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The Zambezi Society and The Biodiversity Foundation for Africa are working as partners within the African Wildlife Foundation's Four Corners TBNRM project. The Biodiversity Foundation for Africa is responsible for acquiring technical information on the biodiversity of the project area. The Zambezi Society will be interpreting this information into user-friendly formats for stakeholders in the Four Corners area, and then disseminating it to these stakeholders.

**THE BIODIVERSITY FOUNDATION FOR AFRICA (BFA** is a non-profit making Trust, formed in Bulawayo in 1992 by a group of concerned scientists and environmentalists. Individual BFA members have expertise in biological groups including plants, vegetation, mammals, birds, reptiles, fish, insects, aquatic invertebrates and ecosystems. The major objective of the BFA is to undertake biological research into the biodiversity of sub-Saharan Africa, and to make the resulting information more accessible. Towards this end it provides technical, ecological and biosystematic expertise.

**THE ZAMBEZI SOCIETY** was established in 1982. Its goals include the conservation of biological diversity and wilderness in the Zambezi Basin through the application of sustainable, scientifically sound natural resource management strategies. Through its skills and experience in advocacy and information dissemination, it interprets biodiversity information collected by specialists like the Biodiversity Foundation for Africa and uses it to provide a technically sound basis for the implementation of conservation projects within the Zambezi Basin.

**THE PARTNERSHIP** between these two agencies was formed in 1996 as a result of mutual recognition of their complementarity. They have previously worked together on several major projects, including the biodiversity component of IUCN's Zambezi Basin Wetland project and the evaluation of biodiversity in Tete province described in detail in the first Four Corners TBNRM Biodiversity Information Package.

#### ISBN 0-7974-2835-6

RECOMMENDED CITATION: Timberlake, J.R. & Childes, S.L. 2004. *Biodiversity of the Four Corners Area: Technical Reviews Volume Two* (Chapters 5-15). Occasional Publications in Biodiversity No 15, Biodiversity Foundation for Africa, Bulawayo/Zambezi Society, Harare, Zimbabwe.

#### ACKNOWLEDGEMENTS

In addition to all the authors of the chapters in this document, The Zambezi Society and the Biodiversity Foundation for Africa wish to thank the following for peer review or additional assistance:-

> John Burrows Colin Craig Barbara Curtis Cornell Dudley Kevin Dunham Peter Frost Debbie Gibson Mike Griffin Michael Irwin Bas Jongeling Linley Lister Gillian Maggs Anthony Mapaura Brian Marshall Susan Ringrose

We also wish to thank Henry Mwima, Nesbert Samu, Othusitse Lekoko, Daudi Sumba, Gitonga Kathurima, Maureen Mashingaidze and Simon Metcalfe of the African Wildlife Foundation

#### CHAPTER 11. SOIL FAUNA OF THE FOUR CORNERS AREA

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#### CHAPTER 11. SOIL FAUNA OF THE FOUR CORNERS AREA

J. Mark Dangerfield



*Macrotermes,* Termites

THE AWF FOUR CORNERS TBNRM PROJECT IS FUNDED BY USAID THROUGH THE REGIONAL CENTER FOR SOUTHERN AFRICA

#### CHAPTER 11. SOIL FAUNA OF THE FOUR CORNERS AREA

#### J. Mark Dangerfield

#### 11.1 INTRODUCTION

Organisms that live for at least part of their lives in the soil, leaf litter and dead wood are ubiquitous, numerous and diverse. They are also poorly known, particularly in their taxonomy but also in their ecologies and specific contributions to ecosystem processes. Their diversity extends to all taxonomic levels with up to 30 Orders and many hundreds of species present in a single habitat. But as with all other groups of organisms, numbers are dominated by just a few taxa with the majority being locally rare. One consequence of the preponderance of locally rare taxa is that composition changes greatly, both within a habitat from sample to sample and between habitats. Variation in diversity at a site (alpha diversity) is consequently high and the sensitive responses of many soil animals to habitat structure means that variation between habitats (beta diversity) is also high.

