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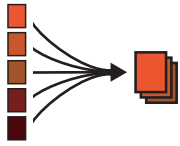

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11. Homeostasis, complexity, and the problem of biological design

Scott Turner
SUNY College of Environmental Science & Forestry, US

The harmonious melding of structure and function – biological design – is a striking feature of complex living systems such as tissues, organs, organisms, or superorganismal assemblages like social insect colonies or ecosystems. How designed systems come into being remains a central problem in evolutionary biology: adaptation, for example, cannot be fully explained without understanding it. Currently, the prevailing explanation for biological design rests on essentially atomist doctrines such as Neodarwinism or self-organization. The Neodarwinist explanation for design, for example, posits that good design results from selection for "good design genes." Along the same lines, self-organization posits that complex systems with sophisticated structures and behaviors can arise from simple interactions among agents at lower levels of organization. There is no reason to doubt the validity of either explanation. Nevertheless, it is doubtful whether such doctrines by themselves can adequately explain the emergence of design in complex systems. In this paper, I argue that the missing piece of the puzzle that can draw forth well-functioning and well-designed "organisms" from the low-level interactions of the myriad agents in a complex system is homeostasis, a classical concept that is not itself inherent in atomist explanations for adaptation and design. I couch my argument in observations on the emergence of a spectacular social insect "superorganism": the nest and mound of the macrotermitine termites.

Introduction

Among biologists, "design" refers to a peculiar coherence between a living structure and a function it performs (Turner, 2007). Bones, for example, are exquisitely constructed cantilevers, built to bear their loads with an elegant economy of form and materials (Currey, 1984). It seems perfectly apt to say that bones are well-designed: indeed, to describe them in any other way seems pedantic. Awkwardness attaches to the word, though, because it readily conjures up the notion of a designer, like that which Plato introduced in his *Timaeus,* that troublesome Master Craftsman that was long the mainstay of natural theology, and that serves that purpose still for the resurgent "natural deism" that imbues the Intelligent Design (ID) movement.

Darwinism convincingly undercuts this type of thinking about biological design, of course, but the persistence of anti-Darwinism nevertheless invites a question: why won't it go away? One doesn't have to be a supporter of Intelligent Design theory (I am not), nor need one be averse to Darwinism (I am not) to see that there are some interesting philosophical issues at play, and that these revolve around the question of biological design: why *are* living things so aptly constructed for the things they do? Darwinism, at least in its Neodarwinist conception, puts forth what is essentially an atomist solution

to the question: biological design arises solely from the interplay of "atoms of heredity" in gene pools, converging over time onto well-functioning phenotypes through natural selection of particular phenotype-specifying genes. As in classical atomism, design emphatically does not arise from evolution being informed by any broader purposefulness or directedness (Dawkins, 1986).

A vast territory of physiology separates genes from fitness, though. Even though much of this territory is *terra incognita,* what *is* known about it exhibits a striking purposefulness that seems quite at odds with the supposedly purposeless process that gives rise to it. This puts the Darwinist stance against purpose into its proper perspective, as more a philosophical position than an empirically demonstrable one.

Complexity, at least as I understand its scientific definition, is cut from the same atomist cloth as Neodarwinism. Both share a goal of deriving emergent phenomena – adaptation in the one case, complex and coordinated function in the other – from simple rules of interaction among myriad low-level agents. Like classical atomism, however, Neodarwinism (and perhaps complexity) is prone to a philosophical quandary: is the phenomenon we seek to explain an emergent product of the agents, or is the phenomenon the agents' driver?

I will say at the outset that I am not a practitioner of complexity science. I have, however, spent several years studying and thinking about a group of social insects that is often cited as one of the more compelling examples of a complex emergent system: the social insect "superorganism." In my contribution to this workshop, I would like to tell you some of what we have learned about how these attributes emerge from the assemblage of agents that comprise these superorganisms. Perhaps these things will pose some interesting questions for complex systems science.

The *Macrotermes* superorganism

I study the colonial physiology of termites, specifically those belonging to an advanced termite family, the Macrotermitinae. This grouping comprises roughly 350 species, distributed among fourteen genera (Table 1). All have in common the cultivation of symbiotic fungi as an adjunct to these termites' normal intestinal digestion of cellulose (Batra & Batra, 1979; Wood & Thomas, 1989; van der Westhuizen & Eicker, 1991). Two of the genera, *Macrotermes* and *Odontotermes,* are renowned for building spectacular above-ground structures (Figure 1). I study one of these species, *Macrotermes michaelseni,* which is widely distributed through sub-Saharan Africas.

