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RESEARCH ARTICLE

From smallholder to commercial farming: the impact of termite mound levelling and spatial heterogeneity in mound morphology on soil organic carbon in Miombo woodlands, Central Africa

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Abstract

Context The recent expansion of commercial agriculture in the Miombo woodlands of central Africa has led to widespread levelling of termite mounds. These mounds contain significantly lower soil organic carbon (SOC) than surrounding soils, and their levelling could largely reduce SOC content in the plough layer, which remains understudied.

Objectives We aim to investigate the effects of mound levelling on SOC of the plough layer in a 1.5 km^2 plot used for commercial farming and quantify the contribution of pre-existing termite mounds to SOC variation in the levelled cropland.

Methods Before and after levelling, we conducted unmanned aerial vehicle (UAV) surveys with structure-from-motion (SfM) technique, and paired soil sampling (0−25 cm) in between-mound areas.

Results Termite mounds were regularly distributed but morphologically heterogeneous in the plot, with volumes ranging from 7.2 m^3 to 820.9 m^3. Large termite mounds clustered in areas with higher topographic wetness index (TWI). Three years after levelling, SOC content in the plough layer of the plot overall reduced by 26% but variability increased by 29%. In the levelled plot, mound morphology, soil texture, and TWI explained over 40% of SOC variation, with mound morphology (characterized by hypsometrical integral, HI) being most influential. Older, larger mounds (with lower HI) were associated with lower SOC after levelling.

Conclusions The immediate and significant reduction of SOC content in the plough layer due to termite mound levelling in commercial farming may affect productivity. Further research is needed to assess its long-term agricultural and ecological impacts at larger scales.

Keywords Termite mound · Soil carbon variability · Landscape heterogeneity · Tropical agriculture · Tillage impact · UAV structure-from-motion (SfM)

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Introduction

Soil organic carbon (SOC) is a key indicator of soil health (Reeves 1997; Shukla et al. 2006), underpinning critical soil functions such as water retention (Olness and Archer 2005), soil structure (Tisdall and Oades 1982), and nutrient storage essential for plant growth (Dignac et al. 2017). Enhancing SOC pools provides multiple ecosystem functions, including improving agricultural productivity (Lal 2006), supporting soil ecological functioning (Wiesmeier et al. 2019), and contributing to climate change mitigation (Aguilera et al. 2013). However, SOC in croplands is highly susceptible to depletion in tropical regions due to intensive land use. Substantial research has shown that in tropical regions, SOC declines rapidly after conversion from forest to cropland (Don et al. 2011; Wei et al. 2014). Long-term cultivation can result in continuous SOC loss (Kapkiyai et al. 1999; Mando et al. 2005), while to reach a new equilibrium may require several decades to hundreds of years (Lobe et al. 2001; Don et al. 2011; Namirembe et al. 2020; Maseko et al. 2022). Appropriate land management practices, such as the application of mineral fertilizers and manure, can help mitigate some of these losses (Bationo and Buerkert 2001; Mando et al. 2005; Namirembe et al. 2020; Maseko et al. 2022; Laub et al. 2023). Recently, the widespread levelling of termite mounds in the Miombo woodlands of central Africa, driven by commercial agricultural expansion, may have significant consequences for SOC. However, the extent and nature of these impacts remain uncertain. To assess these potential consequences, it is essential to consider the ecological role of termite mounds in these landscapes.

Mound-building termites are important ecosystem engineers in tropical and subtropical regions, playing a vital role in shaping the spatial heterogeneity of landscapes (Jones et al. 1994; Sprafke et al. 2024). Among the numerous species, fungus-growing termites are especially noted for constructing prominent mounds that can reach up to 5 m high and 12 m across (Pearce 1997). These termite mounds, containing a substantial amount of material with distinct properties, significantly contribute to the spatial heterogeneity of soil mineralogy, hydrology, and nutrient fluxes in local landscapes (Van Thuyne and Verrecchia 2021). This spatial diversity has cascading effects throughout the system, bringing about spatial heterogeneity in plant and animal species assemblages and functional diversity (Fleming and Loveridge 2003; Holdo and McDowell 2004a; Joseph et al. 2015). Specifically, fungus-growing termites selectively transport finer soil particles to mound surfaces during construction (Jouquet et al. 2002). To sustain suitable living conditions, they form a clayey impermeable layer on mound bottom to store water against dry periods (Van Thuyne and Verrecchia 2021). They also collect dead plant materials into their nests to cultivate symbiotic fungi, which facilitates the decomposition of organic materials for them to digest (Jouquet et al. 2011). In the dry tropical regions of Africa, this foraging zone can extend from 35 to 50 m beyond the mound (Jones 1990). This makes termite mounds important sites for accelerating nutrient cycling in semi-arid regions, where recalcitrant organic materials are more effectively decomposed (Jones 1990). As reported, mound materials usually have significantly different soil properties compared to surrounding soils, with increased soil clay content, alkalinity, and nutrient concentrations such as N, P, Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} (Pomeroy 1983; Holdo and McDowell 2004b; Mills et al. 2009; Tilahun et al. 2012; Seymour et al. 2014; Menichetti et al. 2014; Erens et al. 2015b; Muvengwi et al. 2016; Jembere et al. 2017; Chisanga et al. 2020; Apori et al. 2020). In fact, termite mounds, recognized as nutrient hotspots, have already been widely suggested as a fertilizer for smallholders with limited resources to enhance soil fertility in African regions (Watson 1977; Cadet et al. 2004; Tilahun et al. 2012; Jembere et al. 2017; Chisanga et al. 2020; Apori et al. 2020).

In the semi-arid Miombo woodlands of southern D.R. Congo, the landscape is dotted with large mounds constructed by *Macrotermes falciger* (> 5 m high, > 15 m in diameter, Fig. 1a, b) (Erens et al. 2015b). Some of these mounds are over 2000 years old (Erens et al. 2015a), thus containing materials that far exceed those found in other regions of Africa (Fleming and Loveridge 2003). The recent introduction of large-scale commercial agriculture is profoundly altering the functioning of cropland soils and the overall landscape structure, as termite mounds are being levelled during land preparation (Fig. 1c). Before this shift, most of the croplands were owned by smallholder subsistence farmers (Potapov et al. 2012). Despite being aware of the potential of the mound materials to enhance soil fertility, they

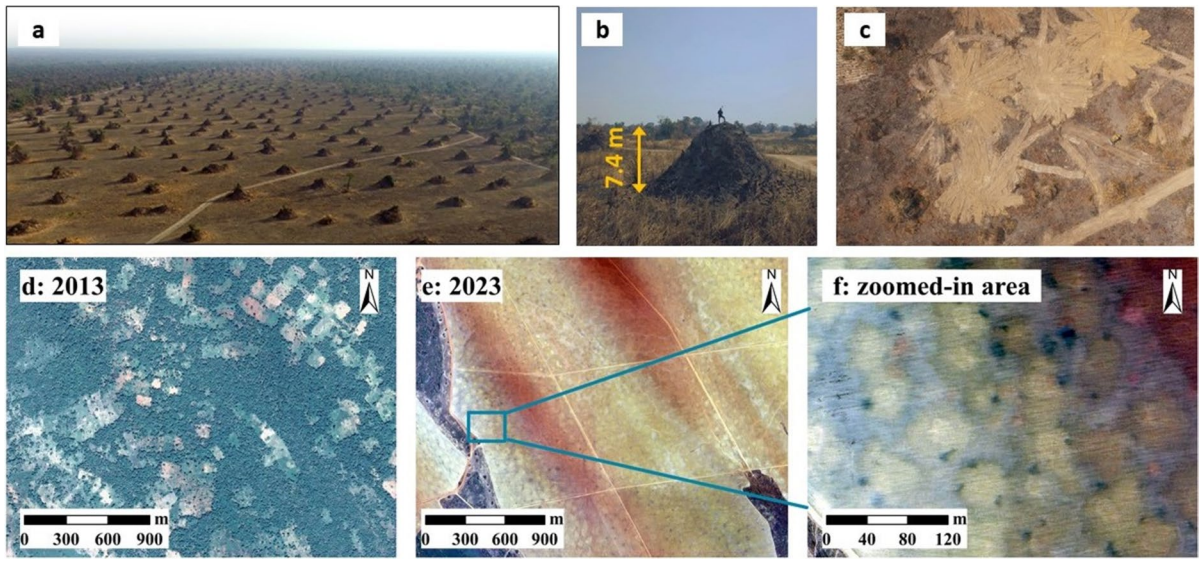

Fig. 1 **a**–**b** Widespread large termite mounds in a cleared Miombo woodland of the D.R. Congo. **c** Appearance of the land surface right after mound levelling, with the soil colour of former termite mound areas appearing brighter. **d**–**e** An example of the transition from smallholder to commercial farms. **f** Zoomed-in area showing the traces of former termite mounds, six years after levelling. Image source (**d**–**f**): Google Earth

usually left the mounds untouched because of their limited capability to manage the land. In recent years, population growth and consequent land use pressure have accelerated the clearing of Miombo woodlands (Jew et al. 2016; Sikuzani et al. 2020). To ensure food security, in 2011, the local government initiated a program aimed at promoting the "agricultural transformation" of the country, which included supporting smallholders and attracting commercial farmers (UNDP et al. 2013). The Copperbelt region of central Africa (Fig. 2a), a mining centre in Haut-Katanga province, D.R. Congo, has been experiencing rapid population growth in recent years (the population of the three major cities: Kolwezi, Likasi, and Lubumbashi, tripled from 2000 to 2020, reaching 3.1 million) (Kemper et al. 2021). We estimated that 22% of the total cropland area in 2021 was used for commercial farming in this region (Fig. 2a.). Now, with this shift from smallholder to commercial farming and the widespread practice of levelling termite mounds, the dispersal and mixing of the substantial mound materials could induce great heterogeneity in local soil fertility and thus affect ecological processes. As shown in the high-resolution Google Earth images, the traces of pre-existing termite mounds are clearly visible even after years of cultivation (Fig. 1f).