It is difficult to estimate from published accounts but perhaps only 5% of soil animal species are formally described. The estimate for insects is 10% (New & Yen 1995). This proportion will remain low as few taxonomists specialise in soil animal groups. As more is discovered about the diversity of soil animals, such as the high diversity of soil feeding termites in tropical forests (Eggleton, Williams & Gaston 1994), estimates of the number of likely species continues to increase. The reality is that there is a huge and mostly underestimated reservoir of species diversity in soil (Andre, Noti & Lebrun 1994) and little formal progress in tapping into the "poor man's rainforest" (Giller 1996).

Soil organisms are critical to decomposition, nutrient cycling, soil formation and moderate many physical and chemical processes in soil. They form soil food webs built on root herbivores and others on decomposers. Many organisms that as adults are key pollinators have larval or pupal stages in the soil. Much is known about the general roles of soil organisms in these ecosystem processes in both temperate and tropical systems, for example the importance of termites in nutrient cycling (Wood & Sands 1978) or earthworms in soil structure modification (Hendrix 1996), but little is known about the specifics of individual species or particular soil animal assemblages. This is an important gap in knowledge because management of soil biological resources is critical to the sustainability of managed systems (Woomer & Swift 1994).

Soil animals are rarely considered by conservation organisations, yet in many cases the functions performed by these animals are critical to the overall performance of the system. For instance, some soil animal species are capable of significant ecosystem engineering, modifying both the magnitude and direction of resource flows in both natural and managed ecosystems (Jones, Lawton & Shachak 1994). It is also likely that some landscapes are a consequence of ecosystem engineering by soil animals (Dangerfield, McCarthy & Ellery 1998). One reason for the lack of attention from conservation groups is that whilst individual species may be sensitive to disturbance, the overall soil animal assemblage may remain quite robust because there will always be tolerant taxa, such as termites, ants, mites and collembola present. There is sound theoretical thinking behind this idea of redundancy (Lawton & Brown 1993), but little empirical evidence.

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It is not uncommon for insects to show dramatic population surges, local extinctions and dramatic shifts in their geographic range (Samways 1996). Highly volatile populations that often become extinct (Dempster 1989) and the need for a flux of individuals to ensure long-term survival (Ehrlich & Murphy 1987) makes it very difficult to apply the usual conservation tools of assessment and reserve selection for individual species, more so given the huge diversity and lack of specific knowledge of invertebrates. Perhaps 100,000 to 500,000 insect species will become extinct in the next 300 years as a result of global change brought about by human activities (Mawdsley & Stork 1995), contributing to the extinction discontinuity (Samways 1996). The extent to which similar principles and likely extinctions apply to soil invertebrates is not known. Some taxa, notably among the collembola and mites, have species with global distributions across many soil types, whilst other species are highly local, dynamic and potentially extinction-prone. Ignorance is not bliss in this case.

Most soil animals are very small. More than 90% of taxa in most habitats are less than 2 mm in body length. Consequently sampling of soil animals is a challenge. As soil and leaf litter are opaque heterogeneous media, searching for specimens by eye, even with the aid of a microscope, is a labourious task. Extraction methods that force the animals out of the media by their own behaviours are more efficient than sorting by eye, but require laboratory machinery (Tulgren funnels, flotation baths, etc.) and so cannot be readily completed in the field. Direct sorting of soil and leaf litter can be achieved in the field but by necessity must focus on the larger, visible taxa. Seasonality and between year variation in rainfall and residual moisture can have dramatic effects on the abundance and behaviours of many taxa, both of which influence sampling performance. Consequently it is very difficult to obtain a complete inventory of soil fauna without repeated sampling effort across seasons and years.

Soil animals are very patchily distributed both within and between habitats (Dangerfield 1990a, 1997). This results in highly variable measures of alpha (site) diversity and local abundance. High variance constrains the interpretive power of most traditional statistical measures of difference. There are also as many specific behaviours and responses to environmental changes as there are taxa. For example, in response to dry conditions some species of millipede will aestivate in shallow burrows, others will burrow up to a metre down, others will seek termite mounds and descend down vent systems, while others will seek moisture in or beneath woody litter (Dangerfield & Chipfunde 1995). One consequence of this is that no one sampling method will adequately sample all millipedes. Sampling of soil fauna is thus restricted to fairly general techniques, such as pitfall trapping or extraction from small soil cores, that sample a subset of the active taxa at the time.

