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Nest structure: termites

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The nests of termites are amongst the most diverse and complex structures among the great diversity of those built by animals. Their intricate architectures and the manner in which termites make use of them have fascinated mankind for centuries, whether it is part of local agricultural practice, as a simple landscape feature, as an inspiration for societal collective building or as a scientific study object on its own. However, their nests remain relatively little understood compared to those of many ants, social wasps and social bees, especially honey bees and stingless bees since termites that actually build mounds or other conspicuous structures are of minor economic importance. The few termites that serve as structural pests -- and so attract the most study -- mostly live inside their food supply without constructing a distinctive nest. My purpose here is to build on the few earlier reviews with an emphasis on mound nests. Many recent advances have been possible thanks to new imaging technics such as Computer Tomography, photogrammetry or automatic tracking and behavior classification. Modelling and simulation techniques further help to link individual construction behavior to emerging architectures.

Diversity of nest structure

Termite nests tend to be quite species-characteristic in their structure. That is, if one comes upon two substantially different nests at a given locality, it is virtually certain that they were built by two different species. Furthermore, anyone familiar with the termites at a given locality quickly learns to distinguish at least the common species by their nests alone.

One-piece nests are the simplest form, in which the termites live inside their food, and the nest structure emerges from their eating activity (e.g. Fig. 1a), thus creating habitable cavities that they sometimes re-arrange with simple constructions to close the nest to the outside. In intermediate nests the living space is enlarged by connecting several food sites by underground galleries (e.g. Fig. 1b). The presence of such simple nests in human-made structures can remain undetected until the infested wood collapses (Fig. 1v).