A study by Erens et al. (2015a) conducted in Lubumbashi (Haut-Katanga province, D.R. Congo) revealed that termite mounds built by *Macrotermes falciger* in Miombo woodlands contained higher nutrients, such as Ca^{2+}, Mg^{2+}, K^{+}, NO_3^{-}, and P, as well as higher pH compared to surrounding soils. However, the soil organic carbon (SOC) in the mounds was significantly lower, ranging from 0.96% to 0.38% (from mound top to bottom), compared to 1.38% in the surrounding topsoil (0−15 cm). This implies that while levelling termite mounds has the potential to increase available nutrients, it could significantly reduce SOC content in the plough layer. In a prior study carried out by Adhikary et al. (2016) on a levelled cropland (Lubumbashi, Haut-Katanga province, D.R. Congo), SOC at the former mound centre ($0.62 \pm 0.08\%$) was significantly lower than in the reference soil which received no mound material ($2.03 \pm 0.15\%$). This presents a concern for these tropical soils, which are already inherently low in SOC due to low carbon stabilization potential and nutrient depletion (Hartemink 2002; Bationo et al. 2007; European Commission 2013; Fujisaki et al. 2018). Some researchers propose there is a critical carbon content, below which some

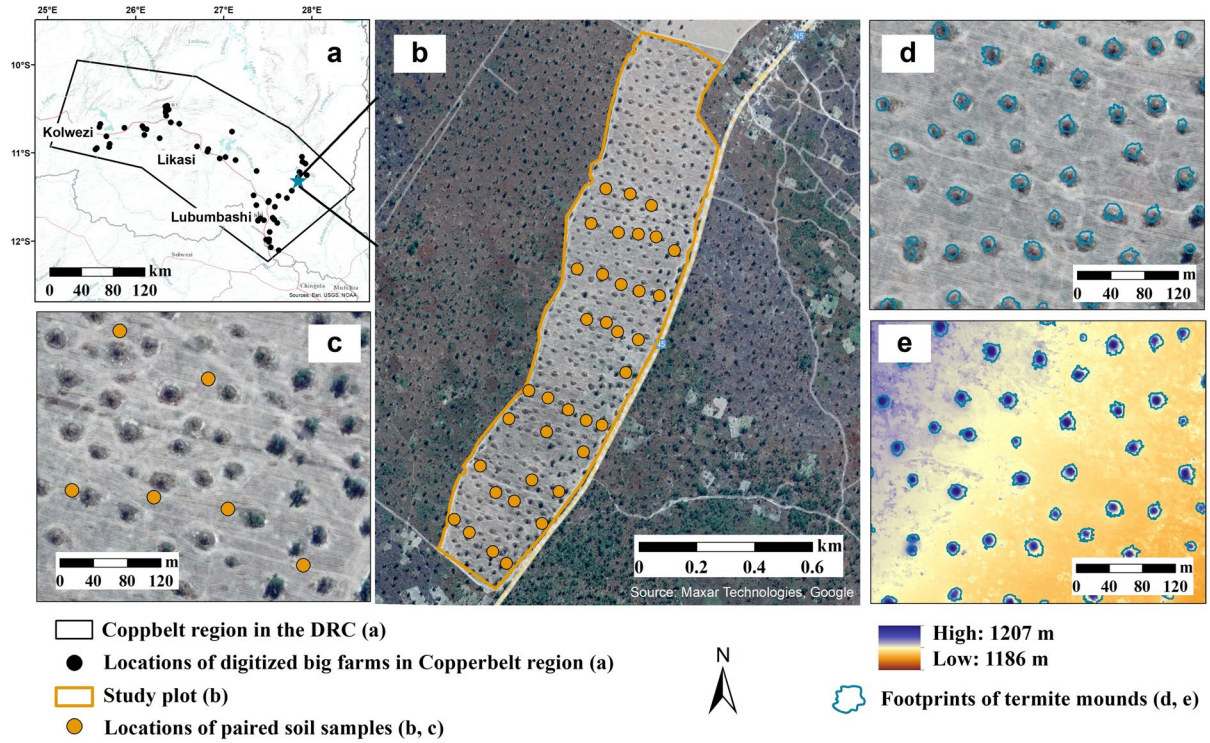

Fig. 2 The study plot (**b**) is located in the Copperbelt region (**a**) of Haut-Katanga province, southern D.R. Congo. The extent of commercial agriculture was determined by digitizing all large farms using Google Earth imagery, as no published data were available. In 2021, commercial farming accounted for 22% of the total cropland area in the Copperbelt region, based on cropland maps from Potapov et al., (2021). A paired sampling campaign was conducted before ($n = 36$, **b**) and after ($n = 36$, **b**) the levelling of termite mounds, from the same locations. All paired soil samples were taken from the plough layer (0–25 cm) in between-mound areas. The sampling locations were randomly selected, with distances to the nearest termite mound ranging from 0 m (adjacent to the mound) to 36 m. **c** provides a detailed view of the sampling locations. The footprints of identified termite mounds were verified and corrected using Google Earth imagery (**d**) and the digital surface model (DSM, **e**) generated from the first unmanned aerial vehicle (UAV) survey as base maps

key soil properties (such as cation exchange capacity, available water capacity and microbial biomass) will be significantly reduced (Grilli et al. 2021). In cropland, soils with carbon below the critical limit can be much less effective in supporting crop growth (Aune and Lal 1997). To ensure food security, which is also one of the sustainable development goals initiated by the United Nations (U.N. 2015), there is an increasing demand to monitor and report changes in SOC in vulnerable hotspots. This allows us to understand localized soil degradation and adapt cropland management strategies accordingly.

Due to the preferences of termites for specific living environments, there remains a considerable spatial heterogeneity in mound morphology, even at the field scale. We therefore hypothesize that this heterogeneity is one of the major factors affecting SOC after levelling. As shown in Fig. 1f, the light-coloured spotted patterns resulting from mound levelling vary in size. A study conducted in Lubumbashi (Haut-Katanga province, D.R. Congo) found that the spatial patterns of mounds built by *Macrotermes falciger* were regular and independent of parent material or soil clay content, but the mound height varied from less than 2 m to over 6 m (Mujinya et al. 2014). Based on existing research, we concluded that there are three key influencing factors on mound morphology: (i) water availability, (ii) clay content of surrounding soil, and (iii) mound age. Water availability is particularly important because *Macrotermes* and the fungi they cultivate are intolerant of dry conditions (Turner et al. 2006). *Macrotermes* need water (in the form of saliva) to bind new soil to mound surfaces, and it was observed that the building activities were

more frequent during the rainy seasons compared to the dry seasons (Turner et al. 2006). Furthermore, termites tend to use finer particles for mound construction, thus the clay content of mound materials is invariably greater than that of the surrounding topsoil (Kang 1978; Pullan 1979; Brossard et al. 2007; Erens et al. 2015b). In soils with finer particles, the regrowth rate of termite mounds has been observed to be faster (Dowuona et al. 2012). Finally, in these areas where living conditions are favourable, larger mounds will form over time through repeated colonization by termites (Erens et al. 2015b). In this context, the spatial heterogeneity in termite mound distribution and morphology acts as a critical landscape variable in determining SOC in the plough layer after levelling: larger termite mounds contain more material with lower SOC, thus affecting a broader area. Quantification of this effect requires accurate identification of termite mounds and calculation of mound morphology (especially volume). Traditionally, this is achieved by manual measurements in the field, which is labour-intensive and spatially limited. Remote sensing approaches like airborne LiDAR, by collecting 3D structural information of the terrain, have been successfully applied to map termite mounds locations and size (Levick et al. 2010; Davies et al. 2014, 2020), The combination of unmanned aerial vehicle (UAV) with structure-from-motion (SfM) technique has also emerged as a rapid and accurate alternative at small scales. By reconstructing dense 3D point cloud data from high-resolution 2D aerial images, it enables detailed characterization of termite mound morphology in three dimensions (D'hont 2021).

