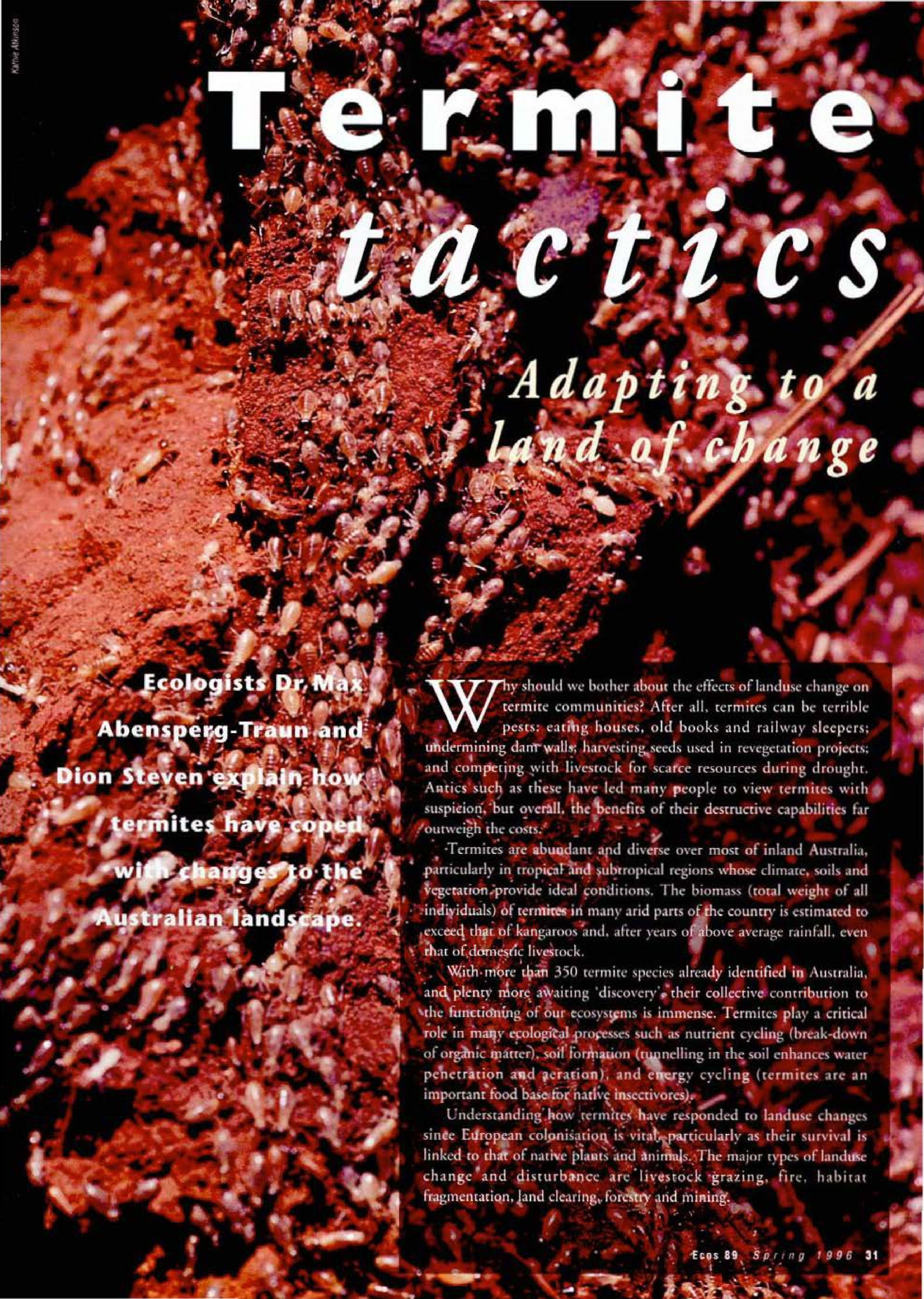


Kathie Atkinson

Termite tactics

Adapting to a land of change

Ecologists Dr Max Abensperg-Traun and Dion Steven explain how termites have coped with changes to the Australian landscape.

Why should we bother about the effects of landuse change on termite communities? After all, termites can be terrible pests: eating houses, old books and railway sleepers; undermining dam walls; harvesting seeds used in revegetation projects; and competing with livestock for scarce resources during drought. Antics such as these have led many people to view termites with suspicion, but overall, the benefits of their destructive capabilities far outweigh the costs.