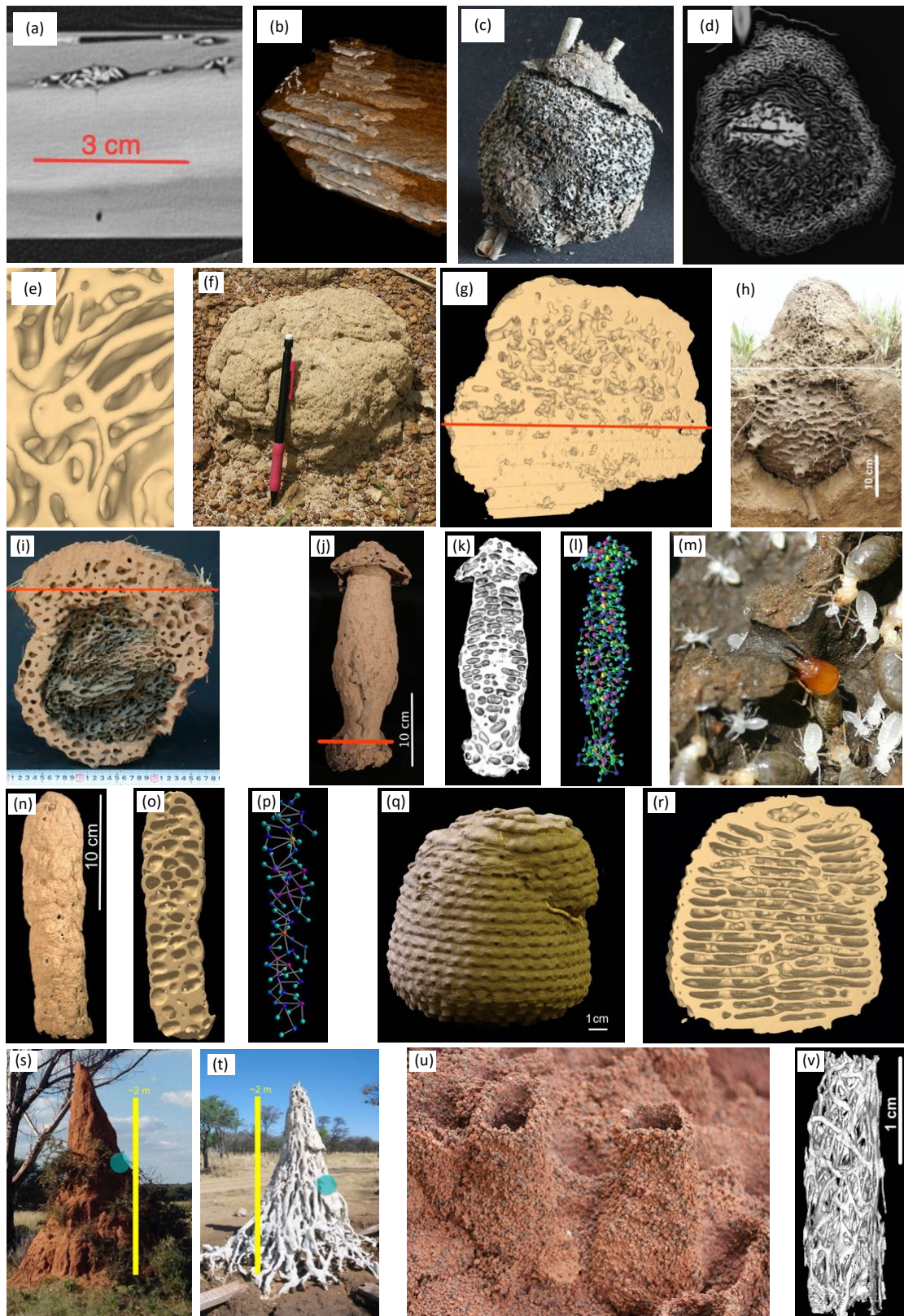


Figure 1. Examples of termite nests. (a) One-piece nest of *Cryptotermes secundus* excavated by feeding in a piece of wood. Tomography by A. Fuchs. (b) Gallery system created by *Reticulitermes flavipes* by feeding in a piece of wood, the galleries following the grain of the wood. Tomography by E. Darrouzet. (c) Arboreal nest of *Nasutitermes ephratae* in French Guiana. The envelope has been removed except for a small part at the top. (d) Long-section of the same nest of *N. ephratae* to show the overall lattice-like

structure with the central royal chamber. (e) Virtual cut showing a 3D reconstruction of these interwoven surfaces. (f) Epigeous part of a *Trinervitermes geminatus* nest in Guinea. (g) Virtual cut through the same nest of *T. geminatus*. The red line indicates the boundary between the hypogeous and epigeous parts, with the latter again a maze of interwoven surfaces. *Trinervitermes* mounds are typically closed, with openings to the outside (see top left) only appearing after heavy rainfall. (h) Partly excavated mound of *Cornitermes cumulans* in the cerrado of Brazil. The solid outer wall is evident even in the hypogeous part, with the empty paraecie separating it from the soil. Tunnels radiate from this nest vertically down more than 3 m to the water table and horizontally 10 cm below the grass cover to a distance of up to 10 m to access the foraging grounds. (i) Young nest of *C. cumulans* that just emerged from the ground, sectioned to show the solid outer wall as distinct from the soft, organic inner part where the colony mostly lives. The red line marks the boundary between the hypogeous and epigeous parts. (j) *Cubitermes* sp. nest from the Central African Republic. The red line marks the boundary between the hypogeous and epigeous parts. (k) Virtual cut through the same nest of *Cubitermes* sp. The broad chambers connected by narrow tunnels reveal the nest as a (l) network of nodes (chambers) and edges (tunnels). (m) The *Cubitermes* sp. soldier's head diameter matches the tunnel width, thus permitting an efficient defence against invading enemies such as ants. Photo by G. Josens. (n-p) Same series of images as (j-l) for a *Thoracotermes* sp. nest. (q) Subterranean nest of *Apicotermes lamani* from the Republic of the Congo. Regularly spaced small pores (connected to circular tunnels, but not to the nest interior) facilitate gas exchange with the surrounding paraecie. (r) Virtual cut of the same nest. The circular tunnels are seen on the periphery. The nest is organized in regular floors connected by linear or spiral ramps. (s) *Macrotermes michaelseni* mound in Namibia. From ref. 10, with permission. (t) Cast of the internal tunnel system: the surface tunnels have been revealed by washing away the soil, the internal tunnel and chamber network (see Fig. 2) is still hidden. From ref. 10, with permission. (u) Chimneys on top of a Brazilian *Syntermes dircei* mound that are connected to a complex tunnel ventilation system. (v) Remains of an agglomerated wood plate after *Coptotermes gestroi* have done their work.

