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Where do South-Indian termite mound soils come from?

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ABSTRACT

This study investigated the origin of the soil termites used to build their above-ground mounds. Termite mounds were surveyed in a ferralsol and a vertisol in a dry deciduous forest in Karnataka, southern India. In these environments, two types of above-ground termite mounds are observed which we describe here as CATHEDRAL and LENTICULAR mounds. Partial Least Squares Regression models (PLSR) were computed from the physical and chemical properties of the soil sampled down to 4 and 2.5 m in the ferralsol and vertisol, respectively. Soils from CATHEDRAL mounds had the same signatures as soils collected at approximately 100 and 50 cm deep in the ferralsol and vertisol, respectively. On the other hand, soil from LENTICULAR mounds had the same signature as soil sampled at 30 and 60 cm deep in the ferralsol and vertisol, respectively. In conclusion, this study highlighted that the source of the soil termites use to build their mounds can be soil (ferralsol *vs* vertisol) and species (CATHEDRAL *vs* LENTICULAR) specific. In light of these findings, we conclude that the impact of CATHEDRAL mounds on soil dynamics appears to be smaller than that of LENTICULAR mounds in terms of soil volume at the landscape scale but it is higher in terms of soil translocation from deeper soil layers to the surface.

1. Introduction

Termites belong to the order Blattodea (infraorder Isoptera) and are one of the most abundant taxonomic groups in tropical soils. Indeed, they are dominant invertebrate decomposers in most tropical ecosystems (Black and Okwakol, 1997; Buitenwerf et al., 2011; Kihara et al., 2015). They are also considered soil engineers due to their effects on soil formation and dynamics (Lobry de Bruyn and Conacher, 1990; Holt and Lepage, 2000). These include the production of soil biogenic structures with different physical and chemical properties to the surrounding soil environment (Dangerfield et al., 1998; Jouquet et al., 2011).

In Africa and Asia, fungus-growing termite nests are some of the largest and most complex invertebrate constructions. To build these structures and ensure their resistance against environmental hazards (e.g., extreme rainfall events, predation by mammals and invertebrates, and the extreme curiosity of scientists…), termites impart specific physical and chemical properties to the soil in mound walls. Indeed, termite mound walls are enriched in fine sized particles, mainly clay, rather than sand, which thus increases hardness and improves water resistance (Contour-Ansel et al., 2000; Fall et al., 2001; Jouquet et al., 2004; Kandasami et al., 2016). The soils in mounds also have different clay mineral compositions to those predominating at the soil surface (Mahaney et al., 1996, 1999; Abe and Wakatsuki, 2010; Mujinya et al., 2013) and are often characterized by lower C contents but higher mineral nutrients, and a higher CEC than the surrounding top-soil (see Bottinelli et al., 2015; Jouquet et al., 2016a for recent reviews). This modification in soil properties may result from termites selecting soil aggregates and translocating soil from various depths of the profile to the soil surface. Nevertheless, the relative importance of these two processes is difficult to assess.

Fungus-growing termites retrieve their material (wet soil particles) very deep in the profile, even down to the water table (which might be as deep as 50 m in places such as the Sahel zone of Senegal) (Holt and Lepage, 2000). This is most likely to find the moisture needed for the colony and their symbiotic fungus (Turner, 2006). For example, Sako

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et al. (2009) analyzed rare earth and trace element concentrations to confirm that *Macrotermes* sp. nests are produced through the accumulation of highly weathered soil originating from the deeper regolith in semi-arid soils in Namibia. Abe et al. (2012) and Mujinya et al. (2013) also examined the nature and abundance of clays and sesquioxides and concluded that termites use soils from the saprolite for building their mound nests in Nigeria and D.R. Congo, respectively. Over time the effects of termites on soil translocation have strong consequences on the soil profile. Thus termites are agents of pedogenesis, influence the distribution of organic and mineral resources in the ecosystem and their constructions impact the growth and diversity of the vegetation and the foraging activity of large herbivores (Awadzi et al., 2004; Pringle et al., 2010; Erpenbach et al., 2013, 2017; Muvengwi et al., 2013, 2014; Seymour et al., 2014; Jouquet et al., 2016a). However, previous studies focused only on African termite species and remained purely qualitative, showing the presence of soil particles from deep soil layers, but without quantitative measurement of the origin and evolution of the soil termites used to produce their nests.

In Southern India, termite mounds are also conspicuous features of the landscape and two types of mounds are usually observed (Jouquet et al., 2016c). The first are the cathedral-shaped mounds that *Odontotermes obesus* (Rambur) (Termitidae, Macrotermitinae subfamily) build. The second type corresponds to lenticular or dome-shaped mounds, which are also commonly observed in Africa. The origin and dynamic of these mounds are unknown but it has been suggested that they originate from the degradation of Macrotermes sp. mounds and their colonization, and subsequently maintenance, by other termite species (Pullan, 1979; Mujinya et al., 2013; Josens et al., 2016). The objective of this study was to use the specific physical and chemical properties of these two types of termite mounds to measure the depth at which termites collect soil for building their mound nests.