The mound-building habit is not unique to the Macrotermitinae, but the use to which these termites put their mounds is. Most termites that build mounds use them as nests, that is, as structures to house the colony: the myriad sterile workers, the queen and the fertile nymphs that will serve ultimately as the colony's propagules. The macrotermitine mound is not the nest, however – few termites, save for occasional patrolling workers, are found there. The nest itself is a compact subterranean structure that is situated below the mound (Figure 2), housing both the colony's complement of termites, and the colony's culture of obligate symbiotic fungi, belonging to the basidiomycete genus *Termitomyces.* The mound's internal architecture departs significantly from the typical architecture of the termite nest, which tends to the

Genus	# species	Mound building
Acanthotermes	1	
Allodontotermes	5	
Ancistrotermes	14	
Euscaiotermes	1	
Hypotermes	10	
Macrotermes	54	*
Megaprotermes	1	
Microtermes	58	
Odontotermes	187	*
Protermes	5	
Pseudacanthotermes	6	
Sphaerotermes	1	
Synacanthotermes	3	

Table 1 *Distribution of mound building among the Macrotermitinae.*

Figure 1 *A mound built by Macrotermes michaelseni, in northern Namibia. Two of my students are in the foreground: Wendy Park (l) and Grace Shihepo (r).*

Figure 2 *A cross section through a nest of a colony of Macrotermes michaelseni. The light-colored bodies are the fungus combs, where the symbiotic fungus is cultivated.*

construction of horizontal galleries, interconnected with small tunnels. The *Macrotermes* mound, in contrast, is permeated with an extensive and broadly connected reticulum of large-calibre tunnels that have a striking vertical bias (Figure 3). These ramify through the mound, integrating with the nest at the bottom, eventually to open to the surface through a number of tiny egress channels.

The egress channels serve two functions. First, they are the principal sites of mound growth. The mound is built by a net translocation of soil by termites from the mound interior and deep soil horizons to the mound surface: the egress tunnels provide the termites access to the mound surface. The egress tunnels are also zones of porosity in the mound's seemingly solid surface, and this serves the mound's principal function as an organ of colonial physiology: it is a wind-driven lung to ventilate the underground nest. The need for nest ventilation is acute. The *Macrotermes* nest is a focus of high metabolic power, which requires a commensurably high collective demand for oxygen, roughly equivalent to that of a mammal the size of a goat. By some estimates, the nest's metabolic rate is equivalent to that of a cow. Without ventilation, the nest's inhabitants would suffocate (Darlington, *et al.*, 1997). Remarkably, most of the nest's collective oxygen consumption is attributable not to the termites but to the cultivated fungi. Because the mound projects upward through the surface boundary layer, it intercepts wind and converts its kinetic energy into a complex field of pressure over the mound surface (Turner, 2000, 2001). Via the porous egress channels, this pressure field drives a complicated flow of air through the mound's internal network of tunnels, ultimately ventilating the nest.

Figure 3 *Plaster filled casts of the internal network of tunnels in Macrotermes mounds. Left: the vertically oriented network surrounding the nest, which is situated in the center. Middle: the large vertically-oriented tunnels in the center of a mound. Right: a partly exposed cast of tunnels situated just beneath the mound surface. Note the numerous egress tunnels projecting to the surface. Mound casts were done in collaboration with Dr Rupert Soar of Loughborough University.*

This association of termites, fungal symbionts and sophisticated mound architecture displays a remarkable integrity. The termites cultivate the fungi, providing them an environment that is rich in nutrients and shielded from their principal fungal competitors (Batra & Batra, 1967; Batra, 1971). The fungi, for their part, serve essentially as an accessory digestive system for the colony, composting the hard-to-digest woody material brought back to the nest into a more easily digestible diet. The mound, meanwhile, is constructed as an accessory organ of physiology that serves the respiratory needs of both termites and fungi. By any conceivable definition of the word, this makes the entire assemblage a superorganism. By my understanding of the word, it also makes it a complex system. The question I wish to pose is whether 'bottom-up' interactions among the agents of this system are sufficient to explain this striking organismal integrity? I will argue in this paper that they can, but only up to a point. The remainder of the explanation, I shall suggest, lies in a concept that is largely lost in the reductionist and atomist mind-set of much of modern biology, complexity science included. That concept is homeostasis, which I believe has to be regarded as essentially axiomatic for any science that presumes to comprehend living systems.

Homeostasis of structure and function in the *Macrotermes* superorganism

Homeostasis is a widely abused word. Usually, is used to describe a generalized tendency to steadiness of particular properties within living systems, like body temperature, blood acidity, and so forth. Abuse of the word usually intrudes when the word is employed without reference to the mechanisms that must underlie it. One finds, for example, mere steadiness of body temperature being described as temperature homeostasis: without an appreciation of what produces the steadiness, one cannot distinguish the temperatures of, say, the

body an elephant from the interior of a large rock.

Homeostasis, I would argue, is properly understood as a regulated dynamic disequilibrium, sustained by the active management of fluxes of matter and energy between environments. Body temperature regulation provides a useful illustration of this concept. A warm body in a cold environment represents a disequilibrium in potential energy between environments – body and surroundings – that can drive a physical loss of heat from the body. The rate of loss is proportionate to the magnitude of the disequilibrium: hence, colder environments elicit greater rates of heat loss from the body than do warmer environments. This applies to both a hot elephant and a hot rock. Temperature *homeostasis* can only occur, however, if these physical heat losses are supplanted by the expenditure of metabolic work, in this instance, directed to thermogenesis. Furthermore, this thermogenesis must proceed at a rate that is *matched* to the physical heat loss rates. Thus, homeostasis is essentially a phenomenon of fluxes: physical fluxes down thermodynamic gradients in potential energy being offset by metabolic work to drive fluxes of matter and energy against these thermodynamic gradients.