Three broad groups of soil macro-organisms are generally accepted - microfauna, mesofauna and macrofauna. Whilst body size formally defines these groupings it is as much to do with the different sampling methods and scale of sampling that have allowed them to become established. It has also meant that most soil biologists have focused on one of these size groupings which further fragments our knowledge of whole soil animal assemblages. Rarely have microfauna, mesofauna and macrofauna specialists worked collaboratively at the same study sites.

There are some taxa such as termites (Isoptera), ants (Formicidae), some beetle families (e.g. Scarabaeoidea, Carabidae), scorpions (Scorpionida) and spiders (Araneae) that have become better known taxonomically and ecologically usually because they are either conspicuous pests, a nuisance or are directly dangerous to humans. However, not all species within these taxa are of economic importance creating further bias in taxonomic and ecological knowledge. Whilst we know that soil fauna are important to ecosystem processes, that their diversity is high and their individual ecologies are complex, we know very little about their conservation status.

#### **11.2 CURRENT KNOWLEDGE**

There are only a handful of biologists who specialise in soil fauna and as with other taxa most of them operate in the northern hemisphere. A few have worked in Africa on occasion but there are few experienced specialists resident in the Four Corners area or surrounds. Whilst we wait for a new generation of young and talented soil biologists to emerge, the knowledge base for soil fauna remains very scant and comes mostly from localized studies in geographically disparate habitats and from broader research programs (such as the International Geosphere-Biosphere Program, IGBP and Tropical Soil Biology & Fertility Program, TSBF). So far none of these have a specific taxonomic or conservation focus.

The TSBF Program developed a protocol for the assessment of soil macrofauna abundance and composition (Anderson & Ingram 1989) and implemented this at several sites throughout Africa (Lavelle *et al.* 1994). The data include abundance, biomass and ordinal level taxonomy for samples from 25 x 25 x 25 cm blocks of soil (soil monoliths) hand-sorted in the field. The nearest sites to the Four Corners area are those from the Marondera District in eastern Zimbabwe where overall densities of soil macrofauna range from 30 to 248 individuals per m<sup>2</sup> and a fresh biomass of 1 to 27 gm per m<sup>2</sup> from nine orders (Dangerfield 1990a). Termites, millipedes, beetle larvae, earwigs and spiders were the most numerous groups with significant shifts in abundance as a result of changes in habitat structure and land use. The conversion of natural woodland to arable agriculture resulted in an order of magnitude decline in abundance and biomass and a loss of half the number of orders (Dangerfield 1990a).

The general pattern from the TSBF dataset is that annual cropping systems have generally depleted soil fauna assemblages, especially in the case of termites, but earthworms seem to be less affected (Lavelle *et al.* 1994). This latter trend is a function of ploughing and the predominance of mound-building termites, especially the smaller mounds of *Nasutitermes* and *Cubitermes* species, versus soil-dwelling taxa (Dangerfield 1990b, Dangerfield *et al.* 1993b). Perennial cropping systems, pastures and plantations generally have less diverse assemblages than the original ecosystem but the biomass can often be higher due to invasive earthworm species (Lavelle *et al.* 1994).

The same methods were used to assess the abundance and ordinal level diversity of soil macrofauna in several habitat types in northern Botswana (Dangerfield 1997) within the Four Corners area. These data were the first from semi-arid systems dominated by long dry seasons and summer rainfall. Samples generated abundances between 100 and 500 individuals per  $m^2$ and an average of 2 to 6 orders per sample. Samples were from soil monoliths (square cores) on 25 x 25 x 20 cm depth and hand-sorted in the field to extract the macro-arthropods. Wooded sites were more diverse than open habitats except along river terraces and other habitats influenced by surface water. The overall abundances are comparable to those in moist tropical forests (Lavelle & Pashanasi 1989, Leakey & Proctor 1987) and many temperate systems (David, Ponge & Delecour 1993). Despite the general absence of earthworms, isopods and molluscs these dry savannas support significant populations of ants, fungus-growing termites and beetle larvae. Only primary rainforest (Lavelle 1988) and deciduous temperate forest (Schaefer 1990, Schaefer & Schauermann 1990) appear to have greater overall abundance of soil macrofauna. The data from Botswana support the general contention that in dry or impoverished habitats soil fauna become an even more important component of the resistance of ecosystems to change, and their resilience once change has happened. Soil fauna are not just important in temperate or moist systems (Whitford 1996).