In this study, we test the hypothesis that the impact of termite mound levelling on soil organic carbon (SOC) is spatially heterogeneous and dominated by the morphological characteristics of the mounds, with larger mounds causing a greater reduction in SOC. We aim to answer the following key questions: (i) are the morphological characteristics of termite mounds spatially variable, i.e. do larger termite mounds tend to cluster in space? (ii) in between-mound areas, how does SOC change after mound levelling? (iii) to what extent does pre-existing termite mound morphology contribute to SOC variation in levelled cropland? We conducted our study in a 1.5 km^2 cleared Miombo woodland plot now used for commercial farming. First, we used a UAV-SfM workflow and 3D point cloud classification to identify and characterize termite mounds. Then, we did paired soil sampling from the same locations in between-mound areas (sampling depth: 0−25 cm), before and after levelling to assess changes in SOC. Finally, we studied the influence of mound morphology on SOC variation in the levelled plot.

Materials and methods

Study area

The study region is located in the Copperbelt region of Haut-Katanga province, Southern D.R. Congo (Fig. 2a). The region is characterized by a humid subtropical climate, with a rainy season from November to March and a dry season from May to September (Kottek et al. 2006; Mujinya et al. 2013). The mean annual precipitation (MAP) is 1231 mm (Funk et al. 2015), and the mean annual temperature (MAT) ranges from 24.7 °C to 34.5 °C (Hengl and Parente 2022). The plot we chose is located in north-eastern Lubumbashi and covers an area of 1.5 km^2 (Fig. 2b), previously dominated by scattered smallholder farms and degraded Miombo woodlands. *Macrotermes falciger* (Isoptera, Macrotermitinae), a fungus-growing termite species, was the main active occupant in this region (Mujinya et al. 2014). In 2014, the commercial farm GoCongo took over the land and cleared all vegetation. After five years of maize cultivation, the termite mounds were levelled by heavy machinery in October 2019. Following the levelling, the plot was continuously cultivated with maize, producing one crop per year for local sale. The maize was typically harvested before June, then the plot remained fallow from July to October, during which it was covered with maize stubble. In this study, UAV surveys and soil sampling were conducted both before and after the levelling event, as summarized in Table 1. The following sections provide detailed descriptions of them.

Termite mounds characterization

UAV survey for termite mounds identification

The first UAV survey was conducted before mound levelling (in July 2019), using an eBee X equipped with a Canon PowerShot ELPH 110 HS camera (16.1 megapixels) to get orthophotos (RGB, nadir view) of the termite mounds. The images from the first flight were first processed in Pix4D mapper to

Table 1 Summary of the field campaigns conducted in this study

Field campaign	Time	Data collected	Aim
UAV survey	Before levelling, July 2019	Orthophotos (RGB, nadir view)	Identify termite mounds
	8 months after levelling, June 2020	Orthophotos (RGB, nadir view)	Map areas that received mound materials after levelling
Paired soil sampling (between-mound areas, depth: 0 – 25 cm)	Before levelling, July 2019	36 soil samples	Assess changes in SOC after levelling
	3 years after levelling, Sept. 2022	36 soil samples (same locations as before)	
Termite mound sampling	Before levelling, July 2019	36 mound samples	Assess mound ages

In 2014, the commercial farm GoCongo took over the land and started cultivating maize. Termite mound levelling in the study plot occurred in October 2019, after five years of cultivation. Maize cultivation continued by the farm after levelling

generate the high-density 3D point cloud dataset, which was then imported into CloudCompare to segment the termite mounds. The plugin Canupo integrates a binary classification algorithm designed for 3D point cloud data, which monitors local cloud geometry behaviour across scales (Brodu and Lague 2012). The segmented point cloud data, containing only the termite mounds, was then vectorized to obtain the footprint (basal area) of each mound in ArcGIS Desktop (v10.8). To validate the results, visual interpretation was performed using the high-resolution (5.22 cm) orthomosaic and DSM generated in Pix4D mapper as reference maps.

Characterization of mound morphology and spatial pattern

First, we extracted the vertical profiles of each mound based on the DSM generated from the first UAV flight to capture the shape of the termite mounds. We identified the peak of each termite mound and, using this peak as the centre, drew a 25-m line in a northeast-southwest direction (to minimize the influence of the gradual elevation decrease from the northwest to the southeast on the shape of the profiles) to extract the elevation values along this line (R packages geosphere, raster). Second, the following parameters were calculated to characterize the morphology of each termite mound based on the footprints and the DSM: (1) basal area, height, and volume (hereafter referred to collectively as size); (2) hypsometric integral (HI, calculated as area under the hypsometric curves) for inferring developmental stages (Pérez-Peña et al. 2009); and (3) the distance between a mound and its nearest neighbour (D1) (Clark and Evans 1954) and Morisita's index (MI) (Masaaki Morisita 1959) to indicate the spatial dispersion/aggregation (Mujinya et al. 2014). The basal area was the footprint area of each mound (R package raster). Height was determined as follows (R packages raster, rgeos): for each mound, we first calculated a base height, defined as the average height of the marginal pixels of mound footprint. The mound height was then calculated as the altitude of the highest pixel in the footprint minus the base height. Volume was computed by multiplying the area of each pixel by its height (altitude minus the base height) and summing these values together (R packages raster, rgeos). The accuracy of the estimated mound size was evaluated against the reference data collected on-site: 48 termite mounds were randomly selected and manually measured for their size, approximating each mound as a cone. Linear regression and Lin's concordance correlation coefficient (CCC) were used to estimate the bias (R package epiR). HI is widely used in geomorphology to indicate the developmental stages of erosional landforms, by quantifying the amount of material left after erosion (Strahler 1952; Luo 2000; Roy 2002; Singh et al. 2008). HI is calculated as the area below the hypsometric curve, which represents the relative proportion of area (a/A) below or above a certain relative elevation (h/H) of a landform, where a is the area of a horizontal section at a specific elevation h, A is the total area, and H is the total elevation range (Strahler 1952). HI is typically inversely related to landscape stability: high HI indicates youthful stages and is associated with active erosion and instability, while low HI indicates older stages and reflects greater stability and more mature or equilibrium states (Roy 2002; Singh et al. 2008). In our study case, we hypothesize that larger termite mounds are

in older developmental stages, thus the area under the hypsometric curve (below a certain relative elevation) decreases, leading to a lower HI. The calculation of HI was performed using the R package hydroTSM, with the script adapted from https://github.com/hzambran/hydroTSM. The mound spatial pattern was analysed based on the MI which was defined as:

$$\mathrm{MI} = Q\frac{\sum_{i=1}^{Q} n_i(n_i - 1)}{N(N-1)} \quad (1)$$

where Q is the number of identical quadrats in the plot, n_i is the number of termite mounds in each quadrat, and N is the total number of termite mounds in the plot. The spatial domain of the mound pattern is first divided into Q quadrats of equal size and shape, and then the numbers of termite mounds falling in each quadrat are counted. MI indicates three types of spatial pattern: random (MI = 1), clustered (MI > 1), or regular (MI < 1). To account for potential scale-dependent spatial patterns, we tested different levels of spatial aggregation with quadrat sizes from 0.25 ha to 9 ha (R packages maptools, spatstat.explore). The lower limit of 0.25 ha was selected to ensure meaningful analysis, as smaller quadrats would often be empty due to the regional mound density of ca. 3 mounds ha^{-1}. The upper limit of 9 ha was determined by the irregular, elongated shape of the study plot (Fig. 2b), which constrained the maximum size of quadrats that could be fitted within.

Spatial heterogeneity of mound morphology

To determine whether larger mounds are spatially clustered, we categorized the mounds into three size classes based on volume using the mean ± standard deviation (SD) as cut-offs (R base functions): small (volume < mean–SD, i.e. 108 m^3), medium (volume within mean ± SD, i.e. 108–453 m^3), and large (volume > mean + SD, i.e. 453 m^3). Morphological parameters for each category are summarized in Table 2. We then performed a two-dimensional density estimation for each category (R package MASS) and visually inspected their spatial clustering trends. Additionally, we tested the correlation between mound volume and three potentially influencing factors (R package stats): (i) water availability, (ii) clay content in surrounding soil, and (iii) mound age. We used the topographic wetness index (TWI) as the indicator of water availability, which was derived from the DSM generated during the first UAV survey. Before calculating TWI, pixels corresponding to the footprints of termite mounds were removed from the DSM to eliminate their influence on local water flow direction, and a low-pass filter was applied to reduce noise in ArcGIS Desktop (v10.8). For each termite mound, the mean TWI within its footprint was calculated, and differences in TWI among small, medium, and large mounds were assessed using the Kruskal–Wallis test (R package stats). Next, for samples collected before the mound levelling (all from between-mound areas, $n = 36$, see Sect. "Field soil sampling and laboratory analysis"), we correlated their clay content with the average volume of the three nearest termite mounds (R package stats). Lastly, the correlation between mound age and volume was analysed (R package stats), using the ^{14}C dating of mound material to estimate mound age (36 samples were taken from within mounds, see Sect. "Field soil sampling and laboratory analysis").

