Termites and nutrient cycles in the north

One of the basic principles of ecology, and one upon which all life on earth depends, is recycling. Many of the elements important to living things move from an inorganic form in the rocks, atmosphere, or ocean to a form that is incorporated inside an organism — and then back again when waste products and dead organisms decompose.

The chief agents of such decomposition are microscopic. (Plenty of large animals scavenge carcasses, but that does not return much of the material to an inorganic form.) Soil bacteria and fungi release, for example, carbon — accumulated in detritus from living things — back to the atmosphere in the form of carbon dioxide for use by plants in photosynthesis and hence reincorporation into the world of the living. Many non-microscopic creatures, such as worms, can also be decomposers, but they usually play only a minute part in the whole process.

In some parts of the world, however, the soil microbes' activity level falls — either because of extreme cold, as in the tundra, or because of heat and lack of moisture, as in the arid tropics. Other creatures may then become more important in maintaining the cycles. In the arid tropics, recent work is suggesting that a candidate for such a role could be the industrious termite.

These insects, often called white ants although in fact they are not ants at all, are distinguished by their architectural inclinations: they build large mounds to harbour their complex societies. Mr John Holt of the CSIRO Division of Soils' Townsville laboratory has been studying some of the termites found around Charters Towers in northern Queensland.

A section through a mound; a soil-sampling grid is in the pit beneath.

Termites occur in many of the world's warm areas and scientists have not been slow to study them — particularly as some of them constitute pests through their destruction of wood — but their importance to the ecology of tropical semi-arid Australia had not previously been investigated. Any visitor to the bush in that part of the country could not fail to notice the enormous number of termite mounds; Mr Holt wanted to know what effect such assiduous builders might be having both on the soil and, through their incessant search for food, on the surrounding ecology.

Looking for carbon

He decided to measure how much carbon dioxide the mounds released, which would help him quantify the extent to which the termites helped recycle carbon. Soil scientists use the term carbon mineralisation to describe the process whereby carbon, coming from the breakdown of organic compounds, is oxidised to form CO_2.

To understand the role of termites in this, Mr Holt picked a study site 40 km south of Townsville. The lightly timbered area is subject to long seasonal droughts, with heavy rainfall from December to April. A large number of termite mounds

Measuring a termite mound 'breathing'; a perspex cylinder is fitted over the mound, so that the air around it can be tested for CO_2.

grace the area, and most of them are built by the species *Amitermes laurensis*.

Now, to measure the amount of CO_2 coming off a termite mound requires a little ingenuity. Mr Holt, and his colleague Mr Malcolm Hodgen, used large perspex cylinders, closed at one end, which would fit over a mound. To prevent mixing with the air, they had to construct water-filled gutters at the base of the mounds, with the open end of the cylinder fitting into the gutter and thus forming an air-tight seal. Each cylinder remained in place for 2 hours. Then another sample was taken.

So every 2 hours, for a 24-hour period once each month for a year, Mr Holt collected gas samples. At the same time, he also collected samples from above normal soil that was not part of a termite mound, and he measured the temperature and humidity in both soil and mound material.

Back in the laboratory, he analysed the gas samples and measured the CO_2 concentrations. The amount in each sample was, as expected, proportional to the size — in terms of volume — of the mound. Extrapolating from his figures, he calculated that in each hectare of that termite country the quantity of carbon released from the mounds is about 101 kg per year. That's an amazing 20 litres of carbon dioxide gas from the larger mounds every day!

Termites produce CO_2 as a product of their metabolism exactly as we do. They eat dead plant material, wood, and cow dung, which they are able to digest thanks to the presence in their guts of millions of symbiotic micro-organisms that provide the necessary enzymes.

The amount of CO_2 they produce depends partly on the temperature. Termites, unable to maintain an absolutely constant internal body temperature, warm up with the environment. The higher their temperature, the faster runs their metabolism — as is the case with any series of chemical reactions — and so they produce more CO_2.

Moisture level in the mounds is also significant. Termites excavate galleries that may extend more than 4 metres down into the soil. At this depth, soil air is almost saturated and the termites obtain water by absorbing it through their skins. They then carry the water up into their mounds, where they release it — thus maintaining an atmosphere of high humidity for themselves.