The nests that have received the most attention are built apart from the food source, so that the termites reach their food supply through an extensive underground gallery system or, less commonly by aerial foraging trails that they cover. While in the first two nest types the structure is mostly limited and shaped by the pre-existing food structure (e.g. seasonal wood rings, Fig. 1a-b), separate nests show a great diversity of architectures that ranges from complex interwoven surfaces (Fig. 1c-i) over networks of chambers connected by tunnels (Fig. 1j-p) to highly regular horizontal floors connected by linear and helicoidal ramps (Fig. 1q-r).

The most complex structures are probably found in fungus growing termites with separate fungus chambers, brood areas, royal chamber and a sophisticated ventilation system for gas exchange (Fig. 1s-t). Nests can be completely below ground (Fig. 1q), mostly below ground with an epigeal part (Fig. 1 f, h, j, n) or entirely above ground (Fig. 1 c,d). They are typically completely closed to the outside, which functions to exclude predators and/or to conserve the internal (humid) microclimate. This closure can consist in simply walling off any potential entry points or by constructing an opaque outer wall (Fig. 1f, h, j, n, q, s) that is sometimes surrounded by an open space (paraecie) that separates it from the surrounding soil (Fig. 1h, q).

Nest growth

As their building materials termites use soil and/or wood or other plant matter mixed with saliva and faecal material (the latter especially in arboreal and humus-feeding species). Nest solidity depends on the clay/sand ratio that some termites seem to be able to manipulate and the chemical structure of saliva and faecal material. As a consequence, different species in the same habitat can produce nests of very different solidity). The founding pair starts the nest with a simple chamber either in wood or the soil. The first workers then begin nest development toward its mature form. Subterranean nests can simply be a network of tunnels or a set of chambers concentrated around the royal cell and separated from the surrounding soil by a limiting wall. Epigeal nests also start below ground with a single chamber and become epigeal as the nest grows upward and outward (Fig. 1h, i). We have very little knowledge of whether arboreal nests start their development in the tree or if the colony is first founded in the soil with a later migration up onto the trunk or a branch. In epigeal and arboreal nests enlargement is often achieved by simply adding new layers or chambers on the top or sides of the existing structure (e.g. Fig. 1h, s), sometimes accompanied by a restructuring of the latter. However, growth can also involve the formation of a discrete nest connected by tunnels to the previous one (e.g. Fig. 1j). The former nest can then be abandoned (nest relocation) or may continue in use by the now polydomous or polycalic colony. Such polydomous colonies are very frequent in underground nests (eg *Sphaeroterme*s or *Apicotermes*, Fig. 1q).

The nest can be seen as part of the colony's extended phenotype. That is, as a physical manifestation of the termites' collective behavior it can be acted upon by natural selection at the whole-colony or superorganismal level. As a result, features of nest structure can be informative in the taxonomy and phylogenetic analysis not only of termites but of other social insects. However, to date this has only been developed with limited success with respect to *Apicotermes* and *Odontotermes* nests. Their use is complicated by the fact that many features (royal cell, an exoecie or ventilation system, an empty or sand-filled paraecie that separates the nest from the surrounding ground) have appeared independently in different lineages. Furthermore, nest-structural features of the same species can be adapted to local environmental conditions.

Functions

Nests provide a closed environment that shields the colony from environmental conditions and predators. The importance of the latter can be readily demonstrated by breaking open a nest and standing back to observe. Very quickly ants, lizards and/or birds will appear to prey on the exposed termites. The most important predators of termites are ants that are roughly the same size. Many nests protect against these with a compact outer wall and very few openings, thus minimizing the soil-nest and air-nest interface. Ants could still dig tunnels, but (depending on species) walls can be almost rock-solid thanks to added saliva and faecal material. And even if ants finally enter the nest termite soldiers are on hand with their strong mandibles and defensive secretions. Nests of the Termitinae, for example, are a tree-like network of chambers connected by narrow tunnels (Fig. 1l, p). A single soldier with its plug-like head can block such a tunnel (Fig. 1m).

