Impacts of fungus-growing termites on surficial geology parameters: A review

John Van Thuyne [a,b,*], Eric P. Verrecchia [a,b]

[a] *Institute of Earth Surface Dynamics, Faculty of Geosciences and the Environment, University of Lausanne, Geopolis, 1015 Lausanne, Switzerland*
[b] *Van Thuyne Ridge Research Center, PO box 301, Kasane, Botswana*

A R T I C L E   I N F O

A B S T R A C T

This review covers more than twenty-five years of research listing and discussing the biogeochemical, mineralogical, and physical impacts of fungus-growing termites (or FGT, Macrotermitinae sub-family) on savanna sediments and landscapes. The main mechanisms by which FGT transform the surficial geological formations in tropical and sub-tropical environments is investigated from a geological perspective and the potential FGT legacies in the sedimentary facies are identified. In order to sustain a twenty million-year symbiosis with the fungus, in which fungi provide digestible food to termites, FGT must optimize the living conditions of the fungus for it to thrive. To do so, they build a biogenic structure maintaining a constant humidity of 80% and a temperature of 30 °C in any kind of environment and all year long. Indeed, FGT adapt to their environment by (i) modifying the grain-size distributions of sediments and soils where they develop, (ii) forming clay horizons below their mounds enabling water to be stored for long period of time in dry environments, (iii) increasing the alkalinity by an order of magnitude of two to three, (iv) mineralizing around 20% of all organic carbon in dry savannas, thus making them the predominant decomposing organisms and crucial actors in the carbon cycle, and (v) concentrating vital nutrients for plants and animals, creating patches of fertile land in sandy semi-deserts. Through their mound-building activities, termites substantially increase the clay fraction compared to the adjacent soil and alter 2:1 clay properties, particularly after the removal of potassium, leading to the formation of smectite layers, demonstrating their biogeochemical effects on silicate mineralogy. Through the binding of aggregates, FGT increase the strength of the mound by a factor of ten and provide exceptional weathering resistance to their mounds. Therefore, termites impact their environment from sub-millimetric transformations to solid voluminous landmarks. The water-holding capacity of a FGT mound leads to an array of positive feedbacks to the savanna landscape by enhancing protection from fires, delaying desertification, supporting rebounds by seedlings and reinforcing dryland resistance and recovery from drought. Termite bioturbation allows sediments to accumulate at a rate averaging 1 mm.y^{-1}.ha^{-1}, and tends to mitigate physical and chemical processes of soil degradation, boosting the heterogeneity at the landscape scale, providing it more resilience. Some of the modifications brought by FGT will remain in the landscape for long periods, testifying to past environmental conditions, and making these mounds potential proxies for paleoenvironmental reconstructions. To conclude, FGT are not only biological actors of the savanna ecosystem, but they act as a geological force by their impact on landscapes as well as by their major role in biogeochemical cycles. Finally, further research is recommended regarding the role of termite's saliva as a binding agent, as well as the age and the evolution of mounds over time.

1. Introduction

Fungus-growing termites (FGT) have long been considered as ecosystem engineers by biologists (Jones et al., 1994, 1997). Indeed, they have a tremendous ability to modify the environment where they live; for example, (i) they are able to modify the grain-size distributions of sediments and soils where they develop (Jouquet et al., 2002b; Van Thuyne et al., 2021), (ii) they are able to mineralize about 20% of all organic carbon in dry savannas (Aanen and Eggleton, 2005), making them the predominant decomposing organisms and crucial actors in the

---

* Corresponding author at: Institute of Earth Surface Dynamics, Faculty of Geosciences and the Environment, University of Lausanne, Geopolis, 1015 Lausanne, Switzerland.
E-mail addresses: john.vanthuyne@unil.ch (J. Van Thuyne), eric.verrecchia@unil.ch (E.P. Verrecchia).

carbon cycle, (iii) their mounds have the potential to retain water for long periods of time in dry environments (Turner, 2006), and (iv) finally, by concentrating nutrients, they create patches of fertile land in sandy semi-deserts (Davies et al., 2016). In other words, FGT are not only biological agents of the savanna ecosystem, but they act as geological players by their impact on the nature and distribution of sediments as well as their extensive involvement in biogeochemical cycles. This review compiles the literature from 1990, when C.G. Jones coined the term of "ecosystem engineer" in the tropical and sub-tropical savanna ecosystems, in reference to the role of termites, particularly the mound building fungus-growing Macrotermitinae (Blattodea; Isoptera; Termitidae; Fig. 1). It is based on more than 140 published papers that investigated biogeochemical, mineralogical, and physical impacts FGT have on sediments and soils covering savanna landscapes. This review intends (i) to enlighten geologists on the capacity of eusocial insects to modify surficial geological formations, and as such, to be considered as geological agents, and (ii), to inform biologists and ecologists on the geological impacts that FGT have in subtropical environments. Last but not least, such a review can also provide some clues to the interpretation of past features that FGT could have left in the geological sedimentary record.

After a general contextualization of the FGT subfamily, a section outlines briefly its origins, traits, and unique characteristics. In addition, a list of the Macrotermitinae species is provided in Table 1. The geographical locations where the referred studies have been undertaken are plotted in Fig. 1 as well as the type of construction they build (Figs. 2

Table 1

Species, taxonomy, and filiation of termites cited in the review.

Taxonomy level	Names	Species
Class	Insecta	
Order	Blattodea	
Infraorder	Isoptera	
Family	Termitidae	
Subfamily	Macrotermitinae	
Genus (12)*	*Acanthotermes*	
	Allodontermes	
	Ancistrotermes (13)*	*cavithorax.*
	Euscaiotermes	
	Hypotermes (17)*	
	Macrotermes (56)*	*annandalei, bellicosus, falciger, jeanneli, michaelseni, subhyalinus.*
	Megaprotermes	
	Microtermes (70)*	
	Odontotermes (203)*	*obesus, pauperans, yunnanensis.*
	Protermes (5)*	
	Pseudacanthotermes (7)*	
	Synacanthotermes (3)*	

Macrotermitinae = (FGT). The Macrotermitinae subfamily encompasses 12 genera and 372 species. In parenthesis the number of species per genus, when known. * refers to Extant Taxa, Termite catalogue, Termite Database http://164.41.140.9/catal/statistics.php
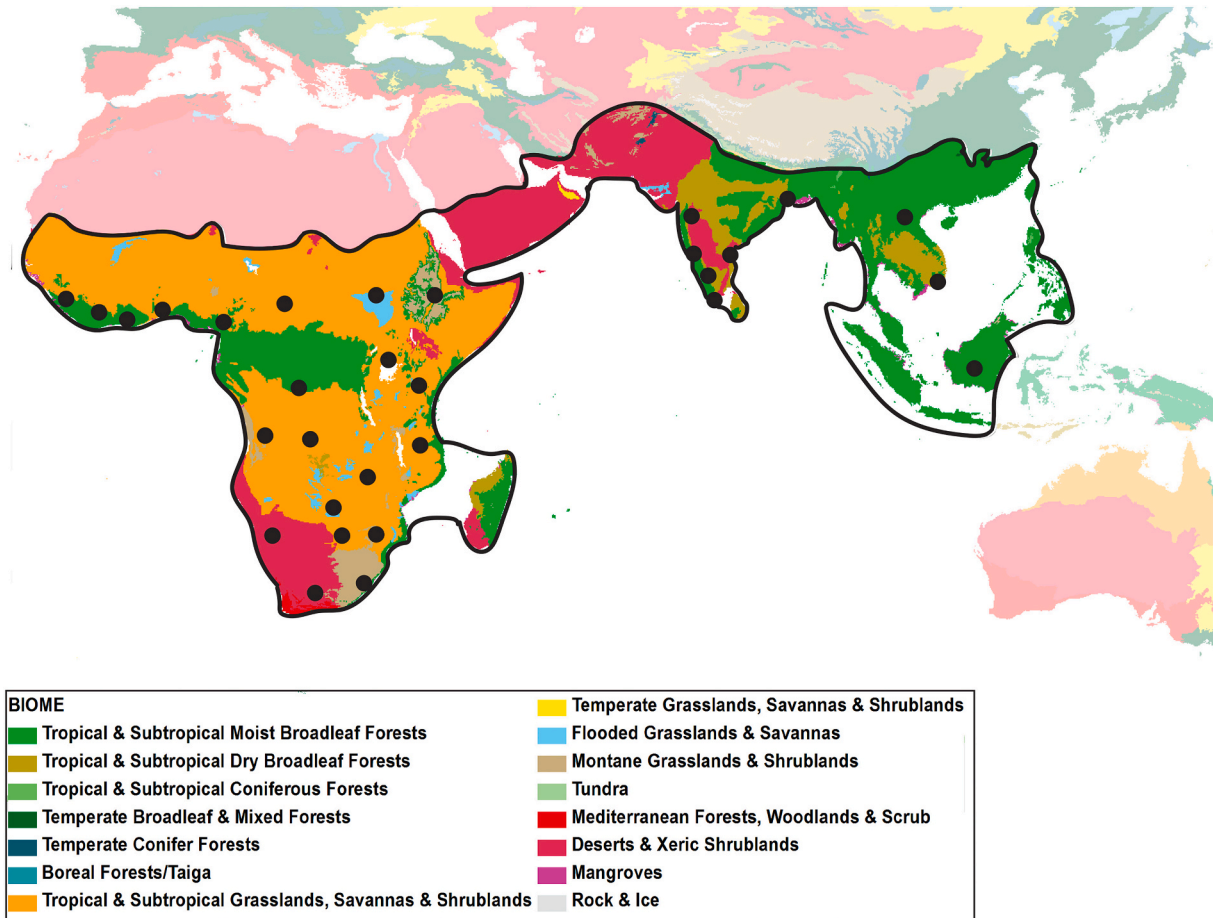

BIOME
- Tropical & Subtropical Moist Broadleaf Forests
- Tropical & Subtropical Dry Broadleaf Forests
- Tropical & Subtropical Coniferous Forests
- Temperate Broadleaf & Mixed Forests
- Temperate Conifer Forests
- Boreal Forests/Taiga
- Tropical & Subtropical Grasslands, Savannas & Shrublands
- Temperate Grasslands, Savannas & Shrublands
- Flooded Grasslands & Savannas
- Montane Grasslands & Shrublands
- Tundra
- Mediterranean Forests, Woodlands & Scrub
- Deserts & Xeric Shrublands
- Mangroves
- Rock & Ice

Fig. 1. Approximated geographical distribution of FGT of the subfamily Macrotermitinae. Black dots represent the 28 studied sites considered in this review. Black line delimits the shaded regions of the world where FGT are absent, including the Americas. Modified from Olson et al. (2001).
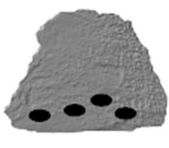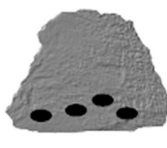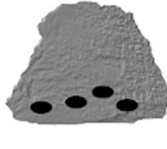
Fig. 2. Schematic illustration of five different aboveground shapes (cathedral, dome, epigeal, buttress, lenticular) of FGT (*Macrotermitinae*) mounds from various species and distinct environments. At the top: environments; on the left side: species. Some species of termites can build two different types of mounds depending on the environment (e.g. *Macrotermes subhyalinus*, *Macrotermes bellicosus*, *Odontotermes obesus*) and different species can build the same types of mound independently of the context. Black rounded forms represent the morphologies of fungus chambers and their respective positions within the mounds. The nests are usually situated just above or below the aboveground limit.

and 3). Sixteen processes triggered by FGT have been identified as impacting factors on savanna sediments and soils. Finally, some gaps and challenges in the available literature are discussed as well as some perspectives and future research opportunities.

2. Biological characteristics of FGT and their relationships with the savannas

The termite fauna of arid savannas is dominated by the fungus-cultivating Macrotermitinae subfamily (FGT). Macrotermitinae termites are characterized by their large body size (2–3 times heavier than other types of termites), large population (1–2 million workers per colony, one to two orders of magnitude more populous than other types of termite colonies), and a higher reproduction rate, up to sixfold (Rouland-Lefèvre and Bignell, 2001) compared to the various taxa of non-FGT. For two specific large mound builders (i.e. *Macrotermes* and *Odontotermes*), termitaria densities can vary between 8.1 and 12.2

termitaria.ha^{-1} (Konaté, 1998). FGT also produce a specific soil fabric structure, ten times greater in strength (Kandasami et al., 2016) in comparison to the surrounding ground, impacting the savanna soils much longer than all other termite species.

2.1. A Paleogene origin of Macrotermitinae

Based on molecular dating, the origin of farming insects is hypothesized to have taken place independently in three different clades of fungus-farming insects, (i) once in termites, (ii) once in ants, and (iii) seven times in ambrosia beetles, all during the Paleogene. A study reported fossil evidence of farming insects in the form of fossilized FGT nests at Laetoli, Tanzania, approximately 3.7 million years ago (Darlington, 2005), as well as in Chad, approx. 7 million years ago (Duringer et al., 2006). Both are probably ancestral forms of species within the *Odontotermes* genus and of the *Macrotermes jeanneli* species, respectively. More recently, a fossilized fungus garden was discovered in a well-
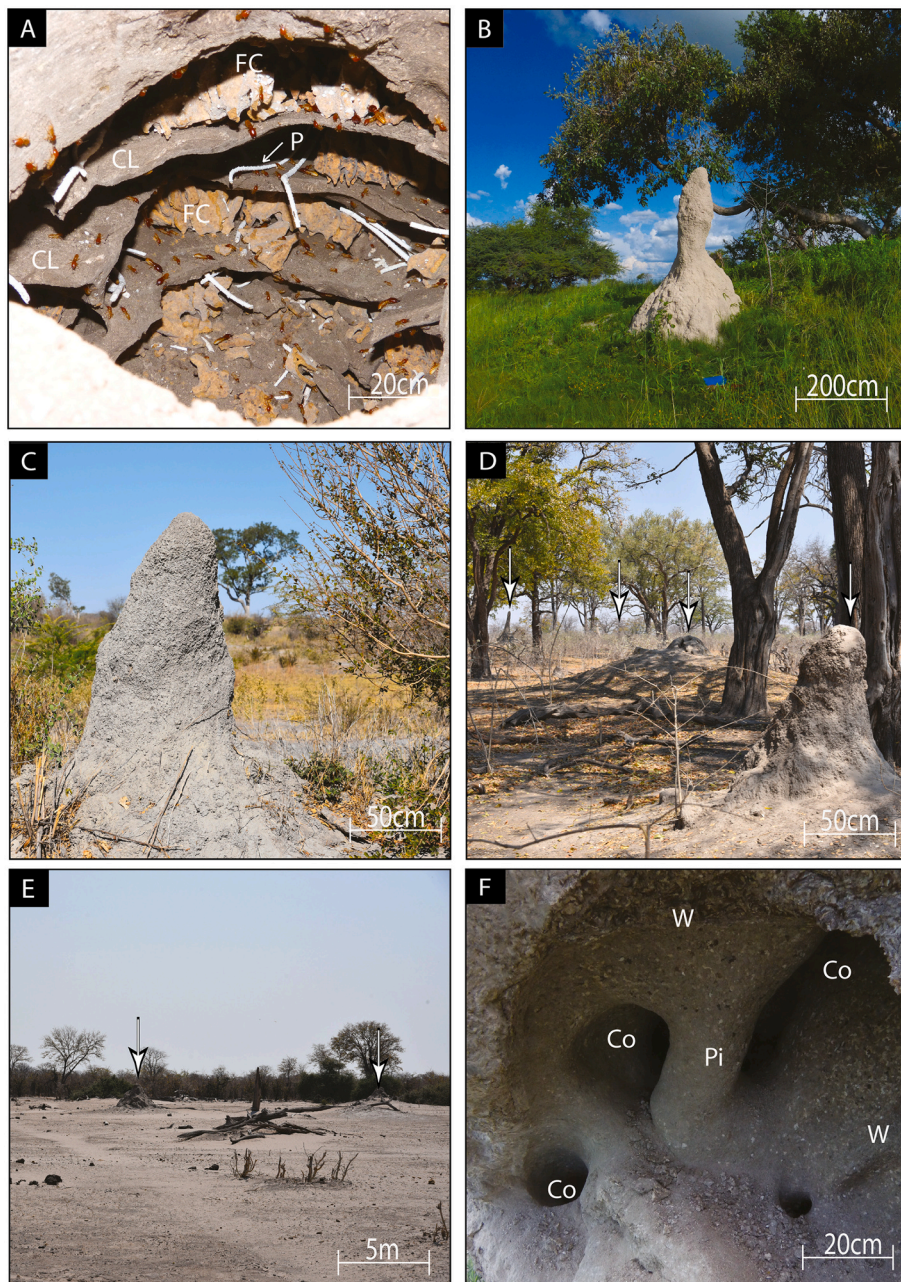
Fig. 3. Field views of termite mounds from Botswana (white arrows point to the mounds). (A) Fungus chamber of a *Macrotermes michaelseni* termite mound: fungus combs (FC) in pale orange deposited one next to other on a clay layer (CL) slowly sloping down in a helicoid shape. The newly scavanged plant material is delivered to the top of the fungus comb while the bottom part is used to feed the colony. White elongated Pseudorhizae (P) are visible sprouting out from some of the combs. (B) *Macrotermes* cathedral mound (see also Fig. 2) on the edge of a carbonate platform in the Chobe Enclave. (C) *Macrotermes michaelseni* epigeal mounds (see also Fig. 2) in an open riverine woodland of the Okavango Delta. (D) *Macrotermes michaelseni* epigeal mound close to an occasional floodplain (Linyanti River). (E) Small Macrotermitinae dome mounds (see also Fig. 2) in a dry open savanna landscape in the Mababe depression; lacustrine deposits are reworked by eolian processes. (F) Conduits (Co) inside a *Macrotermes michaelseni* mound used by termites to transport organic matter and/or sand particles as well as for air circulation; Pi: pillar. The walls (W) of these conduits are extremely solid when dry, but become viscous when wet.

preserved paleosol horizon of the Nsungwe Formation in the Rukwa Rift Basin in southwestern Tanzania, dated between 26 and 24 million years (Roberts et al., 2016). This latest discovery points to an African Paleogene origin of termite agriculture 31 million years ago, which could coincide with the rift initiation and changes in the African landscape (Roberts et al., 2016).

