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Gaia, Extended Organisms, and Emergent Homeostasis

J. Scott Turner

Abstract

Gaia's most remarkable prediction is a biosphere-level physiology and all the organismal traits that implies, including global homeostasis. Gaia's most formidable challenge is to explain how such properties can emerge from the welter of competing genetic interests which the biosphere comprises. This article explores the problem of "emergent homeostasis" in a model experimental system, the colonies of fungus-growing termites, in which a homeostasis of colony atmosphere emerges from a symbiotic assemblage between two heterotrophs, termites and fungi. The termite-fungus symbiosis is a coalition of genetically diverse organisms from which homeostasis emerges, driven by the symbionts' common physiological interests rather than their common genetic interests. This homeostatic system is therefore distinct in origin from the more common *social* homeostasis found amongst bees, ants and wasps, in which the common genetic interest of the colony drives its evolution. I suggest that mechanisms of *emergent* homeostasis, in which common physiological interests are paramount, are a more appropriate model for understanding how Gaia's radical vision of an earth physiology might work.

Introduction

Gaia is a goddess with two faces. On the one side, there is, to paraphrase Daniel C. Dennett's (1995) description of natural selection, "Lovelock's dangerous idea", the radical proposition that the biosphere is, in some sense, alive, and not simply the harbor of life (Lovelock 1987). In this conception, Gaia is an organism, with all the attributes that designation implies: self-sustenance, adaptability, homeostasis, even perhaps a sort of intentionality. Then there is Gaia's more prosaic face, unveiled as Gaia has evolved in recent years into earth systems science (Schneider and Boston 1991; this volume). In this conception, Gaia is a research program concerned with the roles living organisms play in managing flows of matter and energy through the biosphere, and with identifying the feedbacks and potential control points that could give the Earth a semblance of life, if not life itself.

I am a physiologist who came fairly late to the concept of Gaia. I was initially attracted by Gaia's dangerous face, but not, I hasten to say, from any love of danger on my part. Rather, I was intrigued by the challenge "Lovelock's dangerous idea" presents to our understanding of physiology's central principle, homeostasis. To the physiologist, homeostasis is a phenomenon of organisms in the here-and now, and its study is concerned primarily with mechanism: with controls and effectors, how they work and respond to various challenges. Yet homeostasis, like all other attributes of organisms, had to evolve somehow. Commonly, physiologists approach evolution as taxonomists do, taking what nature has provided us in the present - fully functioning organisms "engineered" by natural selection - and working backwards through a process of "reverse engineering" to reconstruct how the organismal contrivances before them could have evolved. Rarely do physiologists ask the more fundamental question: how did homeostasis itself evolve? By and large, homeostasis is assumed to simply be axiomatic to the organismal condition: ultimate questions, such as how homeostasis itself might have evolved, are a troublesome complication. Gaia's radical appeal is that it no longer lets us safely ignore that ultimate question.

For the most part, our thinking on the question "how did homeostasis evolve?" has been shaped by the Neodarwinist conception of homeostasis as

a form of altruism among an organism's cells. Homeostasis requires an investment in physiological "machines" (organs and organ systems) which drive the flows of matter and energy through the organism, and in the control systems that manage those machines' operations. These machines arise through differentiation of the zygote's various cell lineages of the organism's somatic line. The somatic cells will never themselves reproduce: they are sacrificing their genetic interests to ensure the reproduction of the lucky few cells in the germ line. The sacrifice is redeemed for all by the assurance that organisms with well-regulated internal environments - "good" homeostasis - will be more fecund than organisms with poorly regulated internal environments.

Gaia undercuts this tidy explanation, because it posits the emergence of homeostasis in the absence of the common genetic interest that supposedly drives it in organisms. Now the question "how did homeostasis evolve?" becomes more problematic. Why should one organism with its own genetic interests make an investment in homeostasis so that another organism, with disparate genetic interests, might also benefit? This question has presented a major stumbling block for Gaia winning even the grudging acceptance it now enjoys (Dawkins 1982; Doolittle 1981; Joseph 1990; Kirschner 1991; Williams 1992). It is fair to say that acceptance has been won largely at the price of abandoning Gaia's most radical and (to me) appealing idea: the notion of the biosphere as a global organism.

My intent in this paper is to argue that it is too soon to turn away from "Lovelock's dangerous idea." Gaia's proposition of a global homeostasis is in fact one of a large body of similar problems in what might be called emergent homeostasis. Emergent homeostasis asserts that the origin and evolution of homeostasis is driven by a sort of "physiological altruism", that is, pursuit of a common physiological interest by a genetically diverse assemblage of organisms. To the extent that physiological and genetic interests are congruent, as they are in organisms, homeostasis fits comfortably into conventional Neodarwinism. However, common physiological interests can emerge independently of genetic interests, as is the case for most symbioses. Yet, from these genetically disparate coalitions, homeostasis often emerges (Paracer and Ahmadjian 2000). In these instances, the Neodarwinist explanation for homeostasis is less robust (Margulis 1997). The challenge is to explain how homeostasis nevertheless emerges.