2. Materials and methods

2.1. Study site and termite mound models

Soils were sampled in the Mule Hole experimental watershed ($4.1\ km^2$). This dry deciduous forest is located in the Bandipur Tiger reserve in Southern India at 11°44′N and 76°26′E (Karnataka state, Chamarajanagar district). The Mule Hole watershed is located in the sub-humid zone of the sharp climatic gradient induced by the Western Ghats. As a result of the short-term variability of the South-West Monsoon, the experimental watershed is characterized by rainfall ranging from 700 to $1500\ mm\ yr^{-1}$, with an average over the last thirty years of $1100\ mm\ yr^{-1}$. The elevation of the watershed ranges from 820 to 910 m a.s.l. The relief is mostly undulating with gentle slopes. The soil cover of the watershed has been mapped by Barbiero et al. (2007) based on the FAO terminology (IUSS-Working-Group-WRB, 2006). Soil depth is variable but ranging from 1 to 3 m in average (barbioero et al., 2007; Braun et al., 2009). The soil is mainly composed of well-drained ferralsols and impervious vertisols (Barbiero et al., 2007; Braun et al., 2009). The ferralsol and vertisol areas cover 66% and 12% of the watershed, respectively. The distribution of these soils is mainly explained by the topography and the lithology (gneiss and amphibolites) (Barbiero et al., 2007). Ferralsols are developed on granite-gneiss on the hillslopes. Their soils have less than 2% of C in the first soil layer and < 1% below 20 cm depth. The clay content ranges from 30 to 40% and clays are also dominated by non expandable 1:1 clays (kaolinite) (Jouquet et al., 2016b). Vertisols are developed in the lower part of the slope and the flat valley bottoms, on gneiss and mafic rocks. They have high C (> 3% in the 0–20 cm soil layer) and clay contents (from 30 to 50%). Clay mineralogy is dominated by swelling 1:2 clays (smectite), that have higher layer charges and CEC than 1:1 clays (Jouquet et al., 2016b).

In this environment, the fungus growing termite species *Odontotermes obesus* builds abundant cathedral mound nests (CATHEDRAL) with a density of approximately 3.5 mounds ha^{-1} (Jouquet et al., 2016c), which represents a volume of soil equivalent to approximately $3.5\ m^3\ ha^{-1}$. These can reach up to 2 m high with many circumvolutions, ridges and conical turrets and have many similarities in shape to those produced by the African termite species *M. bellicosus* (Roonwal, 1970, 1978; Jouquet et al., 2015, 2016b). On the other hand, lenticular or dome-shaped termite mounds (LENTICULAR) are usually covered in vegetation and occupied by several termite species (e.g., *Odontotermes brunneus*, *O. giriensis*, *O. gurdaspurensis*, *O. microdentatus*, *O. redamanni*, *O. obesus*, and *Ceylonitermes indicola*). LENTICULAR density was approximately 13 mounds ha^{-1} and they represent between 27 and 47 $m^3\ ha^{-1}$ in the ferralsol and vertisol, respectively (Jouquet et al., 2016c).

2.2. Soil sampling

CATHEDRAL varied considerably in size (Jouquet et al., 2015) and only large mounds from 1.5 to 1.8 m high and > 0.5 m^3 were considered in this study (n = 6 replicates in both ferralsol and vertisol). LENTICULAR varied also in size but are mainly a few dozen cm high and between 1 and 3 m^3. To take this variability into account, n = 9 LENTICULAR mounds from 1 to 3 m^3 were selected in both the vertisol and ferralsol areas. Soil samples were collected from the outer wall of CATHEDRAL and from the soil surface layer for LENTICULAR. Soils were also sampled in the surrounding environment (control, distance from any termite mound > 5–10 m ahead of the mound in taking into account the gentle slope of the watershed) at several soil depths down to 4.0 m in four different locations in the ferralsol (n = 39) and down to 2.5 m in three different locations in the vertisol (n = 22). Data describing the evolution of soil properties with depth came from the RBV database (http://portailrbv.sedoo.fr/).

2.3. Analysis of soil properties

The soil physical properties measured included the particle-size distribution, after destruction of organic matter and dispersion with sodium hexametaphosphate (AFNOR, NFX 31 107): clay (< 2 µm) and silts (2–50 µm) were obtained by sedimentation and sand (50–2000 µm) by sieving. To assess Soil Organic Matter (SOM) content, the C and N concentrations were measured using an elemental analyzer Flash 2000 HT. The cationic exchange capacity and the content of exchangeable cations (Ca, Mg, Na, K, Fe, Mn and Al) were determined at soil pH by exchange with cobaltihexamine (AFNOR, NF ISO 23470). Data were grouped according to their depths (0–20, 30–70, 70–100, 100–150, 150–200, 200–250, 250–400 cm for the ferralsol, and 0–20, 30–70, 70–100, 100–150, 150–250 for the vertisol).

2.4. Statistical analyses

Partial Least Squares Regression (PLSR, Mevik and Wehrens, 2007) was used to fit linear regression models by projecting predicted and observable variables from the soil physico-chemical properties at different soil depths. The most significant variables were determined using the variable importance in the projection (VIP) method, which computes scores for each variable (Tenenhaus, 1998). Models were then fine-tuned to minimize the root-mean-square error of cross-validation (RMSECV) and maximize the Q^2 value (cross-validated R^2, which gives the predicting ability of the model). These models were then used to predict the origin of the soil termites used for building their mounds. Differences in soil depths were then compared using a two-way analysis of variance (ANOVA) with soil and termite mound treatments as independent variables, after first verifying that residuals were normally distributed using the Shapiro-Wilk test. Differences in the soil properties between termite mound soils and those of the soil depth, predicted with the PLSR models, were tested with unpaired *t*-test or Kruskal-Wallis test, after verifying that data were normally distributed. For this comparison, only soil properties that have been con-