This definition of homeostasis can be readily applied to the *Macrotermes* superorganism. For example, there is a substantial disequilibrium in the composition of the nest atmosphere with respect to the outside air: nest air is slightly hypoxic, (nest pO_2 is roughly 2 kPa less than atmospheric), slightly hypercarbic (nest pCO_2 is elevated roughly 2 kPa above atmospheric) and very humid (Turner, 2000, 2001). The disequilibrium in partial pressures is established by the nest's metabolic work rate, which I shall call the *metabolic demand*. The disequilibrium also drives a physical flux of these gases across the porous boundary of the mound surface, which I shall call the *ventilatory flux*. The composition of the nest atmosphere is therefore the consequence of a balance between the nest's metabolic demand, and the mound's ventilatory flux. Homeostasis of the nest atmosphere occurs when that metabolic demand is matched with ventilatory flux, which appears to be the case. We know, for example, that mound size is a reliable indicator of the nest's metabolic demand. More populous nests (essentially more engines of soil transport in the form of workers) tend to build larger mounds, and more populous nests have higher overall metabolic demands. If one measures oxygen concentration within the nests of three different size classes of mounds, one finds that the nest pO_2 does not vary, despite the substantial variation of metabolic demand these size classes represents (Figure 4). The homeostasis in this instance is maintained by the expenditure of work to modify the mound's capture of wind energy. More populous, and more metabolically demanding nests build mounds that project higher into the surface boundary layer and into more vigorous winds, which enables the mound to capture more wind energy and effect a more vigorous ventilation. More to the point, the mound's architecture is being adjusted to *regulate* the wind energy captured.

For its part, the structure that mediates nest homeostasis – the mound – itself fits the criteria for homeostasis outlined above. The mound is a structure in disequilibrium with respect to gravity, maintained by a balance between two fluxes of soil. On the one hand, there is a physical flux of soil from the mound onto the ground surface that is driven by erosion by wind or rain. This flux of

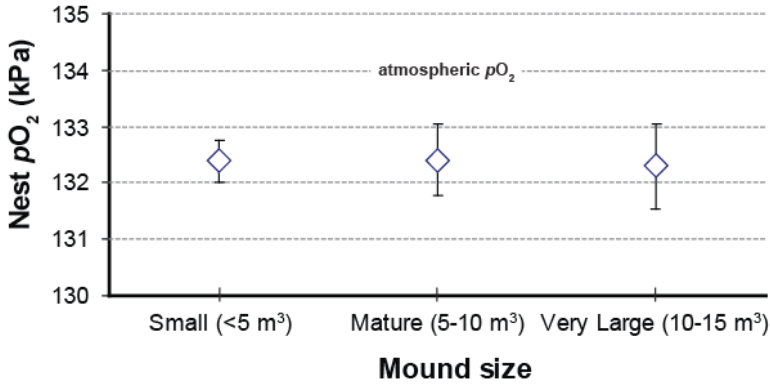

Figure 4 *Partial pressures of oxygen in the nests of three size classes of Macrotermes michaelseni. Despite the large variation of metabolic demand this size variation represents, the concentrations of oxygen in the nest are the same for the three size classes. After Turner (2000).*

soil is substantial, and can amount to several hundred kilograms annually. The mound's disequilibrium is sustained because these physical losses of soil are offset by termites working to carrying soil up into the mound, out through the egress channels, and depositing it ultimately to the mound surface. The mound's architecture is therefore a dynamic disequilibrium maintained by two soil fluxes, not so much a structure as a process, an embodiment of two opposing soil movements.

As such, the mound's architecture can be regulated, just as the nest atmosphere can be. This can be shown dramatically by performing a "complete moundectomy" on a colony, scraping away the mound with a front-end loader (Figure 5). Because this procedure leaves the underground nest intact, the workers are available to rebuild the mound, which they do in remarkably short order. Within 90 days, the mound is rebuilt to its shape prior to the moundectomy, even the point of building a spire that points to the sun's average zenith (Figure 5). The mound is restored to its full function as well, capturing wind to ventilate the nest and regulate the composition of its atmosphere.

The mound's architectural regulation is also evident at a less dramatic scale. Mounds often are subject to injury, such as a breach in the porous surface wrought by animals or erosion. This injury elicits a large-scale rebuilding project to repair the breach and restore the mound to its structure prior to the injury. The project proceeds in three stages (Figure 6). The first, or *recruitment*, stage begins within minutes of the breach, and involves a mobilization of workers from the nest into the mound. The mobilization is elicited by disturbance of the nest atmosphere, wrought by the sudden admission of turbulent wind energy into the mound environment through the breach.