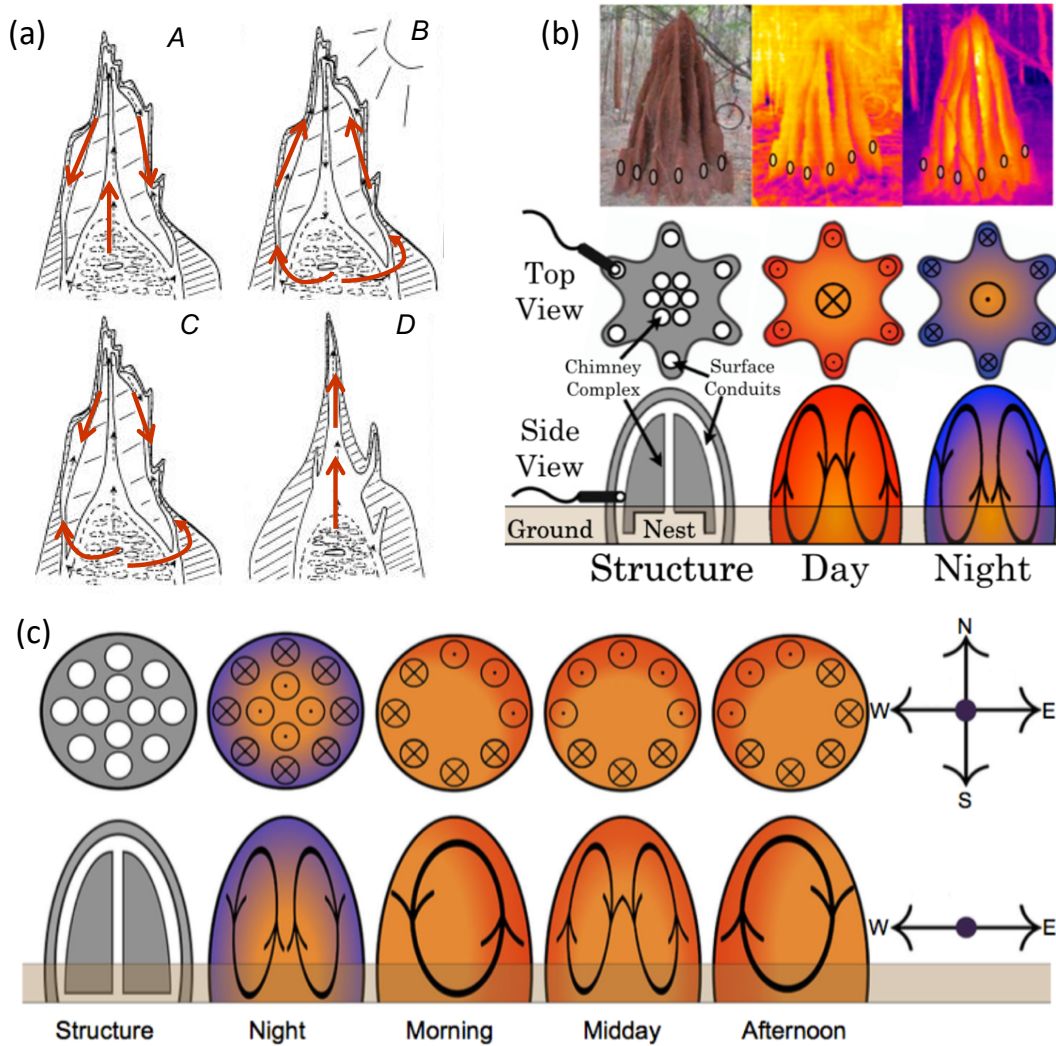


Figure 2. Nest ventilation systems of fungus growing termites. (a) Ventilation systems in the west-African *Macrotermes bellicosus*. From ref. 8, with permission. These mounds have a large central shaft and many lateral tunnels. Subfigure A is the original thermosiphon hypothesis, in which metabolic heat raises the air in the central shaft, which then flows back through lateral tunnels while exchanging gas diffusively through the mound walls. B-C. The refined ventilation scheme for sun-exposed mounds, in which sun-heated air rises in the lateral tunnels during the day while the warmer core air rises through the shaft during the night. D. Non-circulating ventilation in shaded mounds in forest, in which gas exchange mostly occurs through diffusive and buoyant forces. (b) The South Asian *Odontotermes obesus* mound ventilation works similarly to the refined ventilation scheme, but it is enhanced by their star-like shape of the mound with central chimneys and lateral surface conduits in flutes or shafts. Top row: thermal images show the high flute temperatures during the day and the high central temperatures during the night. Bottom row: scheme of air circulation during day and night, crossed circles indicating downward flow and dotted circles upward flow. Illustration from ref. 7, with permission. (c) Ventilation system of the southwest-African *Macrotermes michaelsoni* is slightly different from the previous system due to the higher sun intensity and its position, creating angular surface temperature gradients that lead to dominant air circulation through the lateral tunnels only in the morning and the afternoon (crossed and dotted circles as above). From ref. 10, with permission.

High relative humidity, crucial for these soft-bodied insects, is ensured inside the nest by extensive walling in combination with water sources such as food, respiration (water as a metabolic by-product) and/or active transport from deeper soil levels. However, walling must be complemented by ventilation, since termites consume O₂ while producing CO₂, so that oxygen must be brought in from outside and excess carbon dioxide expelled. In subterranean nests gas exchange mostly occurs by simple diffusion through micropores in the nest wall. The circular aeration tunnels in *Apicotermes* (Fig. 1q) or the empty/sand-filled paraecie around the nest (Fig. 1h, q) are thought to facilitate this diffusion. In epigeal nests gas exchange is mostly wind driven through micropores (e.g. Fig. 1f) with or without a closed or open ventilation system. Especially fungus-growing termites with their high metabolic rates show complex architectural adaptations to enhance ventilation.