2.2. A complex symbiotic system

2.2.1. A first major symbiosis with fungi

The symbiosis between agricultural termites (subfamily Macrotermitinae, lsoptera) and fungi (genus *Termitomyces*, Basidiomycota) is one of the most spectacular examples of mutualistic symbiosis (Fig. 3A). A single transition to agriculture in termites has occurred with no reversions to free-living states (Aanen and Eggleton, 2005). Moreover, the agricultural symbiosis between termites and fungi is (i) symmetrical, (ii) both partners have a single origin, (iii) with no reversals to non-

symbiotic states and (iv) both are obligatorily dependent on this relationship (Aanen and Eggleton, 2005).

Termitomyces is a white-rot fungus, which is among the few organisms that can digest lignin. The optimal conditions (high buffered temperatures and high humidity) for white-rot decay are predominantly found in hot, wet habitats, such as rain forests. The ecological success of FGT in savanna is due to (i) the adoption of a highly successful rainforest process (fungal white-rot decay), (ii) the domestication of this white-rot fungi, (iii) providing the domesticated fungi with a constant supply of growth substrate, by (iv) replicating rainforest conditions in their fungus-garden (Aanen and Eggleton, 2005).

Plant materials consist mainly of lignocellulose, in which cellulose is protected by lignin against enzymatic attack (Reid, 1989). Hyodo et al. (2000) inferred that lignin is an obstacle for termites to acquire energy and carbon sources from cellulose. Grassé and Noirot (1958) were the first to propose the "lignin degradation hypothesis" of how symbiotic fungi have the ability to degrade lignin, which makes cellulose more

easily attacked by the termites' own cellulase (Hyodo et al., 2000). A more recent hypothesis suggests a cellulose degradation, where bacteria degrade the simple sugars from which FGT take in the cellulose acetate (Poulsen et al., 2014). Therefore, the fungus gardens of FGT (Fig. 3A) can be considered as a functioning external rumen. Roberts et al. (2016) emphasized that FGT ingest and masticate woody material, which are then excreted into round pellets (Fig. 4A), known as mylosphere, composed of undigested plant fragments and *Termitomyces* spores. The latter can germinate and colonize the plant material, thus forming a fungal garden. Collins (1983) described this symbiosis with the fungus as a way for termites to have an "external digestive system", which decomposes their faeces and decreases the C/N ratio of organic products by metabolizing carbohydrates prior to consumption. The first gut passage serves to mix fungal and termite enzymes and spores with the substrate. According to the "ruminant hypothesis" (Nobre and Aanen, 2012), initially the fungi benefit from their own enzymes and from termite-acquired enzymes using the termites to efficiently combine these enzymes with the substrate and their own asexual spores (nevertheless, it must be kept in mind that a rumen refers to an anaerobic fermentation, which is different from the aerobic digestion that takes place within the comb). This was later confirmed by da Costa et al. (2018). The termites secondarily profit from these enzymes in the form of degraded, nitrogen-enriched, plant material and fungal biomass, when old fragments of the comb (see next paragraph) are consumed (Nobre and Aanen, 2012).

What gives *Termitomyces* the advantage over its fungal competitors appears to be specific properties of the nest environment, e.g. the C/N ratio and the relatively dry environment of the mound. Indeed, and as
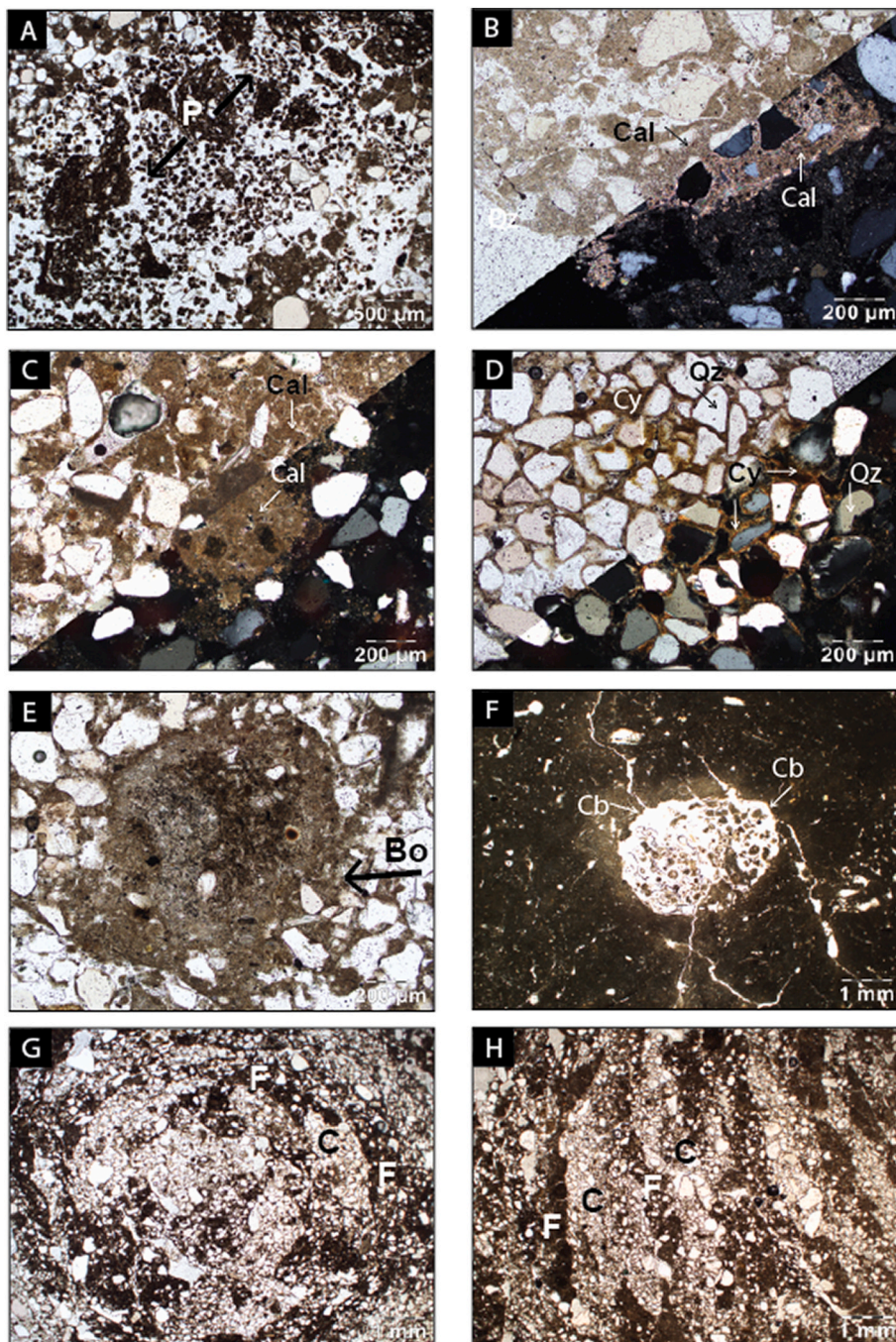
Fig. 4. Thin sections taken from FGT mounds (northern Botswana; unpublished authors' samples used as illustration for mound features). (A) Accumulation of pellets (P) (termite excretions), averaging from 50 μm to 100 μm, also called the "mylosphere": it is composed of undigested plant fragments and *Termitomyces* spores. Plane polarized light (PPL). (B) Calcium carbonate in the form of sparitic calcite (Cal). Upper left side: PPL; lower right side: crossed-polarized light (XPL). (C) Calcium carbonate fraction (brown-beige colors) as micritic calcite (Cal) inside the center part of the mound. Same as (B) for PPL and XPL views. (D) Chitonic c/f distribution showing clay coating (Cy) surrounding medium size sub-angular quartz grain (Qz). Same as (B) for PPL and XPL views. (E) Bolus (Bo) is a building brick used by termites to construct their mounds. These boluses have a wide variability in sizes, averaging between 200 μm and 800 μm. They are made of an aggregation of mineral grains of different particle sizes, mixed with saliva, and a given water content. The size of the particles determines the size of the bolus. PPL view. (F) A chamber (Cb) within a fine micromass, partly infilled by mineral grains and organic matter. PPL view. (G) The "lamellar fabric" of Mermut et al. (1987), i.e. a banded arrangement of aggregates with a specific fabric corresponding to the alternation of coarse (C) and fine (F) material. This circular shape relates to the pillar observed in the conduit zone of the mounds (see Fig. 3F (Pi)). PPL view. (H) Same arrangement, but this time in a parallel alignment, showing alternating coarse (C) and fine (F) material. PPL view. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

underlined by Turner (2004),"potential competitors are numerous and diverse, evidenced by the presence of roughly two dozen other types of fungal spores. [But] within the nest, the spores of all of *Termitomyces'* potential rivals remain dormant". However, it is also known that termites employ elaborate behavioral mechanisms for controlling parasitic fungi in their mounds (Visser et al., 2012). Therefore, *Termitomyces* grow as a single-strain on a special substrate, the fungus comb, a structure maintained by termites through the continuous addition of pre-digested plant material. The consumption of comb material varies between species. ln some cases, there is a continuous turnover of comb material, with primary faeces (including fungal inoculum) being deposited on top and the older comb material and the bottom being consumed (*Macrotermes* and *Odontotermes*). In other species, for example in the genus *Pseudoacanthotermes*, the entire comb is consumed before building a new one in an empty chamber (Nobre and Aanen, 2012). Macrotermitinae select fungi that (i) can slowly degrade the litter, enabling termites to have access to a constant source of food, and (ii) cannot grow too fast to potentially cause the destruction of the mound. ln conclusion, entering the symbiosis has allowed the fungi to overcome highly unfavorable seasonal conditions (e.g. temperature fluctuation and low moisture), and the termites to exploit complex plant substrates (e.g. lignocellulose).

2.2.2. A second major symbiosis with bacteria

Termites host a gut microbiota made of diverse and essential symbionts that enable the consumption of dead plant material, an abundant but nutritionally imbalanced food source (Brune, 2014). Since the first observations by Cleveland (1925) of termites surviving on pure cellulose, many biologists continued to explore the mechanisms through which termites overcome the two inherent problems of this diet: the decomposition of plant-cell walls and the acquisition of sufficient nitrogen (Higashi et al., 1992). Furthermore, Sugimoto et al. (2000) emphasized that termites are necessarily associated with symbiotic microorganisms, mainly gut bacteria. Termite gut microbiota provides the enzymes needed to degrade plant polymers, synthesize amino-acids, recycle nitrogenous waste, and fix atmospheric nitrogen. The role symbionts play in balancing the N economy - called "the second major symbiosis in termites" by Higashi et al. (1992) - has not been thoroughly investigated. Indeed, fixation takes place within the termite gut and not in the external fungus comb. Furthermore, FGT may be less nutritionally constrained by their lifestyle than other termites, but this does not rule out that N_2 fixation may be functionally important. Nevertheless, this challenges the notion of an important N_2 fixation in FGT, based on the assumption that the fungal diet obviates the need for costly fixation (Sapountzis et al., 2016). The combination of substrate processing and inoculation at first gut passage, followed by a second digestive phase, make the termite gut the central operational compartment of the symbiosis. Poulsen et al. (2014) finally concluded that "it is here that the entire genetic potential of all members of the symbiosis comes together, presumably shaped by natural selection for optimal collective performance in two sequential digestive phases".

2.3. Savanna expansion

FGT are restricted to the Old-World tropics (Fig. 1), with the highest diversity in the African tropical rainforest. This habitat has also been reconstructed as the center of origin, likely just before the expansion of the savanna, about 30 Ma ago. After originating from continental African rainforests, FGT have later repeatedly dispersed into savannas of Africa, and then, of Asia. The expansions of savannas and FGT might have occurred at similar geological times. ln order to maintain the rainforest conditions for the fungi within the nest, Macrotermitinae had to construct a biogenic structure (Fig. 3B-C). They form a large-scale "super-decomposition factory" to which a large amount of dead material is carried and processed into stored food, in order to be completely decomposed and consumed (Batra and Batra, 1979). The geographic expansion of FGT into more arid regions (Fig. 3D-E; Wood and Thomas,

1989) was made possible through three mechanisms: (i) termites created impermeable zones by adding fine clays to their structures, enabling water retention and reserves to develop in very dry environments; (ii) they gather water in deep sediment layers, a super-organismal equivalent of drinking (Turner, 1994, 2006), and (iii) due to the heterotrophic respiration of fungi and termites, large quantities of water are stored inside the biogenic structures for long periods of time. These factors helped FGT colonize dry habitats probably more efficiently than any other termite sub-families. Nevertheless, the number of FGT species is higher in rainforest habitats, but their relative contribution to the ecosystem decomposition is the highest in savannas, with up to 20% of all carbon mineralization (Nobre and Aanen, 2012).

2.4. Functional aspects of FGT and their mound

The species belonging to the Macrotermitinae sub-family are the only termite species that build a variety of biogenic structures (Fig. 2; Ocko et al., 2019). They do it in order to host the exosymbiotic *Termitomyces* fungus, often as a big epigeal mound with large fungus comb-chambers (Figs. 2 and 3A). This sub-family is only present in tropical and subtropical regions of Africa and Asia but is absent from Australia and the Americas (Fig. 1). Genera of this sub-family, such as *Macrotermes*, and in some cases *Odontotermes*, are the predominant ones, constructing big mounds with wide fungus chambers (Table 1).

2.4.1. Inter- and intra-species variability

Three genera suitably represent the variability of nest constructions encountered within the Macrotermitinae sub-family: *Ancistrotermes* and *Odontotermes* respectively forming lenticular mounds (Josens et al., 2016) and buttress mounds in forested areas, and *Macrotermes* forming epigeal mounds in all kinds of environments (Fig. 2). Darlington (1984), after research on two distinct epigeal mounds encountered in two different environments in Kenya, concluded that the observed termites belonged to the same species, i.e. *Macrotermes subhyalinus*. Mermut et al. (1984) noted that building behavior of different termite species with the same climate, vegetation, and parent material, appeared to be quite similar, whereas construction units by the same species under different conditions may be different (Fig. 2; Korb and Linsenmair, 1998, Korb and Linsenmair, 1999). Moreover, Turner (2000) stressed that variations within species behavior can be more important than variations between species. The impact of FGT is therefore not species specific but varies depending on the study site (Jouquet et al., 2005a). Last but not least, major differences are observed within a mound of a given species, as different parts of it require different structures and textures to fulfill distinct functions (Abe et al., 2009; Van Thuyne et al., 2021).

2.4.2. Saliva

In contrast to non-fungus growing termites, FGT do not incorporate faeces in their constructions, or do it extremely rarely (e.g. for comb construction). Instead, they enrich their construction with saliva, which acts as a binding agent. Jouquet et al. (2011) proposes that the incorporation of saliva in mound construction could influence clay mineralogical properties. These authors explain this mechanism by the grinding of soil particles by termites in the buccal cavity, which increases the surface area exposed to the surrounding solution, "leading to a release of interlayer K as well as the adsorption of hydrated or polar ions between the layers". Jouquet et al. (2002b) relate the mineralogical alterations observed in FGT mounds to (i) a direct effect of saliva, (ii) an indirect effect by the stimulation of microflora with saliva, (iii) an incorporation of fungi within their constructions, or (iv) a combination of these effects. Zachariah et al. (2020a) suggest that saliva does not directly increase the cohesion between soil aggregates, but its adhesive properties do substantially improve the resistance of the mound to erosion.

2.4.3. Time factor and age of mounds

Time can impact termite mounds at different scales. For example,

Chen et al. (2018) noted that the concentration of NO_3^- declined significantly following the transformation from active to abandoned mounds. Schwiede et al. (2005) suggested that leaching and erosion continued until the complete disappearance of the mound, causing a diminution of nutrients within the old mound and a rise in the adjacent soils. It can be inferred from field observations that FGT mounds, once abandoned, will tend to crumble down rather quickly; but as time passes, this process becomes exponentially slow (Ali Mainga's observations in Botswana, pers. comm.). Once the colony at the origin of a mound dies, inquiline species, soil invertebrates, and specific plant species colonize the nest structure and continue to maintain it, increasing the spatial heterogeneity of this specific biotope for a long time. FGT mounds are generally important geomorphological features standing out in otherwise relatively flat landscapes of savanna. Their volume is considerable: a mound studied by the authors in the Chobe Enclave (Botswana) had an above ground volume of 1350 m^3. They also can remain for long periods of time: two FGT relic mounds have independently been dated by Optically Stimulated Luminescence (OSL) (Kristensen et al., 2015) and ^{14}C (Erens et al., 2015a) at 4′000 and 2′200 yr BP in Ghana and the D.R. Congo, respectively.