In another study, Mr Holt and his colleagues Dr Keith Bristow and Mr Steve Bailey found that evaporation of water cools the mounds by up to 5°C. Thus, the process of keeping high moisture levels in their mounds is an important adaptation that enables termites to survive in a very inhospitable environment.

While this improves the quality of life for the termites, it also raises the moisture content of the mounds and so directly affects the microbes living there — they flourish under moist conditions. (The microbes' moisture requirements account for the low mineralisation rates in arid soils.) The researchers indeed found that there were greater numbers of microbes living in a mound than in the surrounding soil.

Termites' monumental contributions

Mr Holt's figures show that a hectare of soil without mounds releases 3400 kg of carbon in a year. As termite mounds — at the density of 212 to the hectare found in his study site — typically only increase the figure by about 100 kg, the effect of the mounds may seem very slight.

One, two, three...

In the study of ecology, scientists often need to know the population size of a particular species. Counting directly can be either tedious in the extreme or impossible. But a simple mathematical technique that involves only a small amount of counting can solve the problem.

Called 'mark–release–recapture', it relies on a statistical approach and is valid with reasonably large numbers. The principle is simple enough: you select at random a number of the organisms you are studying, say 100, and mark them in some way. Then you release them back into the original population. Allow time for them to mix back in, and then sample the population at random again. Among your new hundred, a small proportion of the marked originals will turn up by chance. From this fraction, you can calculate the total size of the population.

The number of marked organisms in your second sample, divided by the total in that sample, will approximately equal the number of organisms originally marked divided by the population size. The last term is the only unknown in the equation and can therefore be calculated.

For example, if we took 200 on our second sample, and recaught 10 of our previously marked 100 individuals, then those original 100 must have comprised 10/200, or one-twentieth, of the total population, which must therefore have been 20×100—2000. So in this example we only counted two batches totalling 300 from which we were able to deduce the population size and save ourselves a laborious count to 2000.

Of course, for the procedure to give accurate results, you must make certain assumptions, the most important of which is that no substantial change in the population — whether by movement or births and deaths — has occurred between sampling periods. To minimise the chance of this, you must conduct the second sampling soon after the first, unless you can be sure that your population size is not subject to significant change over a longer period.

Applying the technique to count the number of termites in a colony, Mr Holt and Dr Easey marked about 500 or more workers with a radioactive isotope — iodine-131 or gold-198. To do so, they left the termites on isotope-impregnated agar; this, being sticky, covered the animals, which then cleaned themselves and, in the process, ingested some of the radioactive agar. The scientists were able to confirm that this occurred by detecting the *gamma*-ray emission from the animals.

After leaving them on the agar long enough for them to become well marked by radioactivity, the scientists carefully replaced the insects in their mound, sealing it with mud to prevent predatory ants from gaining access. About 3 days later — sufficient time for the labelled workers to mix randomly with the rest of the population — they took a large sample of 2000–3000 termites, and counted the radioactivity in batches of 100. Termites share food by regurgitation, and so small amounts of radioactivity were spread around the colony — but the scientists found that it was present only at a very low level. A sudden very large peak in radioactivity showed the presence of one of the marked originals.

This work made the assumption, which Mr Holt has some evidence to justify, that termites taken from the periphery of a mound represent a truly random sample of the whole population. (The researchers sampled from the edge in order not to destroy the mound.) To test the validity of the results Mr Holt also courageously performed a manual count of some small termite colonies, varying in size from about 10 000 to 25 000 individuals, and the numbers agree very closely with those derived from the mark–release–recapture method.

However, we have to consider another factor: much of the soil CO_2 comes from the respiration of plant roots underground. These parts of a plant are 'breathing' just like us — combining oxygen with foodstuffs and giving off CO_2. This does not count as carbon mineralisation because no decomposition is taking place. The source of the CO_2 is the plants' own sugar in the sap. When root respiration is subtracted from the totals for soil, then the significance of termites becomes much greater.

Mr Holt has recently performed a series of experiments to estimate the extent of root respiration in these soils, and his early results suggest that it may account for up to half of the total carbon release.

With root respiration discounted, he has calculated that the colonies of *Amitermes laurensis* would contribute about 7% of the total carbon mineralised in the area. Termites as a whole may account for more than this; other species present on the site were not investigated in this study.