Since the early speculative explanations (Fig. 2a), detailed case studies have advanced our understanding of the actual mechanisms involved. The Asian *Odontotermes obesus* with its closed ventilation system harnesses diurnal temperature variations due to sunlight to drive ventilation. This is possible through a simple combination of geometry, heterogeneous thermal mass, thermal lag and porosity (Fig. 2b). The African *Macrotermes bellicosus* also has a closed ventilation system. In cathedral-shaped mounds in open savanna the ventilation seems to be driven by temperature gradients within the mound and between the mound and its exterior environment (Fig. 2a), leading to heat convection similar to the system in *O. obesus*. However, dome-shaped mounds of the same species in forest lack such external temperature gradients and are sheltered from wind, so that non-circular ventilation seems to be driven by buoyant forces that raise the air from the center of the nest to the top of the mound where gases are exchanged through thin walls of turrets and a central spire (Fig. 2a). The East African *Macrotermes michaelseni*'s ventilation system strongly resembles that of the *O. obesus*. In addition, the direct savanna sunlight creates angular thermal gradients in addition to the radial thermal gradients seen in *O. obesus*. This creates more complex bulk air flows (Fig. 2c).

Some termites also use open ventilation systems. Large ducts traverse the whole nest with openings to the outside (Fig. 1t). Air flow in these ducts is mostly wind driven through direct channelling or suction. *M. michaelseni* may also be in this category through seasonally open egress tunnels. External turbulent wind in this case enhances gas exchange at the mound surface. Note that even in open mounds the ducts or mound ventilation system are usually not directly connected to the colony's living space, so that gases diffuse through the porous walls and mix with the inner air space that moves thanks to buoyant forces created by the colony's heat production (the Pendelluft mechanism).

Despite these sophisticated ventilation systems, CO₂ concentrations in the nest can be up to 50 times above atmospheric levels. Depending on species and environmental conditions CO₂ concentrations can be homogeneous or with internal gradients that may fluctuate throughout the day. The termites as well as their fungus cultivars (in the case of macrotermitines) must adapt to these conditions.