3. Geochemical impacts of Macrotermitinae

3.1. Macrotermitinae and soil chemical properties

3.1.1. Alkalinity

The pH in mounds – The soil fraction associated with termites usually displays a more alkaline pH compared to the surrounding soil (Fig. 5A; Brauman, 2000; Holt and Lepage, 2000; Erens et al., 2015b). Mujinya et al. (2010) measured the following soil pH_{KCl}: 5.8 in the central hive, 6.2 in the chamber wall, 4.9 in the mound foot, and 4.5 in the control soil; the pH can even reach values up to 8.4_{H2O} in the inner cone (Mujinya et al., 2011). Jouquet et al. (2004a) also measured a pH almost always higher in the termite mounds than in the control soil, with alkaline values up to 8, the control soil remaining slightly acidic throughout the profile.

Potential causes of alkaline pH – The processes inducing high pH values are (i) saturation status by alkali and alkaline-earth cations, (ii) lowering the point of zero charge, and (iii) the microbial activity associated with termites. Indeed, the concentrations of four cations (Ca^{2+}, Mg^{2+}, Na^+, K^+; see next section) are 21, 20, and 12 times greater in the central hive, the chamber wall, and the mound foot (respectively), than in the control soil (Mujinya et al., 2010). Consequently, this increased saturation status may explain the trend towards high pH observed in the mound interior (Fig. 3F). In addition, Mujinya et al. (2010) demonstrated that the termite activities are able to considerably lower the point of zero charge values, contributing to increase the soil pH. Finally, a specific biogeochemical chain of reaction, the oxalate-carbonate pathway (Cailleau et al., 2011), could also explain the shift in the pH, as this process is always accompanied by a substantial alkalinization (Verrecchia et al., 2006). Indeed, Mujinya et al. (2011) noted that "the formation of all observed weddellite is related to fungal activity, formed from released oxalic acid in contact with hyphae or at a greater distance". Calcium oxalate is then locally transformed into carbonate ions by bacterial oxalotrophy (Verrecchia et al., 2006), leading to a significant increase of pH.

3.1.2. Cation exchange capacity (CEC)

CEC values within the mound – Termite mounds usually display greater CEC values compared to control soils (Jones, 1990; Jouquet et al., 2004a; Mujinya et al., 2010; Erens et al., 2015b). Mujinya et al. (2010) showed that termite activities considerably lowered the preferential adsorption of Al^{3+} on the exchange complex. At field soil pH, they measured average values of CEC_B (base cation exchange capacity) of the central hive to be 9.9 cmol Kg^{-1}, 9.6 cmol Kg^{-1} in the chamber wall, and 6.7 cmol Kg^{-1} in the mound foot. All samples values were greater than

those of the control soils (2.1 cmol Kg^{-1}). Moreover, they obtained an average CEC_T (total cation exchange capacity) values at soil pH, four times greater in the central hive and chamber wall samples, and three times greater in the mound foot soil, than in the control soils. Contour-Ansel et al. (2000) also found a CEC value in walls of 18 cmol Kg^{-1}, which was significantly higher than in the reference soil, i.e. 7.5 cmol Kg^{-1}. The differences between CEC_T and CEC_B generally decrease in the following order: control soil > central hive > mound foot > chamber wall (Mujinya et al., 2010). Erens et al. (2015b) measured the highest CEC values in the center of the mound (22.4 cmol Kg^{-1}) and locally in the outer mantle (15 cmol Kg^{-1}), and all their results, regarding the mound samples, were higher than those of the upper part of the surrounding soils (8.32 cmol Kg^{-1}). Jouquet et al. (2004a) demonstrated that the level of exchangeable Mg^{2+} and K^+ was greater in the termite mound. Conversely, the concentration of Al^{3+} was greater in the control soil; but they also found that the level of Ca^{2+} did not differ significantly.

Possible causes influencing the CEC – After many years of research performed by J. A. Jones in the 90's, three different reasons were postulated to explain the high CEC encountered in FGT mounds: (i) the presence of calcareous materials collected by termites, (ii) alkaline groundwater brought up by termites, and (iii) seasonal evaporation of shallow groundwater by suction effect through the mound chimneys. Jouquet et al. (2004a) indicated that no difference was found between CEC at soil pH and CEC at pH = 7, suggesting that the CEC is not pH dependent. In addition, these authors mentioned that soil organic matter (SOM; see next section) may play a negligible role in the CEC. Therefore, these remarks imply that 2:1 clay minerals can be responsible for the high CEC values, since these clays often have an elevated CEC (Dangerfield et al., 1998). The presence of higher amounts of smectite in the termite nest soils is another reason put forward by Jouquet et al. (2016a) to explain the increasing CEC despite the reduced C and N contents. In conclusion, the higher CEC values encountered in FGT mounds is probably not pH and SOM dependent but rather due to the presence of 2:1 clays, specifically high amounts of smectite.

3.2. Macrotermes and chemical elements

3.2.1. Nitrogen and C:N ratio

Jouquet et al. (2004a) noted that the N content associated with clays used by termites is not significantly different from the clays in the control soil. Conversely, the N content was significantly higher in the sand used by termites for building sheeting and galleries. Jouquet et al. (2003) also determined that N in the chamber wall was significantly greater than in the gallery. Erens et al. (2015b) showed that the center of the mound exhibited extreme concentrations of NO_3^- (1069 mg Kg^{-1}), which gradually decrease outwards. Jouquet et al. (2005c) also recorded an enrichment in nitrate, ammonium, and mineral nitrogen. These respective enrichments were attributed by Erens et al. (2015b) to a low pH, at locations where NO_3^- accumulates in the mound. They suggested that a nitrification process takes place predominantly after leaching of NH_4^+ came to a halt, and consequently, NO_3^- is not leached further down. An additional soluble salt analysis performed by Erens et al. (2015b) revealed that NO_3^- could occur predominantly as Ca^{2+} and Mg^{2+} salts. Chen et al. (2018) measured decreasing concentrations of NO_3^- in a sequence as follows: active mound, abandoned mound, and surrounding soil. Another study by Menichetti et al. (2014) detected significantly higher nitrification rates in all termite mounds (active and non-active) compared to adjacent soils. The ammonification rates were also significantly higher in the colonized termite mounds than in their adjacent soils, but not in the abandoned nests.

Moreover, organic carbon contents measured by Jouquet et al. (2004a) were greater in the control soil than in the termite mound soil, whereas there was no significant difference in their respective nitrogen content. Consequently, the C:N ratio was significantly less in the mound. According to these authors, soils could be ranked by their decreasing C:N ratio as follows: control soil > galleries > chamber walls (Jouquet et al.,
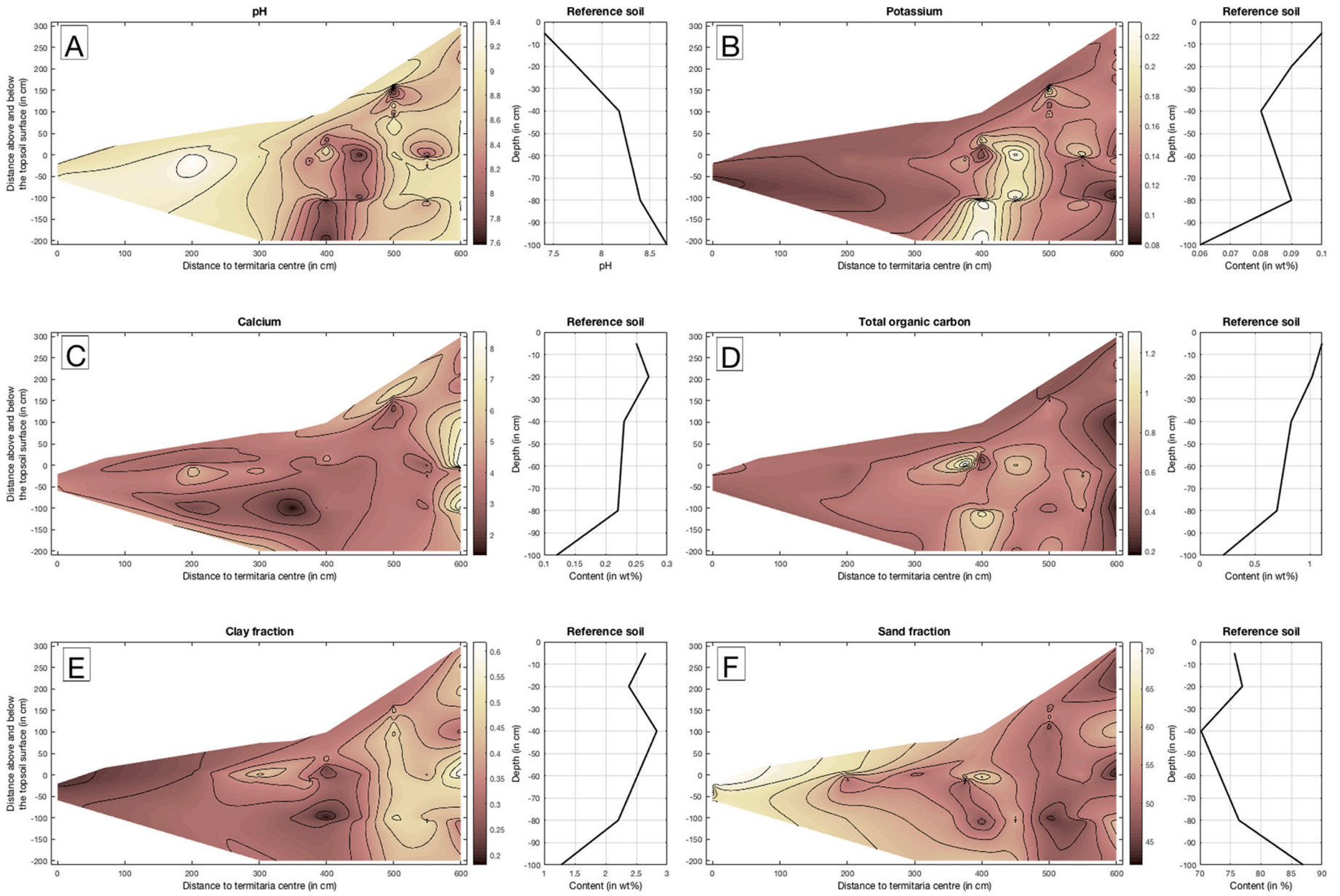
Fig. 5. Maps of pH, % wt of elements and grain-size distributions in one half of a termitarium of *Macrotermes* from the Chobe Enclave district (Botswana, unpublished authors' samples used as illustration for mound features; pH measured in a 1:2.5 soil:water mix with a Metrohm 682 titroprocessor; K and Ca measured with a PANalytical Axios X-ray fluorescence device on bulk fraction; total organic carbon assessed with a Rock-Eval 6 pyrolyser; grain-size distribution obtained with a Beckmann Coulter Laser grain-sizer). On the x axis, distance from the periphery of the mound to its center; on the y axis, distance above (> 0 cm) and below (< 0 cm) the topsoil surface (at 0 cm). (A) pH. (B) Total potassium in % wt. (C) Total calcium in % wt (almost exclusively as calcite in this case). (D) Total organic carbon in % wt measured by Rock Eval pyrolysis. (E) Clay fraction in % (size ≤2 μm). (F) Sand fraction in % (63 μm ≤ size ≤2000 μm). Same variables are used in graphs on the right-hand side of each map: these plots refer to a reference soil, 20 m from the termitarium. The mound is clearly separated into three distinct zones (i) the outer mantle, (ii) the central column comprising the nest, the chimney and an accumulation zone, and (iii) a transition zone, which lies between the former and the latter. Elevated pH values are found inside the central column and the outer mantle. High concentrations of K border the central column, while low contents are detected inside the column and above and below ground in the transition zone. Calcium is mainly abundant in the central column, whereas the central part seems depleted. The clay fraction is therefore characterized by high pH values, high calcium and clay contents. On the other hand, potassium and total organic carbon are concentrated around the transition zone, whereas sands and pH reach high values in the outer mantle. Reference soils provide distributions of the variables for comparison with the various parts of the termitarium. They are one to two orders of magnitude less alkaline than the termitarium, with low contents of K, Ca, and clays compared to the mound.

2004a). Tilahun et al. (2012) calculated that a termite mound can store of 27–53 kg ha^{-1} of total N. Furthermore, Chen et al. (2018) showed that the mound structures inhabited by *Odontotermes yunnanensis* contain higher NH_4^+ concentrations than the mounds of *Macrotermes annandalei*, but no variations between mounds were found in NO_3^- concentrations. This difference in species clearly indicates that the ammonification rate was higher in *Odontotermes* mounds.

In conclusion, it appears obvious that FGT have the ability to concentrate nitrogen, its greatest concentration being in the center of the mound, in the comb chamber. The accumulation of NO_3^- in the center of the mound can be explained by the leaching of ammonium from the upper layers, which takes place before the nitrification process, precluding leaching of nitrate afterwards. The observed concentrations of N in the comb seem to be due to the symbiont fungus. Moreover, termite gut microbes provide the mean to fix great quantities of atmospheric nitrogen within their gut.

3.2.2. Macrotermes and potassium

High concentration of potassium in mounds – Erens et al. (2015b) noted elevated exchangeable K^+ contents along the wide central column in a mound, compared to lateral parts of the same structure and the control soil. The highest values were observed in the active nest (1.94 cmol kg^{-1}) and around the ground level (2.02 cmol kg^{-1}). Tilahun et al. (2012) showed that the available P and the exchangeable Mg^{2+} and K^+ contents of a termite mound were significantly higher than in the adjacent soils by 90%, 36%, and 188%, respectively. Whatever the sites and the observations performed by researchers, potassium seems to systematically reach high levels inside the inner part of the termite mound (Fig. 5B).

Processes involved in the concentration of potassium – Erens et al. (2015b) explained the elevated exchangeable K^+ contents observed in the central column of mounds by the mineralization of organic matter brought into the nest area. Another reason could be the slowdown of element leaching due to retention by the cation exchange capacity, mainly represented by the clay mineral fraction. Mujinya et al. (2013) proposed a complementary explanation based on laboratory experiments simulating the clay mineral transformation inside the mound. Indeed, during their analysis, they observed an increase in the proportion of expandable layers in clays. The authors attributed this transformation to the release of non-exchangeable potassium from illite interlayers, due to interactions with termite saliva and associated microorganisms. In addition, Mahaney et al. (1999) measured an exchange of potassium for calcium (Fig. 5C) in *Macrotermes* and *Pseudoacanthotermes* termite nests. Finally, in one of their experiments, Jouquet et al. (2005b) also found a modification of the clay properties due to the termite action on 2:1 minerals. The aging of mounds has also been put forward by Menichetti et al. (2014) as a key factor influencing the nutrient distribution (including K) in termite-colonized soils. This property has also been emphasized by Erens et al. (2015b) and Chen et al. (2019), who found that nutrient accumulations increase once a mound reaches a given size and decrease once abandoned. Jones (1990) was among the first researchers to propose that the nutrient enrichment of termite mounds resulted from termite harvesting of plant litter from the upper soil organic layers. This litter matter, transferred into the mounds, decayed inside the fungus garden. Moreover, it has been suggested by Sako et al. (2009) that a slight increase in Total Organic Carbon (TOC; Fig. 5D) content in mounds, relative to the surrounding top soil, may enhance the accumulation of most of the micro-nutrients (K^+ included) in the mounds.

In conclusion, four processes can be put forward to explain the enrichment in K encountered in termite mounds: (i) the mineralization of organic matter, K^+ being leached down and trapped by the high cation exchange capacity of the mound soil, (ii) the transformation of illite into smectite, (iii) the litter transfer inside the mound, and (iv) the aging of the mound. The first two processes can mainly be attributed to a "termite and mound effect", whereas the third one is clearly a "termite

effect", and the last one a "mound effect".

3.2.3. Macrotermes and phosphorus

All mounds studied by Erens et al. (2015b) showed an accumulation of total P in the lower central part. Unlike the patterns of exchangeable K^+, those of P displayed no maxima around the current nest position of the mound, suggesting that P, derived from mineralization of organic matter in the nest, is leached downwards. Menichetti et al. (2014) showed that the phosphate content was significantly higher in the colonized termite mounds than in the adjacent soils. However, they also discovered that, despite the larger microbial biomass and respiration, all measured enzyme activities involved in phosphate pathways were lower in the mound walls than in the adjacent soils. Jouquet et al. (2011) noted that only a few studies have been conducted on the effect of termites on soil P, although this nutrient is often deficient in tropical soils. They remarked that the influence of termites on the total and available P fractions seemed to vary according to termite functional groups. Seymour et al. (2014) confirmed the lack of P availability in savanna soils. Thus, having a source of available P in termite mounds could be of interest for plants and farmers. They also demonstrated that, although more P was found in FGT mounds, the woody plants growing on mounds did not seem to be distinctively enriched in P. Therefore, even if the concentration of P is higher in FGT mounds (Tilahun et al., 2012), this does not necessarily mean that P is more bioavailable (Edosomwan et al., 2012). It depends on the type of construction and the quantity of clay incorporated in the mound. Clay enriched materials have high P-sorbing capacities and, consequently, a lower P availability than adjacent soils. Jones (1990) noted that the high N and P observed in mounds resulted from *Termitomyces*, as their efficiency reaches 80% in the decaying of cellulose and lignin in the macerated litter. Phosphorus pathways differ from those of N, because, although N is concentrated in mounds, it still remains available for plants (Dangerfield et al., 1998). In addition to the elevated sorbing capacities generally observed in FGT mounds, the availability of P is dependent on the pH found inside the mound, the latter often being higher than 7 (see section 3.1.1). Erens et al. (2015b) suggested that, above a pH = 7, phosphate can precipitate and be fixed in the form of calcium phosphate, rendering the availability of P difficult.