The recruitment phase is lasts for roughly an hour, and merges into the second, or *stigmergic building* phase. Stigmergy (literally, "driven by the mark") is a self-organized building process (Stuart, 1972). A termite lays down a grain of soil onto a surface and cements it into place with a salivary glue containing an attractive pheromone: the pheromone-laden grain of soil is the "mark."

Figure 5 *Rebuilding of a mound following a complete moundectomy. Top: Mound prior to the moundectomy. Middle: The same mound (photographed from a different angle) following the moundectomy. Bottom: The rebuilt mound roughly five weeks later.*

Other termites are attracted to this mark, and are driven deposit new grains of soil onto it, each new grain, in its turn, accompanied by another dollop of the attractive pheromone. This produces a still more powerful enticement to other termites to deposit *their* grains of soil there. The overall effect is an organized translocation of soil to form large-scale orderly structures, either pillars or sheets initially (Courtois & Heymans, 1991), merging over the longer term into a complex space-filling architecture called a *spongy build* (Figure 7).

Following an injury, stigmergic building is initiated widely throughout the mound (Figure 6). This is elicited apparently by strong transients in the atmosphere of the breached mound, driven by turbulent wind energy that had previously been excluded from the mound interior, but which are now admitted via the breach. The most intense transients occur near the breach, of course, and these elicit the most intense stigmergic building there. Immediately following the injury, however, the transients are sufficiently intense throughout the mound to elicit foci of stigmergic building nearly everywhere in the mound. The subsequent course of the stigmergic building phase is determined by the respective rates of soil movements at the various foci. The rate of stigmergic building is most intense near the site of injury, and the spongy build there will be filled in faster than spongy build elsewhere in the mound, sealing the breach before any of the deeper tunnels. Although this limits the wind-induced transients within the mound, stigmergic building continues for a time everywhere in the mound, sustained initially by the pheromone-mediated positive-feedback process driving it until it eventually decays, and stigmergic building ceases, terminating the stigmergic building phase.

The stigmergic building phase leaves the mound with a sealed spongy build at the site of the breach, and sites of comparatively open build elsewhere in the mound. This initiates the final *remodeling* phase, which plays out over the space of several weeks, and involves restructuring the sites of spongy build throughout the mound, restoring the tunnel architecture to what it was prior to the breach (Figure 6). The remodeling phase appears to be tied in to another aspect of nest homeostasis, in this instance, the nest's water balance.

Although termites are generally intolerant of dry conditions, the Macrotermitinae are capable of inhabiting habitats with annual rainfalls as little as 250 mm (Deshmukh, 1989). Termites have this capability because they construct a mesic environment within the nest (Turner, 2006). Even though this saves termites from having to adapt to arid conditions, it nevertheless comes with a cost, because the mesic nest environment is in disequilibrium with the surroundings, which include dry surface soils and dry air. This disequilibrium can drive substantial fluxes of water between the nest and surroundings. As in all homeostatic systems, this disequilibrium is sustained by a balance of physically- and biologically-driven water flows through the nest and mound (Turner, 2007, Figure 8). During dry periods, the termites work to offset physical water losses from the nest to the dry surroundings by actively bringing water into the nest via transport in moist soil. This is not a casual process: termites will go to great depths to obtain this water, as deep as a hundred meters or so by some anecdotal accounts. They also actively reconstruct the soil environment for several tens of meters around the nest, modifying soil porosity and subsurface catchments so that sparse rainfalls can be gathered into shallow perched