Mapping levelling-affected area

After mound levelling, we conducted a second UAV survey in June 2020 using a DJI Phantom 3 Professional equipped with a GoPro HERO3 (12 megapixels). Based on our field observation (Fig. 1c) and the findings from Adhikary et al. (2016) in the nearby Lubumbashi region (Haut-Katanga province, D.R. Congo), mound material

Table 2 Morphological parameters (mean ± standard deviation) of small, medium and large termite mounds

Parameter	Category of termite mounds ($n = 457$)		
	Small ($n = 116$)	Medium ($n = 226$)	Large ($n = 115$)
Basal area (m^2)	64.6 ± 22.4	161.7 ± 45.0	274.7 ± 44.8
Height (m)	2.4 ± 0.7	4.7 ± 1.1	6.7 ± 0.8
Volume (m^3)	60.3 ± 26.4	270.2 ± 97.1	556.7 ± 93.0
HI	0.55 ± 0.08	0.43 ± 0.07	0.36 ± 0.04

is noticeably brighter in colour compared to surrounding soils. This colour difference is likely due to the substantial accumulation of carbonate in Macrotermes mounds (Mujinya et al. 2011) and its comparably low SOC content (Erens et al. 2015b). With the drone-derived orthophotos of the levelled plot, we used this colour distinction to map the areas that received mound material after levelling (hereafter referred to as levelling-affected area). In addition, the decrease in land surface altitude was used as complementary information to enhance the mapping accuracy. During this second UAV survey, we employed a post-processed kinematic (PPK) workflow for precise positioning (Zhang et al. 2019). The images were processed in Pix4D mapper to generate the orthomosaic and DSM, with a root mean square error (RMSE) values in each direction (X, Y, Z) of 0.48 m, 0.4 m, and 0.29 m. The decrease in height caused by mound levelling was obtained by calculating the differences in DSMs (DoD) of two flights (before and after the mound levelling). In doing so, it was essential to align the two DSMs as accurately as possible, especially in the Z-direction. We used the second DSM as a reference to correctly position the DSM from the first flight, which did not use real-time kinematic positioning (RTK). We manually selected 17 stable ground features (such as road intersections, road markings and field boundaries) as ground control points (GCPs), and the resulting RMSE in each direction (X, Y, Z) was 0.56 m, 0.54 m, 0.17 m. Combining the geolocation errors from both flights, the RMSE of the DoD in each direction (X, Y, Z) was 0.74 m, 0.67 m and 0.34 m. Subsequently, a random forest classifier was trained using the following variables as input (R package caret): the pixel values of the DoD and the digital number (DN) of the RGB bands of the orthomosaic generated from the second flight. Three sets of training samples were collected randomly: from the centre of mounds ($n = 137$), the surrounding affected area ($n = 138$), and the unaffected area ($n = 87$). The model was evaluated using overall accuracy and kappa coefficient (tenfold cross-validation).

Field soil sampling and laboratory analysis

The paired soil samples were taken from between-mound areas (locations see Fig. 2b), with the aim of assessing SOC changes in these cultivated areas after levelling. Before mound levelling (in the fallow period of 2019), we collected 36 soil samples with their distances to the nearest termite mound ranged from 0 m (adjacent to the mound) to 36 m (mean: 16.1 m, SD: 8.5 m). The varying distances ensured comprehensive coverage of the between-mound areas. After levelling (in the fallow period of 2022), we used a Garmin 64S GPS device to relocate the same sampling locations and collected another set of 36 soil samples. All samples were collected in the plough layer at a depth of 0 – 25 cm, using an Edelman hand auger. As we focus on a very small scale, we took one single sample instead of a composite of subsamples for each location, after removing surface litter. As part of the soil sampling campaign of our research project in the Copperbelt region, the samples taken for this study were analysed together with samples collected from the entire region ($n = 522$). We used mid-infrared (MIR) spectroscopy to analyse the target properties for these samples, including SOC, clay and silt content. This method offers a rapid, precise, and cost-effective alternative to conventional wet chemistry analysis, which typically relies on harmful reagents and costly equipment (Jimenez and Ladha 1993; Chatterjee et al. 2009). MIR spectroscopy works by detecting specific molecular vibrations that encode information about soil properties, such as SOC, through characteristic absorptions at different wavelengths (Viscarra Rossel et al. 2016). Many studies have demonstrated the reliability and efficiency of MIR spectroscopy in assessing soil characteristics, particularly carbon-related properties (McCarty et al. 2002; Soriano-Disla et al. 2014; Hong et al. 2017; Baumann et al. 2021). To do this, the samples were first scanned by an Alpha II FT-IR spectrometer (DRIFT module, Bruker Optik GmbH, Germany) to obtain MIR reflectance, following the method detailed by Zhao et al. (2023). The Kennard-Stone algorithm was then applied to select a representative subset ($n = 171$) for wet chemical analysis (SOC and soil texture) (Kennard and Stone, 1969). SOC was determined using a VarioMax CN analyzer (Elementar GmbH, Germany), after being sieved at 2 mm and pretreated with 10% HCl to remove inorganic carbon (Shi et al. 2020). Soil texture was measured through laser diffraction (LS13320, Beckman Coulter, USA). For each sample, about 1 – 2 g of soil was taken using a sample splitter and treated with 10%

HCl to remove inorganic carbon and 35% hydrogen peroxide to remove organic matter. Before the measurement, the samples were treated with ultrasound for one minute to fully disperse aggregated clay particles. The results of wet chemical analysis were used to calibrate the spectroscopic models, which were then applied to predict soil properties of the remaining samples (R packages dplyr, simplerspec, prospectr, resemble). The model performances were as follows: (i) for SOC: $R^2 = 0.84$, RMSE = 0.18%; (ii) for clay (< 0.002 mm): $R^2 = 0.81$, RMSE = 5.65%; (iii) for silt (0.002 – 0.63 mm): $R^2 = 0.71$, RMSE = 6.33%.

Additionally, we collected 36 mound samples from termite mounds of varying sizes, ranging in volume from 52 m^3 to 805 m^3 (mean: 314 m^3, SD: 187 m^3). Sampling was guided by visual assessment to capture a range of mound sizes, as precise volumes were unknown at the time. Based on the volume cut-offs used in this study, these samples contained 2 small, 27 medium and 7 large termite mounds. Mound materials were collected by a metal soil tube with a length of 20 cm and a diameter of 5 cm, from the central canal, at a position of 1.5 m above the mound base. Radiocarbon (^{14}C) of the mound samples was measured using the accelerator mass spectrometry (AMS) facility of the Max-Planck Institute for Biogeochemistry, Jena, Germany (Steinhof 2013) and measured on a mini carbon dating system (Micadas, IonPlus, Switzerland). The results were expressed as years before present (yr BP), where "present" refers to AD 1950. Given that the samples were taken horizontally above the base of the mounds, the mound age tended to be slightly underestimated.

Statistical analysis

For the paired soil samples taken before and after mound levelling, we compared their mean SOC content using paired t-tests (for normal distribution) or paired Wilcoxon tests (for non-normal distribution) and calculated the mean difference to quantify the changes in SOC content (R package stats). Additionally, we compared the interquartile ranges (IQR) to assess changes in SOC variability before and after levelling (R package stats). Afterwards, we constructed two models to assess the contribution of the former mounds on SOC variation (i.e. SOC of the samples taken after levelling). A random forest model was used to explain the potential non-linear relationships within the data (R packages pdp, ranger, mlr). Given that the model makes minimal assumptions about input variables, all available predictors were incorporated, including the average morphology (basal area, height, volume, HI, D1) of the three nearest pre-existing mounds to each sampling point, soil texture (clay and silt content), and TWI. To achieve a less biased statistical inference and alleviate overfitting caused by spatial autocorrelation between neighbouring samples, spatial cross-validation was adopted (Lovelace et al. 2019). The dataset was partitioned into five spatially disjoint subsets, with each subset used to train 50 models to search for the optimal hyperparameter combination. Partial dependence plots (PDPs) were then used to graphically examine the relationship between the predictors and SOC (Greenwell 2017). Apart from machine learning, a linear model was also built to quantitatively assess the contribution of the former termite mounds to SOC variability on the levelled cropland (R package stats). To avoid multicollinearity, based on prior knowledge and the PDPs, we selected four independent variables: clay, HI, D1, and TWI, representing the influences of soil texture, termite mounds, and soil moisture (Western et al. 2002). Z-score standardization was applied to ensure the comparability of coefficients among predictors (R package bestNormalize).

Results

Overall, the results of mound segmentation were accurate as checked by visual interpretation (Fig. 2d,e), but there were still some inconsistencies: 28 termite mounds, mainly small mounds (mean volume: 72 m^3) near the plot edges, were missed, likely due to lower 3D point cloud density in the marginal areas. Additionally, 13 non-termite mounds (mostly grass bumps) were misclassified, and in 15 cases, two closely adjacent termite mounds were misclassified as one. Given that an accurate identification of termite mounds is the basis of this study, and considering the relatively small size of the study area, any misclassified or missed termite mounds were manually corrected. After manual correction, we identified a total of 457 termite mounds in the plot area of 1.5 km^2. The calculated mound size parameters from the UAV-SfM workflow were in great agreement with the reference dataset ($R^2 > 0.9$,

CCC > 0.8, Fig. 3). The basal area was slightly greater than the manual reference measurements, especially for larger termite mounds, possibly influenced by surrounding grass or an underestimation of the basal area based on field observations only. The height and volume were more accurately calculated, with a CCC of 0.95 and 0.93 respectively. These results provided a solid basis for subsequent analyses.