In conclusion, phosphorus in mounds appears to be dependent on (i) the quantity of clays, (ii) *Termitomyces* elevated decomposition rate of cellulose, (iii) the type of construction, (iv) the species studied, and (v) the pH value inside the mound. Finally, the concentration of macronutrients, such as P, is strongly correlated to the mound size, which is also strongly correlated to mound age (Seymour et al., 2014). Once the FGT mound is abandoned and washed out in the piedmont, the stored quantities of P could eventually become available in the surrounding soil, but this will depend on its speciation, the soil pH, as well as other local edaphic factors.

3.3. Carbon-bound compounds

3.3.1. Carbon dioxide

A two-fold increase in CO₂ emissions – Jones (1990) suggested that organic carbon is transformed in termite mounds and emitted (i.e. *mineralized*) as CO_2 and CH_4. Apparently, 80% of the organic carbon ingested by Macrotermitinae may be digested by *spp*, with CO_2 as the main end product. Konaté et al. (2003) observed that, whatever the savanna type, the CO_2 emission from the soil surface did not differ between the control soil and the soil of the eroded termite mound. However, this emission was significantly higher in areas associated with fungus comb chambers compared to areas without them (10–19 μmol CO_2 m^{-2} s^{-1} compared to 5–10 μmol CO_2 m^{-2} s^{-1}, respectively). In grassy savanna, where most of the termite activity is concentrated in mounds, Konaté et al. (2003) estimated that the CO_2 emission due to *Odontotermes* was about five times higher than that attributed to *Ancistrotermes* (28 nmol m^2 s^{-1} and 6 nmol m^2 s^{-1}, respectively). They further

calculated that the total respiration rate from an individual fungus comb chamber was around 60 μmol CO_2 h^{-1} and 150 μmol CO_2 h^{-1} for *Ancistrotermes* and *Odontotermes*, respectively. At the landscape scale, the total CO_2 emission was estimated at 27.2 g C m^{-2} y^{-1}, representing almost 5% of the total aboveground net primary production in a savanna ecosystem and 11% of the carbon not mineralized by annual fires. They conclude that the "total CO_2 emitted by FGT ranged from 118.8 to 290.4 g C m^{-2} y^{-1} on termite mounds, compared with 7.2 to 27.6 g C m^{-2} year^{-1} in the surrounding soils" (Konaté et al., 2003).

Diversity in respiration and sources of CO₂ – Konaté et al. (2003) observed that the Macrotermitinae species, which have the highest respiration rates (e.g. *Macrotermes bellicosus* and *Odontotermes n. pauperans*), ingest enzymes from the fungus and combine them with their own enzymes for the digestion of their nutrient sources. Other FGT species, which exhibit lower respiration rates, (e.g. *Ancistrotermes cavithorax)*, do not. Therefore, Konaté et al. (2003) concluded that the respiration from the walls of fungus comb chambers represents a heterotrophic activity, mainly a microbial metabolism, and could be a good indicator of the quantity of organic carbon mineralized by the microflora. Furthermore, they showed that the *Termitomyces* fungus is able to release the majority of the organic carbon ingested by termites. This illustrates the role of the fungus comb in achieving the C:N balance in termite mounds, the release of inorganic C through the fungus respiration being an additional way to concentrate nitrogen in the comb. Sugimoto et al. (1998) observed that methane emitted from termite mounds had heavier $\delta^{13}C$ than the methane directly released by FGT, meaning that CH_4 had been partly oxidized during its emission into the atmosphere. In conclusion, the differences between the respiration rates, when comparing species, can probably be related to their digestive metabolism, as the rate of carbon dioxide production by different termite species represents a good estimation of their trophic status. Finally, Aanen and Eggleton (2005) arguably presented the FGT as the predominant decomposer organisms in dry savannas, where they are responsible for around 20% of all C_{org}-mineralization.

3.3.2. Organic carbon at the ecosystem-soil scale

Variability in contents of soil organic carbon – According to Holt and Lepage (2000) and Jouquet et al. (2002a, 2004a), FGT seem to significantly modify their environment by increasing the content of SOM in their mounds. Jouquet et al. (2005a) hypothesized that the differences observed between the structure of bacterial communities found on walls of fungus comb chambers and on walls of lenticular mounds built by *Odontotermes* could be explained by their SOM content. Indeed, these authors found greater quantities of carbon and a greater content of microbial biomass within the lenticular mounds compared to the control soils. This points to an important content of SOM available to microbes in these constructions. In another study, Jouquet et al. (2011) suggested that an intense humification process is mediated by FGT during the gut transit, where a re-organization and re-integration of SOM with the mineral soil fraction takes place. The resulting clay-humic complexes are then combined as micro-aggregates and then integrated in the termite structures, which protect soil organic matter from mineralization (Romanens et al., 2019). Jouquet et al. (2011) characterized termite nests as "carbon sinks", since they withdraw large quantities of litter and soil organic matter from the aerial/aerobic decomposition pathways. Aging of the mounds seems to lead to higher concentration of C_{org} (Fig. 5D) and total N in the abandoned mounds than in active mounds (Chen et al., 2018). On the other hand, the concentrations of organic carbon (C_{org}) and total N in the active termite mounds were significantly lower than those in the surrounding top soils (Chen et al., 2018). Jouquet et al. (2015b) noted that the lower SOM content observed in the active mound can usually be attributed to either a selection by termites of small aggregates enriched in clay and/or the use of material from the deep soil layers, which have a lower SOM content but a higher clay content.

Variations in soil organic matter incorporation and the priming effect – It

was first suggested by Jouquet et al. (2002a) that termites are able to modulate the quantity of SOM in their epigeal mounds. In a laboratory experiment, Jouquet et al. (2002b) further showed that the amount of SOM incorporated (via the termites' saliva) depends on the nature of the soil used and the type of construction. Konaté et al. (2003) showed that the direct respiration of termites is accompanied by a priming effect of labile carbon sources, enhancing soil organic matter mineralization. Jouquet et al. (2007b) found concurring results when they observed lower C and N in sheeting built from clay, implying a priming effect, which increases SOM mineralization after the addition of fresh organic matter (saliva). They further emphasized the role of FGT as important soil organic matter decomposers through their capacity to initiate these particular priming effects. Following in situ field analyses, Jouquet et al. (2007b) highlighted that SOM content in constructions of FGT can vary substantially when compared to bulk soil. These observations are in accordance with other studies reporting that SOM contents in FGT were similar (Eschenbrenner, 1986), higher (Jouquet et al., 2003), or lower (Brauman, 2000; Contour-Ansel et al., 2000; Jouquet et al., 2004a; Jouquet et al., 2015b) than the surrounding soils. Recently, a study by Shanbhag et al. (2017) revealed that termite mounds tended to be enriched in C_{org} when the surrounding control soil had C_{org} contents <1.4% but became impoverished in C_{org} for concentrations >1.4% in the surrounding soils. This finding provides an interesting explanation for the apparent contradictory results stipulating that termite constructions can have higher, lower, or similar C contents when compared to the surrounding soil (Shanbhag et al., 2017). Indeed, this result suggests that concentrations of C_{org} in a termite mound depends on the richness of the organic matter in the adjacent soil rather than the termite species (Chen et al., 2018). Finally, in an experiment conducted by Chenu et al. (2000), walls of the fungus chambers were more effective in holding water than walls of the connecting galleries: this property could be the consequence of SOM as, "since, the two constructions had the same texture, the increase of the soil water retention was probably caused by the change in SOM quality" (Chenu et al., 2000).

3.3.3. Soil organic carbon at the mound scale

Based on the turnover of the fungus comb mass, Josens (1972) estimated that FGT consumption of organic matter in a savanna environment varied between 1300 and 1600 kg ha^{-1} year^{-1}, which is equivalent to 645 kg C ha^{-1} y^{-1} (64.5 g m^{-2} y^{-1}). Tilahun et al. (2012) calculated that a termite mound can store 186–306 kg ha^{-1} of organic carbon. Konaté et al. (2003) measured respiration rates as representing roughly 42% of the carbon consumed by the Macrotermitinae populations. Furthermore, it was observed by Jouquet et al. (2007b) that, while the carbon content was significantly lower in the biogenic structures built from clay compared to the control soil, an increasing C content was found when termites used sand. Other research, conducted by Erens et al. (2015b), showed that the outer mantle samples were associated with high C_{org} levels, and positioned opposite to the accumulation zone characterized by relatively high concentrations of NO_3^-, P, CEC, and exchangeable K^+. They also mentioned that outliers corresponded to the chimney structure (low C_{org}) and the active nest (high C_{org}). In conclusion, due to the high decomposition rate and the rapid carbon turnover, small quantities of organic carbon are stored in FGT mounds. Generally, more organic carbon is found in the outer mantle and in the central nests compared to the rest of the mound.

Moreover, Jones (1990) proposed that organic matter (OM) decomposition progresses much faster in soils occupied by termites than in soils without termites, because of their litter harvesting and fungus cultivation by Macrotermitinae. More recently, results from Contour-Ansel et al. (2000) showed that the walls of *M. subhyalinus* mounds had a low organic matter content (2.5 mg g^{-1}), about half of the reference soil (4.1 mg g^{-1}) with an amount of organic nitrogen essentially the same in walls (0.23 mg g-1) as in the reference soil (0.30 mg g^{-1}). As a consequence, the walls of FGT mounds contain little organic matter, and hence, low levels of polysaccharides, which are mainly of plant origin

(Contour-Ansel et al., 2000). Jouquet et al. (2003) observed that organic carbon was incorporated in galleries and walls, but the quality of this OM differed between galleries and chamber walls; it seems that termites can adjust the quantity and the quality of OM supplied in the structure they edified, according to their requirements. Sako et al. (2009) suggested that the labyrinth of *Macrotermes* was more exposed to termite activities, and therefore contained higher amounts of clay and organic matter compared to galleries and external sheeting. Jouquet et al. (2011) came to similar conclusions and proposed that temporary structures built by Macrotermitinae can be created from the immediately adjacent soil, and relatively little organic matter was supplied as a binding agent; conversely, in the case of nests, termites gather components deeper in the soil and incorporate more organic matter. Observations made by Erens et al. (2015b) supported these findings as well, and they also emphasized that the organic matter content in the mound was high at the surface and decreased in the lower central part of the mound, yielding a pattern that matched variations in pH (see section 3.1.1). Estimations of plant litter transported to the nest can vary between 1 and 1.5 t ha^{-1} y^{-1} (Lepage, 1979). In semiarid African savannas, 90% of the dead wood was found to be degraded (Ferrar, 1982). Wood and Sands (1978) estimated that, in such environments, termite biomass could be between 70 and 100 kg ha^{-1}. These values are comparable to the ungulate biomass of African savannas, i.e. 10 to 80 kg ha^{-1} (Bell, 1982). Jouquet et al. (2011) hypothesized that termites can mechanically reduce plant material size, thereby, significantly increasing the surface area accessible to microorganisms. One aftermath is a feedback of organic matter to the biomass of termite bodies, their biogenic structures, and the associated soil. Furthermore, Jouquet et al. (2011) postulated that termite sequester SOM for considerable periods in their nests, mounds, and galleries, until the breakdown and erosion of nest structures return this incorporated organic matter and nutrients to the sedimentary environment.

In conclusion, termite activities tend to accelerate organic matter decomposition, lowering OM concentrations in mounds compared to the control soil. However, more OM is found and concentrated in the nest labyrinth compared to the galleries and sheeting (Jouquet et al., 2015a). The major factors involved in this process are the capacity of FGT to adjust (i) the quantity of OM to the different parts of their constructions, and (ii) the quality of the OM, by adding more saliva or more plant material, wherever necessary.

3.3.4. Macrotermitinae and sugars

Contour-Ansel et al. (2000) showed that the reference soil contained more sugars than the walls of the *M. subhyalinus* mound, clearly demonstrating that the glucose originated from cellulose. Moreover, although it was present in the reference soil samples, the almost complete absence of stachyose (a tetra-saccharide) from the walls confirmed that plant organic matter was not used to build termite mounds (Contour-Ansel et al., 2000). Therefore, it seems that termites use instead the deep soil, which contains little or no humus. After a thorough investigation of the mutualistic symbiosis between Macrotermitinae termites and *Termitomyces* fungus, Hyodo et al. (2000) demonstrated that the digestibility of cellulose on an old fungus comb was approximately three times higher than in the fresh part, suggesting that the lignin degradation was progressively taking place in the fungus comb. These results confirm (i) the lignin degradation hypothesis (see section 2.2.1.), and (ii) the role of the mutualistic fungi to degrade lignin and enhance the digestibility of cellulose by FGT.

4. The mineralogical and physical impacts of Macrotermitinae

4.1. Macrotermitinae and minerals

4.1.1. Calcium carbonate in termite mounds

Distribution of the carbonate fraction – Many mounds of Macrotermitinae, especially *Macrotermes*, contain a $CaCO_3$ phase. $CaCO_3$

content is generally higher in mounds compared to the adjacent soils (Figs. 4B, C, 5C). Inside a large termite mound in the D.R. Congo, Mujinya et al. (2011) measured the following calcite contents: 25–38% in the inner cone, 6–25% in the middle cone, 0–5% in the outer cone, and no calcium carbonate in the adjacent soils. Erens et al. (2015b) observed a distribution pattern of carbonate similar to pH (see section 3.1.1; Fig. 5A, C), with the highest calcite concentrations in the zone between the hive centre and the mound surface layers: in some mounds, the highest $CaCO_3$ contents were observed in their lower parts, extending to layers below the epigeal part of the termite mound. Comparatively, Mujinya et al. (2011) observed carbonate coatings in the mound, mainly between 1 m above and below the soil surface. In addition, they noted the presence of carbonate nodules, with a specific distribution pattern at each of their sites. Finally, Erens et al. (2015b) attributed the presence of high proportions of carbonate in the lower part of the mounds to the dissolution and leaching from the upper parts. But invariably, the surrounding soils remained totally depleted in carbonate at both Erens et al. (2015b)'s and Mujinya et al. (2011)'s sites (see Fig. 5C and its reference soil).

Origin of the calcium carbonate fraction – As early as the 1940's, Milne (1947) already hypothesized that the $CaCO_3$ accumulated in the termite mounds could have resulted from upward movement of Ca^{2+} and HCO_3^--rich groundwater, a hypothesis, partially supported by Hess (1955) and Weir (1973). But these two latter authors also emphasized the necessary presence of evaporation processes from the raised mound surface, in order to trigger the precipitation of carbonate within the mound. Watson (1969) intended to confirm these assumptions by using a radioactive tracer, but concluded that, unless the mound is extremely old, the Ca^{2+} included in the carbonate phase of termite mounds could not have originated from underground waters. He imputed the elevated concentration of calcium to a process termed "differential leaching", outlining that termite mounds are generally less leached than their respective control soils. Sako et al. (2009) observed that carbonate species tended to form stable complexes with Heavy Rare Earth Elements (HREE) and inferred that HREE were accumulated in mounds due to the co-precipitation of these elements with calcite, after an evaporation process took place. Whatever the hypothetical processes involved, three critical characteristics are needed for calcite precipitation: the presence of (i) Ca^{2+} ions, (ii) a dissolved inorganic carbon source, (iii) and alkalinity.

Concerning the carbonate ions, they can easily originate from the large, almost infinite, compartment of soil CO_2 permanently fed by the biota respiration and the organic matter decay. Mujinya et al. (2011) also emphasized such a process, partially relating the precipitation of carbonate accumulated in mounds to microbial respiration. For them, the carbonate phase precipitated in equilibrium with the soil CO_2, originating from the decaying SOM. On the other hand, the question of the alkalinity remains more difficult to solve. Many mounds are presently observed in silicate/siliceous watersheds worldwide, where the soil parent material, as well as the most widespread classes of soils on which mounds initially developed, are slightly neutral to outright acidic. As mentioned in section 3.1.1, the oxalate-carbonate pathway can be proposed as an efficient process to explain a rise in alkalinity. The oxidation of Ca-oxalate from fungi or plants by oxalotrophic bacteria can locally significantly increase the soil pH (sometimes by three units; Erens et al., 2015b), making the precipitation of $CaCO_3$ possible in an overall acidic environment. Alkalinity remains clearly an issue.

During the 1970's, complementary arguments were put forward by Watson (1975) and Trapnell et al. (1976), who suggested that the increase in Ca^{2+} content in *Macrotermes* mounds might stem from consumed plant tissues. Mujinya et al. (2011) proposed that calcium in FGT mounds could derive from plant tissues incorporated inside the mound. This is not surprizing as, in the tropical zone, the main cation source remains the plant reservoir, in which ions are permanently recycled, from the SOM to the living plants, and back to the soil as incorporated litter (see section 3.3.2). Finally, Liu et al. (2007) proposed

an upward transportation of $CaCO_3$ particles by termites.