Understanding emergent homeostasis would be aided by a model system, a sort of Gaia-in-microcosm, which could be studied experimentally. Below, I will outline such a model system: the colonial respiration of fungus-growing termites of the Macrotermitinae (subfamily of the Termitidae; Ruelle 1970). The macrotermitines are marked by a sophisticated digestive symbiosis between termites, cellulolytic bacteria, and at least two types of cellulolytic fungi, which reaches its pinnacle in the mound-building genera *Macrotermes* and *Odontotermes*. Emerging from this symbiosis is a remarkable degree of homeostasis of the nest climate (Lüscher 1961; Ruelle 1964). The macrotermitines also are pivotal controllers of the physiology of the savanna ecosystems they inhabit (Dangerfield *et al.* 1998), and this ability is, in large measure, a consequence of the regulated environment in the termite nest. We have recently come to better understand this homeostasis and how it arises (Turner 1994; Korb and Linsenmair 1998a, 1998b, 2000; Turner 2000a, 2001). These findings may illuminate how homeostasis might emerge at any organizational level, ranging from cells and endosymbionts, to the colonies of termites, to the purported biosphere-level homeostasis posited by Gaia.

The symbiosis

Termites are well known for their digestive symbioses with micro-organisms (Wilson 1971; Breznak 1984; Wood, 1988; Wood and Thomas 1989). The rationale for these associations is straightforward. The principal component of the termite diet is lignified cellulose, which termites have only limited ability to digest. Termites thus use micro-organisms that can digest cellulose, commonly bacteria and protists composing an abundant gut flora. These intestinal symbionts express a rich array of cellulases and other enzymes that readily degrade cellulose to more easily digestible cellobiose, xylose and oligosaccharides (Martin 1987).
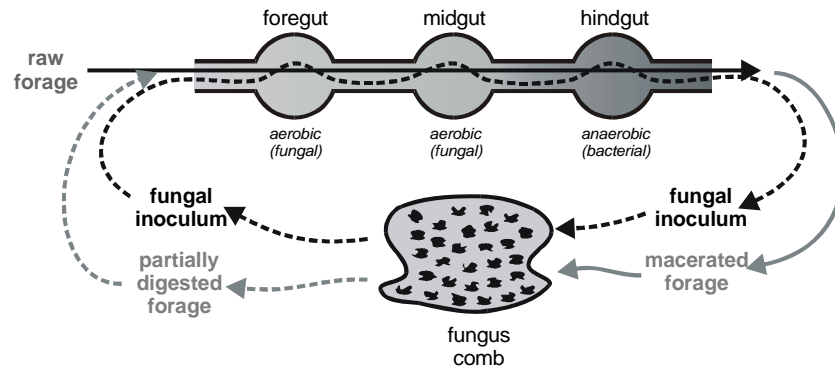
Figure 5.1
Scheme of the digestive symbiosis between *Macrotermes* and *Termitomyces*. Details in text.

For most termites, the association with their digestive symbionts is obligatory and confined to the intestine. Termites sterilized of their gut flora macerate and pass cellulose through their intestines normally, but cannot extract useful energy from it, and so starve to death. The gut flora are maintained by repeated inoculation of individuals' digestive tracts by other members of the colony, both upon hatching and following each molt. The macrotermitines have taken the digestive symbiosis a step further, however, "outsourcing" cellulose digestion to extracorporeal fungi (Martin 1987; Batra and Batra 1979). The fungi are cultivated on structures called fungus combs, built by the termites and maintained by them within the nest. This association probably arose from opportunistic invasions by soil fungi into termites' cached supplies of surplus food. This was gradually refined into the close symbiosis between the macrotermitine genera *Macrotermes* and *Odontotermes* and basidiomycete fungi of the genus *Termitomyces* (Mora and Rouland 1995; Rouland *et al.* 1991, 1988; Thomas 1987a, 1987b, 1987c).

The fungus combs are sites for conversion of low-quality lignified cellulose to a high quality food of simpler sugars (Rouland *et al.* 1988a, 1988b, 1991; Veivers *et al.* 1991). Foraging termites ingest food, mostly grass, but also bark, dead wood and undigested material in fecal pats, and transfer it to minor workers and nurse workers upon return to the nest (Figure 5.1). These pass the raw forage rapidly through the gut, which contains the usual culture of bacterial symbionts, but which is also replete with fungal spores. These are mixed with the slurry of macerated raw forage as it passes through the gut. When defecated, the inoculated slurry is daubed by the workers onto the top of the fungus comb. The *Termitomyces* spores then germinate, and infiltrate their hyphae through the comb, digesting the raw forage (spores of other fungi remain dormant). Simultaneously, termites consume digested material from the bottom of the comb, and pass it again through the intestine, where it is digested by the termites' normal intestinal symbionts and by fungal enzymes which remain active in the intestine (Leuthold *et al.* 1989). Thus, the fungus comb is a sort of flow-through composter, with new material added continually to the top, and digested material continually being consumed from the bottom.

Energetics of Digestion Among the Macrotermitines

Most termites rely solely on intestinal digestion, which imposes upon them constraints in the extraction rate for energy from food. A termite intestine is analogous to a plug-flow digestive reactor, with the absorption rate optimized only at a certain feeding rate (Penry and Jumars 1986, 1987). If the feeding rate of individual termites is already at this optimum, the colony can increase its energy intake rate only by increasing the number of workers in the colony - the number of individual plug-flow reactors. However, each worker itself represents an energy investment in development and maintenance, which increases exponentially by about the 0.4 power for each increment of termite biomass (Peakin and Josens 1978). This must be repaid before the colony can accrue a net energy profit. These and other constraints conspire to limit both the body size and

colony population of termites that rely solely on intestinal digestion.

