier sand particles. This is supported by significant correlations between soil texture and soil moisture found in transects from grasslands (higher relative sand content) to riparian forests (higher relative clay content) at the same site studied here (Munhoz et al. 2008).

The majority of the species found on the mounds are from savanna and only about 18% are of forest origin. No correlations between the presence of forest species on the mounds and their distance relative to the forest were found and the species/area curve within the mounds matches the savanna saturation (Fig. 5). All these observations support the presence of a savanna ecosystem prior to mounds formation, which supports the erosion hypothesis. However, some floristic metrics were quite different compared to the savannas. For example, the basal area in the mounds ( $14 \text{ m}^2 \text{ ha}^{-1}$ ) was greater than those of the savanna ( $7 \text{ m}^2 \text{ ha}^{-1}$ ), but much lower than in the forest ( $42 \text{ m}^2 \text{ ha}^{-1}$ ), and the diversity on the mounds ( $3.1 H'$ ) was lower than those observed in the gallery forest ( $3.6 H'$ ) and the neighbouring savanna ( $3.5 H'$ ). We propose that these contrasting characteristics were developed after the mound formation. In other tropical systems, increased tree density and basal area in small islands may result from habitat fragmentation due to changes in dispersion and reduced seeds predation (Wright and Duber 2001). This along with expected increases in seedling recruitment near conspecific species may in time reduce diversity (Wright and Duber 2001). Likewise, our results suggest that limited mound area, or the fragmentation of the savanna, may

lead to higher density and lower diversity of woody plants.

However, the conclusions raised from the comparison of such floristic data have to be taken cautiously. Floristic composition vary greatly within both savannas and forests of cerrado region, thus any extrapolation based on the particular site studied here would be inappropriate. Additionally, because different sampling designs were used on each of these vegetation types (systematic design—continuous strip layout—in the forest; sets of randomized plots in the savanna; and complete census in the mounds), comparing vegetation features may be not as straight forward as one would think. The reason why different designs are used is to produce the most representative data set of each given ecosystem. Considering that each of the above vegetation physiognomies was satisfactorily described (Fig. 5) and that the criteria of inclusion for woody species was the same (>5 cm), here the floristic features of these different ecosystems are comparable (Felfili 1995).

The isotopic and chemical signature of the soil profile as well as its texture and the floristic composition of the mounds all suggest that they were formed by erosion. This site was most likely a savanna site that gradually eroded to the *campos de murundus* landscape with small tree islands in a matrix of seasonally flooded grassland. Much of the previous evidence regarding the termite origin of *campos de murundus* was circumstantial and only based on the observation of the presence of termite nests on the mounds. However, it is not known whether the termites became established after mound formation or were the actual cause of the mound formation. One study in particular (Oliveira-Filho 1992) proposes a succession of different termite species in mound genesis, which initiates with *Armitermes euamignathus* (Silvestri), a species more tolerant of moist conditions than other termites. According to this interpretation, the succession of termite species culminates in *Cornitermes snyderi*, which is least tolerant of moist conditions. Our isotopic data do not support the above scenario in that the SOM isotopic signature below the mound is characteristic of savanna and not the moist grassland rich in C<sub>4</sub> grasses. The evidence for erosive processes in mound genesis has also been circumstantial and based on the observation that *campos de murundus* are usually found in seasonally flooded gentle slopes.

Although our results do not support the termite origin hypothesis, their association with earth mounds may actively alter the physical environment and vegetation dynamics. For instance, termite activity (hollowing out soil, mining clay etc.) may have affected the height or area of the mounds through time, perhaps intensifying differential erosion. Additionally, the predominance of wind-dispersed species on the regional open savannas (Ribeiro and Tabarelli 2002) can be replaced by species that depend on biotic agents for dispersal. The fast response of insects to current changes in climate should also be of relevance towards such dynamics. It has been shown in southern Africa that termitaria density is positively correlated with rainfall (Picker et al. 2007), furthermore, they may reach more than 20,000 years in age, becoming a stable part of the landscape (Midgley et al. 2002) and altering vegetation composition (Rahlaio et al. 2008). While a potential association between termitaria and woody species distribution in *campos de murundus* of central Brazil remains to be investigated, there are similar landscapes in Africa and Australian savannas, as well elsewhere in the Neotropics, which may indeed be caused by termite or other biotic-mediated activity (Cox et al. 1989; Ellery et al. 1998; McCarthy et al. 1998; Brossard et al. 2007). In such places the isotopic profiling of SOM as used here would certainly improve our confidence in the assessments of whether they are truly of a biogenic nature or not.

**Acknowledgements** We thank Doyle McKey (Centre D'Écologie Fonctionnelle Et Évolutive (CEFE)-CNRS), Norton Polo Benito (EMBRAPA-Cenargen), José Carlos Sousa Silva (EMBRAPA-Cerrados) for helpful comments.

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