In conclusion, the origin of carbonate accumulation in FGT mounds must be seen as a result of complex pedogenic processes (Fig. 4B, C), involving both indirect biotic action of bacteria, fungi, and plants (i.e. as sources of carbon and alkalinity) and abiotic reactions (e.g. leaching processes, dissolution-precipitation of crystals). In addition, significant differences in Ca concentrations can be found between mounds of *Odontotermes* versus *Macrotermes* genus, as observed by Mujinya et al. (2014).

4.1.2. Clays

Mounds seem to concentrate clay minerals – One of the most interesting features regarding grain size distributions in mounds is the ability of termites to create a stone-free A horizon in savanna soils. Indeed, Dangerfield et al. (1998) showed that (i) many clay minerals are mined from the rocks beneath the mound, and (ii) large fragments of the parent soil material subsequently fall to lower levels in the soil profile. Contour-Ansel et al. (2000) confirmed that the termite mounds of *M. subhyalinus* were highly enriched in clay (30%) and silt (13%), and proportionally depleted in sand, compared to control soils (Fig. 5E, F). The amount of organo-clay material (i.e. the clay fraction associated to organic matter) in the mound walls was 27% compared to 10% in the reference soil. The proportion of clays is always higher in termite mounds than in the bulk soil and often the most in the royal cell and the least in the outer wall (Jouquet et al., 2002b). Using soil micromorphology, Mujinya et al. (2013) provided direct evidence of clay dispersion and translocation by *Macrotermitinae*. These authors also showed that the water dispersible clay content (WDC) is always much higher (4–87 fold) in the epigeal part of the mounds in comparison to the control soils.

Macrotermitinae as accelerating weathering agents? – Converging studies from Jouquet et al. (2002b, 2005b, 2007b, 2015b) point to a possible selection by FGT of building material from different clay minerals. It appears that, when the material is relatively homogenous, the selection focuses only on a higher proportion of fine clays. These authors suggest that (i) the soil chosen by FGT is not based on a clay-type criterion but on grain size, as also illustrated in Van Thuyne et al. (2021), and (ii) clay weathering by termites, which was obvious in laboratory conditions, was not discernible in FGT mounds when compared to the surrounding soils. Jouquet et al. (2007b) noted that reactions, such as conversion of illite into smectite, are faster under the influence of termites than during geological processes. It can be inferred from these results that FGT are catalysts for clay transformation, particularly in tropical regions. They also demonstrated that "termite handling can lead to an increase in expandable layers of the component clay minerals, and that heating and saturation with potassium of modified clays do not completely close the newly formed clay layers" (Jouquet et al., 2007b, p. 128). In addition, Sako et al. (2009) noticed a surge in the U—Th ratios as well as a probable collapse of biotite. In this case, *Macrotermes* species could contribute to speed up the outcome of chemical weathering. These authors further remarked a prevalence of certain minerals (e.g. smectite, muscovite, illite) in *Macrotermes* mounds, and explained these occurrences by less-weathered material brought up from the deep layers to the surface. In soils undergoing a lot of weathering, alkaline elements and soluble silica are often leached out from the topsoil, leaving in the surrounding soil only residual 1:1 clay-minerals with low negative charges. Termite mounds are, in general, more resistant to leaching, and show an enrichment in 2:1 clays with high negative charges (Sako et al., 2009). To explain the observed mineralogical differences between mounds and top soils, Sako et al. (2009) proposed that mounds could be highly resistant to leaching, a process called "differential leaching" by Watson (1969) or the "umbrella effect" by Lee and Wood (1971): this effect prevents conversion of primary clay minerals into secondary phases. Furthermore, clay mineral transformations inside the mounds have been simulated in laboratory conditions by Mujinya et al. (2013). They observed the release of non-exchangeable potassium from illite interlayers, increasing the proportion of expandable layers, and related

these changes to termite saliva and associated microorganisms. When measuring clay compositions, Jouquet et al. (2015b) found higher amounts of smectite in termite mounds compared to the surrounding soil, explaining the increase of the CEC despite lower C and N contents. Jouquet et al. (2002b, 2004b) had already remarked that, if clay charges were not pH dependent, it was due to the clay mineral composition, which was predominantly attributed to 2:1 clay. Two processes can describe the presence of diverse clays (Fig. 4D) in the walls of termite mounds compared to their control soil. The first is the supplementation of fine grains within the mound, and the second is the alteration of 2:1 clay properties, particularly after the removal of potassium, leading to the formation of smectite layers. In sheetings built by FGT, Jouquet et al. (2007b) observed large proportions of poorly crystallized illite (PCI, with less than 5% of smectite layers), at the expense of well crystallized illite (WCI with 100% illite). This can be explained by an augmentation of smectite layers and/or a diminution of layers in the crystallites highlighting a modest, but compelling weathering effect of termites on silicate mineralogy. Jouquet et al. (2002b) further observed differences between chamber walls and galleries. Indeed, galleries enclose weakly non-reversibly expanded clays (smectites with large charges), while chamber walls enclose strongly non-reversibly expanded clay (smectites with small charges). These differences in charges can be traced to the distinct purposes of the structures: chamber walls are lasting constructions, which help to shelter fungus and termites as well as conserving humidity, while galleries are provisional constructions used for foraging activities. These clay materials can be graded following their content in expandable and small charges in the following order: chamber walls > galleries > control soil (Jouquet et al., 2002b).

Species, soils, and construction types – The morphological characteristics observed in termite mounds relate to the parent material (Mujinya et al., 2014; Van Thuyne et al., 2021). Mujinya et al. (2013) detected the unexpected presence of montmorillonite in mounds built by *Macrotermes* species on kaolinite rich soil in the Lubumbashi region (D.R.of Congo). As a matter of fact, Jouquet et al. (2015b) remarked that the mound walls of *Odontotermes obesus* were more enriched in clays in Luvisols than in Ferrasols, suggesting a more passive process rather than a particle size selection. In contrast, soils of the Okavango Delta (Botswana) are mainly derived from eolian sands, with a very poor clay content. Nevertheless, *Macrotermes michaelseni* preferentially select particles of kaolinite and illite, which become an order of magnitude more concentrated below the mounds (Dangerfield et al., 1998). Additionally, Jouquet et al. (2007b) found differences in clay mineralogy between control soils and the sheeting in *Pseudacanthotermes* mounds, but no difference between the surrounding soil and the galleries. These authors also showed that a greater vermiculization effect took place in the fungus comb chamber walls of *Odontotermes pauperans* compared to their galleries. Furthermore, Kandasami et al. (2016) demonstrated that, when presented with a choice of sand grains encompassing a wide range of mineralogy, termites, in order to form boluses (see section 4.2.1), may strategically select certain types of clay minerals, such as kaolinite and montmorillonite, based on a water-availability criteria (liquid limits of 58% for kaolinite, and 600% for montmorillonite; Mitchell and Soga, 2005). However, Sako et al. (2009) also highlighted the predominance of smectite, muscovite, and illite in mounds, which can be attributed to the physical transport by *Macrotermes* of less weathered materials from soil deep horizons.

4.1.3. Iron-sesquioxide forms

Abe and Wakatsuki (2010) provided the first evidence of the influence of termites on the form and composition of free sesquioxides in soils, due to a direct enrichment effect on fine soil particles in the mound. These authors suggested that *Macrotermes bellicosus* preferentially collected clay particles, which are formed by the association of phyllosilicate minerals and short-range order sesquioxides. For them, FGT integrate these fine particles in the mound, prompting an increase in the dithionite-extracted iron content (crystalline free iron; Fe_d)

compared to the oxalate-extracted iron fraction (mostly complexed with organic matter; Fe_O). In addition, there is an indirect effect of fluctuations in redox conditions within the ground, probably affected by the transportation of soil from a reductive to an oxidative environment (Abe and Wakatsuki, 2010). This last proposition was confirmed by Mujinya et al. (2013), who observed variations in the moisture regime, inducing differences in the nature and the quantity of sesquioxides between the mound and the surrounding soil. Indeed, alternating reducing/oxidizing conditions affect the basal parts of the mounds, in contrast to the surrounding well-drained soils. Mujinya et al. (2013) found lower Fe_d and higher Fe_o contents in the epigeous part of the mound compared to the control soil. This advocates that the higher Fe_o/Fe_d ratios found in this part of the mound should contain greater relative amounts of poorly crystalline oxides. Mujinya et al. (2013) refer to the work by Boero and Schwertmann (1987) stating that "high Fe_o/Fe_d ratios generally indicate periodic redox conditions that promote dissolution of pre-existing well-crystallized oxides and inhibit formation of secondary crystalline oxides by periodic dissolution and relatively fast precipitation of iron oxides" (Mujinya et al., 2013, p. 310).

In conclusion, only two studies specifically mention the dynamics of iron-sesquioxides. Nevertheless, these two studies have been performed on the same termite genus, but two different species: *Macrotermes falciger* and *Macrotermes bellicosus*. They seem to be contradictory, as one shows an increase in Fe_d (Abe and Wakatsuki, 2010) whereas the other emphasizes a decrease in Fe_d (Mujinya et al., 2013). Even if the results are in opposition, two main mechanisms put forward to explain the influence of termites on free sesquioxides in the soil remain effective: (i) input of clays from deep horizons and (ii) alternating redox conditions inside the mound.

4.2. Physical impacts of Macrotermitinae

4.2.1. Building blocks of a mound ("boluses")

FGT alter the soil significantly by cohering grains through their secretions into units called *boluses* (Fig. 4E). These boluses are the bricks used by termites to build their mounds (Zachariah et al., 2017; Mess et al., 2021). To hold together these boluses, termites need to modify the ambient water availability to a water content that is almost equal to the plastic limit of the soil (Kandasami et al., 2016). Furthermore, FGT use their secretions and/or excretions as a cementing agent in order to enhance the strength of the soil. In an experiment conducted in the laboratory of the department of civil engineering in Bangalore (India), a termite mound soil was subjected to unconfined uniaxial compression. Results displayed a strength of about 1500 kPa in comparison to 150 kPa for the control soil (Kandasami et al., 2016). It was presumed that it is both the cementation effect of the secretion and the particle segregation that achieved this tenfold increase in strength. Kandasami et al. (2016) further observed that, when the termite mound soil was re-molded to remove the cementation due to the secretion, no more differences were observed in the frictional strength between control and termite soils. This implies that termite secretion is involved in this strengthening. Moreover, it appears that the enhancement of strength is aided by the significant matrix suction due to unsaturated conditions (Mitchell and Soga, 2005). In addition, Cheng et al. (2013) proposed that termites use microbially induced calcite precipitation in order to build these boluses (Fig. 4E). This biomineralization process, which dates back to the Precambrian, involves bacteria able to produce calcium carbonate precipitates as "bio-cement" between the sand grains (Cheng et al., 2013).

4.2.2. Porosity and humidity

Dangerfield et al. (1998) were among the first to emphasize that gathering of specific minerals by termites for construction and moisture collection can reach considerable depths in the soil profile: respectively 52 m (Lepage, 1984), 70 m (Lock, 1985) and 84 m (Marais and Irish, 1989). This achievement extends biotic activity from the upper horizons into the parent and/or geological material. Mills and Sirami (2018)

reported that, in Zimbabwe, West (1970) observed greatly swollen termites moving upwards and non-swollen termites moving downwards. It was proposed by Boyer (1975) that alteration brought by FGT on soils surrounding termite mounds can modify the water infiltration pattern and runoff, as many cavities and chambers run through the mound (Fig. 4F). In this context, Dangerfield et al. (1998) explained that moisture can return to the centre of the mound either (i) passively through the heat pump of the turret, (ii) through the capillary action of the fine mineral fraction, or (iii) through the soil particles collected by termites for construction.

Soil porosity – On mounds built by various genus of FGT (e.g. *Odontotermes*, *Ancistrotermes* and *Microtermes*), Konaté et al. (1999) found a higher soil:air ratio in clods in the mound than in the control areas, particularly in deep layers. For instance, in one of the measured termite mounds, clod porosity was estimated at 46% while, in the control soil, it was only 33%. King et al. (2015) also measured a high porosity (37–47% air, by volume) in *Odontotermes obesus*' mound walls. Konaté et al. (1999) investigated the maximum soil water content available for plants (AWC*max*) at different depths within a mound and a control soil profile. They did not find differences in the first layer (i.e. 0–0.30 m), but in the layer below (i.e. 0.30–0.60 m), the soil water content available for plants was much higher in the mound (58 mm) compared to the control soil (34 mm). This difference in AWC*max* was considered by Konaté et al. (1999) of significant importance. Moreover, it was hypothesized by Jouquet et al. (2002a) that if the control soil and the mound top soil had similar textures but different water-holding capacities, the increase in water-holding capacities observed in the mound must be attributed to a supplementation of organic matter (e.g. saliva) or a change in SOM quality (Chenu et al., 2000). In comparison, the variations in water-holding capacities observed in deep layers must be credited to shifts in textures as well as organic matter content.

Water vapor and perched water tables – Although the diurnal/annual ambient temperature variations related to ventilation observed in termite mounds have been largely assessed (King et al., 2015; Ocko et al., 2019), the annual variations of their moisture and the mechanisms involved in the regulation in their water flow outside/inside are currently under debate (Chen et al., 2019). Following many years of research in southern Africa and northern Namibia, Turner (1994, 2006) observed that the air in an active *Macrotermes'* nest was always much more humid compared to the atmosphere. What the author measured is a large difference in the partial pressure of water vapor between the exterior air and the air contained within the nest of a *Macrotermes michaelseni* mound (Turner, 2001), occurring during the warm summer months when the activity of termites is at its highest. The value for the nest interior was calculated at 3.4 kPa and is 2.6 kPa above the surrounding atmospheric humidity, on average. Three types of water bodies are suggested by Turner (2006) in order to explain inputs of liquid water into the mound: (i) metabolic water, (ii) matric water, wicked up from deep layers, and (iii) water carried up from deeper ground. Turner (2006) confirmed what Dangerfield et al. (1998) had speculated; indeed, impermeable hollows were present, often developed under mounds through biogenic deposition of calcite (see section 4.1.2; Fig. 4B, C), and a continuous and widespread re-mobilization by termites of below ground soils (at depths reaching 12 m). These characteristics enable perched water tables to run into the structure (Turner, 2006). At two sites of the Lubumbashi region of the D.R. Congo, Mujinya et al. (2011) further noticed that, even in the middle of the dry season, the excavated mound material remained moist. They explained the recharge of the aquifer by the percolation of rainwater from the wet season into the mound because of a more permeable soil surrounding the mound, due to termite bioturbation (Arveti et al., 2012). As a waterproof layer forms below the mound (a common feature of FGT mounds), rainwater can accumulate and flow back to the structure. Because of this water resource, Jouquet et al. (2011) observed that during the dry months of the year, when rain is scarce and nights are cold, FGT were the only group of insects and bioturbators which persistently stayed active.

4.2.3. Stability of the mound

Factors influencing the stability of the mound – Contour-Ansel et al. (2000) measured the sizes of aggregates in mounds and control soils to assess the structural stability *of Macrotermes subhyalinus* mounds in Senegal. Their results show that 50% of the aggregates encountered in the mound walls were > 0.2 mm in diameter. This value is what Le Bissonais and Le Souder (1995) consider as a reasonable size for a stable structure. On the other hand, the surrounding soil aggregates had an average diameter < 0.2 mm, which reflects unstable structures. These authors immersed both materials in water: interestingly, both materials broke down immediately and completely. Furthermore, even if the mound material was considered to be fairly stable, no difference could be detected in terms of stability between the mound and the control soil material. Jouquet et al. (2003) found Mean Weight Diameter (MWD) values almost six times higher in *Ancistrotermes cavithorax* structures than in surrounding soils ($\pm$ 2.4 versus $\pm$0.4 mm) in Ivory Coast, making these structures much more stable than the control soils. Regarding MWD results for *Macrotermes subhyalinus* and their control soil, Contour-Ansel et al. (2000) measured values of $\pm$0.32 versus $\pm$0.19 mm, respectively, with a low structural stability for both sets of samples. This illustrates differences in soil properties between *Macrotermes* and *Ancistrotermes* genera and emphasizes the importance of considering differences between termite species, types of nest, and compartments within the structure (Jouquet et al., 2003). It remains difficult to propose definitive results regarding the stability of FGT mounds compared to their surrounding soils, although Le Bissonais and Le Souder (1995) stated that control soils are generally unstable compared to soils rearranged by termites. In a broader perspective, Jouquet et al. (2003) proposed that the structural stability increases in the following manner: control soil < gallery < chamber walls.

The role of soil organic matter and clays – Jouquet et al. (2004a) hypothesized that the structural stability of soils is usually correlated with their soil organic matter content, which is generally considered as a cement guaranteeing the stability of the mound soil. But in this particular study of *Macrotermes'* nests in the Ivory Coast, they demonstrated that SOM is not as influential as expected, whereas the clay content appeared as the key component to explain the structural stability of the mound. Thus, two antagonist trends seem to regulate the structural stability of FGT mounds. On one hand, the clay content inside the mounds can reduce the pore sizes, thereby increasing the mound stability. On the other hand, smectite-type clays can contribute to the breakdown of the mound during alternating swelling and shrinking phases.