Although about 80% of the site's mounds are those of *A. laurensis*, underground termite species may exist in large numbers. Mr Holt therefore speculates that all termites together may be responsible for up to 20% of the carbon mineralisation occurring in the ecosystem.

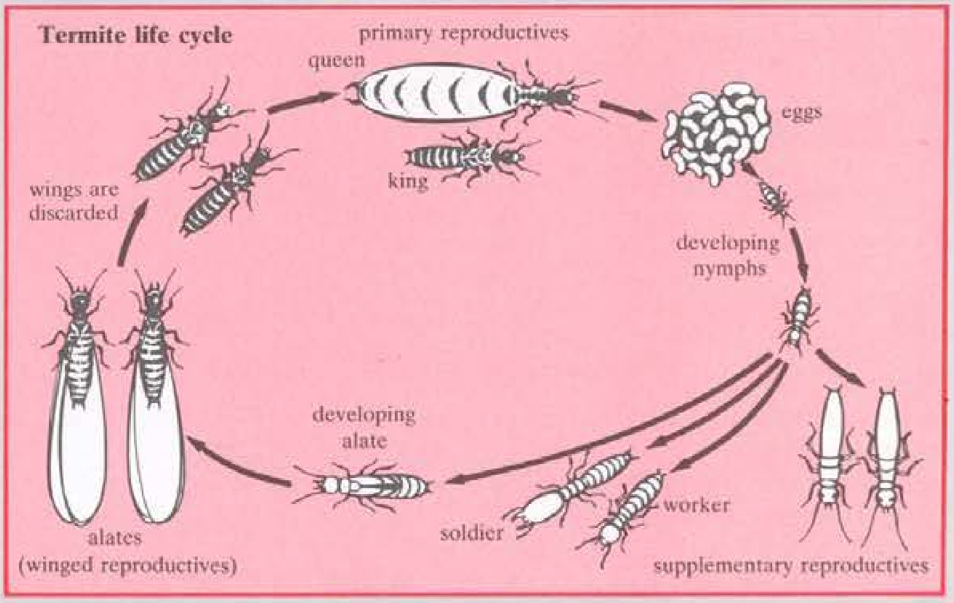
Fertiliser

Soils in much of arid Australia inherently have a low fertility. Scientists have noticed that termite mounds — throughout the world — contain high levels of organic matter and compounds essential for good plant growth. Indeed, some have even suggested that termite mounds be crushed and the resulting powder used as a crop fertiliser!

Mr Holt and his colleagues Dr Ross Coventry, also of the Division of Soils, and Dr Dennis Sinclair, formerly of the Division of Mathematics and Statistics, examined the situation, again in the inland of northern Queensland. On a cattle-grazing property near Charters Towers, they studied the influence that three species of mound-builders might have on soil pH and on a whole range of soil nutrients. They compared the concentrations in the mounds with those in soils unmodified by termite activity, and estimated rates of soil turnover.

Mr Holt and his collaborators collected samples from various positions in the mounds, from the soil beneath the mounds, and (as a control) from soil that appeared not to have had any recent mounds on it. The results confirmed the low fertility of the soil types — red and yellow earths —

The world of a social insect



A termite colony can be thought of as a 'superorganism' with cells represented by individuals specialised for different functions. The alates correspond to gametes.

Termites live predominantly in the tropics. Most species eat grass and organic debris and are not therefore pests of buildings. Those that are digest the cellulose, starch, and sugars occurring in wood. Some species culture fungi in the moist confines of the colony, and use them as a protein source.

Biologists have long been fascinated by these insects, and not just because of the damage that some of them can wreak on human dwellings. They are intriguing creatures because of their complex behaviour, their mounds, and their social organisations based upon the occurrence of different forms or castes. Termites belong to a different taxonomic order from the other social insects (the ants, bees, and wasps), and unlike them are unable to sting. In fact, they are most closely related to cockroaches.

A termite colony starts when winged forms leave another colony on the romantically termed 'nuptial flight'. A male and female pair up and, discarding their wings, find a suitable spot to start another colony. They copulate and tend the resulting 10–20 offspring. The original pair are the new colony's king and queen and may live for 30–50 years.