The macrotermitines have escaped this constraint by "outsourcing" cellulose digestion to the extracorporeal fungus combs, which are analogous to continuous-flow stirred tank reactors (Penry and Jumars 1986, 1987). Expanding the colony's digestive capacity now involves the relatively cheap expansion of biomass in fungus combs. Pre-digestion by the fungi also enriches the diet, improving the digestive capacity of each worker termite. As a consequence, macrotermitine colonies are metabolically very active, consuming enormous quantities of food and releasing enormous amounts of energy for physiological work (Rohrmann 1977; Rohrmann and Rossman 1980; Darlington et al. 1997; Peakin and Josens 1978). This has remarkable consequences for all aspects of these termites' biology. Macrotermitine body sizes are typically two to three times larger than other termites' (Coaton and Sheasby 1972), and their colony populations are, on average, one to two million workers, roughly an order of magnitude larger than the typical colony populations of species that rely solely on intestinal digestion (Wiegert 1970; Darlington 1990, 1994; Darlington et al. 1992). These factors combine to give a *Macrotermes* colony a high collective metabolic rate, similar to that of large ungulate herbivores (Table 5.1). Finally, the presence of a colony stimulates soil respiration around it, which elevates the energy consumption rate of the "extended colony" further (Darlington *et al.*, 1997). This metabolic effervescence makes these termites dominant components of the savanna ecosystems they inhabit (Dangerfield *et al.* 1998; Tables 2 and 3). Their biomass exceeds that of all the other soil invertebrates combined, carbon flow through them is similar to that for all the ungulate herbivores combined (Table 5.2), and they perturb soil at rates exceeding that of other mound-building termites in the environment (Table 5.3).

The Nest and Its Infrastructure

The macrotermitines' most striking attribute is the nests and associated structures they build, most obviously the large above-ground mounds that are prominent features of the savannas they inhabit (Harris 1956; Ruelle 1964; Figure 5.2). The mound is not the habitation for the colony. The queen, workers, fungus combs and young reside in an underground nest, and are confined into a dense mass roughly 1.5 to 2 meters in diameter (Figure 5.3). This, combined with a typical nest's high metabolic rate, results in the colony having a high metabolic power density (W m^{-3}). This substantially alters the concentrations of respiratory gases in the nest atmosphere. Carbon dioxide mole fractions commonly range from 0.5% to 1%, with concomitant reductions in oxygen concentrations (Korb and Linsenmair 2000; Turner 2001; Darlington *et al. 19*97). The nest atmosphere is also rich in the gaseous products of the anaerobic and methanogenic bacteria that reside in termites' hindguts, and the volatile acids, alcohols and other hydrocarbons produced by the fungi (Darlington *et al.* 1997). The nest atmosphere is also very humid, the water vapor supplied by a high production rate of metabolic water supplemented by soil water (Darlington *et al.* 1997; Weir 1973; Turner 2001).

The Mound and Nest Ventilation

The mound is the nest's physiological infrastructure. The colony's high metabolic power density requires that the nest be ventilated: if it were not, the colony would suffocate. The mound serves this function by capturing kinetic energy in winds. The ebb and flow of turbulent winds powers a tidal ventilation of the mound's peripheral air spaces, similar to the in-and-out movements of air during the respiratory cycle of the mammalian lung (Turner 2000a). A similar pattern of ventilation has been observed in nests of the leaf-cutter ant *Atta vollenweideri* (Kleineidam and Roces 2000; Kleineidam *et al.* 2001), and in nests of another macrotermitine *Odontotermes transvaalensis* (Turner 1994). The mound's elaborate tunnel network (Figure 5.3) integrates wind-induced ventilation in the peripheral air spaces with metabolism-induced buoyant forces that loft spent air from the nest into the mound's chimney. The colony's respiratory gas exchange is therefore analogous to the three-phase gas exchange in the mammalian alveolus (Figure 5.4): a forced convection phase in the bronchi and bronchioles, a diffusion phase in the alveoli themselves, and a mixed convection-diffusion phase in the alveolar ducts and lower bronchioles.

Table 5.1
Estimates of whole colony metabolic rates (in watts) of three nests of *Macrotermes jeanneli*.

	Nest 1		Nest 2		Nest 3	
	MR (W)	M (kg)	MR (W)	M (kg)	MR (W)	M (kg)
Method A						
Worker total	75.61	61.25	49.54	34.31	24.93	13.39
Fungus combs	104.29	95.14	92.86	81.15	48.45	33.29
Nest totals	179.90	200.79	142.39	145.76	73.38	58.78
Method B(1)						
Worker total	85.33	72.28	51.07	35.78	7.17	2.43
Fungus combs	122.50	118.61	72.45	57.76	8.34	2.99
Nest totals	207.83	244.68	123.52	119.97	15.50	6.99
Method B(2)						
Worker total	73.33	58.73	58.51	43.11	23.90	12.65
Fungus combs	104.97	95.99	83.31	69.94	32.36	19.15
Nest totals	178.30	198.35	141.82	144.96	56.26	40.85
Method C						
Nest totals	227.95	277.70	373.51	551.47	75.23	61.06

Note: Method A estimates colony metabolic rate from biomass determinations in combination with estimates of mass specific metabolic rates of each of the components. Methods B estimate colony metabolic rates from measurements of diameter of outflow air tunnels. Method C estimates colony metabolic rate from enrichment of carbon dioxide and volume flow rate of the outflow stream from the exhaust tunnels of intact nests. The latter includes the stimulation of soil respiration as well as respiration of the termites and fungi themselves. Conversion of carbon dioxide enrichment to metabolic rate in watts was made assuming a respiratory quotient of 0.8. After Darlington *et al.* (1997).