Role of rain – In savanna regions, rainfall is one of the main natural factors impacting soils: raindrops destroy soil surface aggregates, splash detaching particles from aggregates, and runoff removing top soil layers. But in the context of termite mound stability, the shape of epigeous structures responds more favorably to raindrop impacts, because raindrops transmit less energy when hitting a steep surface rather than a flat one; they also tend to rebound, preventing any accumulation of a sufficient volume of erosion on small and steep faces, compared to horizontal surfaces (Jouquet et al., 2004a). Additionally, Erens et al. (2015b) described similar rainwater repellence of termite mounds due to their glossy and pronounced slopes. More recently, Jouquet et al. (2016a) confirmed that the key to rain resistance of mounds is the lower penetration of water into soil particles, i.e. because of lower porosity of soil clods and/or water repellence of soil aggregates, and not the resistance of soil aggregates to water. Kandasami et al. (2016) observed the same water repellence in mound material, and attributed it to elemental bonds around organic matter.

Mound stability: a multifactorial challenge – As stipulated above, FGT usually tend to increase the soil structural stability of their mounds compared to the surrounding soil. Nevertheless, antagonist processes seem to influence the soil structural stability of the mound in opposite directions. According to the literature, five main factors are expected to increase the stability of the mound: (i) iron sesquioxides (by

cementation of soils particles); (ii) the higher quantity and quality of SOM (i.e. it can enhance soil microparticle adherence and help to bond negatively charged clay minerals to cations; Jouquet et al., 2016a); (iii) clay content (i.e. it decreases the pore sizes and water diffusion); (iv) the mound shape; and (v) a high salt content and a decreased exchangeable sodium percentage (ESP) of the termite soil, which reduce clay dispersion, mitigating the infiltrability (Mills and Medinski, 2021). But two other compelling factors can also challenge the mound stability: (i) a low SOM content and (ii) the presence of smectite clays, which reduce the macro-aggregate stability (Jouquet et al., 2016b) because of their properties. Moreover, a share of organic matter is decisive in the strength equation, but exactly how much is not known. In addition to the factors increasing the stability of the mound mentioned above, Zachariah et al. (2020a) added some characteristics responsible for strengthening the mound, such as the soil suction, the self-weight consolidation, and a moisture level of approximately 30% (close to its liquid limit). The latter contradicts earlier findings by Kandasami et al. (2016), who proposed that termite secretions played an important role in the stability and the strength of the mound. Further research is thus needed to sort out the true contribution of saliva to mound strength compared to the control soil. Nevertheless, even considering all the above-mentioned binding agents, Zachariah et al. (2020b) found that strengths of the mound and the control soils are finally not so different, confirming what Le Bissonais and le Souder (1995) had already stated. In conclusion, clays, depending on their type (1:1 versus 2:1), where they are concentrated, and in what quantities, remain one of the most important parameters influencing the structural stability of termite mounds. Finally, if the mound strength is obviously crucial to the colony survival, the resistance of the mound to erosion is even more important. Zachariah et al. (2020a) emphasized the extraordinary capacity of FGT mound material to resist weathering by water. Saliva, as a sticky additive adhering soil particles and secretion gluing boluses together, seems to be responsible for this substantial increase in resistance. Nonetheless, mechanisms by which this viscous secretion is able to increase the weathering resistance of the mound is not yet known. In addition, mound strength and mound resistance to weathering can both be increased by the densification of the mound due to gravity, as well as repeated cycles of wetting and drying (i.e. soil stress history) or alternating wet and dry climatic cycles (Mahaney et al., 1999).

4.2.4. Sediment transport

When building their mounds, termites transport and repack soil particles. For example, Mermut et al. (1984) observed a striking feature in thin sections, described as a "lamellar fabric", from constructed parts of a *Macrotermes subhyalinus* mound made of fine sand and silt. This peculiar fabric is found when the skeleton grains (coarse groundmass) and micromass alternate in parallel alignments forming banded arrangements of aggregates (Fig. 4G, H). Moreover, Jouquet et al. (2002a) noticed that, in order to build galleries, FGT can arbitrarily select either top or deep soils, but for energy cost effective reasons, they tend to select the grains and matter from the top soil. However, when building chamber walls, the special needs for the exosymbiosis with *Termitomyces* appear to explain the preferential use of finer deep soil, where present. Turner (2000) calculated that *Macrotermes michaelseni*'s mounds occupy a volume of 5–7 m^3, of which roughly 80% is matter excavated from the deep soil and brought up into the mound by termites. He further explained that the mound is a dynamic structure, with approximately a cubic metre of soil per year being transported up to replace the soil lost from the mound through erosion (Pomeroy, 1976a). Kristensen et al. (2015) compared the construction and erosion processes observed in termite mounds, as being compared to an upward "conveyor belt", where superficial sediments are interred by new sediment carried up from deeper ground. In the savanna ecosystem of Ghana, these authors measured the surface deposition rate and evaluated it at approximately 0.28 mm y^{-1}, a process that probably started 4000 years ago, and was periodically stopped and re-started many times (Kristensen et al., 2015).

Following this quantification of soil transport by FGT, they concluded that most of the material originated from the top meter of soil. This observation seems to contradict the conventional model of mound building in which sand grains are collected from deeper horizons (Holt and Lepage, 2000; Abe and Wakatsuki, 2010). Indeed, the collection of fine materiel is needed by FGT in order to reach a mandatory particle size distribution in the mound, with an approximate clay content of 12%. Kristensen et al. (2015) did not find this proportion in the top layer (only <7%). Consequently, they suggested that termites must have excavated at least some sediment below 100 cm, as these layers are in most cases richer in clays (> 18% of clay at the site studied in Ghana). Jouquet et al. (2017) made similar conclusions for cathedral mounds in Vertisols and Ferrasols from southern India. The depth at which termites collected the soil was very shallow (110 cm for Ferrasols and 70 cm for Vertisol). The authors inferred that termites did not need to dig deeper as these soils were already rich in clays in the first meter. In conclusion, it can be hypothesized that unless the top soil (< 100 cm) is rich in a clay fraction, termites will mine deeper to look for clay size particles.

5. Discussion

Surficial geology investigates ancient and present-day processes and landforms that shape the Earth surface. It includes visible traces observed in the surficial sediments and soils due to past transformations, sometimes allowing dating, and interpreted in order to reconstruct paleoenvironments. The aim of this review is to evaluate the contribution of termites in these transformations, i.e. asking the questions: what is the main mechanisms by which FGT transform the surficial geological formations, and what is their legacy in the sedimentary structures left once termites are gone? Before discussing the above questions, it is important to outline the contexts in which FGT settle and thrive. Indeed, a set of conditions must be met before FGT establish in a specific environment and, once these conditions are reached, they must remain.

The main factor controlling the establishment of a termite mound is the depth of the water table (Ahmed et al., 2019). If the water table is permanently too deep, FGT do not settle, and if the water table is too close to the surface, mounds are only observed in a far lesser density (Davies et al., 2014). The most suitable location is therefore an intermediate water table position. Furthermore, Davies et al. (2014) noticed that termite mounds were bigger and steeper when conditions were drier, with a lower diversity of species per hectare. In a rain forest, Ashton et al. (2019) observed that during drought conditions, the number of mounds increased. Jouquet et al. (2017) provided evidence that rainfall can substantially impact the abundance of *Odontotermes* mounds. Environmental characteristics (e.g. outdoor temperatures) can also exert a strong influence on mound construction, to the point of regulating its shape within the same species and between species (Mermut et al., 1984). To summarize, epigenic factors (i.e. climate, soil types, temperatures) are the dominant criteria affecting mound dynamics. Consequently, the variation of these factors, along with the water table level, creates optimal to suboptimal environments for the development of FGT mounds, making these mounds potential proxies for paleoenvironmental reconstructions.

5.1. Can FGT be regarded as geological agents?

The first way FGT modify the surficial geological formation starts with deep digging in the ground, a process called *mining* (Mills et al., 2008; Williams, 2019), which refers to their ability to dig through the soil into the saprolite. By this process, termites collect moist and clay-size mineral fractions adapted to their construction (Fig. 5E). Moreover, Pomeroy (1976b) calculated that the upward transport of soil material by termites reaches 0.1 mm/ha/yr; the average bulk density of a *Macrotermes* mound being 1.8 g/cm^3 (Holt and Lepage, 2000), the quantity of reworked material, which would be equivalent to 1.8 t/ha/yr. Bagine (1984) calculated a figure of 1.05 t/ha/yr, which is

equivalent to 0.06 mm/ha/yr. Whitford and Eldridge (2013), who summarized data from the literature on this topic, found ranges between 0.03 and 5.8 t/ha/yr. More recently, Jouquet et al. (2020) calculated that, only for their sheeting purposes, termites can dig out up to 1 t/ha/yr. These incessant upward-downward movements by termites slowly damage the parent material and deepen the alteration zone (Eschenbrenner, 1986). These activities of mining, transporting, bioturbating, accumulating, and depositing are all one and the same process, lately coined as "mounding" (Bétard, 2021). Termite mounding affects the grounds surrounding the mound, by creating stone free zones, buried stone lines, or buried gravel layers (Watson, 1960; Soyer, 1987; Stoops, 1989; Johnson, 1990; Phillips, 2009). During landscape evolution, and depending on their density and their distribution pattern (Pringle et al., 2010), an entire area will be improved by this modified finer material, as it becomes enriched in nutrients and sometimes in organic matter redistributed at its surface. Aloni and Soyer (1987) calculated that, over a period of a thousand years, 37 cm of soil had been translocated from termite mounds and deposited in the surrounding environment. Some voluminous mounds (a few thousand cubic meters big and more than 20 m wide) took up to hundreds of years and become prominent geomorphological landmarks in savanna environments (Viles et al., 2021). They can remain intact for very long periods of time thanks to their extremely high resistance to weathering (Zachariah et al., 2020a). The succession of ancient eroded large mounds often ends up as kilometric hill-shape formations, which are then capped by sand deposits and vegetation cover. Termitic horizons (a term coined by Romanens et al., 2019) are found in present-day soils as well as destroyed or inherited mounds forming plurimetric landforms, with their unique geochemical, mineralogical, and physical characteristics. Some of these environments have been sustained during the last thousands of years but some have changed and no longer offer the necessary conditions for termite expansion.

In addition, a suite of conditions (i.e. concentration of cations, lowering of the point of zero charge, microbial activity, oxalate-carbonate pathway) linked to the building of the mound, triggers an increase in alkalinity by a factor of three within it (Fig. 5A). During the development of the mound, calcareous materials can be brought into the mound, groundwater collected, and vegetation carried inside, leading to the concentration of cations such as Ca^{2+}, Mg^{2+}, Na^+, K^+, and thus substantially increasing the CEC. Other vital nutrients (e.g. N and P) necessary for FGT development, plant growth, and animal feeding, build up within the mound and are kept for long periods of time, even after its dismantlement. Moreover, bioturbation influences the infiltration rate, the micro- and macro-porosity, as well as moisture levels, allowing water to drain into an impermeable depression formed below the mound by the biogenic deposition of calcite-cemented or clay-rich layers, leading to large quantities of stored water. The formation of calcite-cemented patches inside the mounds (Fig. 4B, C) is likely due to a favorable set of conditions, i.e. the presence of Ca^{2+}, a source of dissolved inorganic carbon, and alkalinity. Finally, overprinting all the material modifications brought by termites, pedogenic processes affect the mineral and organic phases, giving them additional physical and chemical properties, ultimately leading to the formation of new sedimentary bodies and rocks by termites. By their soil particle uptake, termites accumulate large quantities of manipulated clays in the topsoil and have the ability to transform illite into smectite (Mujinya et al., 2013), to breakdown biotite and primary clays in the mounds (Sako et al., 2009), as well as to create expandable clay minerals (Jouquet et al., 2016a): therefore, termites definitely act as accelerating geochemical weathering agents.

5.2. What are the geological effects of FGT on savanna landscape?

Termite impact on soils relates to the outcome of three main forces: behavioral, physical, and climatic (Harris, 1956). Once the FGT colony is established and the building of the upper part of their mound has

started, the influence of termites on their proximate environment begins. Termite bioturbation tends to mitigate physical and chemical processes of soil degradation (Edosomwan et al., 2012). The first noticeable effect is the initiation of a nutrient hotspot, with higher chemical fertility (Mujinya et al., 2013) than the surroundings, attracting plants and animals. This influences the recycling rate of nutrients, their availability and redistribution. The clustering of nutrients and clay at the top soil helps certain plant species to establish, where they would normally not grow (Joseph et al., 2013). After mound abandonment, nutrients are generally leached into the adjacent soils (Schwiede et al., 2005). The water holding capacity status of FGT mound, as well as their reduced (ESP) (Mills and Medinski, 2021), lead to an array of positive feedback to the savanna landscape by enhancing protection from fires, delaying desertification, supporting rebounds by seedlings (Traoré et al., 2015; Tarnita et al., 2017), and reinforcing dryland resistance and recovery from drought (Bonachela et al., 2015). Moreover, in the tropical rainforest, increased landscape heterogeneity, higher moisture level, and removal of combustible material fostered by termites, tend to weaken the effects of drought (Ashton et al., 2019). In addition, greater concentrations of rare earth and trace elements were observed by Sako et al. (2009) in FGT mounds in Namibia. These authors attributed this enhancement to the concentration of in situ alteration products, which were brought up by termites from the bedrock, as well as solute accumulation from the collection of groundwater (Mills and Sirami, 2018). Furthermore, Mills et al. (2008) suggested that micro-nutrient enrichment (e.g. Mn, Co, Cu, and Se) in FGT mounds are advantageous for wildlife and plants. It is hypothesized that these accumulations do not take place when FGT are not present and as such, could deprive wildlife from vital nutritional elements, therefore threatening the survival of some of them. The improved availability of these scarce elements has therefore important ecological consequences, particularly in semi-arid regions. In conclusion, the concentrated actions of termites in a specific place, as "intended engineers" versus "accidental engineers" (Jones et al., 1994; Jouquet et al., 2006, 2016c), undoubtedly boost the heterogeneity at the landscape scale (Jouquet et al., 2007a), providing it more resilience (Arveti et al., 2012).

Islands can be initiated by termites in regions such as the Okavango Delta in Botswana (McCarthy et al., 1998), when built mounds remain above the maximum flood level (Bétard, 2021). Fluvial systems can be modified by termites through a series of feedback mechanisms between biota and geomorphic processes (Boyer, 1975; Dangerfield et al., 1998). Moreover, in terms of pedogenic processes, termites relocate clays from the subsoil to the surface, these being eluviated back from the surface into the subsoil during time, contributing to soil forming processes (Abe et al., 2012) and increasing the nutrient holding capacity of the landscape. In addition, Dangerfield et al. (1998) noted that grain-size and mineralogical clays modified by termites are likely to have "medium spatial scale impact but long-term temporal effects" in the environment. Large quantities of altered soil are accumulated and remain in termite mounds.

5.3. Future challenges

Identification of future challenges – Some gaps and challenges have been identified while compiling the literature for this review. (i) Further research is needed on termite saliva in order to explain the mechanisms by which it influences clay properties. Studies are also required to elucidate the true contribution of saliva to the rigidity of the soil fabric compared to the control soil, as well as the mechanisms through which termite secretion interacts with soil organic matter, increasing the weathering resistance of the mound. (ii) No straightforward reasons have been advanced to explain the mechanism by which FGT are able to extract un-exchangeable potassium from illite interlayers, leading to the creation of smectite layers. It appears difficult to differentiate if this extraction is produced by the saliva, or the action of associated microorganisms. Furthermore, the release of potassium to the outer solution

leading to a mineralogical alteration is not fully understood. (iii) It seems that the age of large termite mounds still remains poorly assessed and only a few studies have been undertaken on abandoned mounds. A comparative study between an active mound, a recently abandoned mound, and a relic mound could provide interesting results. (iv) Supplementary investigations are encouraged to reveal the key role FGT play in the surface deposition of material mined from below the stone line and their possible implication in the formation of tropical soils. (v) One chemical element, sodium, remains overlooked in the literature and consequently in this review, although recently emphasized as a major contributor to infiltrability (Mills and Medinski, 2021). Indeed, the importance of sodium has been stressed in the context of research related to termites (Jouquet, pers. comm.; Mills and Medinski, 2021). Documenting its geological provenance, biogenic sources, and availability within the mound would open new issues on the elemental biogeochemistry of FGT mounds.

New tools to address future challenges – (i) Optically stimulated luminescence (OSL) is often used to date geological sediments and is especially appropriate for dating landforms, features and paleo-environments in recent geological times, i.e. the Late Quaternary. OSL methods could be proposed in order to more precisely date the age of various termite mounds, or to estimate the accumulation rate of sand deposited by FGT. (ii) Mid-Infrared Spectroscopy (MIRS) is a rapid, precise and cost-effective analytical tool used to determine soil properties and to identify biogenic aggregates (Jouquet et al., 2018). This method, which is new to this field of study, could be used to observe how the soil properties and biogenic aggregates evolve with time. (iii) Rapid image-based field analyses (i.e. photogrammetry, cross-sectional image analysis) has recently been used to measure volume, surface areas, porosity and gas exchange in termite mounds (Nauer et al., 2018). These tools could be used to acquire rapid and accurate data and to quantitatively characterize different types of mounds at various stages of their existence. (iv) Finally, Electrical Resistivity Tomography (ERT) is a geophysical technique widely used in many research fields (e.g. in investigations on ground water table, fault presence, or soil moisture content). It could be an efficient tool to interpret clay variations in the mound and to access mound strength and stability through their densities and porosities. 2D and 3D Electrical Resistivity Tomography offers a highly attractive tool for cheap and non-invasive investigation of the subsurface structure of mounds in terms of variable physical properties.