Morphological parameters of termite mounds

The size parameters of the termite mounds were as follows (mean ± standard deviation): height 4.6 ± 1.6 m, basal area 163.1 ± 75.2 m^2, and volume 280.6 ± 172.4 m^3. Significant positive correlations were observed between basal area, height, and volume, with correlation coefficients ranging from 0.83 to 0.95 (Fig. 4). Among the size categories (small, medium and large termite mounds), the strength of these relationships varied. The correlation between basal area and volume remained strong across all mound size categories ($r = 0.72 - 0.86$), whereas the correlation between height and volume weakened for large mounds ($r = 0.45$).

Figure 5 further illustrates the variability in termite mound morphology as represented by vertical cross-sections (Fig. 5a) and hypsometric curves (Fig. 5b). Generally, termite mounds had a conical vertical cross-section (Fig. 5a), suggesting a "dome-like" mound shape. Termite mounds with larger volumes (red) were taller and broader in profiles compared to smaller mounds (blue), which tended to be shorter and narrower, meaning the increases in mound volume was achieved by both the expansion of basal area and rise in height. Irregularities in the edges of some cross-section curves likely resulted from vegetation interference, while irregularities near the centre may reflect erosion processes at different stages. These differences in mound developmental stages were captured by hypsometric curves (Fig. 5b): termite mounds with larger volumes (red) showed concave hypsometric curves, while smaller termite mounds showed convex hypsometric curves. Statistically, there was a significant negative correlation between HI (area under the hypsometric curves) and all mound size metrics ($r = -0.68 - -0.8$, Fig. 4). The average HI for small, medium, and large mounds (see Table 2 for the size parameters of the three categories) was 0.55, 0.43, and 0.36, respectively.

Spatial clustering of large termite mounds

Spatially, the distance between a mound and its nearest neighbour (D1) varied, averaging 28.8 ± 9.5 m. No significant differences were found in D1 among small, medium, and large termite mounds. Overall, the termite mounds were regularly distributed (MI < 1, quadrat sizes ranged from 0.25 ha to 9 ha), with a density of 3 mounds ha^{-1}. From the density maps (Fig. 6), we observed distinct spatial patterns among mound size categories. Small (Fig. 6a) and medium termite mounds (Fig. 6b) were more evenly distributed across the plot, while large termite mounds were more clustered (hotspot in red, Fig. 6c). TWI analysis revealed significant differences among mound size categories ($p < 0.0001$,

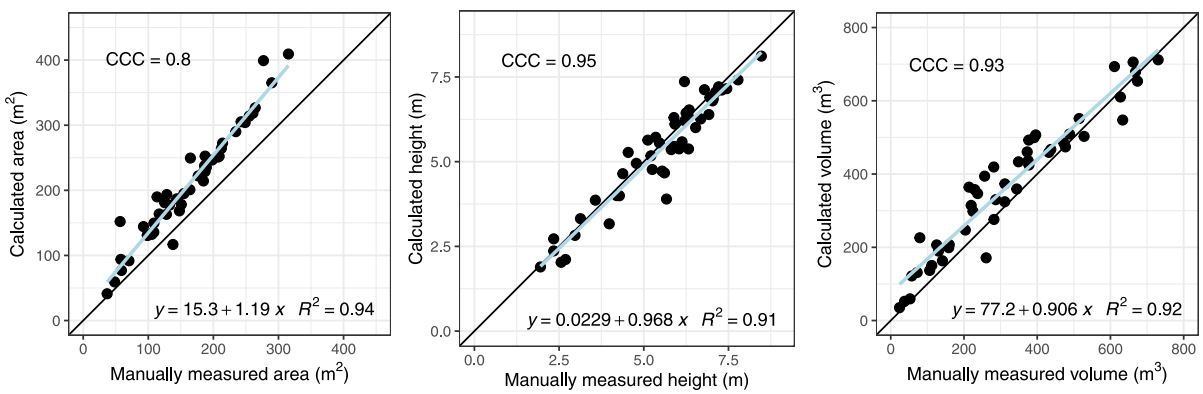

Fig. 3 Linear regressions between the manually measured and calculated mound size parameters ($n = 48$). The blue line is the fitted regression line, and the black diagonal line is the 1:1 line. *CCC* Lin's concordance correlation coefficient

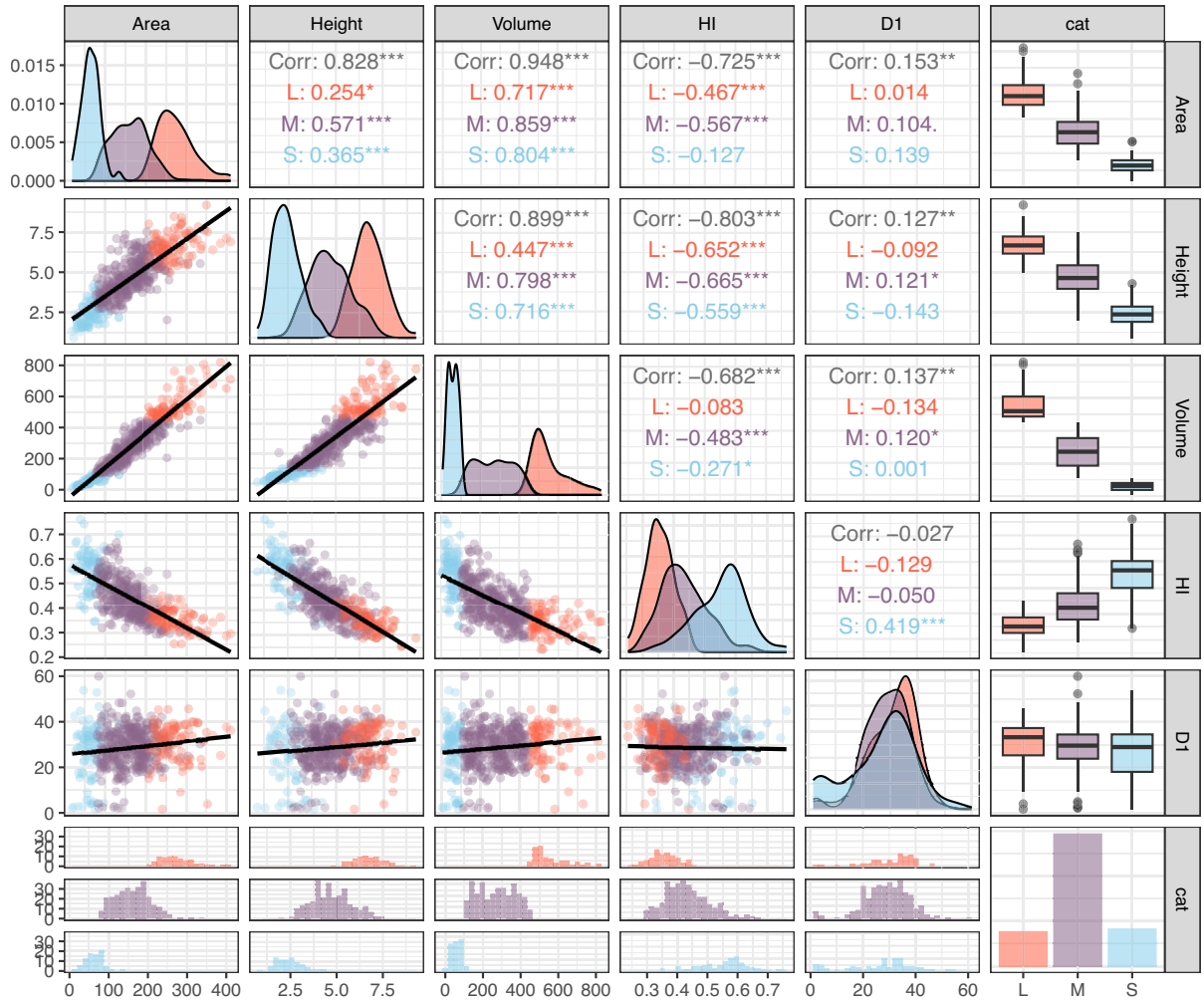

Fig. 4 Correlation plots of the morphological parameters of termite mounds. The mounds were divided into small, medium and large (see Table 2) for comparison. HI: hypsometric integral (area under the hypsometric curves); D1: distance between a mound and its nearest neighbour. The symbols in the upper right corner of the correlation matrix represent p-values: $p<0.001$ (***), $p<0.01$ (**), $p<0.05$ (*), $p>0.05$ (no symbol)

Kruskal–Wallis test). TWI increased from areas located by small to medium to large termite mounds.