Table 5.2
Some estimates of the metabolic impact of macrotermitine termites on tropical ecosystems. After Dangerfield et al. (1997)

Measure	Location
account for 40-65% of soil macrofauna biomass	African savanna
standing biomass of 70-110 kg ha^{-1}	African savanna
ungulate biomass of 10-80 kg ha^{-1}	African savanna
annual turnover of termite biomass of 120 kg ha^{-1}	African savanna
consume 1.0-1.5 t litter ha^{-1} y^{-1}	African savanna
consume 23% of annual litter production	Nigerian forest

In the *Macrotermes* mound, the convection phase, driven by wind, is located primarily in the surface conduits and lateral connectives close to the surface. A natural convection phase, analogous to the diffusion phase in the alveolus, occurs in the nest and lower chimney, driven by relatively weak buoyant forces induced by colony metabolism. The upper chimney and inner parts of the lateral connectives, finally, form a mixed-regime phase, where both forced convection and natural convection are roughly equivalent (Turner 2001).

Homeostasis in *Macrotermes* Colonies

Many social insect colonies exhibit *social* homeostasis, in which the collective activities of the inhabitants are coordinated to regulate the colony environment. For example, honeybee colonies regulate the temperature of the hive in ways that individual bees cannot (Southwick 1983). As temperatures fall, for example, the hive's inhabitants cluster into a compact ball, conserving heat. Part of this involves behavioral differentiation among the members of the colony: certain bees in the cluster form an insulating layer,

Table 5.3
Rates of soil movements and standing crop of soil in mounds of various Ugandan termites (after Pomeroy 1976).

Site	Species	Soil standing crop (m^3 ha^{-1})	Upward soil transport rate (m^3 ha^{-1})	Downward soil transport rate (m^3 ha^{-1})
Natete (well drained ridge)	*Macrotermes bellicosus* (Macrotermitinae)	8.08	0.90	1.15
	Pseudacanthotermes spp (Macrotermitinae)	0.28	0.10	0.12
Naluvule (poorly drained bottomland)	*Macrotermes bellicosus* (Macrotermitinae)	4.22	0.41	0.39
	Pseudacanthotermes spp (Macrotermitinae)	1.88	0.60	1.00
	Cubitermes spp (Termitinae)	0.02	0.02	0.00

Figure 5.2.
A mound of *Macrotermes michaelseni* in northern Namibia.

certain others generate the bulk of the heat to warm the cluster, and so forth. Social homeostasis is manifest in other ways, including matching of foraging rates to energy stores in the colony, control of reproduction and so forth.

Homeostasis in the *Macrotermes* colony appears directed largely to regulating the composition of the nest atmosphere (Turner 2001). There are several lines of evidence for this. For example, concentrations of oxygen in *Macrotermes michaelseni* nests atmosphere do not vary appreciably with colony size, despite the large variation of colony metabolic rate that entails (Darlington *et al.* 1997). This constancy can only occur if ventilation keeps pace with the colony's growing demands for respiratory gas exchange (Figure 5.5). Furthermore, metabolically active parts of the colony are ventilated more vigorously than relatively quiescent parts (Figure 5.6). Finally, the nest atmosphere is steadier in composition and less susceptible to environmental perturbations during the active summer season than during the winter, when the termites are relatively inactive (Turner 2001).

Homeostasis of the *Macrotermes* nest atmosphere arises from adaptive modification of mound architecture, which matches the capture of wind energy for ventilation to the rate of respiratory gas exchange in the nest. At its simplest, the matching is brought about through adjustment of mound height (Turner 2001). The surface boundary layer presents a gradient in wind velocity. Consequently, the higher the mound, the more energetic will be the winds that the mound intercepts. If a colony's metabolic rate increases, as it might as the colony matures, demand rate for respiratory gases also grows. To regulate the composition of the nest atmosphere, the ventilation rate must increase commensurably. This is readily accomplished by building the mound upwards through the surface boundary layer until it encounters winds sufficiently energetic to match ventilation rate with respiration rate (Turner 2000a, 2001).
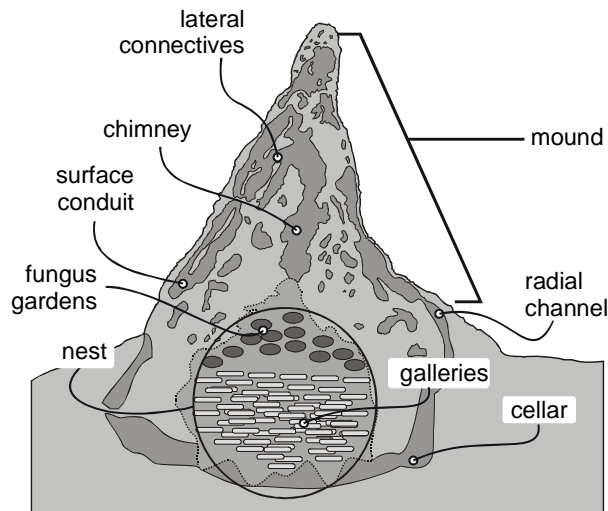
Figure 5.3.
Cross section of a colony of *Macrotermes michaelseni*, showing locations of nest, galleries and fungus gardens, mound and associated air passageways. From Turner (2000a).