Termites are abundant and diverse over most of inland Australia, particularly in tropical and subtropical regions whose climate, soils and vegetation provide ideal conditions. The biomass (total weight of all individuals) of termites in many arid parts of the country is estimated to exceed that of kangaroos and, after years of above average rainfall, even that of domestic livestock.

With more than 350 termite species already identified in Australia, and plenty more awaiting 'discovery', their collective contribution to the functioning of our ecosystems is immense. Termites play a critical role in many ecological processes such as nutrient cycling (break-down of organic matter), soil formation (tunnelling in the soil enhances water penetration and aeration), and energy cycling (termites are an important food base for native insectivores).

Understanding how termites have responded to landuse changes since European colonisation is vital, particularly as their survival is linked to that of native plants and animals. The major types of landuse change and disturbance are livestock grazing, fire, habitat fragmentation, land clearing, forestry and mining.

Above: Termite mounds are a common feature in many areas of inland Australia that are subject to heavy grazing by livestock.

Left: Spinifex grass collected for storage by the mound-building harvester *Drepanotermes perniger* in the north-west of WA.

Hoofbeats on the horizon

In most parts of southern Africa, termites have co-existed since ancient times with a range of large herbivores, including elephants, buffalos, antelopes, gazelles, giraffes, hippopotamus and rhinoceros. But in Australia the story is different. All large native herbivores became extinct during the Pleistocene (more than 10 000 years ago) possibly due to factors such as climate change and Aboriginal hunting.

The introduction by European settlers of large herbivores such as cattle and sheep might have influenced the survival of termites. This could occur through competition for food, and the modification of soil moisture/humidity and soil temperature regimes to which termites are known to be vulnerable. Livestock cause these micro-climatic changes in the soil by destroying shrubs and trees, by preventing regeneration, by compacting the soil, and through the loss of the litter layer by trampling, especially when overstocked.

Most evidence suggests, however, that Australia's termites have coped well with introduced stock. Livestock-grazing and trampling on their own have had no drastic effects on termite abundance or diversity in northern Australia (water buffalo) and in south-western Australia (mostly sheep). On the contrary, the abundance of harvester termite (*Drepanotermes tamminensis*) mounds in the south-west was found to be higher in grazed than in ungrazed areas. General surveys of termite activity in central Australian rangelands give a similar picture.

In the mulga (*Acacia aneura*) lands in arid parts of Australia, harvester termites coexist with cattle with no significant levels of competition; the cattle eat green material while the harvesters collect predominantly dead grasses and litter. During years of normal or above average rainfall, colonies of *D. perniger*, a specialised grass-eater, increased markedly in abundance. In some areas, their low and flat mounds (up to three metres in diameter) were almost contiguous, with up to 350 mounds per hectare. But harvester colonies perished during a severe drought when competition with cattle would have been greatest.

Harvester termites benefit from livestock dung which many species eat when dry. Livestock may also increase the nutritional quality of the harvested grasses through the recycling of nutrients. This can occur through the burying of dung by dung beetles and the activity of the soil microbiota which results in the incorporation of the nutrients into the soil for subsequent uptake by plants, and ultimately by termites.

Burning down the house

Much of the vegetation in inland Australia has been subjected to fires since prehistoric time. With the exception of rainforest and semi-arid shrublands, fire remains an important tool for ecosystem management in many parts of the country. Native animals, such as termites, that depend directly on plants for food, appear to be vulnerable to intense fire.

Colonies of wood-eating termites with nests in above-ground wood are likely to perish in a high-intensity fire. Wood-eating species nesting in the soil or protected by mound walls will have higher survival chances both during and after fire when they can eat roots and unburnt surface wood.

About the authors

DR Max Abensperg-Traun and Dion Steven work at the WA laboratory of CSIRO's Division of Wildlife and Ecology. Most ecological research on Australian termites was initiated by the division in the early 1950s, in recognition of the insect's importance in Australian ecosystems. Since then, the Division of Entomology has dominated termite research, mostly on taxonomy and termite biology at the scale of individual colonies and species.

Intensive studies on the effects of various landuse strategies on termite communities began in earnest in the late 1980s. This new impetus to termite research was associated with the initiation by the Division of Wildlife and Ecology of a long-term research project into the ecological dynamics of remnant vegetation is the central wheatbelt of WA. The authors have been associated with that research since its inception. Ongoing studies by the authors focus on questions of termite diversity in different parts of the landscape, and their role as indicators of the diversity of other groups of animals.