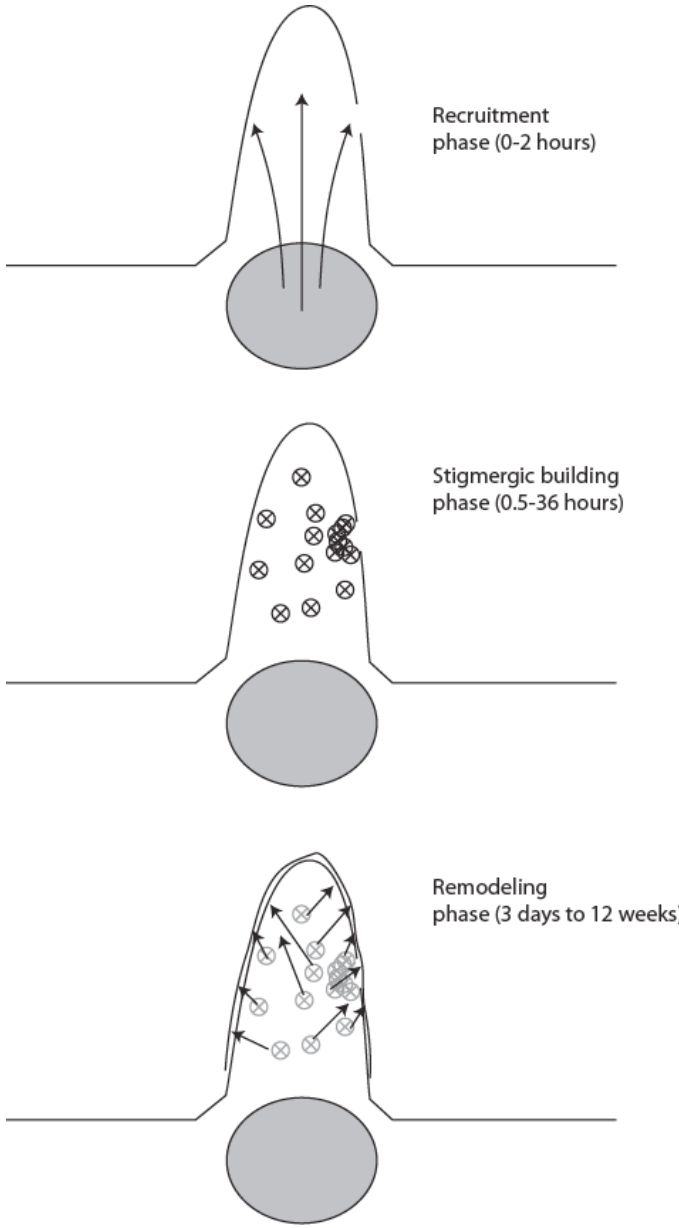

Figure 6 *The three phases of mound recovery from injury.*

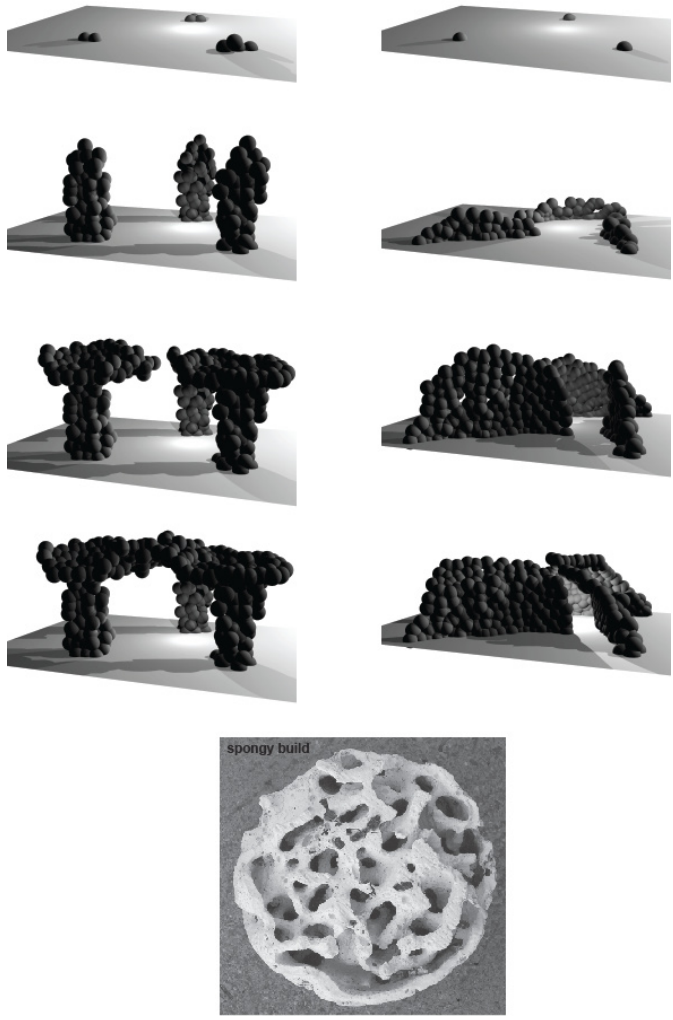

Figure 7 *Stigmergic building and the spongy build. Left series: Stigmergic building that produces pillars. Right series: Stigmergic building that produces walls. Bottom: The space-filling spongy build.*