The mound can be an effector for the regulation of the nest atmosphere because the mound's architecture is adjustable, and because mound morphogenesis is coupled to the nest's physiological state. Termites in the nest monitor local concentrations of CO_2, oxygen and water vapor, and any disturbance of these properties indicates a mismatch between respiration and ventilation. When a disturbance is sensed, worker termites are recruited from the nest, where they normally reside, to the mound surface, where they either build new surface, excavate vent holes, or seal porous layers of soil (Figure 5.7; Turner 2000a). Consequently, the termites' building activity alters the mound's capture of wind energy, which feeds back onto the stimulus (the perturbation in nest atmosphere) that initiates the building in the first place.
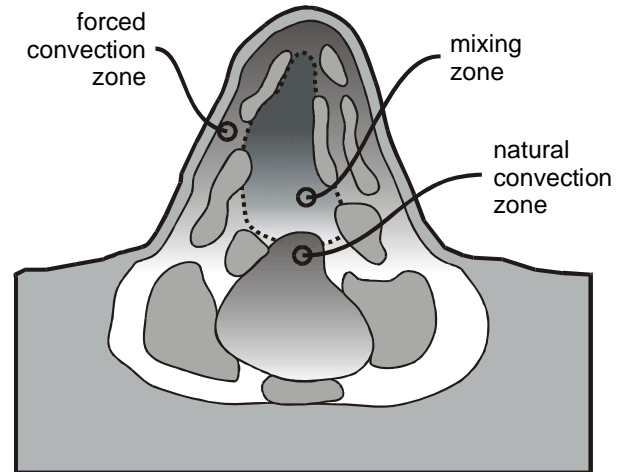
Figure 5.4
Postulated zones of gas exchange in a *Macrotermes michaelseni* mound and nest. Details in text. After Turner (2001).

More generally, homeostasis in the *Macrotermes* nest arises through coupling of mechanisms of mound morphogenesis to large-scale gradients of potential energy in the mound (Turner 2000a). Worker termites can be thought of as conveyors of soil along metabolism-induced gradients in concentration of respiratory gases. If the nest produces carbon dioxide at a certain rate, for example, this will establish gradients of pCO_2 within the mound that radiate away from the nest. How steep these gradients will be is determined by both the nest's metabolic rate and by the resistance to gas flux through the mound's air spaces. If worker termites convey soil down that pCO_2 gradient, the mound surface will grow outward and upward. This growth, in turn, itself alters the distribution of pCO_2 within the mound. Thus, the mound is both cause and effect of the gradients of carbon dioxide within itself. Homeostasis of the nest atmosphere follows when the intensity of soil transport is "tuned" properly to the changes of CO_2

distribution that result. Because the "tuning" involves adjusting the likelihood that individual termites will pick up or deposit grains of sand in response to a stimulus (say pCO_2), emergent homeostasis can arise through straightforward natural selection on variations in these likelihoods.
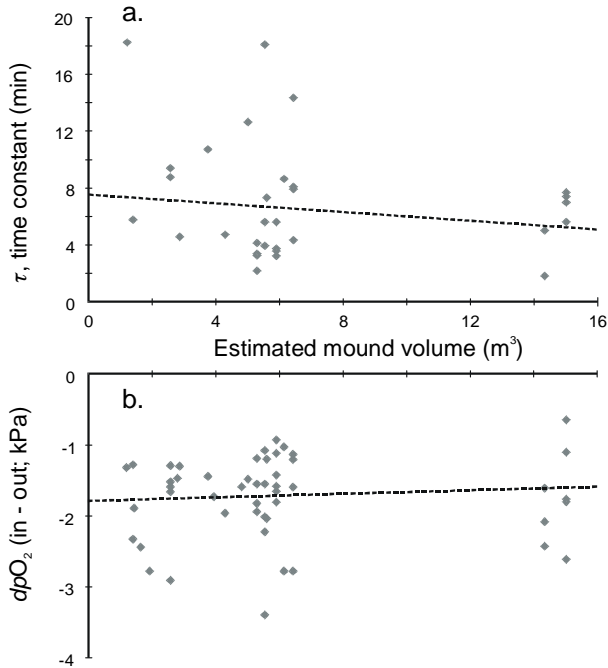

Figure 5.5
Homeostasis of nest atmosphere in mounds of *Macrotermes michaelseni*. *a:* Time constant for clearance of tracer gas from *M michaelseni* nests of various sizes. The time constant is the inverse of the rate constant for exponential clearance, and so is inverse to the ventilation rate. Roughly 95% of the air in a space is replaced within a period of roughly three time constants. Time constant does not vary significantly with mound size. *b*: Partial pressure differences for oxygen (dpO_2) between the nest atmosphere and external atmosphere. Despite large variation of colony metabolic rate with size, the depletion of oxygen within the mound is invariant with respect to colony size. Dotted lines indicate least squares regressions for both panels.

Why homeostasis of the nest environment?

For homeostasis to be selected for, some selective benefit must accrue to more precise regulation of the nest atmosphere. The macrotermitines have the most sophisticated mechanisms for nest homeostasis of all the termites. However, it is still an open question what purpose the nest

homeostasis serves. Commonly, homeostasis was thought directed to regulation of nest temperature, which presumably allowed the macrotermitines to extend their ranges into thermal environments that were hostile to termites with less well-regulated nests. This is now doubtful, because manipulation of ventilation does not appreciably alter temperatures of underground nests of social insects (Turner 1994; Kleineidam *et al.* 2000). More likely, the homeostasis arises to reinforce the symbiosis between *Macrotermes* and *Termitomyces*.
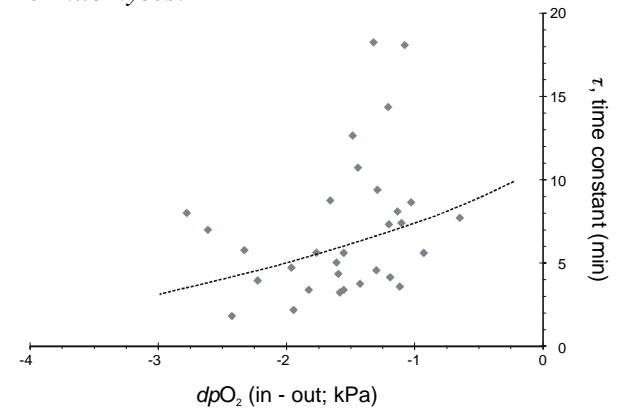

Figure 5.6
Relationship between time constant for clearance and oxygen partial pressure difference for mounds of *Macrotermes michaelseni*. Metabolically active areas (indicated by substantial oxygen depletion) are more intensely ventilated (indicated by short time constants) than metabolically more inert areas (indicated by little oxygen depletion). Dotted line indicates least squares polynomial regression.