The queen continues to produce eggs, which develop into wingless workers and soldiers. They take over the work of tending new offspring; they also search for food (only when humid outside), feed the queen, build, maintain, and clean the colony, and, in the case of soldiers, protect it from other insects. But they do not reproduce because, although they include both sexes, they are sterile.

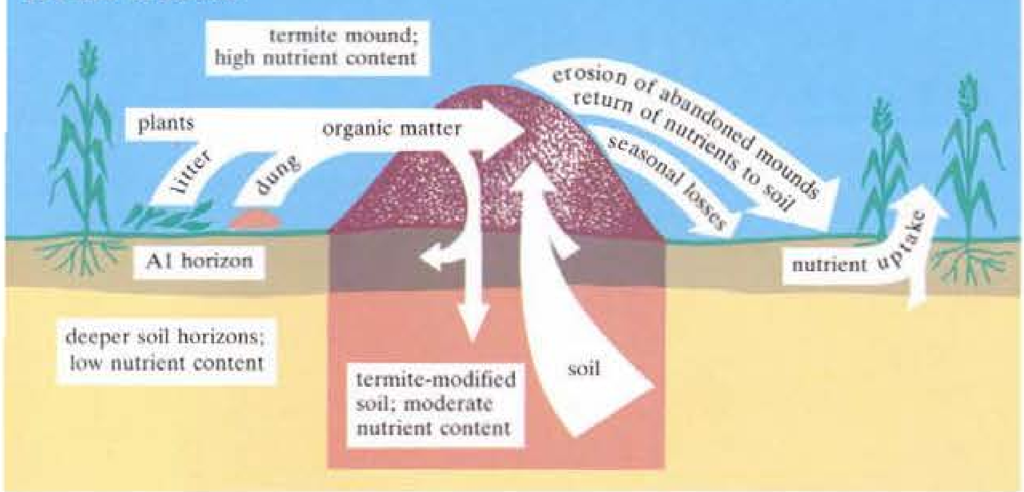
After some years, the queen is really in her stride and, with no other duties, produces about 1000 eggs a day, replacing the soldiers and workers, which live from about 1 to 5 years. The original king fertilises her from time to time.

A third caste appears whose forms are not sterile. These 'reproductives' found new colonies. They have a hard cuticle better able to withstand the often-dry conditions of the outside world. Most importantly, they also have wings and well-developed eyes. They are future kings and queens and will fly away from the colony to start a brave new world.

Termite societies are not necessarily limited by the already long life of their queens. If a queen dies or produces too few eggs, supplementary queens are selected from developing reproductives. Of course, they will not then fly away. Often they are smaller and less productive than the main queen; nevertheless, the colony will continue.

The great termite city with its ostentatious mound relies almost entirely on a vast army of microscopic creatures for its survival. These are the bacteria, or in some species protozoa, which live inside the termites and produce the necessary enzymes to convert cellulose to sugars, a process most animals generally can't perform by themselves. (However, some of the very latest research shows that the majority of termite species appear capable of producing their own cellulose-digesting enzyme from the wall of the gut. How much of the enzyme they produce and how effective it is, we have yet to find out.)

The flow of carbon



in that area. They showed that vital organic carbon and nitrogen were in short supply, and became even scarcer with increasing depth. Phosphorus was also insufficient for many crops.

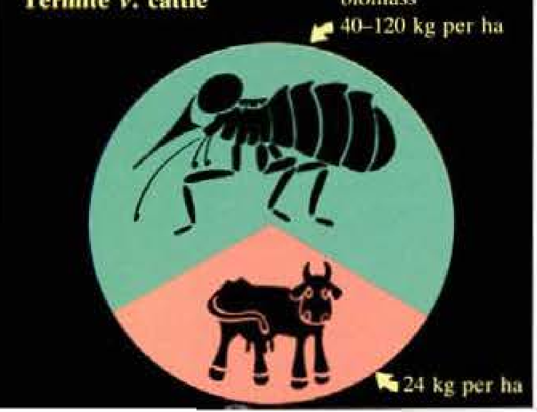
By contrast, the termite mounds contained these nutrients in abundance. Depending on the species of termite, concentrations in the mounds ranged from 2·3 to 6·5 times greater than in the soil for organic carbon, and from 1·4 to 5·4 times more for nitrogen. Mound material was also rich in phosphorus, calcium, magnesium, and potassium.