More cellulose please!

WHEN starved of nutrients, some termites have been known to turn from plant-eating to cannibalism, eating their nest mates to survive periods of food shortage. Some termites have been observed to eat carrion and bone. Otherwise, termites eat all cellulose-based organic materials in varying stages of decay. This includes wood, bark, leaves, seeds, grasses/herbs, and dung of mammalian herbivores (when dry).

Available food is usually partitioned between the different co-existing species. Species of *Coptotermes*, for example, can eat living, dead but undecayed, as well as decayed wood. In contrast, most species of *Schedorhinotermes*, *Amitermes*, and many others, eat decomposed wood only, being unable to deal with plant chemical substances in living and undecayed wood.

Several species, particularly in the high rainfall regions of tropical Australia, play similar roles to earthworms by eating the most decomposed stages of plant-based materials, humus and soil. A single, large log of a fallen eucalypt, for instance, thus often supports six to eight different species occupying different layers of the wood while feeding. Each of these different species makes a significant contribution to the log's break-up and eventual return to the soil as part of the nutrient-cycling process. Other species are specialised harvesters collecting a wide variety of plant debris ranging from bits of bark and leaf to seeds, grasses and herbs.

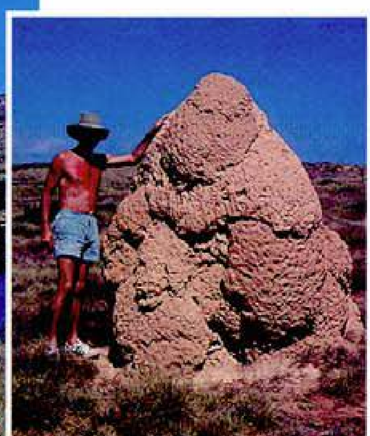
Harvester termites are particularly common in grasslands and open savanna of central and northern Australia. The only truly polyphagous termite (eating all types of different plants in all stages of decay) is *Mastotermes darwiniensis* which is restricted to tropical Australia and is capable of causing significant damage to agricultural crops and timber structures. This species has also been known to attack leather, wool, horn, and even bitumen and rubber. *Coptotermes* is a timber pest throughout Australia.

With few exceptions, termite communities at high Australian latitudes consist largely, if not entirely, of wood-eaters. This is because cold ambient temperatures are unsuitable to support harvesting by these small, soft-bodied arthropods. Wood-eaters benefit by the insulating effects of the wood. One of the exceptions is the specialised harvester *Tumulitermes westraliensis* whose flat, pavement-like mounds are a common feature in parts of the Fitzgerald River National Park on the south coast of WA.

The effects of fire on harvester termites depend on fire intensity and plant regeneration before stored supplies are depleted.

Studies in WA show that intense fires in vegetation types that are rich with plant species have lesser effects on harvester termite colonies than in plant-species poor vegetation, such as a spinifex grassland. Different plant species often have different powers of regeneration after fire: some being fast (many resprouters), others slow (many seeders). There is a greater likelihood of rapidly-regenerating species occurring in plant-rich vegetation types providing alternative food sources for the termites.

Many other factors will influence the survival of harvester termites after fire. Small colonies with smaller food requirements may suffer less from fire; regeneration will be more rapid where fire is followed by rainfall; and termite mound colonies weakened by fire are more easily invaded by predatory ants which may further weaken the colony. Both the frequency and the intensity of fires will also affect the survival of termites.



Mounds of the spinifex termite (*Nasutitermes triodiae*) on the coast near Exmouth in the far north-west of WA. This termite inhabits large areas of Australia where fire is an important element of the environment.

Demolition and decline

Removal of trees will have an immediate effect on arboreal termite species which depend entirely on them for food and within which they maintain their entire nest system. In Australia, arboreal species include *Nasutitermes walkeri* and *N. graveolus* in the Tropics, and the so-called drywood termites (such as *Kalotermes*) to which all Tasmanian species belong.

Subterranean and mound-building wood-eaters maintain an active gallery system within the soil for foraging on surface wood and the roots of trees. Such species may be more resilient to clearing. In fact, clearing often increases the availability of edible (dead and decomposing) wood, and this may cause a temporary increase in the abundance of wood-eaters. All studies to date show a general decline in termite diversity after clearing for pasture establishment.

