Vast 4000-year-old termite population persists in NE Brazil

Brazilian 4000-yr-old termite mounds

Over-dispersed mound patterns generated in a semiarid climate with a unique plant-termite ecology, and not by inter-mound aggression

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Martin et al. show that in NE Brazil an estimated 200 million, regularly spaced, termite mounds are up to 4000 years old. Each mound is 2-4m high by 9 m in diameter; they occupy 230,000 km², and arise from the excavation of 10 cubic km of soil during the construction of a vast tunnel network that still allows termites' safe access to their food.

Due to the demise of their bio-engineering species, many large-scale 'biogenic' earthen structures have controversial origins, especially when they form regular (over-dispersed) self-organized vegetation patterns[1]. Here we describe a 'population' of soil mounds constructed by *Syntermes dirus* termites that has persisted for up to 4000 years and covers an estimated 230,000 km² of seasonally dry tropical forest in a relatively undisturbed and climatically stable region of NE Brazil. The mounds are not nests, but rather they are generated by the excavation of vast inter-connecting tunnel networks, resulting in approximately 10 km^3 of soil being deposited in 200 million conical mounds that are 2.5 m tall and approximately 9 m in diameter. The *S. dirus* termites are still present in the soil surrounding the mounds and we found that intra-specific aggression occurred at a scale much larger than an individual mound. We suggest that the complex network of tunnels built to access episodic leaf-fall has allowed for the optimization of waste soil removal, which over thousands of years has formed an over-dispersed spatial pattern of mounds.

Largely hidden from view in the fully deciduous, semiarid, thorny-scrub *caatinga* forests unique to northeastern Brazil exist tens of millions of 2-4 m high, conical, densely packed earth mounds locally known as *'murundus'*. Based on established distributions of mounds[2], a MAXENT model predicted their potential distribution. Subsequent ground searches covering thousands of kilometers, and inspection of satellite images, indicated that the mounds cover approximately 230,000 km^2 – roughly the size of Great Britain (Figure 1a), and similar to a previous study[3]. The oligotrophic, clayey, and acidic *caatinga* soils support little agricultural activity, so that the core mound area has remained largely undisturbed by anthropogenic interventions

Soil samples collected from the centers of 11 mounds (Figure 1a) and dated using single-grain Optically Stimulated Luminescence and the Minimum Age Model, indicated mound fill dates between 690 to 3820 years ago (Table S1a). Those ages are comparable to the world's oldest known termite mounds in Africa [4]. During that period, the *Syntermes dirus* termites constructed vast tunnel networks (Figure 1c, Movie S1) that generated huge volumes of extracted material that was discarded to form uniformly large (~2.5 m tall and 9 m Ø) conical mounds (Figure 1c). The mounds do not create any surrounding vegetation patterns (Movie S1) as commonly seen in other systems[1,5].

Another striking feature of the mounds is their over-dispersed spatial pattern (Figure 1b), which is similar to North American '*mima* mounds', South African '*heuweltjies*', and Namibian fairy circles [1, 5]. We confirmed using neighbor-distances and Ripley's K-functions the mounds over-dispersed spatial pattern at 20 locations (Table S1b). The mean inter-mound distance is 20 m, giving mound density of 1800/km^2 (Table S1b), leading to an estimated 200 million mounds. Each is composed of approximately 50 cubic meters of soil and requiring the excavation of over 10 km^3 of earth, equivalent to ~4000 great pyramids of Giza – making this the greatest known example of ecosystem engineering by a single insect species.

Inspecting hundreds of mounds bisected by road construction, supplemented by our own excavations, revealed that each mound is simply an amorphous mass of soil without any internal structure. Newly forming mounds contain a single large (~10 cm Ø) central tunnel descending into the ground that intersects with an extensive network of underground tunnels (up to 10 cm Ø) and narrow horizontal galleries containing harvested discs of dead leaves or brood; to date no royal chamber has been located either in or below a mound, despite extensive searching. The tunnels are never left open to the environment, ruling out their use as a ventilation system [6]. At night, when food is available, groups of 10-50 workers and soldiers emerge onto the forest floor between the mounds from an array of small (~8 mm Ø) temporary tubes excavated from below; those temporary tubes are sealed shut after use. As the mounds exhibited none of the complex architecture normally associated with termite mounds[6], we investigated if their spatial pattern was driven by mound associated intra-specific competition[1]. Multiple aggression bioassays between *S. dirus* soldiers and workers (various combinations) failed to elicit any aggression at the mound level, but when individuals were artificially forced to encounter *S. dirus* termites 50 km away, aggression was immediate - demonstrating that the over-dispersed spatial mound pattern was not generated by mound-specific aggression[1, 5]. Instead, we propose the mound pattern arose through self-organizational processes facilitated by the increased connectivity of the tunnel network, which is driven by the episodic leaf-fall in the *caatinga*. The spatial distribution of chemicals[7] such as alkene and alkadiene isomers that we found *S. dirus* produces, could create a pheromone map, allowing the termites to minimize their travel time from any location in the colony to the nearest waste mound (Figure S1). This vast permanent tunnel network allows safe access to a sporadic food supply, similar to *Heterocephalus* naked-mole rats that also live in arid regions and construct very extensive burrow networks to obtain food [8].

This system is characterized by adverse environmental conditions where a limiting resource (leaf-fall) has driven the modification of the environment by the construction of a complex network of inter-connecting tunnels. This allows negative feedback in the form of competition for a depleted resource often associated with an over-dispersed formation pattern[9]. As aggression cannot explain waste mound distribution, we propose that minimising the energetic costs of waste disposal, made possible by the inter-connected tunnels, an over-dispersed spatial pattern can emerge (Figure S1). This would support the idea that there may be several mechanisms capable of generating over-dispersed spatial patterns[1].

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Figure 1. The distribution of *Syntermes dirus* termite waste mounds across NE Brazil and tunnel network.

a, Core area (orange) of *S. dirus* mounds confirmed by ground visits. The MAXENT model predicted suitable area, and new mound sites confirmed by visits (orange triangle) or using satellite images (black triangles). Dated mounds indicated by red squares. Great Britain outline illustrates the extent of the mound fields; **b**, Satellite image with the position of each mound indicated by a black dot, indicating an over-dispersed spatial distribution; **c**, Sketch showing the mound structure and network of major tunnels (solid lines) and smaller vertical foraging tunnels (dashed lines). The images illustrate the various aspects of the sketch.