The soil below each mound was also enriched, although not to the same high concentrations found in the mounds. As you might expect, the nutrient increase tapered off with increasing depth until little effect was noticeable beyond 50 cm.

The important question is whether or not these nutrient stores are shared out around the pasture that the termites inhabit. Obviously termite mounds must eventually decay, but nobody really knows how long they remain inhabited. Unlike a bee colony, the termite society is not limited by the life span of its queen. When she dies, other individuals develop as egg-layers so that the colony can continue. Mr Holt makes an 'educated guess' (based partly on an analysis of the number of unoccupied mounds in an area) of an average life of 20–40 years for a colony.

Calculations indicate that in the red-earth cattle country around Charters Towers termites outweigh (per hectare) their bovine competitors.

Termite *v.* cattle



But how long do the empty mounds remain? Their rate of erosion obviously depends a lot on rainfall — on the duration of spells of heavy rain rather than the total annual precipitation. Some preliminary studies of mound erosion have enabled Mr Holt to estimate that a period of 30 years is probably required to erode the commonest mound type in the climate of his study area. Knowing this, and assuming that the redistributed mound materials stay in the surface soils, one can estimate the effect of the mounds on the pasture in which they stand.

It turns out that the rate of soil cycling through them is the equivalent of adding 300–400 kg of fertiliser per hectare every year. This 'fertiliser' contains between 4 and 10 times the concentration of nutrients found in the top layer of soil (the A1 horizon as it's called) in that region.

Also, the soil beneath the mounds will provide nutrient-rich islands once the mounds have eroded away. This may encourage the growth there of species less tolerant of the surrounding low-fertility soil. So undoubtedly, by their recycling of plant nutrients, termites play an important role in northern Australia's harsh arid inland.

Pests?

But the question naturally arises: where do the termites get their nutrients from? The answer varies from one species to another. The termites in the lightly timbered pasture near Charters Towers are not the species that cause problems for wooden houses. Instead, they are scavengers, and eat detritus and litter. Some of Mr Holt's laboratory experiments suggest that one of the relevant species could, each year, eat up to 300 kg of plant dry matter per hectare — at the density at which they occur on the study site. Production of this quantity of dry matter may only occur about 2 years out of every 10 in the kind of country studied. Therefore the termites, which

As a result of the termites' activity, much of the surrounding soil is enriched with organic matter.

probably eat several of the same things as cattle, may be significant competitors during bad years.

If tiny termites can compete with cattle, this leads us to another question: just how many termites are there? What is the actual mass of termite flesh?

Although not an easy question to answer, Mr Holt, together with Dr John Easy and Mr Graham Spellman, of the Australian Nuclear Science and Technology Organisation, have ingeniously succeeded. Using the well-established biological technique of mark–release–recapture (see the box on page 16), and with a radioactive isotope as a marker, they proved that small mounds contain from 10 000 to 25 000 individuals and larger mounds many more. The mean for colonies of *Amitermes vitiosus*, the most common mound-builder in their area, was about 40 000. (Other species, incidentally, can have far larger populations.)

The four species in the study area have a combined population density of from 10 to 22 million per hectare. This staggering figure converts to a weight of termites of 40–120 kg per hectare. As the land is so poor, cattle here graze at the very low rate of one beast to 25 hectares, on average. This means that the biomass of the termites is actually greater than that of the cattle — whose weight would average out at only about 24 kg per hectare.

In effect, the termites are far more efficient creatures than the cattle when it comes to converting the scant resources of the region into their own flesh. (Perhaps we should eat termites rather than beef!) That they have the numbers to represent a significant pest during dry years is true; but the benefits they confer by decomposing plant litter in an area where soil bacteria are less effective than elsewhere, and then spreading the resulting nutrients when their mounds erode, almost certainly outweigh any occasional disadvantages.

Roger Beckmann

More about the topic

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Some aspects of the biology and pedological significance of mound-building termites in a red and yellow earth landscape near Charters Towers, North Queensland. J.A. Holt, R.J. Coventry, and D.F Sinclair. *Australian Journal of Soil Research*, 1980, **18**, 97–109.