Cultivation has an immediate, catastrophic impact on termite communities. Few, if any, species survive prolonged ploughing and application of herbicides and pesticides. However, subterranean termites in central Queensland and south-west WA have been observed to re-invade quite rapidly from adjacent native habitat after the adoption of zero tillage and stubble retention.

Left: A mound of *Amitermes obeuntis*. This species is known to disappear when native forests are replaced with exotic pine.

Below: A nest of *Coptotermes acinaciformis*. Colonies of this species survive when native forests are replaced with pine plantations.

In the WA wheatbelt, we have studied regenerated heath and shrubland plant communities that were once cultivated for varying periods (some for over 40 years), and that were subsequently abandoned more than 20 years ago. Today, termites have recolinised these regrowth areas to the extent that their communities are largely indistinguishable in their diversity from those in comparable but undisturbed native vegetation in adjacent areas.

We will never know whether large-scale clearing has caused the extinction of species unique to agricultural regions. Based on what we know of the biogeography of Australian termites, many species do show restricted distributions and are therefore potentially at higher risk of extinction, as are colonies in very small vegetation islands in farm paddocks.

A fragmented existence

In the central wheatbelt of WA, extensive agriculture has created a scatter of native vegetation remnants within an matrix of mostly grazing paddocks, wheat and lupins. A similar situation exists in the south-east of the continent. The result has been a huge reduction of termite populations, and possibly a decline in termite diversity. The great majority of species are now restricted to these native vegetation fragments.

A critical issue is that most fragments are very small (many are less than 2 ha), supporting only small termite populations. These are most vulnerable to unpredictable events such as drought and fire, in addition to competition for food with other consumers such as sheep, cattle, kangaroos and other termites.

If the remnant population perishes for some reason, successful recolonisation depends on its degree of isolation from potential recolonisers in other fragments. Such fragments are often many hundreds of metres away, separated by an agricultural landscape which is hostile to aerially-dispersing termite alates (high visibility to predators, unsuitable nesting conditions).

Of 1000 alates that leave the parent colony, more than 95% will be eaten by a wide range of predators including birds, mammals, frogs, lizards and many invertebrates, ants in particular. Those that reach the isolated fragment (largely driven by winds) need to run the gauntlet of ever-present predators before finding a mate as well as a suitable spot for nesting. The chances of a new colony being established are slight. These odds can be improved when termite species synchronise their maiden flights, thus swamping potential predators.

Our studies within woodland fragments (gimlet, *Eucalyptus salubris*) in the WA wheatbelt show that termite abundance and diversity, particularly the harvesters, has declined markedly in very small fragments. Some fragments (<1 ha) have lost all harvester termites. Small fragments are more disturbed than larger ones, with prolific weed growth and the loss of virtually all native plant species other than old and senescent eucalypts. With their demise the remnant will disappear. Wood-eaters may survive somewhat longer than the harvesters.

Successful recolonisation of small, senescent vegetation remnants is unlikely unless the remnant is replanted with native species and connecting corridors to other fragments, through which dispersing termites can move, are established. Termite alates dispersing along vegetated road-verges/corridors, rather than across ploughed land or paddocks, are far more likely to reach vegetation fragments because micro-environmental conditions in these habitat corridors are more conducive to nest establishment. Remnants would then eventually be reached by the progressive advance of newly established colonies following maiden flights.

The only Australian termite that inflicts considerable damage to agricultural crops (such as sugar cane) is *Mastotermes darwiniensis* in northern Australia. This species is 'polyphagous', which means it eats all kinds of plant material in all stages of decay. It probably benefits by clearing and cultivation which replaces a comparatively poor-quality (low nutrient), low quantity food resource (native plants) with a readily available, high quantity supply of nutritious (fertilised) food. This contrasts with many parts of Africa where several species reach enormous population densities in cultivated fields and cause great damage to food and cash crops.

Stumped by alien trees

The process of establishing pine plantations typically includes the clear-felling of all native trees followed by a burn. Logs of large trees that survive the fire are left on the ground. The area is then ploughed and seedlings planted. Pine plantations generally occur in temperate climates where harvester termites are either scarce or absent. Several studies show that few wood-eating species survive the replacement of native woodland with exotic pine.