In addition, larger termite mounds were observed in areas where the clay content of the surrounding soil was lower, with a significant negative correlation between mound size and clay content ($r=-0.53$, $p=0.00086$, Fig. 7a). In these low-clay areas, the TWI was typically higher, showing a strong negative correlation with clay content ($r=-0.5$, $p=0.0021$, Fig. 7b). The analysis of ^{14}C indicated that the average age of termite mounds was 1046 ± 548 yr BP. Our results support this intuitive relationship, showing that mound volume increased over time, with a significant positive correlation between mound age and volume ($r=0.57$, $p=0.00033$, Fig. 7c).

The effect of mound levelling on SOC

Levelling-affected area

A model with a strong predictive power (overall accuracy = 0.91, kappa coefficient = 0.96) was developed to map the original mound centre, the area affected by mound levelling and the unaffected areas (Fig. 8). After the levelling of the termite mounds, the soil was unevenly mixed, as inferred

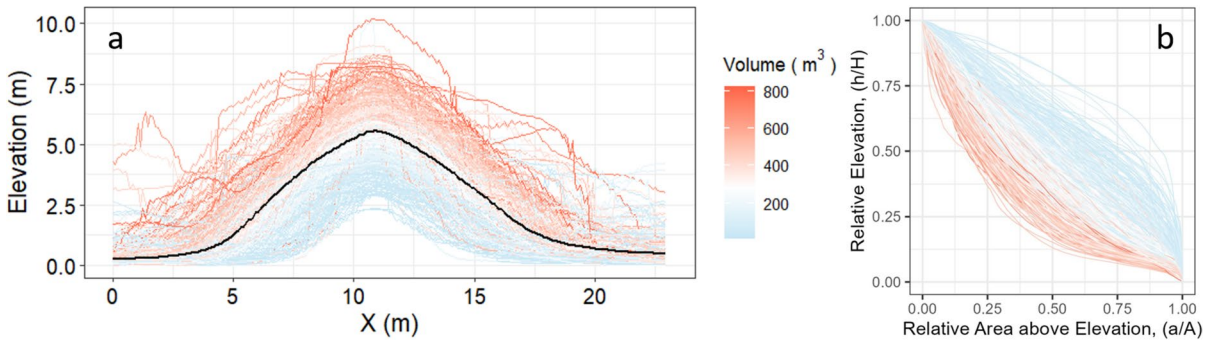

Fig. 5 Vertical cross-sections (**a**) and hypsometric curves (**b**) of all termite mounds ($n = 457$) in the study plot. In panel (a), each coloured line represents the vertical cross-section of a termite mound along the x-axis (m), with mound volume increasing from blue (smaller mounds) to red (larger mounds). The black curve is the median of all profiles. Panel (b) shows the hypsometric curves, which represent the relationship between relative area (a/A) and relative height (h/H) for each mound, coloured by mound volume

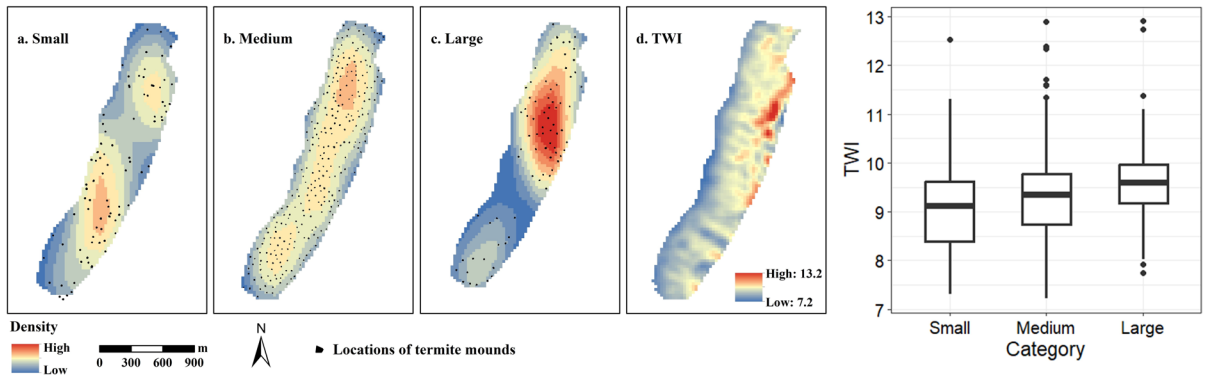

Fig. 6 Density maps of small (**a**), medium (**b**), and large termite mounds (**c**). The boxplot shows topographic wetness index (TWI) of areas located by the three groups, and the Kruskal–Wallis test indicated a significant difference among them ($p < 0.0001$)

from the varying soil colours from the orthomosaic. Specifically, soil colour at the mound centre appeared the lightest, clearly delineating the circular footprint of the mounds. Radiating outwards from the centre, the soil colour in the surrounding area was less bright, while the unaffected area was darker. Based on our predictive maps (Fig. 8), we estimated that the affected area (i.e. mound centre plus surrounding affected area) represented about 45% of the plot.

Changes in SOC in between-mound areas

The scatterplot in Fig. 9a compared SOC content before and after levelling for paired soil samples taken in between-mound areas. In the plough layer (0 − 25 cm), termite mound levelling led to a significant reduction in SOC (on average 26%, from 1.30 ± 0.32 g/100 g to 0.96 ± 0.33 g/100 g, $p < 0.0001$). After levelling, soil samples showed a wider IQR compared to pre-levelling samples (Fig. 9b), with an increase of 29%.

Contribution of former mound morphology on SOC variation

On the levelled cropland, 46% of the SOC variation (RMSE = 0.24 g/100 g) could be explained by the RF model. According to the PDPs, HI was the most important variable in predicting SOC after levelling, while the remaining variables had little effect (Fig. 10). When HI ranged from 0.35 to 4

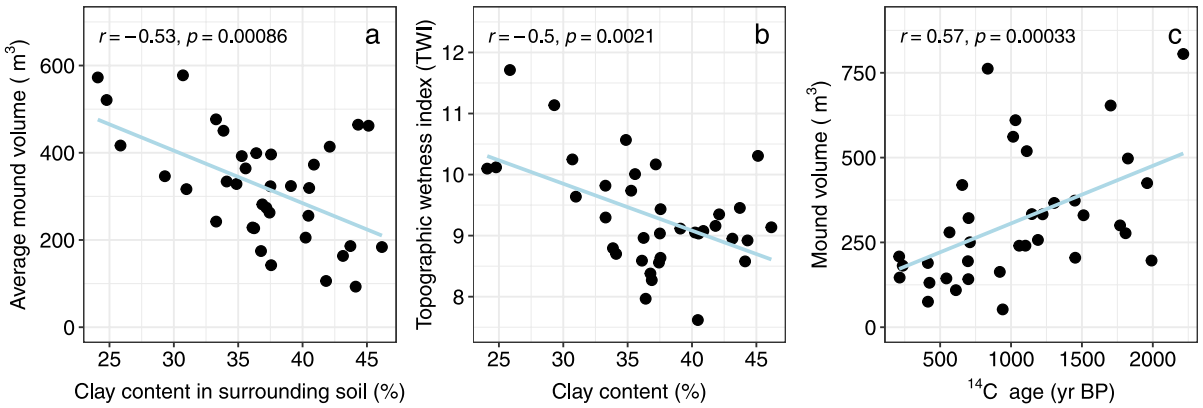

Fig. 7 **a** Correlation between clay content of surrounding soil ($n = 36$; samples were collected in 2019 from between-mound areas) and mound volume of neighbouring sampling locations. On the y-axis: for each soil sample, the average volume of its three nearest mounds was plotted. **b** Correlation between soil clay content ($n = 36$; samples were collected in 2019 from between-mound areas) and the topographic wetness index (TWI) of the sampling locations. **c** Correlation between ^{14}C age and mound volume ($n = 36$, collected from within mound)

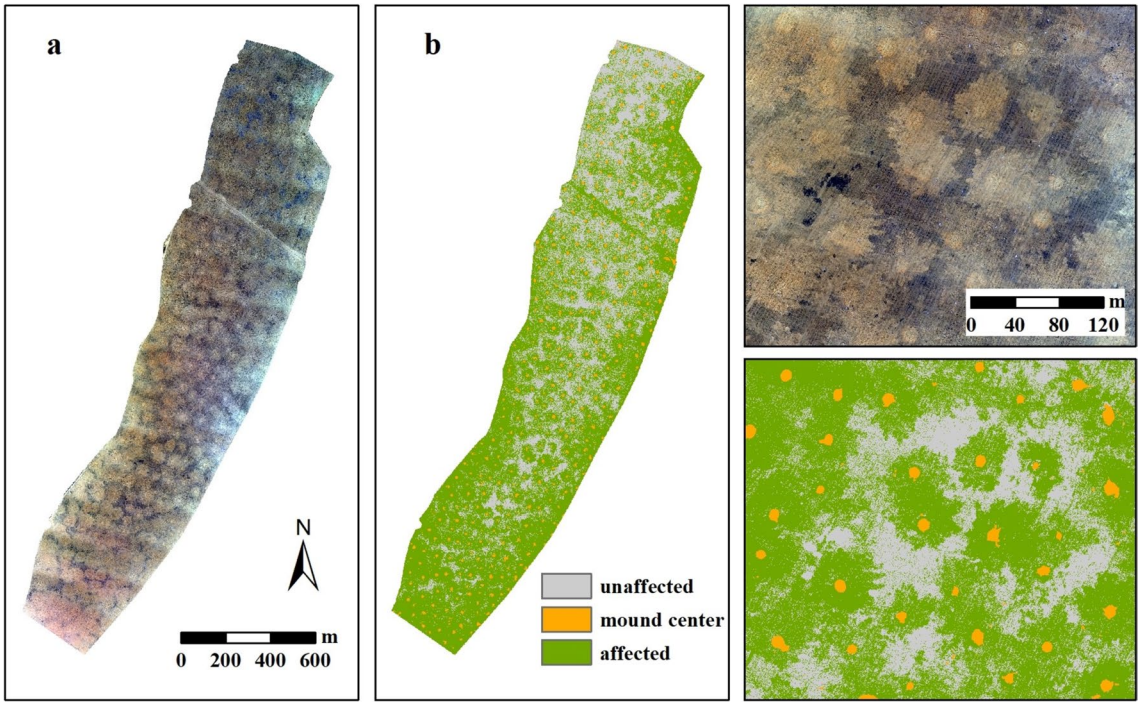

Fig. 8 a) Orthomosaic of the plot after mound levelling. b) Predicted map showing the affected area