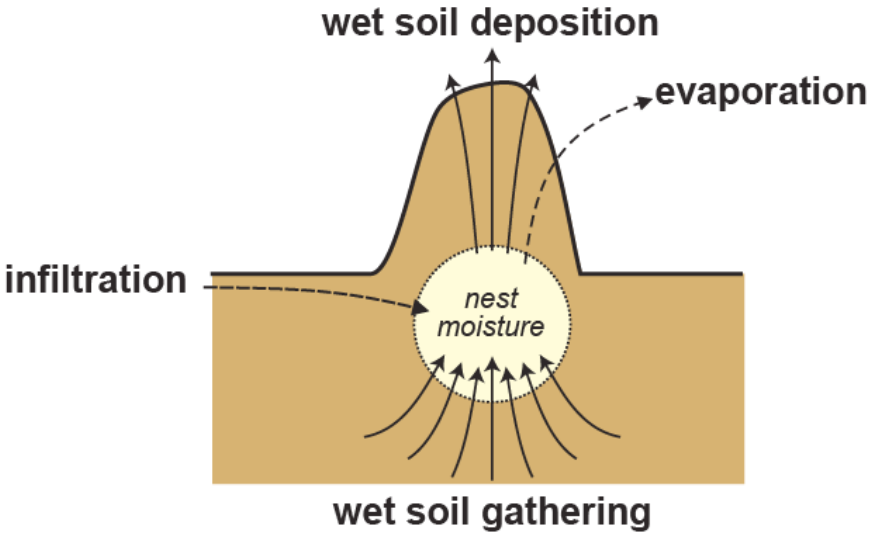

Figure 8 *Water balance of a Macrotermes superorganism. Solid arrows signify work-driven water transport by termites. Dashed arrows represent passive movements of water due to infiltration from wet soils and evaporation through the mound.*

water tables that the termites can readily access. During wet conditions, such as episodes of intense rainfall, water can percolate into the nest from the now moister surroundings, and termites will work to offset this as well, by actively transporting water in moist soil up out of the nest, into the mound, and ultimately to the mound surface where it can evaporate away (Turner, 2007). The end result is an impressive regulation of nest moisture throughout the year (Figure 9).

During the dry winter, moisture regulation is confined to the nest, which becomes a narrowly circumscribed *zone of homeostasis* (Figure 10). The mound, meanwhile, is allowed to dry. During the spring, as prevailing humidity rises, the mound gets wetter until its moisture also appears to be regulated. This gradual moistening results not from the mound being wetted by rainfall, but from termites transporting water-laden soil from the nest up into the mound. The mound moistening also represents an expansion of the zone of homeostasis, which had been confined to the nest during the dry season, until the entire mound becomes a zone of homeostasis. Once the entire mound is ensconced in this zone of homeostasis, soil deposition onto the mound surface begins (Figure 11).

Remodeling occurs as part of this expanding zone of homeostasis (Turner, 2007). Soil in a dry mound is essentially immobile: termites avoid the dry areas of the mound, and there is little rain to drive erosion. As the mound moistens, the soil within becomes mobile: erosion rates kick up, and termites are no longer hesitant to move about the more equable mound. Remodeling occurs as part of a general outward translocation of the now-mobile mound soil to the surface. How termites choose which soil grains to pick up and move and which

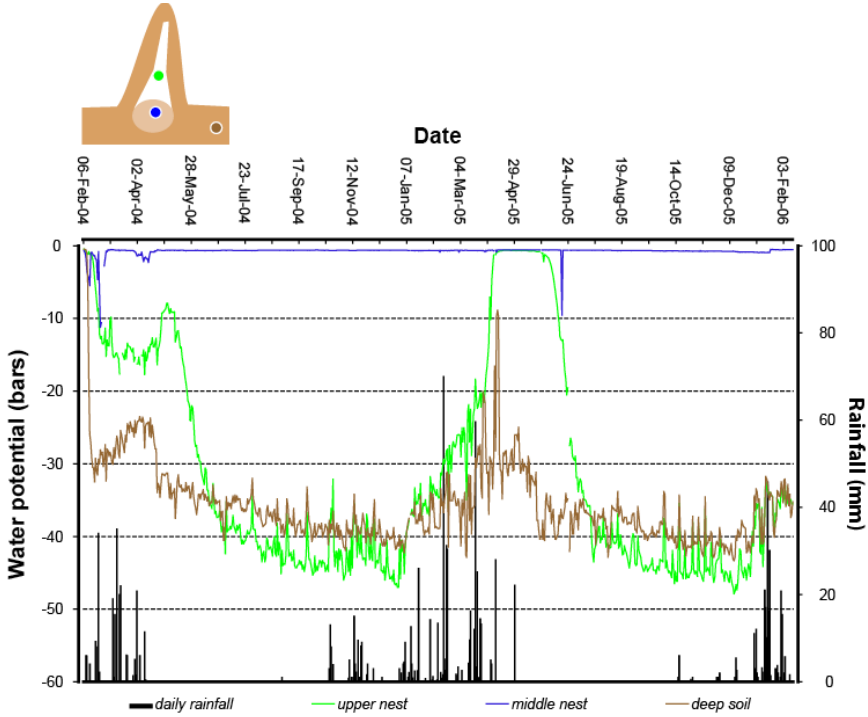

Figure 9 *Moisture homeostasis in the nest of Macrotermes michaelseni. The moisture in the nest (blue trace) is maintained throughout the year, even as moisture in the adjacent soils (brown trace) dries considerably through the year. The center of the mound (green trace) is allowed to dry during the dry season, but becomes regulated during the rainy season. After Turner (2007).*

to leave in place is unclear, but previously deposited spongy build appears to be one important source: termites are attentive to edges, the spongy build provides an abundance of edges, and this probably enhances the probability that soil grains there will be picked up and carried to the surface. As a consequence, the spongy build is eventually demolished, restoring the smooth tunnel to what it was previously.

Is self-organization enough?