Only a small number of species (mostly species of *Coptotermes*, *Heterotermes*, *M. darwiniensis*) can eat pine wood, possibly because the chemical composition of this exotic timber makes it unpalatable. Survival of other termite species therefore depends on the retention of an underground root system, and large logs of the native trees. The closed canopy and thick layer of pine needles on the soil surface also results in a drop in soil temperature which is unsuitable for nesting. This is known to have caused the demise of *Nasutitermes exitiosus* colonies in eastern Australian pine plantations.

With age, the trees are periodically thinned and the pine litter burnt, which marginally improves conditions for termite activity. Re-invasion is slow, however, and does not occur as readily as it does by some other soil and litter invertebrates such as ants. Termite survival in other kinds of plantations (such as 'blue-gum') appears not to have been investigated although *M. darwiniensis* is known to be a pest in tropical orchards.

Colonies mined out

Information on the effects of open-cut mining on termites come from bauxite mined areas in the extreme south-west of WA. Here, Alcoa of Australia Limited has led the way in terms of ecological restoration of abandoned minesites.

Local ecologists monitoring termite recolonisation found that no species survived the initial mining operation, and that recolonisation depends on suitable colonisers being able to reinvade from adjacent native habitat. The reproductive elements of the termite colony (so-called 'alates', or future kings and queens) disperse by air in spring or autumn of each year. This enhances the recolonisation process which follows a successional trend based largely on food preference of the different termite species.

The first recorded recolonisation took place some three years after minesite rehabilitation. In the early successional period (less than five years), only termite species capable of eating sound (undecayed) wood recolinised.

With time, species feeding on decayed wood were recorded, while litter-feeders appeared last. Most of the species present prior to mining were recorded 25 years after the minesite was rehabilitated. The return of termite species was enhanced by the use of fresh topsoil, the planting of a diverse range of tree and shrub species, and the use of mulch to provide a litter habitat. Information from other areas of Australia gives a similar picture. With further improvements of methods of minesite rehabilitation, recolonisation rates are also likely to improve.

The comparatively recent colonisation by European settlers has meant that Australian termites have had to deal with changes to their environment on a faster and higher scale of time and intensity than has taken place on most other continents in recent times. Data from a wide range of landuse types have shown termites do cope reasonably well with environmental change associated with European colonisation, probably because of their sociality, soil-living and decomposer habits, and aerial dispersal.

Although populations may temporarily decline or become locally extinct for a variety of reasons, ecosystem restoration (replanting), passive regeneration of abandoned farmland and the creation of linkages (corridors) to other vegetation fragments, is likely to result in their successful recolonisation as long as native vegetation is within reach of potential colonisers.

More about termites

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A winning combination

A RANGE of traits enables termites to thrive in desert environments where most other invertebrates, with the exception of ants and grasshoppers, are comparatively scarce.

• Their social organisation permits the effects of environmental fluctuations, both physical (moisture, temperature) and biotic (food availability), to be buffered to a large extent. Physical fluctuations are minimised by creating a controlled microclimate in the nest. Biotic stability is enhanced by storing food. Maximum benefits of sociality would thus be felt in the most variable environments, and it is no accident that the most successful and influential organisms in desert habitats (termites and ants) are among the few insect groups with social organisation. Their sociality enables them to be active throughout the year and thus have a much more profound influence on ecosystem processes than that of the more spectacular, but intermittent, outbreaks of plague locusts.

• Termites can sustain themselves on relatively poor food. This is in part achieved by nitrogen fixation of their gut flora and by digestive efficiency. For example, spinifex grassland is renowned for its low food value yet supports an extremely abundant termite fauna, particularly the harvesters. A well-known participant is the 'spinifex termite' *Nasutitermes triodiae* whose large, dome-shaped mounds characterise many north-western landscapes. Its large colonies are sustained almost entirely by spinifex which occurs in large amounts and (with the exception of new shoots) is eaten by few other animals.

• Predatory animals are highly susceptible to population fluctuations of their prey as a result of temperature extremes (such as seasonal effects on insect abundance), drought or fire. The decomposer habit of termites is less strongly affected by such environmental influences.

Termites cope well even in the most inhospitable environments.

• Termite colonies succumb to a range of factors such as predation or food shortage after prolonged drought or fire. However, when each colony is seen as an individual organism, which, in ecological terms, is how it functions, colonies can be very long-lived (several decades) and are potentially immortal. Should the king or queen die, a replacement rapidly takes its place to ensure reproductive continuity.