The fungal partner in the symbiosis seems to benefit the most from nest homeostasis. *Termitomyces* is in competition with another common soil fungus, *Xylaria*, for the rich trove of cellulose transported to the nest by the termites (Batra and Batra 1979). *Xylaria* is fast-growing, presumably because its uptake of cellulose digestate is very rapid. In contrast, *Termitomyces* is slower-growing, perhaps because its uptake of cellulose digestate is slower. This may explain why *Termitomyces* rather than *Xylaria* is the favored fungal symbiont*: Termitomyces'* slower uptake of digestate leaves more for consumption by the termites. The exclusion of *Xylaria* appears to be through suppression of its reproduction and growth in the nest. Spores of both species of fungus are abundant in the nest soils, termites'
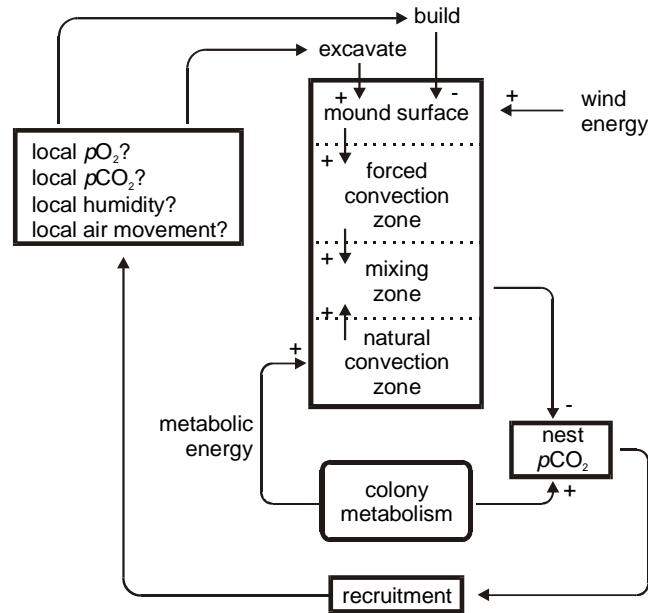
Figure 5.7
Simple operational scheme of homeostasis of nest atmosphere in *Macrotermes michaelseni*. For example, if concentration of carbon dioxide in the nest is too high, the ventilatory flux is too low to meet the colony's respiratory flux. This recruits workers from the nest, which build the mound upwards, where it encounters more energetic winds, powering a more vigorous ventilation (gray symbols). Once ventilation flux and respiratory flux are brought back into balance (indicated by a return of nest carbon dioxide concentration to normal), worker recruitment ceases, as does the further upward extension of the mound. After Turner (2001)

intestines and the fungus combs (Thomas 1987a, 1987b, 1987c), yet only *Termitomyces* grows: germination and growth of all other fungal species is suppressed. Apparently, some aspect of the nest environment is responsible. Removing the comb from the nest invariably results in *Xylaria* spores germinating and aggressively taking over the comb, even if termites are given full access to it. Only within the nest is *Xylaria* germination and growth suppressed while *Termitomyces* growth is favored (Martin 1987; Batra and Batra 1979).

Precisely what aspect of the nest environment controls fungal growth is unknown at present, but the most intriguing hypothesis comes from Batra and Batra (1979), who suggest that the nest's high concentrations of carbon dioxide suppresses *Xylaria* growth, similar to the CO_2-induced suppression of fungal growth in nests of leaf-cutter ants (Kleineidam *et al.* 2001). If so, it points to why homeostasis of the nest atmosphere is crucial for the success of the symbiosis. If nest carbon dioxide concentrations are too low, the nest's culture of *Termitomyces* is threatened by enabling the runaway growth of *Xylaria*. In short, nest homeostasis may reinforce flow of energy through

a particular *association* (*Macrotermes / Termitomyces*), while cutting out a competing *association* (*Macrotermes/Xylaria*).

Social homeostasis vs emergent homeostasis

The macrotermitines exhibit what seems to be a unique type of social homeostasis, differentiable from the more familiar form found among, say, honeybees. In bee colonies, physiological and genetic interests are congruent: social homeostasis involves behavioral and physiological interactions only between genetically related members of the colony (Figure 5.8). The honeybees are the principal source of carbon dioxide production in the hive, and pCO_2 regulation is brought about through the activities of the worker bees (Seeley 1974; Southwick and Moritz 1987). In the *Macrotermes/Termitomyces* colony (Figure 5.9), physiological and genetic interests are divergent. The nest's largest perturber of carbon dioxide concentration is not the termites, but the fungi. Yet, it is the termites that do all the work of regulating the nest atmosphere. The termites clearly gain from the symbiosis, but so too do the fungi, because the regulated nest atmosphere
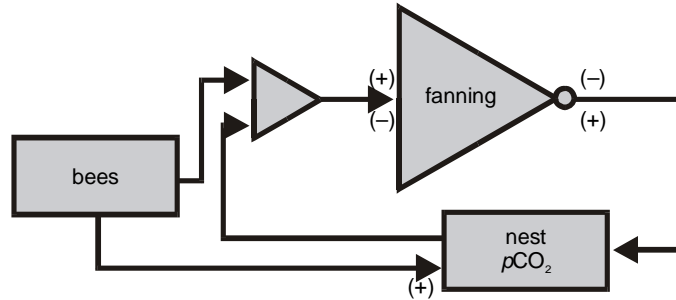
Figure 5.8