6. Conclusions

The aim of this paper was to propose to the geological audience a review on the role FGT play as geological agents. Similarly, it invited the interested biological audience to pay attention to the influence and legacy FGT may have on surficial geological deposits and landscapes. Through a thorough analysis of approximately 140 published papers and identifying sixteen processes, what stands out is, for millions of years (>20 My), the symbiosis between FGT and the fungus generated an efficient biogeological agent, capable of transforming sediments, storing water, increasing the alkalinity, and concentrating vital nutrients in subtropical semi-arid conditions. By doing so, FGT create, convert, and build landforms, imprinting past environmental conditions in the sedimentary record. Their capacity to adapt the environment to their requirements is impressive. Indeed, termites form impermeable layers for water to be stored. They modify the grain-size distributions of sediments and soils where they develop, thereby increasing the clay fraction. Through their mounding activities, termites change the clay properties, leading to the formation of smectite layers, and act as weathering agents of silicate minerals. Termites can also increase the strength of their mound, drastically improving its resistance to weathering. Termites act at various scales, from sub-millimetric features to landscapes: they not only concentrate nutrients and increase the pH surrounding the mounds, but they also foster more highly fertile grounds, attracting plants and animals. Litter brought back to the nest and partially decomposed

account for 20% of all organic carbon present in dry savannas. The mineralized part of organic carbon by termites make them the predominant decomposer organisms and crucial actors in the carbon cycle. The water holding capacity status of FGT mounds enhances protection from fires, delays desertification, supports rebounds by seedlings and reinforces savanna resistance and recovery from drought. Finally, termite bioturbation contributes to decrease soil degradation and boosts the heterogeneity of the landscape habitats providing it more resilience. Therefore, FGT are not only biological agents of the savanna ecosystem, but they obviously act as *geological players* by their impact on soils, sediments, and biogeochemical cycles.

Author's Contributions

Both authors contributed equally to the conceptualization, investigations, methodology, resources, software applications, formal analysis, as well as to the writing, review and editing. John van Thuyne particularly proposed the original draft and managed the bibliography research; Eric P. Verrecchia was responsible for the project administration, the funding acquisition, and the supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

References

Aanen, D.K., Eggleton, P., 2005. Fungus-growing termites originated in African rain forest. Curr. Biol. 15, 851–855.

Abe, S.S., Wakatsuki, T., 2010. Possible influence of termites (*Macrotermes bellicosus*) on forms and composition of free sesquioxides in tropical soils. Pedobiologia 53, 301–306.

Abe, S.S., Yamamoto, S., Wakatsuki, T., 2009. Soil-particle selection by the mound-building termite *Macrotermes bellicosus* on a sandy loam soil catena in a Nigerian tropical savanna. J. Trop. Ecol. 25, 449–452.

Abe, S.S., Kotegawa, T., Onishi, T., Watanabe, Y., Wakatsuki, T., 2012. Soil particle accumulation in termite (*Macrotermes bellicosus*) mounds and the implications for soil particle dynamics in a tropical savanna Ultisol. Ecol. Res. 27, 219–227.

Ahmed, I.I.J.B., Pradhan, B., Mansor, S., Tongjura, J.D.C., Yusuf, B., 2019. Multi-criteria evaluation of suitable sites for termite mounds construction in tropical lowland. Catena 178, 359–371.

Aloni, K., Soyer, J., 1987. Cycles des matériaux de construction des termitières d'humivores en savane au Shaba méridional (Zaïre). Revue Zool. Afr. 101, 329–358.

Arveti, N., Reginald, S., Kumar, K.S., Harinath, V., Sreedhar, Y., 2012. Biogeochemical study of termite mounds: a case study from Tummalapalle area of Andhra Pradesh, India. Environ. Monit. Assess. 184, 2295–2306.

Ashton, L.A., Griffiths, H.M., Parr, C.L., Evans, T.A., Didham, R.K., Hasan, F., Teh, Y.A., Tin, H.S., Vairappan, C.S., Eggleton, P., 2019. Termites mitigate the effects of drought in tropical rainforest. Science 363, 174–177.

Bagine, R.K.N., 1984. Soil translocation by termites of the genus *Odontotermes* (Isoptera: Macrotermitinae) in an arid area of northern Kenya. Oecologia 64, 263–266.

Batra, L.R., Batra, S.W.T., 1979. Termite-fungus mutualism. In: Batra (Ed.), Insect-Fungus Symbiosis: Nutrition, Mutualism, Commensalism. John Wiley, New York, pp. 117–163.

Bell, R.H.V., 1982. The effect of soil nutrient availability on community structure in African ecosystems. In: Huntley, B.J., Walker, B.H. (Eds.), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 193–216.

Bétard, F., 2021. Insects as zoogeomorphic agents: an extended review. Earth Surf. Process. Landf. 46, 89–109.

Boero, V., Schwertmann, U., 1987. Occurence and transformations of iron and manganese in a colluvial terra rossa toposequence of northern Italy. Catena 14, 519–531.

Bonachela, J.A., Pringle, R.M., Sheffer, E., Coverdale, T.C., Guyton, J.A., Caylor, K.K., Levin, S.A., Tarnita, C.E., 2015. Termite mounds can increase the robustness of dryland ecosystems to climate change. Science 347 (6222), 651–655.

Boyer, P., 1975. Action de certains termites constructeurs sur l'évolution des sols tropicaux III. Les différents aspects de l'action de Bellicositermes sur les sols tropicaux. Ann. Sci. Nat. Zool. Paris 12 (17), 447–504.

Brauman, A., 2000. Effect of gut transit and mound deposit on soil organic matter transformations in the soil feeding termite. A review. Eur. J. Soil Biol. 36, 117–125.

Brune, A., 2014. Symbiotic digestion of lignocellulose in termite guts. Nat. Rev. Microbiol. 12, 168–180.

Cailleau, G., Braissant, O., Verrecchia, E.P., 2011. Turning sunlight into stone: the oxalate-carbonate pathway in a tropical tree ecosystem. Biogeosciences 8, 1755–1767.

Chen, C., Liu, W., Wu, J., Jiang, X., 2018. Spatio-temporal variations of carbon and nitrogen in biogenic structures of two fungus-growing termites (*M. annandalei* and *O. yunnanensis*) in the Xishuangbanna region. Soil Biol. Biochem. 117, 125–134.

Chen, C., Wu, J., Zhu, X., Jiang, X., Liu, W., Zeng, H., Meng, F.R., 2019. Hydrological characteristics and functions of termite mounds in areas with clear dry and rainy seasons. Agric. Ecosyst. Environ. 277, 25–35.

Cheng, L., Cord-Ruwisch, R., Shahin, M.A., 2013. Cementation of sand soil by microbially induced calcite precipitation at various degrees of saturation. Can. Geotech. J. 50 (1), 81–90.

Chenu, C., Le Bissonnais, Y., Arrouays, D., 2000. Organic matter influences on clay wettability on soil aggregate stability. Soil Sci. Soc. Am. J. 64, 1479–1486.

Cleveland, L.R., 1925. The effects of oxygenation and starvation on the symbiosis between the termite, termopsis, and its intestinal flagellates. Biol. Bull. J. 48 (5), 295–308.

Collins, N.M., 1983. Utilization of nitrogen resources by termites (Isoptera). In: Lee, J.A., McNeill, S., Ronson, I.H. (Eds.), Nitrogen As an Ecological Factor. Blackwell Scientific, Oxford, pp. 381–412.

Contour-Ansel, D., Garnier-Sillam, E., Lachaux, M., Croci, V., 2000. High performance liquid chromatography studies on the polysaccharides in the walls of the mounds of two species of termite in Senegal, *Cubitermes oculatus* and *Macrotermes subhyalinus*: their origin and contribution to structural stability. Biol. Fertil. Soils 31, 508–516.

da Costa, R.R., Hu, H., Pilgaard, B., Vreeburg, S.M.E., Schückel, J., Pedersen, K.S.K., Kracun, S.K., Busk, P.K., Harholt, J., Sapountzis, P., Lange, L., Aanen, D.K., Poulsen, M., 2018. Enzyme activities at different stages of plant biomass decomposition in three species of fungus-growing termites. Appl. Environ. Microbiol. 84 (5), e01815–e01817.

Dangerfield, J.M., Mc Carthy, T.S., Ellery, W.N., 1998. The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. J. Trop. Ecol. 14, 507–520.

Darlington, J.P.E.C., 1984. Two types of mound built by the termite *Macrotermes subhyalinus* in Kenya. Int. J. Trop. Sci. 5 (6), 481–492.

Darlington, J.P.E.C., 2005. Distinctive fossilized termite nests at Laetoli Tanzania. Insect. Soc. 52, 408–409.

Davies, A.B., Levick, S.R., Asner, G.P., Robertson, M.P., van Rensburg, B.J., Parr, C.L., 2014. Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. Ecography 37, 852–862.

Davies, A.B., Baldeck, C.A., Asner, G.P., 2016. Termite mounds alter spatial distribution of African savanna tree species. J. Biogeogr. 43, 301–313.

Duringer, P., Schuster, M., Likius, J.F.G.A., Mackaye, T.H., Vignaud, P., Brunet, M., 2006. The first fossil fungus gardens of Isoptera: oldest evidence of symbiotic termite fungiculture (Miocene, Chad basin). Naturwissenschaften 93, 610–615.

Edosomwan, N.L., Edosomwan, E.U., Oke, O., 2012. Physical and chemical characteristics of termite mounds and associated soils in tropical forest-savanna transitional area of southern Nigeria. Indian J. Agric. Res. 46 (4), 338–343.

Erens, H., Boudin, M., Mees, F., Mujinya, B.B., Baert, G., Van Strydonck, M., Boeckx, P., Van Ranst, E., 2015a. The age of large termite mounds-radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo. Palaeogeogr. Palaeoclimatol. Palaeoecol. 435, 265–271.

Erens, H., Mujinya, B.B., Mees, F., Baert, G., Boeckx, P., Malaisse, F., Van Ranst, E., 2015b. The origin and implications of variations in soil-related properties within *Macrotermes falciger* mounds. Geoderma 249-250, 40–50.

Eschenbrenner, V., 1986. Contribution des termites à la micro-agrégation des sols tropicaux. In: Cahier ORSTOM Série Pédologie, 4, pp. 397–408.

Ferrar, P., 1982. Termites of a south African savanna. IV. Subterranean populations, mass determinations and biomass estimates. Oecologia 52, 147–151.

Grassé, P.P., Noirot, C., 1958. La meule des termites champignonnistes et sa signification symbiotique. Ann. Sci. Nat. 11 (20), 113–128.

Harris, W.V., 1956. Termite mound building. Insect. Soc. 3, 261–268.

Hess, P.R., 1955. A chemical and physical study of the soils of termite mounds in East Africa. J. Ecol. 43, 449–461.

Higashi, M., Abe, T., Burns, T.P., 1992. Carbon-nitrogen balance and termite ecology. Proceed. Royal Soc. Biol. Sci. 249, 303–308.

Holt, J.A., Lepage, M., 2000. Termites and soil properties. In: Holt, J.A., Lepage, M. (Eds.), Termites: Evolution, Sociality, Symbioses, Ecology. Chapter 18. Kluwer Academic Publishers, pp. 389–407.

Hyodo, F., Inoue, T., Azuma, J.I., Tayasu, I., Abe, T., 2000. Role of the mutualistic fungus in lignin degradation in the fungus-growing termite *Macrotermes* gilvus (Isoptera; Macrotermitinae). Soil Biol. Biochem. 32, 653–658.

Johnson, D.L., 1990. Biomantle evolution and the redistribution of earth materials and artifacts. Soil Sci. 149, 84–102.

Jones, J.A., 1990. Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. J. Trop. Ecol. 6, 291–305.

Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.

Jones, C.G., Lawton, J.H., Shachak, M., 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78, 1946–1957.

Josens, G., 1972. Etudes Biologique et Écologique des Termites (Isoptera) de la Savane de Lamto-Pakobo (Côte-d'Ivoire). PhD Thesis. Université Libre de Bruxelles, Brussels (262p).

Josens, G., Dosso, K., Konaté, S., 2016. Lenticular mounds in the African savannahs can originate from ancient *Macrotermes* mounds. Insect. Soc. 63, 373–379.

Joseph, G.S., Seymour, C.L., Cumming, G.S., Cumming, D.H.M., Mahlangu, Z., 2013. Termite mounds as islands: woody plant assemblages relative to termitarium size and soil properties. J. Veg. Sci. 24 (4), 702–711.

Jouquet, P., Lepage, M., Velde, B., 2002a. Termite soil preferences and particle selections: strategies related to ecological requirements. Insect. Soc. 49, 1–7.

Jouquet, P., Mamou, L., Lepage, M., Velde, B., 2002b. Effect of termites on clay minerals in tropical soils: fungus-growing termites as weathering agents. Eur. J. Soil Sci. 53, 521–527.

Jouquet, P., Mery, T., Rouland, C., Lepage, M., 2003. Modulated effect of the termite *Ancistrotermes cavithorax* on soil properties according to the internal mound structures. Sociobiology 42 (2), 403–412.

Jouquet, P., Tessier, D., Lepage, M., 2004a. The soil structural stability of termite nests: role of clays in *Macrotermes bellicosus* (Isoptera; Macrotermitinae) mound soils. Eur. J. Soil Biol. 40, 23–29.

Jouquet, P., Boulain, N., Gignoux, J., Lepage, M., 2004b. Association between subterranean termites and grasses in a West African savanna: spatial pattern analysis shows a significant role for *Odontotermes* n. *pauperans*. Appl. Soil Ecol. 27, 99–109.

Jouquet, P., Ranjard, L., Lepage, M., Lata, J.C., 2005a. Incidence of fungus-growing termites (Isoptera, Macrotermitinae) on the structure of soil microbial communities. Soil Biol. Biochem. 37, 1852–1859.

Jouquet, P., Barré, P., Lepage, M., 2005b. Impact of subterranean fungus-growing termites (Isoptera, Macrotermitinae) on chosen soil properties in a West African savanna. Biol. Fertil. Soils 41, 365–370.

Jouquet, P., Tavernier, V., Abbadie, L., Lepage, M., 2005c. Nests of subterranean fungus-growing termites (Isoptera, Macrotermitinae) as nutrient patches for grasses in savannah ecosystems. Afr. J. Ecol. 43, 191–196.

Jouquet, P., Dauber, J., Lagerlöf, J., Lavelle, P., Lepage, M., 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. Appl. Soil Ecol. 32 (2), 153–164.

Jouquet, P., Mathieu, J., Barot, S., Choosai, C., 2007a. Soil Engineers as Ecosystem Heterogeneity Drivers. Ecology Research Progress. (Chapter 7).

Jouquet, P., Bottinelli, N., Lata, J.C., Mora, P., Caquineau, S., 2007b. Role of the fungus-growing termite *Pseudoacanthotermes spiniger* (Isoptera, Macrotermitinae) in the dynamic of clay and soil organic matter content. An experimental analysis. Geoderma 139, 127–133.

Jouquet, P., Traoré, S., Choosai, C., Hartmann, C., Bignell, D., 2011. Influence of termites on ecosystem functioning. Ecosystem services provided by termites. Eur. J. Soil Biol. 47, 215–222.

Jouquet, P., Guilleux, N., Chintakunta, S., Mendez, M., Subramanian, S., Shanbhag, R.R., 2015a. The influence of termites on soil sheeting properties varies depending on the materials on which they feed. Eur. J. Soil Biol. 69, 74–78.

Jouquet, P., Guilleux, N., Shanbhag, R.R., Subramanian, S., 2015b. Influence of soil type on the properties of termite mound nests in Southern India. Appl. Soil Ecol. 96, 282–287.

Jouquet, P., Guilleux, N., Caner, L., Chintakunta, S., Ameline, M., Shanbhag, R.R., 2016a. Influence of soil pedological properties on termite mound stability. Geoderma 262, 45–51.

Jouquet, P., Chintakunta, S., Bottinelli, N., Subramanian, S., Caner, L., 2016b. The Influence of Fungus-growing termites on soil macro and micro-aggregates stability varies with soil type. Appl. Soil Ecol. 101, 117–123.

Jouquet, P., Bottinelli, N., Shanbhag, R.R., Bourguignon, T., Traoré, S., Abbas Abbasi, S., 2016c. The neglected soil engineers of tropical soils. Soil Sci. 181 (3–4), 157–165.

Jouquet, P., Caner, L., Bottinelli, N., Chaudhari, E., Cheik, S., Riotte, J., 2017. Where do South-Indian termite mound soils come from? Appl. Soil Ecol. 117-118, 190–195.

Jouquet, P., Pando, A., Aroui, H., Harit, A., Capowiez, Y., Bottinelli, N., 2018. Evidence from mid-infrared spectroscopy (MIRS) that the biochemical fingerprints of *Odontotermes obesus* colonies change according to their geographical location and age. Insect. Soc. 65, 77–84.