(medium-sized mounds), with higher HI (which indicates smaller and younger termite mounds), the model predicted an increase in SOC. However, for HI < 0.35 (old mounds) or HI > 0.4 (young mounds), predicted SOC remained unchanged.

We observed similar results in the linear regression analysis (Table 3): 42% of the SOC variation was explained ($p = 0.0018$), and HI was the only statistically significant variable with the highest coefficient (0.45).

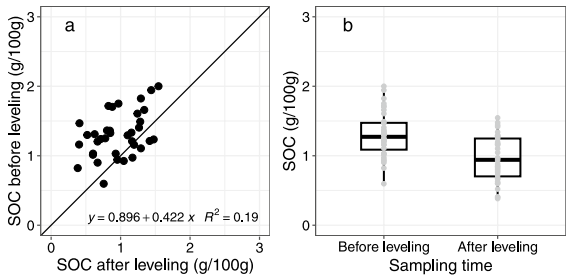

Fig. 9 SOC of paired samples taken in between-mound areas (sampling depth: 0 – 25 cm) before and after the levelling of termite mounds. The Student's t test indicated a significant reduction in SOC after the levelling ($p < 0.0001$)

Table 3 Linear regression of SOC with clay content, HI, D1, and TWI ($n = 36$; $R^2 = 0.42$; $p = 0.0018$)

Variable (normalized)	Coefficient	*p*-value
Clay content	0.12	0.45
HI	0.45	0.01
D1	0.18	0.25
TWI	0.24	0.12

HI hypsometric integral (area under the hypsometric curves), *D1* distance between a mound and its nearest neighbour (m), *TWI* topographic wetness index

Discussion

Mound morphology and spatial pattern

The morphology of termite mounds varies among termite species and environmental conditions (Ocko et al. 2019). For the fungus-growing termites (Macrotermitinae), the primary aboveground mound forms include cathedral, dome, epigeal, buttress, and lenticular (Van Thuyne and Verrecchia 2021). The same termite species may adapt their building strategies based on the specific environment, in order to balance temperature, gas exchange and humidity within the mound (Korb and Linsenmair 1998, 1999; Ocko et al. 2019; Seymour et al. 2023). For instance, *Macrotermes bellicosus* constructs cathedral-like mounds with ridges and turrets (higher surface complexity for thermoregulation) in the warmer but thermally variable shrub savanna, while in the cooler and more stable gallery forest, the mounds are dome-like and compact, designed for heat conservation (Korb and Linsenmair 1998). In our study, termite mounds built by *Macrotermes falciger* were dome-shaped, likely reflecting an adaptation to the Miombo woodlands environment, where conserving heat is more critical than facilitating heat exchange (Korb 2003). Erens et al. (2015a) also suggested

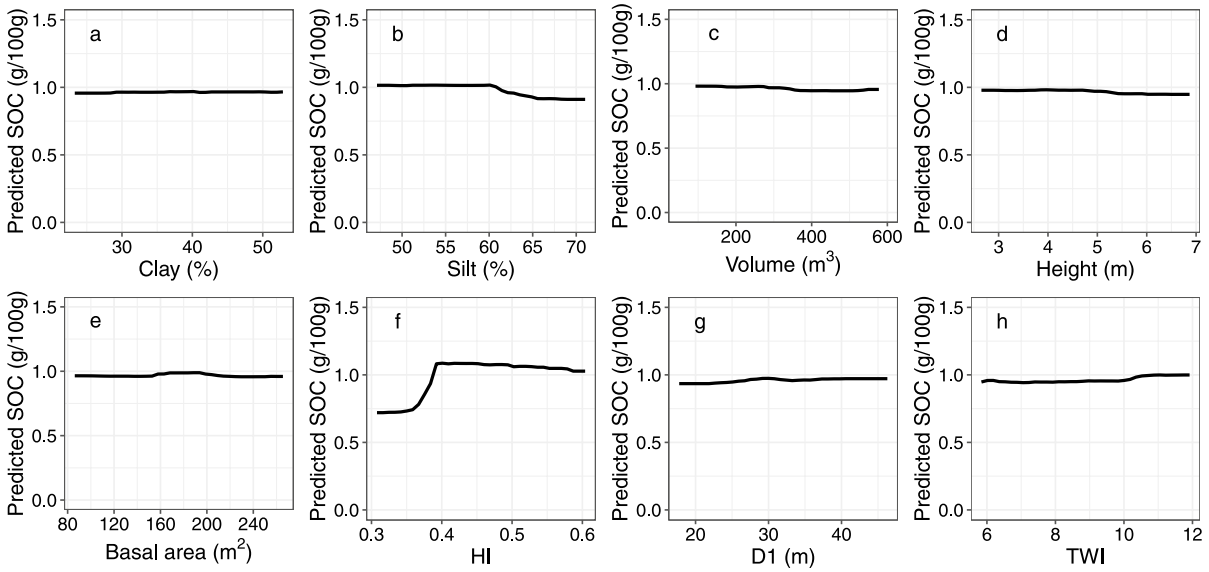

Fig. 10 Partial dependence plots (PDPs) of the predictors derived from the random forest model. *HI* hypsometric integral (area under the hypsometric curves), *D1* distance between a mound and its nearest neighbour (m), *TWI* topographic wetness index

that for *Macrotermes falciger*, temperature might be a key factor influencing not only mound shape but also mound density and growth rate, as suitable temperature conditions (about 30 °C) are necessary for fungus cultivation. Additionally, for mounds constructed by the same termite species within the same environment, the morphology at a certain stage is determined by the balance between mound construction and erosion. Termites continuously transport soil to the mound surface, and at the same time soil erosion leads to deposits on the side and foot of the mound (Pullan 1979; Turner et al. 2006). However, this process applies only to active mounds. In the Lubumbashi region, anthropogenic activities, particularly deforestation, have resulted in a high proportion of abandoned termite mounds (Mujinya et al. 2014). Thus, the abandoned mounds in our study plot are progressively reshaped by erosion, with little new construction occurring. Jouquet et al. (2011) noted that erosion occurs rapidly in the initial years after abandonment but gradually decreases over time, eventually becoming negligible as vegetation growth stabilizes the remaining structure. As hypothesized, larger termite mounds were associated with lower HI, indicating greater stability in morphology. In other words, larger termite mounds are in more advanced stages of erosion, where material has been redistributed from the peak to the base. This redistribution also explains the weaker height-volume correlations observed in large mounds. In contrast, basal area, compared to height, is a better easy-to-measure proxy for mound volume. These findings emphasize that HI is a reliable indicator of both the size and developmental stage of erosional termite mounds.

The density of termite mounds is constrained by mound size (Ocko et al. 2019). Larger mounds are typically constructed by larger termite colonies, such as fungus-growing termites (Pullan 1979). These large termite mounds are often at lower densities because they require much longer periods to develop than small mounds (Ocko et al. 2019). In our study plot, termite mounds built by *Macrotermes falciger* had a density of 3 mounds ha^{-1}, comparable to the reported density of 3–5 mounds ha^{-1} in the south-eastern Katanga miombo ecosystem (Mujinya et al. 2013). In contrast, smaller termite species can construct mounds at much higher densities. In the South African savanna, *Cubitermes* mounds have been recorded at densities of 385–496 mounds ha^{-1}, with the mound height ranging from 1.2 m to 2.2 m (Ferrar 1982). The spatial distribution of termite mounds remains consistent in stable environments (Pullan 1979). However, in areas with optimal temperature and humidity, mound density tends to be higher due to accelerated construction rates (Korb and Linsenmair 1998, 1999).