I could go on, but I hope my principal point is made: this system is the most impressive example of a superorganism of which I am aware. It exhibits coordination, integrity and design. It is also a complex system, with self-organized behaviors like stigmergy playing a foundational role in the emergence of these superorganismal traits from the myriad interacting agents the system comprises (Bonabeau, *et al.*, 1997). It is now apt to revisit the question I posed in my opening comments: is this foundation sufficient to produce the emergent superorganism?

My answer is "no", and my reason is simple. Self-organized behaviors like stigmergic building are not confined to the Macrotermitinae, but are widespread throughout the termites. Yet, it is only among the Macrotermitinae,

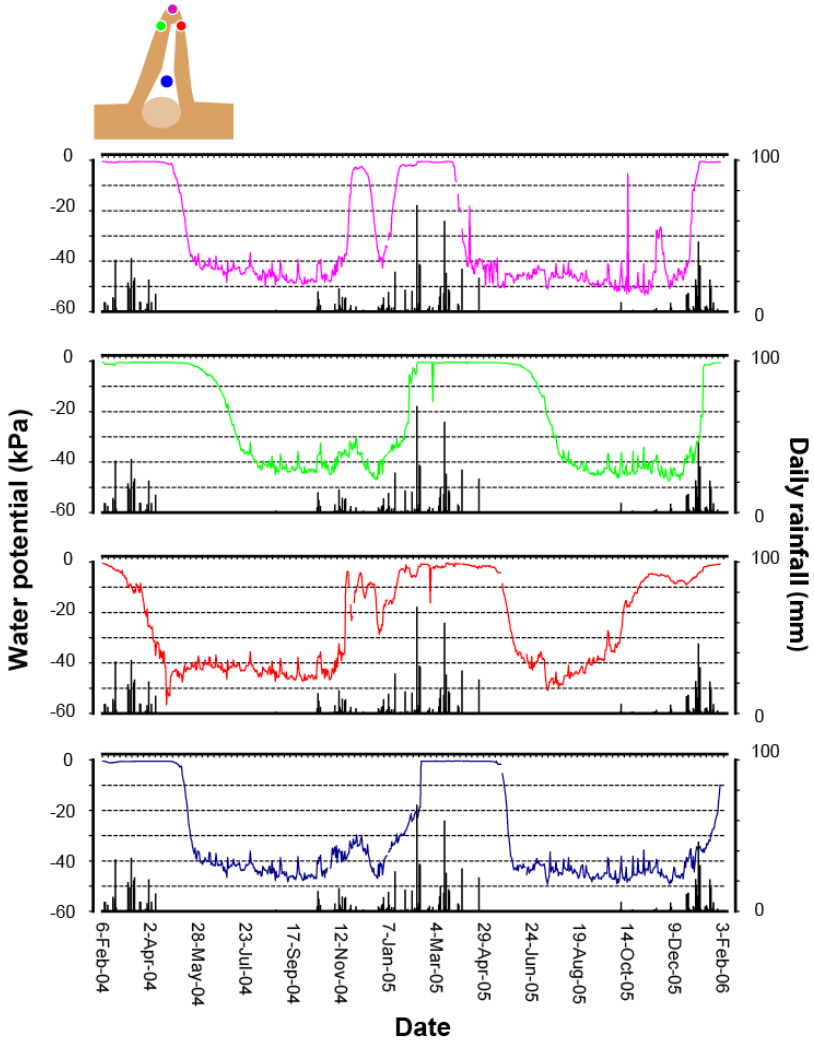

Figure 10 *The expanding zone of moisture homeostasis in a Macrotermes michaelseni mound. As the rainy season proceeds, moisture throughout the mound comes to be regulated. After Turner (2007).*

and from only a few genera among them, that the impressive *Macrotermes* superorganism arises. The question therefore becomes: what, if not stigmergy, draws forth this emergent superorganism? The answer, I argue, is something that is not inherent in atomist explanations for the emergence of such things: the phenomenon of homeostasis.

Termites are agents of homeostasis, whose *modus operandi* is to create new environments upon which homeostasis can be imposed (Turner, 2007). In the case of termite colonies, that new environment is the nest interior, created by excavating spaces in soils that are partitioned from the surroundings, and regulated by constructed organs of physiology. *Macrotermes* are not unique among the termites in being agents of homeostasis. The unique *Macrotermes*