Jouquet, P., Jamoteau, F., Majumdar, S., Podwojewski, P., Nagabovanalli, P., Caner, L., Barboni, D., Meunier, J.D., 2020. The distribution of Silicon in soil is influenced by termite bioturbation in south Indian forest soils. Geoderma 372, 114362.

Kandasami, R.R., Borges, R.M., Murthy, T.G., 2016. Effect of biocementation on the strength and stability of termite mounds. Environ. Geotech. 3 (2), 99–113.

King, H., Ocko, S., Mahadevan, L., 2015. Termite mounds harness diurnal temperature oscillations for ventilation. PNAS 112 (37), 11589–11593.

Konaté, S., 1998. Structures, Dynamique et Rôle des Buttes Termitiques Dans le Fonctionnement d'une Savane Préforestière (lamto, Côte d'Ivoire): Le Termite Champignonniste *Odontotermes* Comme Ingénieur De L'écosystème. PhD Thesis. Université Pierre et Marie Curie, Paris (245 pp).

Konaté, S., Le Roux, X., Tessier, D., Lepage, M., 1999. Influence of large termitaria on soil characteristics, soil water regime, and tree leaf shedding pattern in a West African savanna. Plant Soil 206, 47–60.

Konaté, S., Le Roux, X., Tessier, D., Verdier, B., Lepage, M., 2003. Effect of underground fungus-growing termites on carbon dioxide emission at the point and landscape-scales in an African savanna. Funct. Ecol. 17, 305–314.

Korb, J., Linsenmair, K.E., 1998. The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. Insect. Soc. 45, 51–65.

Korb, J., Linsenmair, K.E., 1999. The architecture of termite mounds: a result of a trade-off between thermoregulation and gas exchange? Behav. Ecol. 10 (3), 312–316.

Kristensen, J.A., Thomsen, K.J., Murray, A.S., Buylaert, J.P., Jain, M., Breuning-Madsen, H., 2015. Quantification of termite bioturbation in a savannah ecosystem: Application of OSL dating. Quat. Geochronol. 30, 334–341.

Le Bissonais, Y., Le Souder, C., 1995. Mesurer la stabilité structurale des sols pour évaluer leur sensibilité à la battance et à l'érosion. Etudes Gestion Sols 2, 43–56.

Lee, K.E., Wood, T.G., 1971. Physical and chemical effects on soils of some Australian termites, and their pedological significance. Pedobiologia 11, 376–409.

Lepage, M.G., 1979. La Récolte en Strate Herbacée de *Macrotermes aff. Subhyalinus* (Isoptera : Macrotermitinae) dans un Écosystème Semi-aride (Kajiado-Kenya). Comptes Rendus Union Internationales Pour L'étude des Insectes Sociaux, Lausanne, 7-8 sept. 1979, pp. 145–151.

Lepage, M.G., 1984. Distribution, Density and Evolution of *Macrotermes Bellicosus* Nests (Isoptera: Macrotermitinae) in the North-East Ivory Coast. MSc Dissertation. The University of Queensland.

Liu, X., Monger, H.C., Whitford, W.G., 2007. Calcium carbonate in termite galleries-biomineralization or upward transport? Biogeochemistry 82, 241–250.

Lock, N.P., 1985. Kimberlite exploration in the Kalahari region of southern Botswana with emphasis on the Jwaneng Kimberlite province. In: Davis, G.R. (Ed.), Prospecting in Areas of Desert Terrain. Institute of Mining and Metallurgy, London, pp. 183–190.

Mahaney, W.C., Zippin, J., Milner, M.W., Sanmugadas, K., Hancock, R.G.V., Aufreiter, S., Campbell, S., Huffman, M.A., Wink, M., Malloch, D., Kalm, V., 1999. Chemistry, mineralogy and microbiology of termite mound soil eaten by the chimpanzees of the Mahale Mountains, Western Tanzania. J. Trop. Ecol. 15, 565–588.

Marais, A.V., Irish, J., 1989. *Typhlops schlegelii petersii* (Squamata : Thyphlopidae) in a cave: accidental or incidental? Cimbebasia 11, 145–146.

McCarthy, T.S., Ellery, W.N., Dangerfield, J.M., 1998. The role of biota in the initiation and growth of islands on the floodplain of the Okavango alluvial fan, Botswana. Earth Surf. Process. Landf. 23, 291–316.

Menichetti, L., Landi, L., Nannipieri, P., Katterer, T., Kirchmann, H., Renella, G., 2014. Chemical properties and biochemical activity of colonized and abandoned litter-feeding termite (*Macrotermes* spp.) mounds in chromic Cambisol Area on the Borana Plateau, Ethiopia. Pedosphere 24 (3), 399–407.

Mermut, A.R., Arshad, M.A., St Arnaud, R.J., 1984. Micropedological study of termite mounds of three species of *Macrotermes* in Kenya. Soil Sci. Soc. Am. J. 48, 613–620.

Mess, F., Mujinya, B.B., Baert, G., Van Ranst, E., 2021. The construction of terrestrial mounds and arboreal nests by termites – a micromorphological approach for species from Katanga, DR Congo. Catena 202, 105287.

Mills, A.J., Medinski, T., 2021. Ecological effects of clay mining by *Macrotermes* termites. S. Afr. J. Sci. 117 (7/8).

Mills, A.J., Sirami, C., 2018. Nutrient enrichment of ecosystems by fungus-growing versus non-fungus-growing termites. J. Trop. Ecol. 34 (6), 385–389.

Mills, A.J., Milewski, A., Fey, M.V., Groengroeft, A., Petersen, A., 2008. Fungus culturing, nutrient mining and geophagy: a geochemical investigation of *Macrotermes* and *Trinervitermes* mounds in southern Africa. J. Zool. 278, 24–35.

Milne, G., 1947. A soil reconnaissance journey through parts of Tanganyika Territory, December 1935 to February 1936. J. Ecol. 35, 192–265.

Mitchell, J.K., Soga, K., 2005. Fundamentals of Soil Behavior. Wiley & Sons, Inc, Hoboken, NJ, USA.

Mujinya, B.B., Van Ranst, E., Verdoodt, A., Baert, G., Ngongo, L.M., 2010. Termite bioturbation effects on electro-chemical properties of Ferralsols in the Upper Katanga (D.R. Congo). Geoderma 158, 233–241.

Mujinya, B.B., Mees, F., Boeckx, P., Bodé, S., Baert, G., Erens, H., Delefortrie, S., Verdoodt, A., Ngongo, M., Van Ranst, E., 2011. The origin of carbonates in termite mounds of the Lubumbashi area, D.R. Congo. Geoderma 165, 95–105.

Mujinya, B.B., Mees, F., Erens, H., Dumon, M., Baert, G., Boeckx, P., Ngongo, M., Van Ranst, E., 2013. Clay composition and properties in termite mounds of the Lubumbashi area, D.R. Congo. Geoderma 192, 304–315.

Mujinya, B.B., Adam, M., Mees, F., Bogaert, J., Vranken, I., Erens, H., Baert, G., Ngongo, M., Van Ranst, E., 2014. Spatial patterns and morphology of termite (*Macrotermes falciger*) mounds in the Upper Katanga, D.R. Congo. Catena 114, 97–106.

Nauer, P.A., Chiri, E., de Souza, D., Hutley, L.B., Arndt, S.K., 2018. Technical note: Rapid image-based field methods improve the quantification of termite mound structures and greenhouse-gas fluxes. Biogeosciences 15, 3731–3742.

Nobre, T., Aanen, D.K., 2012. Fungiculture or termite husbandry? The ruminant hypothesis. Insects 3 (1), 307–323.

Ocko, S.A., Heyde, A., Mahadevan, L., 2019. Morphogenesis of termite mounds. PNAS 116 (9), 3379–3384.

Olson, D.M.E., Dinerstein, E.D., Wikramanayake, N.D., Burgess, G.V.N., Powell, E.C., Underwood, J.A., D'Amico, I., Itoua, H.E., Strand, J.C., Morrison, C.J., Loucks, T.F., Allnutt, T.H., Ricketts, Y., Kura, J.F., Lamoreux, W.W., Wettengel, P., Hedao, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51, 933–938.

Phillips, J.D., 2009. Soils as extended composite phenotypes. Geoderma 149 (1–2), 143–151.

Pomeroy, D.E., 1976a. Studies on a population of large termite mounds in Uganda. Ecol. Entomol. 1, 49–61.

Pomeroy, D.E., 1976b. Some effects of mound-building termites on soils in Uganda. Eur. J. Soil Sci. 27, 377–394.

Poulsen, M., Hu, H., Li, C., Chen, Z., Xu, L., Otani, S., Nygaard, S., Nobre, T., Klaubauf, S., Schindler, P., Hauser, F., Pan, H., Yang, Z., Sonnenberg, A.S.M., de Beer, W., Zhang, Y., Wingfield, J., Grimmelikhuijzen, C.J.P., de Vries, R.P., Korb, J., Aanen, D. K., Wang, J., Boomsma, J.J., Zhang, G., 2014. Complementary symbiont contributions to plant decomposition in a fungus-farming termite. Proc. Natl. Acad. Sci. U. S. A. 111 (40), 14500–14505.

Pringle, R.M., Doak, D.F., Brody, A.K., Jocqué, R., Palmer, T.M., 2010. Spatial pattern enhances ecosystem functioning in an African savanna. PLoS Biol. 8 (5), e1000377.

Reid, I.D., 1989. Solid-state fermentation for biological delignification. Enzym. Microb. Technol. 11, 786–803.

Roberts, E.M., Todd, C., Aanen, D.K., Nobre, T., Hibert-Wolf, H.L., O'Connor, P.M., Tapanila, L., Mtelela, C., Stevens, N.J., 2016. Oligocene termite nests with in situ fungus gardens from the Rukwa Rift Basin, Tanzania, support a Paleogene African origin for insect agriculture. PLoS One 11 (16), e0156847.

Romanens, R., Pellacani, F., Mahinga, A., Fynn, R., Vittoz, P., Verrecchia, E.P., 2019. Soil diversity and major soil processes in the Kalahari basin, Botswana. Geoderma Reg. 19, e00236.

Rouland-Lefèvre, C., Bignell, D.E., 2001. Cultivation of symbiotic fungi by termites of the subfamily Macrotermitinae. In: Seckbach, J. (Ed.), Symbiosis. Springer, Dordrecht, pp. 731–756.

Sako, A., Mills, A.J., Roychoudhury, N., 2009. Rare earth and trace element geochemistry of termite mounds in central and northeastern Namibia: Mechanisms for micro-nutrient accumulation. Geoderma 153, 217–230.

Sapountzis, P., de Verges, J., Rousk, K., Cilliers, M., Vorster, B.J., Poulsen, M., 2016. Potential for nitrogen fixation in the fungus-growing termite symbiosis. Front. Microbiol. 7, 1993.

Schwiede, M., Duijnisveld, W.H.M., Böttcher, J., 2005. Investigation of processes leading to nitrate enrichment in soils in the Kalahari Region, Botswana. Phys. Chem. Earth 30 (11), 712–716.

Seymour, C.L., Milewski, A.V., Mills, A.J., Joseph, G.S., Cumming, G.S., Cumming, D.H. M., Mahlangu, Z., 2014. Do the large termite mounds of *Macrotermes* concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas? Soil Biol. Biochem. 68, 95–105.

Shanbhag, R.R., Kabbaj, M., Sundararaj, R., Jouquet, P., 2017. Rainfall and soil properties influence termite mound abundance and height: a case study with *Odontotermes obesus* (Macrotermitinae) mounds in the Indian Western Ghats forests. Appl. Soil Ecol. 111, 33–38.

Soyer, J., 1987. Rôle des termites dans la formation du complexe de la stone-line. Geo-Eco-Trop 11, 97–108.

Stoops, G., 1989. Contribution of in situ transformation to the formation of stone-layer complexes in Central Africa. Geo-Eco-Trop 11, 139–149.

Sugimoto, A., Inoue, T., Kirtibutr, N., Abe, T., 1998. Methane oxidation by termite mounds estimated by the carbon isotopic composition of methane. Glob. Biogeochem. Cycles 12 (4), 595–605.

Sugimoto, A., Bignell, D.E., MacDonald, J.A., 2000. Global Impact of Termites on the Carbon Cycle and Atmospheric Trace Gases. Termites: Evolution, Sociality, Symbioses, Ecology, pp. 409–435.

Tarnita, C.E., Bonachela, J.A., Sheffer, E., Guyton, J.A., Coverdale, T.C., Long, R.A., Pringle, R.M., 2017. A theoretical foundation for multi-scale regular vegetation patterns. Nature 541, 398–401.

Tilahun, A., Kebede, F., Yamoah, H., Mujinya, B.B., Verdoodt, A., Van Ranst, E., 2012. Quantifying the masses of *Macrotermes subhyalinus* mounds and evaluating their use as a soil amendment. Agric. Ecosyst. Environ. 157, 54–59.

Traoré, S., Tigabu, M., Jouquet, P., Ouédraogo, S.J., Guinko, S., Lepage, M., 2015. Long-term effects of *Macrotermes* termites, herbivores and annual early fire on woody undergrowth community in Sudanian woodland, Burkina Faso. Flora 211, 40–50.

Trapnell, C.G., Friend, M.T., Chamberlain, G.T., Birch, H.F., 1976. The effects of fire and termites on Zambian woodland soil. J. Ecol. 64, 577–588.

Turner, J.S., 1994. Ventilation and thermal constancy of a colony of a southern African termite (*Odontotermes transvaalensis*: Macrotermitinae). J. Arid Environ. 28, 231–248.

Turner, J.S., 2000. Architecture and morphogenesis in the mound of *Macrotermes michaelseni* (Sjöstedt) (Isoptera: termitidae, Macrotermitinae) in northern Namibia. Cimbebasia 16, 143–175.

Turner, J.S., 2001. On the mound of *Macrotermes michaelseni* as an organ of respiratory gas exchange. Physiol. Biochem. Zool. 74 (6), 798–822.

Turner, J.S., 2004. Extended phenotypes and extended organisms. Biol. Philos. 19, 327–352.

Turner, J.S., 2006. Termites as mediators of the water economy of arid savanna ecosystems. Dryland Ecohydrol. 303–313.

Van Thuyne, J., Verrecchia, E.P., Darini, I., Mainga, A., 2021. Are fungus-growing termites super sediment-sorting insects of subtropical environments? J. Arid Environ. 193, 104566.

Verrecchia, E.P., Braissant, O., Cailleau, G., 2006. The oxalate-carbonate pathway in soil carbon storage: The role of fungi and oxalotrophic bacteria. In: Gadd, G.M. (Ed.), Fungi in Biogeochemical Cycles. Cambridge University Press, British Mycology Society, pp. 289–310.

Viles, H.A., Goudie, A.S., Goudie, A.M., 2021. Ants as geomorphological agents: a global assessment. Earth Sci. Rev. 213, 103469.

Visser, A.A., Nobre, T., Currie, C.R., Aanen, D.K., Poulsen, M., 2012. Exploring the potential for Actinobacteria as defensive symbionts in Fungus-growing Termites. Microb. Ecol. 63, 975–985.

Watson, J.P., 1960. Some observations on soils horizons and insect activity in granite soils. In: Proc. 1st Fed. Sci. Congr. Rhodesia and Nyasaland, pp. 271–276.

Watson, J.P., 1969. Water movement in two termite mounds in Rhodesia. J. Ecol. 57, 441.

Watson, J.P., 1975. The composition of termite (*Macrotermes* spp.) mounds on soil derived from basic rock in three rainfall zones of Rhodesia. Geoderma 14, 147–158.

Weir, J.S., 1973. Air flow, evaporation and mineral accumulation in mounds of *Macrotermes subhyalinus* (Rambur). Anim. Ecol. 43, 509–520.

West, W.F., 1970. The Bulawayo symposium papers, No2: termite prospecting. Chamber Mines J. 30, 32–35.

Whitford, W.G., Eldridge, D.J., 2013. Effects of ants and termites on soil and geomorphological processes. In: Shroder, J.F. (Ed.), Treatise on Geomorphology. Academic Press, San Diego, pp. 281–292.

Williams, M.A.J., 2019. Termites and stone lines-traps for the unwary archeologist. Quat. Sci. Rev. 226, 106028.

Wood, T.G., Sands, W.A., 1978. The role of termites in ecosystems. In: Brian, M.V. (Ed.), Production Ecology of Ants and Termite. Cambridge University Press, Cambridge, pp. 245–292.

Wood, T.G., Thomas, R.J., 1989. The Mutualistic Association between Macrotermitinae and *Termitomyces*. Insect-Fungus Interactions. The Royal Entomological Society of London. Academic Press.

Zachariah, N., Das, A., Murthy, T.G., Borges, R.M., 2017. Building mud castles: a perspective from brick-laying termites. Nat. Sci. Rep. 7, 4692.

Zachariah, N., Murthy, T.G., Borges, R.M., 2020a. Moisture alone is sufficient to impart strength but not weathering resistance to termite mound soil. R. Soc. Open Sci. 7, 200485.

Zachariah, N., Singh, S., Murthy, T.G., Borges, R.M., 2020b. Bi-layered architecture facilitates high strength and ventilation in nest mounds of fungus-farming termites. Nat. Sci. Rep. 10, 13157.