Termite mounds have also been said to control temperature throughout the year, a manifestation of nest homeostasis. However, near-constant temperatures seem only to be possible in very large mounds. Studies indicate that mean mound temperature tracks the annual mean temperature, as the heat capacity of the surrounding soil seems to overpower the mound's heat capacity. Inside the mound temperature propagates according to classical heat diffusion. The final nest temperature is a mixture of this buffering effect on external fluctuations and internal metabolic heat production. Further work is required to assess how internal architecture and building material influence the associated diffusion coefficient. Mean mound temperature can still be influenced by the termites' choice of particular sites to build their nest or by

changing the nest shape. For example, epigeal nests catch more sunlight and are on average warmer than the surrounding soil. The slab-shaped magnetic termite mounds of northeastern Australia, with their long axis north-south (Fig. 3c), catch sunlight mostly in the morning and late afternoon, but little during mid-day, thus moderating the temperature extremes early in the morning and in the early afternoon. However, compared to a roundish, conical mound, the slab shape might be advantageous due to food conservation in the nest: there is a higher microbial load in the food stored in the mound when the slab is experimentally thickened, suggesting that the quicker drying of a slab helps to reduce this microbial load. Local temperature can also be controlled by evaporative cooling: some termites seem to carry water to the most sensitive nest parts to cool them (for example the nursery).

