Correspondence

A vast 4,000-year-old spatial pattern of termite mounds

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The origins of many large-scale ‘biogenic’ earthen structures are controversial, because often the species that built them have vanished. This is especially true when they form regular (over-dispersed), self-organized vegetation patterns [1]. Here, we describe a vast array of soil mounds constructed by termites (*Syntermes dirus*) 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 Northeast Brazil. The mounds are not nests, but rather they are generated by the excavation of vast inter-connecting tunnel networks, resulting in approximately 10 km³ of soil being deposited in 200 million conical mounds that are 2.5 m tall and approximately 9 m in diameter. *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, there are 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 km² — roughly the size of Great Britain (Figure 1A) [3]. The oligotrophic, clayey, and acidic *caatinga* soils support little agricultural activity, so that the core mound area has remained largely undisturbed by human intervention.

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. Those ages are comparable to the world’s oldest known termite mounds in Africa [4]. During that period, *S. dirus* termites constructed vast tunnel networks (Figure 1C; Video S1) that generated huge volumes of extracted material that was discarded to form uniformly large (~2.5 m tall and 9 m diameter) conical mounds (Figure 1C). The mounds do not create any surrounding vegetation patterns (Video 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*

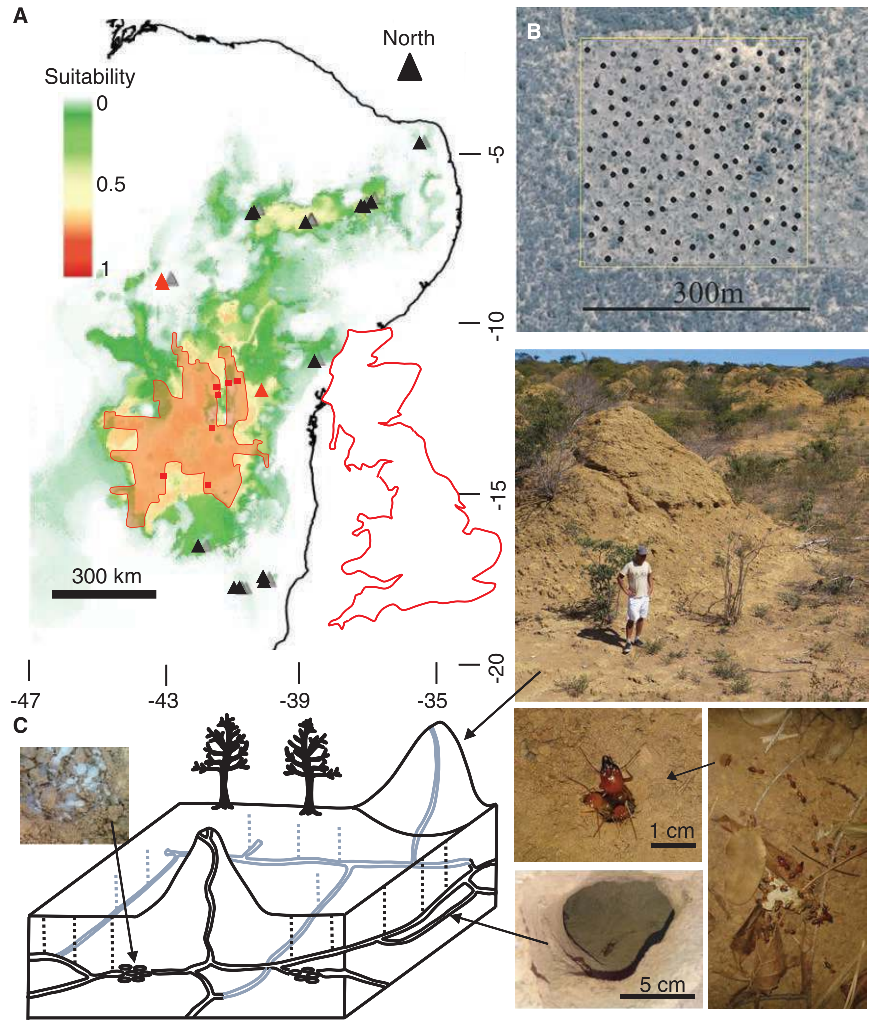

Figure 1. The distribution of *Syntermes dirus* termite waste mounds across Northeast Brazil and associate tunnel networks.
(A) Core area (orange) of *S. dirus* mounds confirmed by ground visits. The MAXENT model predicted suitable area, and new mound sites confirmed by visits (orange triangle) or using 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.

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 (Supplemental Information). The mean inter-mound distance is 20 m, giving mound density of 1800/km^2 (Supplemental Information), leading to an estimated 200 million mounds. Each mound is composed of approximately 50 cubic meters of soil that required 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.

Inspection of hundreds of mounds bisected by road construction, supplemented by our own excavations, has revealed that each mound is simply an amorphous mass of soil without any internal structure. Newly forming mounds contain a single large (diameter of ~10 cm) central tunnel descending into the ground that intersects with an extensive network of underground tunnels (diameter of up to 10 cm) 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 (diameter of ~8 mm) 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, which 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 (Supplemental Information). 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 (Supplemental Information). This would support the idea that there may be several mechanisms capable of generating over-dispersed spatial patterns [1].

SUPPLEMENTAL INFORMATION

Supplemental Information including experimental procedures, one figure, one table, a video and a Data S1 file can be found with this article online at https://doi.org/10.1016/j.cub.2018.09.061.

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