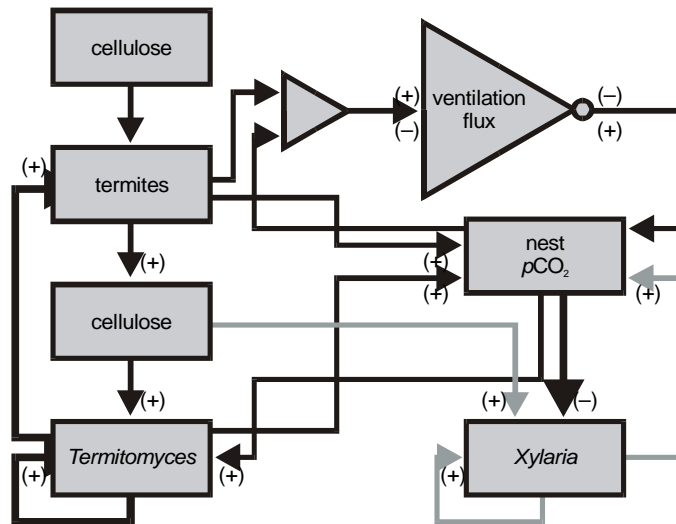Social homeostasis of nest pCO_2 in a honeybee colony. Details in text. After Seeley (1974).

Figure 5.9

Emergent homeostasis of nest pCO_2 in a nest of *Macrotermes michaelseni.* Autocatalytic loops are represented by heavy arrows. Gray arrows represent potential avenues for flux of carbon that are not realized because of *Xylaria*'s sensitivity to the nest pCO_2.

suppresses the growth of their principal competitor, *Xylaria*. In short, the homeostasis is maintained by a physiological interaction between genetically disparate partners in a symbiosis. This type of homeostasis we might call *emergent*, to distinguish it from the more commonly recognized *social* homeostasis where physiological and genetic interests converge.

Emergent homeostasis and Gaia

Emergent homeostasis offers a different way of thinking about the evolution of homeostasis generally, and in particular, for thinking about how the global homeostasis posited by Gaia might arise. The early and more radical conception of Gaia sought to paint the biosphere as a sort of superorganism writ large (Lovelock 1987). This

may have assured Gaia's initial controversial, even hostile, reception, because the superorganism concept has a long and troubled history (Wilson 1971; Golley 1993; Bowler 1992). Since its heyday in the Clementsian ecology that spawned it, the superorganism idea has largely faded away, swept aside by the dominance of the philosophically incompatible doctrines of Neodarwinism. It survives principally among students of the social insects. Its survival there is largely because it poses no essential challenge to Neodarwinist conceptions of sociality, such as kin selection and inclusive fitness, which assume genetic and physiological self-interest to be congruent (Wilson 1971). Yet, if Gaia is to represent a biosphere-level homeostasis, it cannot involve any analog of *social* homeostasis, because Gaia must involve assemblages of organisms in

which genetic and physiological self-interests are dissociated. A Gaian biosphere-level homeostasis must therefore be an *emergent* homeostasis, similar in principle to that which arises among the genetically disparate organisms that enter into symbioses (Paracer and Ahmadjian 2000). The challenge for Gaia is not to demonstrate whether or not there is a global homeostasis, but to explain how homeostasis arises from assemblages of genetically disparate partners. Understanding how emergent homeostasis works is the true research program of Gaia.

What lessons can be drawn from the "test case" of the *Macrotermes/Termitomyces* symbiosis? Certain features of this association stand out as conducive to emergent homeostasis, and these may be at the heart of Gaian homeostasis as well. Ranked in rough order of increasing unconventionality, these are:

- *Complementarity of metabolism:* In the *Macrotermes/Termitomyces* symbiosis, each partner brings a metabolic capability to the association that the other partner does not. The complementarity exists at many levels. On the one hand, the fungi contribute a variety of enzymes that digest woody material, lignases and endocellulases from the fungi, while termites may contribute an exocellulase. The cocktail of enzymes from both breaks down woody material faster than would be possible for each partner alone. In addition, the termites bring capabilities for mechanical transport, location and harvesting of food which the fungi obviously lack. With respect to Gaia, all agree that metabolic complementarity is the foundation upon which a purported homeostasis of the biosphere can be built (Volk 1998). So far, much of the effort in study of Gaia has focused on microbes, because most of the biochemical diversity of the biosphere resides in them. Complementarity can exist at many levels of organization beside the biochemical, however, and Gaia will have to account for those.