Termite mounds in ecological context

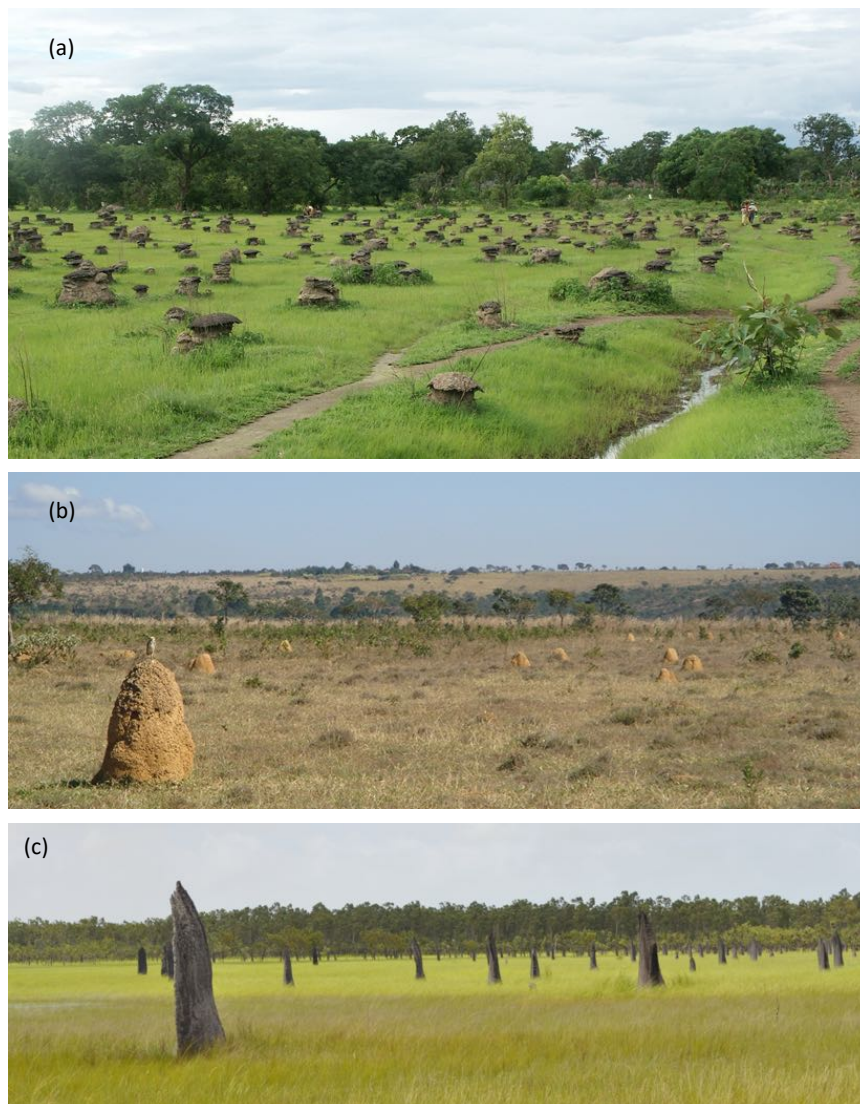


Figure 3. Mound nests sometimes dominate landscapes in the tropics. (a) *Cubitermes* mounds in Guinea, West-Africa. Note the two humans on the right side for scale. (b) *Cornitermes* mounds in the Brazilian cerrado. The owl sitting on the mound to the left is approximately 20 cm tall. (c) Magnetic termite *Amitermes meridionalis* mounds in northern Australia. Photo by J. Korb.

Termite nests are often conspicuous features of tropical landscapes (Fig. 3), so that their colonies can be veritable ecosystems engineers. They accumulate water and sometimes also nutrients, thus forming fertile islands in otherwise arid savanna that are host to many other species, invertebrates (spiders, ants, scorpions) as well as vertebrates (snakes, lizards, birds). Most importantly, they speed the recycling of detritus, such as dead vegetation and animal excretions. A recent work also shows that they increase the resistance of dryland ecosystems to climatic change.

Nest construction behavior

How do termites build these nests? It is generally recognized that no central coordination is at work, and the queen and king are certainly not in command of the operations. Nest construction is a decentralized, self-organized process, in which each worker acts on its locally available information. The basic idea was long ago set forth by Pierre-Paul Grassé as his concept of stigmergy, based on observations of mound-building termites in Africa. Individual actions cause local environmental change, which in turn modifies the subsequent behavior of the same or other individuals. Several studies in more recent times have shown that self-organization, often in combination with environmental or animal made templates, can account for much of social insect construction in general. These studies required a combination of minute experimental work, on both the individual and collective level, and appropriate modelling techniques to validate the detailed behavioral mechanisms. In termites such studies are less advanced. Most models of mound construction are still freely inspired by Bruinsma's work on queen chamber construction (3), without validating the suggested mechanisms with proper quantitative experimentation. Given the non-linear plasticity in such self-organized processes this methodology is only a weak validation of the proposed mechanisms. To advance our understanding how termites construct their mound we need much more quantitative experimental work on individual construction behavior and its modulation by environmental parameters, combined with modelling to formalize these behaviors quantitatively and link the individual behavior with the emerging mounds.

Termite mounds in the human environment

Termite ventilation systems take advantage of their environment and require little energy input. As a result, they have thus inspired architects to build air-conditioning systems based on similar principles. The best known example is the Eastgate Centre in Harare, Zimbabwe by architect Mick Pearce, and other bio-mimetic engineering solutions are discussed in dedicated workshops. The self-organized nature of mound construction has inspired roboticists to design robot swarms that can collectively build large structures based on similar principles. The mentioned accumulation of nutrients in termite mounds is already exploited in many traditional agricultural practices. It has been tested for large-scale use in sustainable agriculture (termite mound material as fertilizer), but mound growth seems to be too slow. Furthermore, termite mounds are rather perceived as a nuisance/obstacle for mechanized modern agriculture (Fig. 3) and many methods exist to kill the mounds before they become too tall. However, mound building termites are not pests in any usual sense. This role is clearly taken by some wood eating termites whose one-piece or intermediate nests weaken human constructions (Fig. 1v) or by sugar-cane eating *Coptotermes* who extend their nests to the stems of their host plants.

Termite mounds also have a place in human culture. They have several functions in sub-Saharan Africa: geochemical prospecting, indicators of soil quality, food supplements, material for bricks or pots, plastering for houses, storage, and burial sites associated with traditional funerary practices. The practice of termite fishing through holes in mounds, first

observed in chimpanzees, has become a key example of the kind of cultural transmission that presumably existed in our human ancestors.

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Synonyms: mound nest, nest mound