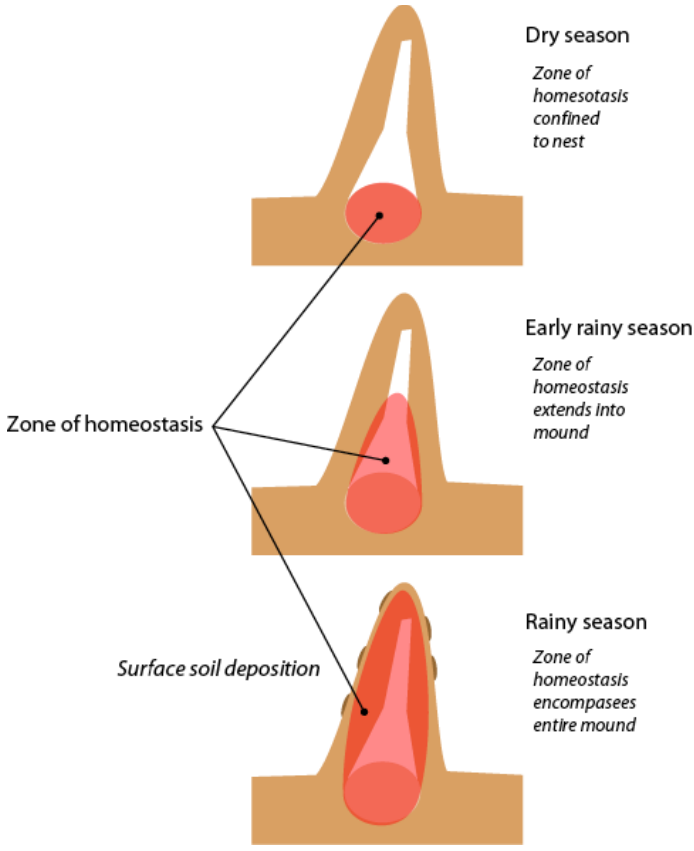

Figure 11 *The link between expanding zones of homeostasis and soil transport. Once the entire mound is enveloped in a zone of moisture homeostasis, soil deposition to the surface commences.*

superorganism emerges when these termite agents of homeostasis are coupled to strong physiological drivers of matter and energy. These strong drivers are, of course, the symbiotic fungi. This is aptly demonstrated by two phenomena, one that has played out over the evolution of the Macrotermitinae, and another that plays out over the life history of individual *Macrotermes* colonies.

The fungus-growing habit among the Macrotermitinae probably got its start as a hygienic measure. Fungi are usually serious parasites on the cellulose food that termites bring back to their colonies. As a consequence, termite colonies often store food in numerous caches that are remote from the colony: if a cache becomes infected, it can be abandoned and isolated both from the colony and from other caches. The symbiosis between *Macrotermes* and *Termitomyces* probably began when the ancestors of *Termitomyces* proferred digestive benefits to the termites that parasitic fungi could not. The evolutionary trend among the Macrotermitinae has been to gather these "beneficial" caches together, presumably to protect them from infection by parasitic fungal competitors, culminating in the consolidated fungus gardens that characterize *Macrotermes* and *Odontotermes.*

With consolidation of fungal biomass, however, has come concentration of metabolic demand (expressible in units of watts), culminating in nests that are characterized by a high metabolic power *density* (expressible in units of watts per cubic meter of nest). This elevating metabolic power density appears to be the primary driver of the evolution of the mound-building habit among the Macrotermitinae (Turner, 2007). When food caches, and the metabolic power they embody, are widely dispersed, there is little evidence of organized soil transport. With increasing metabolic power density, however, comes the power to severely perturb the nest environment: driving up nest temperatures, nest carbon dioxide concentrations and levels of nest moisture. When these fungal-driven perturbations are coupled to the termite agents of homeostasis, the well-designed mound is the result. Locally high carbon dioxide recruits termites to translocate soil. Locally high temperatures impart buoyant forces to the nest air that direct this soil transport upward. Locally high moistures promote the ongoing upward movement of soil, and as the mound grows upward, it begins to encounter the strong wind-driven transients that promote soil translocation from the mound interior to the surface, opening the large vertically-oriented voids within the mound.

This process can be seen in reverse in the life history of individual *Macrotermes* colonies. Even though a colony's fungus gardens are typically consolidated into a compact nest, so-called accessory fungus gardens often become established peripheral to the main nest. Why these accessory fungus gardens arise is unknown. However they arise, though, an accessory fungus garden represents a new focus of high metabolic power density that is peripheral to the main nest. Remarkably, an accessory fungus garden invariably is associated with a "moundlet", the built representation of a small focus of intense upward transport of soil, driven by the same strong fungal perturbations that drive the construction of the principal mound. And they have the same consequence: construction of a designed "organ of physiology" to meet the metabolic demands of this new focus of metabolic power.

Whence the superorganism?

All this points, in my opinion, to a philosophical conclusion that perhaps some will find troubling. One of life's most striking attributes is the tendency of living agents to assemble into what we might call "organism-like" entities: cells into tissues, tissues into organs, organs into organisms, or organisms into superorganisms (Turner, 2000, 2006). Why should this be? Atomist doctrines, like self-organization, or Neodarwinism, assert this tendency emerges spontaneously from simple agent-level interactions, with no overarching goal to direct it: no "skyhooks" as Daniel C Dennett has compellingly put it (Dennett, 1995). In the emergence of the *Macrotermes* superorganism, such agent-level processes clearly operate, but they alone are inadequate to explain the emergent phenomenon. What does draw forth the superorganism is itself a kind of a "skyhook" – large-scale, constructed environments that are maintained by agents of homeostasis.

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