- *Competition between loops and pathways for mass and energy flow:* The symbiosis between *Macrotermes* and *Termitomyces* persists in the face of a strong competitive challenge from *Xylaria*. The competition superficially involves the two fungal species, but it is really a competition between two supra-organismal pathways for

energy flow. The termites convey cellulose to a focal point where it is available to both fungal species. Whether one fungal species or the other prospers depends not only on available food, but upon how the termites bias the environmental conditions for each fungus' germination and growth. In an important sense, the real competition is not between two species of fungi for the same abundant resource, but between alternate pathways for carbon flow which involve plants, termites and the fungi. One pathway channels carbon from plants to termite to *Xylaria*, leaving the fungus as the ultimate beneficiary. The other "closes the loop", channeling carbon from plant to termite to *Termitomyces* and then back to the termites. Closing the loop enhances biological work for both *Macrotermes* and *Termitomyces*, while the open loop only enhances growth of *Xylaria*. In the case of Gaia, all nutrients flow through the biosphere in closed loops (Barlow and Volk 1990). The loops that persist and grow will be those that successfully retain nutrient flow within themselves, as in the high cycling ratios observed for rare nutrients like phosphorus or nitrogen (Volk 1998).

- *Coordination of metabolism:* A successful symbiosis exhibits both complementarity *and* coordination of metabolism. In either an open pathway or a closed loop for energy flow, conservation of mass will dictate that flow through one partner in a symbiosis be matched to the other. A mismatch in rates will result in a "spillover" of material, either to other competing loops, or into energy sinks where it is hard to retrieve (Turner 2000b). In either case, the nutrient flow, and the capacity for physiological work that goes with it, is lost to the loop or pathway. In the *Macrotermes/Termitomyces* symbiosis, metabolic capacities are matched largely by adjustments in biomass of the respective partners. A high collective metabolism of the fungi makes energy available that can fuel increases in termite biomass, which can in turn increase transport rate of carbon to the fungi. Conversely, an elevated transport rate of carbon to the colony is matched by an expansion of fungal biomass and their metabolic capacity. This requirement for "tuning" the metabolism of the respective partners in a symbiosis acts as a natural check on one or the other partners pursuing its own selfish interests

(Turner 2000b). This is a somewhat controversial idea, because it asserts that the unbridled pursuit of selfish interests on the part of individual organisms may be counter-productive, while restraint of selfish interest in favor of the partnership may enhance fitness of both.

• *Co-opting the physical environment into an "extended organism"*: A symbiosis that joins the partners intimately, such as endosymbiosis, or the close associations found among lichens or mycorrhizae, facilitates the closing of loops of nutrient flow and the coordination of metabolism that is required for emergent homeostasis. A Gaian physiology must emerge from less intimate partnerships, the partners separated to some degree by an unpredictable physical environment. In this circumstance, the controlled flow of nutrients between the partners could be disrupted, diminishing the likelihood that the metabolism of symbiotic partners could be attuned (Turner 2000b). The disruption could be avoided, however, through adaptive modification of the physical environment, so that the flow of matter and energy between the partners could be controlled. The *Macrotermes*/*Termitomyces* association provides a dramatic example of this. The flow of carbon and energy through the association is subject to a variety of disruptive influences, like chaotic variations in the strength of prevailing winds. Disruption is prevented by the termites building an adaptive interface, the mound, between the outside environment and the environment of the nest, so that carbon can flow reliably between *Termitomyces* and *Macrotermes*. This extension of physiology beyond organisms' integumentary boundaries is a common feature of plants, animals and microbes (Turner 2000b). An emergent homeostasis for Gaia implies the biosphere comprises a variety of such complementary and mutually-coordinated extended organisms. The adaptive modification of the physical environment need not be something as tangible as a termite mound: it could include modifications of fluid density, wind speed, concentration of particular substances, oxidation state, and so forth.

• *Ecological inheritance:* The notion of a homeostatic biosphere has been most severely criticized for its supposed incompatibility with widely accepted principles of evolutionary biology, such as competition and differential reproduction, as well as for its purported failure to reconcile "selfish" genetic interests with the altruism that global homeostasis seems to demand. This is less serious a criticism now than it was when Gaia was first introduced: the collective pursuit of genetic self-interest among the partners in a symbiosis is not such a controversial idea anymore. However, biosphere-scale homeostasis implies biosphere-scale physiology operating through the physiological outreach of extended organisms. This implies the perpetuation not only of the organisms that modify the environment, but of the modifications of the environment itself (Jones et al. 1997). Thus, Gaia may require a sort of ecological inheritance, in which the physical modifications of the environment take on a sort of extracorporeal genetic memory, shaping the selective *milieu* in which operate the biosphere's many extended organisms (Laland *et al.* 1996, 1999). In the *Macrotermes/Termitomyces* symbiosis, for example, the modifications of the soil environment associated with the colony outlast any of the individuals within the colony, and the success of future generations of workers and fungi depends in part upon the structural legacy left to them by previous generations. The structural legacy survives the death of the colony, enduring for centuries or even millennia, with substantial effects on the distribution and evolution of all the biota associated with it.

• *Telesymbiosis:* Finally, a homeostatic biosphere implies a level of symbiosis that extends biosphere-wide. This implies symbiosis between organisms that are vastly separated from one another in space and time, linked by an extended physiology controlled by the organisms that comprise it, a sort of symbiosis-at-a-distance, or telesymbiosis. There is evidence that telesymbiosis is present, as in the ecosystem-wide coordination of metabolism implied by the high cycling ratios of certain nutrients (Volk 1998). What is uncertain is how such telesymbioses could work. This is the real challenge faced by both supporters and critics of Gaia's radical conception of a homeostatic biosphere. For both, gathering evidence that the Earth's climate is, or is not, regulated by the biosphere, is a dead end. Gaia will stand or fall on whether a convincing case can be made for how the telesymbiosis implied by Gaia could work.

Acknowledgments

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