Across the study plot, termite mounds showed a regular spatial pattern, which is typically due to the intraspecific competition for the termite mounds to maintain their foraging zones (Darlington 1985; Korb and Linsenmair 2001). However, previous research has demonstrated that the spatial distribution of termite mounds is scale-dependent, shaped by both biotic and abiotic factors (Davies et al. 2014). For example, Davies et al. (2014) found that at the catchment scale, mound distribution was dominated by environmental factors such as rainfall, geology, and hydrology, resulting in clustered patterns. In contrast, at the hillslope scale, endogenous competition between termite colonies led to over-dispersed, or regular, patterns. Similarly, Mujinya et al. (2014) also observed this scale-dependent phenomenon. In Miombo woodlands, termite mounds built by *Macrotermes falciger* were regularly spaced within small plots (< 9 ha), likely driven by resource competition among colonies. However, at larger scales, mound distribution appeared more random, suggesting the influence of ecological factors beyond competition.

Water-regulated clustering of large termite mounds

Our findings showed that large termite mounds tended to cluster in areas with higher water availability and lower clay content. The negative correlation between mound volume and clay content differed from our initial hypothesis and contradicted most previous studies, which reported a positive correlation between mound size and clay content (Umeh et al. 1999; Dowuona et al. 2012; Shanbhag et al. 2017). This discrepancy is notable given that termites typically gather finer soil particles, (Noirot and Darlington 2000; Jouquet et al. 2002, 2011), in order to maintain the structural stability and moisture of the mounds (Van Thuyne and Verrecchia 2021). However, some studies suggest that when clay content is already high or when the soil profile has minimal texture variation with depth, termites do not prioritize clay

selection for mound construction (Ackerman et al. 2007). While we lack direct data to check the texture with depth in our study area, the observed negative correlation between mound volume and clay content was likely because areas with lower clay content corresponded to higher TWI (Fig. 7b). Given the long dry season in the region (May to September), we argue that at this plot scale, microtopography-induced variations in water availability, rather than clay content, is the primary factor influencing termite activities. Areas with more favourable conditions can promote termite occupancy and mound growth (Korb and Linsenmair 1998, 1999; Erens et al. 2015a), resulting in the observed clustering of large mounds. Since the lifespan of *Macrotermitinae* does not exceed 20 years (Collins 1981), the growth of these large termite mounds relies on repeated re-colonization by new generations of termites (Erens et al. 2015b). Consequently, these high-TWI areas, where mound expansion is most sustained, are likely to experience more significant impacts following mound levelling.

Effect of mound levelling on SOC

Eight months after levelling, termite mound material covered 45% of the study area (1.5 km^2). Based on our on-site observations after levelling, the termite mounds were not completely flattened but rather formed slightly raised bumps, with a height of about 0.5 m. As the levelling was carried out by bulldozers, we expect that the layer of mound material thinned when moving further away from the centre of the mound. While in the areas where larger termite mounds cluster (Fig. 6c), thicker deposits of mound materials should form a broader affected area. In theory, this height variation could be calculated through the DoD, yet there are two challenges. First, the RMSE of the DoD equalled 0.34 m in the z-direction. Second, during the first flight, the area around the termite mounds was covered with grass, obscuring the true altitude of the land surface. However, we could consider it this way: the total volume of all termite mounds amounted to 85,333 m^3 km^{-2}, equivalent to 144,213 t km^{-2} of material, based on the reported average bulk density (1.69 t m^{-3}) of mounds built by *Macrotermes falciger* in Miombo woodlands (Erens et al. 2015b). If we assume that all the termite mound material was evenly distributed over the entire area, this would form a soil layer of up to 8.5 cm thick, equivalent to one-third of the current plough depth (0 – 25 cm). When only the affected areas are considered, this corresponds to an average uplift of the ground surface of about 19 cm.

In between-mound areas, SOC content reduced significantly over a short period (three years) after mound levelling. Given the relatively slow natural changes of SOC in agricultural land over time (Shukla et al. 2006) and the fact that all samples were taken during the fallow period (before any fertilisation), we argue that the uniform mechanized management practices had a limited impact on this reduction. Therefore, the observed SOC reduction in between-mound areas was primarily due to the mixing of low-SOC termite mound material with the surrounding soil, which initially had a higher SOC content (Erens et al. 2015b). Since the distances from the locations of the paired soil samples to the nearest termite mounds varied, and mound morphology exhibited spatial heterogeneity, the extent of termite mound material redistribution differed across the between-mound areas. This uneven mixing of mound material with the original surrounding topsoil led to an increase in SOC variability after levelling. Among all considered explanatory variables, morphology of the former termite mounds (quantified by HI) had the strongest influence on SOC in the levelled plot. Areas previously occupied by larger, older termite mounds contained more low-SOC material, thus leading to lower SOC content in the plough layer after levelling. However, the PDPs from the RF model (Fig. 10) revealed a nonlinear relationship between HI and SOC: when HI was below 0.35 (corresponding to the large mound group, Table 2) or above 0.4 (corresponding to the small mound group), predicted SOC content remained unchanged as HI varied. This suggests that for large mounds, the extensive coverage of mass mound material likely led to a more uniform change in SOC across the plot. Conversely, for small mounds, the limited area covered by mound material after levelling might reduce its overall influence on SOC. Thus, only for medium-sized termite mounds, an increase in HI (indicating smaller and younger mounds) corresponded to a discernible increase in predicted SOC content.

Limitations and the way forward

First, we observed that the impact of mound leveling on SOC was evident in the short term (three years). With time, mechanised farming will continue to spread the substantial low-SOC material into surrounding soils, expanding the affected area spatially and causing long-term impacts on soil functionality. The immediate significant reduction of SOC in the plough layer may directly affect crop productivity (Johnston et al. 2009), while increased SOC heterogeneity complicates soil management and fertility maintenance. Beyond SOC reduction, researchers have observed surface sealing within those circular zones of former mound sites, indicating poorer soil structure (Mujinya, unpublished data). Degraded soil structure may further affect carbon sequestration potential (Six et al. 2000) and increase soil erosion risk (Pimentel 2006), impacting long-term land degradation. However, a more comprehensive assessment of soil functioning would also require further research considering additional soil fertility properties, such as pH, available N, P, K, Ca^{2+}, and Mg^{2+}, and soil structure. These factors are intrinsically linked and collectively influence nutrient cycling, microbial activity, and overall soil resilience (Bronick and Lal 2005). Second, while our findings on the plot scale provide preliminary insights into the effects of mound levelling on SOC, expanding the analysis to larger spatial scales is essential. At larger scales, environmental factors may drive different mound distribution patterns, which, in turn, could influence the extent and impact of mound levelling. Understanding these patterns in the context of expanding commercial agriculture is crucial for evaluating the wider ecological and agricultural consequences of land-use changes. Third, the negative impact of mound levelling on SOC observed in this study is based on the fact that large termite mounds built by *Macrotermes falciger* in Miombo woodlands contain significantly lower SOC than the surrounding reference soil. However, the role of termite mounds in SOC dynamics remains unclear. As reported so far, mound material could contain significant higher (Watson 1976; Ilse L. Ackerman et al. 2007; Mthimkhulu et al. 2019; Bera et al. 2020; Clarke et al. 2023), lower (Umeh et al. 1999; Jouquet et al. 2004, 2007; Tuma et al. 2022), or similar SOC content (Hesse 1955; Ekundayo and Aghatise 1997; Tilahun et al. 2012) compared to the surrounding reference soil, with the underlying mechanisms still not fully understood. It has been argued that this variability depends on initial soil properties (Jouquet et al. 2011). On the other hand, despite these uncertainties, the crucial role of termites as ecosystem engineers and decomposers is undeniable. The widespread levelling of termite mounds not only destroys their habitats but may also have cascading ecological effects, which remain largely unexplored. These uncertainties further emphasize the need for site-specific studies and larger-scale investigations across a wider variety of tropical termite savannah and woodland systems to better understand the impacts of mound levelling across different landscapes, which is crucial for developing sustainable land management practices in rapidly intensifying agriculture.

Conclusions

The shift from smallholder to large-scale commercial farming in Miombo woodlands, accompanied by the widespread levelling of large termite mounds built by *Macrotermes falciger*, has significantly altered landscape structure and SOC dynamics. Our findings reveal that mound levelling led to a 26% reduction in SOC content and a 29% increase in SOC variability within the plough layer of the investigated plot, driven by the uneven spatial redistribution of low-SOC mound material. Larger termite mounds, which clustered in areas with higher water availability, were associated with lower SOC content in the levelled plot. The immediate SOC reduction in the plough layer may directly affect crop productivity, but a more comprehensive understanding of soil functioning requires further research on additional soil fertility properties and soil structure. Given the substantial volume of mound material, which could form an 8.5 cm thick layer if evenly distributed across the study plot, continued mechanized tillage will likely expand the affected area spatially. These findings highlight the impact of mound levelling on altering SOC dynamics, posing major agricultural and ecological challenges in regions experiencing rapid commercial agricultural expansion.

Author contributions All authors contributed to the study conception and design. Field survey and data collection were

performed by KVO, BBM, and GDS. XO and KVO performed the data analysis and prepared the first draft of the manuscript. All authors provided feedback on earlier versions of the manuscript.

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Data availability The datasets generated and analysed in the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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