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An ecological study on the effects of DDT use in the control of tsetse flies was undertaken in the Siabuwa Communal Area in NW Zimbabwe that included information on soil fauna from pitfall trap data collected in winter (Tingle, Lauer & Armstrong 1992). No effect of spraying was apparent on the relative abundance or diversity of surface active (epigeal) soil fauna but some ants (*Camponotus* sp.) were suspected of carrying the chemical through the food chain to affect insectivorous birds (Tingle 1995). DDT applications changed the proportion of detrivorous cryptostigmatid mites and an overall trend was seen for slower degradation of leaf litter in areas with a low level of DDT contamination of the woodland floor (Tingle & Grant 1995). This study provided one of the more thorough taxonomic appraisals of soil animal assemblages in the Four Corners area and contains the best inventory lists available for family, genus and species levels. However, all samples were from one method (pitfall traps) and only one season.

In 2001, the Government of Botswana instigated a tsetse fly reduction program involving the blanket aerial application of deltamethrin insecticide over the Okavango Delta. An environmental monitoring program was conducted in which there was some sampling of soil fauna using pitfall traps. The focus of this monitoring was on non-target invertebrates in tree canopies and has generated more than 200,000 specimens, more than a quarter of which have been identified to family and or genus and then morphospecies in less than five months. This capacity to process significant numbers of specimens is the result of advances in both approaches to taxonomy and information technology (Oliver *et al.* 2000). The morphospecies voucher specimens and their associated digital images are lodged with the Harry Oppenheimer Okavango Research Centre, University of Botswana in Maun.

Other information for lower taxonomic ranks is very sparse and taxon specific. There have been some collections of termites (Mitchell 1980) and minor taxa such as the Philoscidae, a family of terrestrial isopods (Taiti & Ferrara 1980), but the situation for millipedes illustrates the more general case well. The only substantial collection of millipedes for the region, identified only to sub-order, was housed in the Natural History Museum in Bulawayo until the 1980s when it was requested for exchange by taxonomists in the USA. In the late 1990's the material was still in the USA and no publications offering taxonomic details have been forthcoming to date. This illustrates one major difficulty with species-based conservation programs for invertebrates in poorly known areas. The taxonomic expertise is only found overseas and is already overworked. Answers to taxonomic questions are not easily obtained.

Less than 1% of named insect species are pests but they are the most studied of insects (Samways 1993). Their specific ecologies, population dynamics, physiologies and responses to pesticides are often well documented (Jepson, Efe & Wiles 1995, Sherratt & Jepson 1993, Stark, Jepson & Thomas 1995). This said, there is little published literature on the extent of pest species in the Four Corners area.

The extensive use of chemical pesticides has generated both methods for the assessment (Grant 1988, Kovach *et al.* 1992) and data on non-target organisms, including soil fauna (Murphy, Jepson & Croft 1994, Theiling & Croft 1988, Vickerman 1988). These studies remain one of the best sources of information on soil fauna and insects in general for areas like the Four Corners where taxonomic expertise and funds for surveys are scarce.

Levels of endemism for southern African insects varies from less than 20% of species in the dragonflies (Odonata) to nearly 50% in grasshoppers (Acridoidea), 75% in crickets (Tettigonioidea) and 85% in bees (Apoidea) (Samways 1993). The poor taxonomic base makes estimates for the soil fauna difficult. The only reliable species-level data on biogeography would

be for the termites. Here the key fungus growing groups appear to have many widespread species.

There are, however, some local endemics in other taxa such as the woodlouse *Aphiloscia victoriana* that occurs only in rainforest in the spray zone of Victoria Falls and for which there is some ecological data (Dangerfield & Telford 1991a, 1995). In general, however, levels of endemism, species richness within habitats and turnover of species within and between habitats for soil fauna in savannas in general remains obscure and mostly uncharted.

#### 11.3 PHYSICAL AND ECOLOGICAL PROCESSES

Soil fauna are most strongly affected by changes in moisture and temperature regimes that are outside the normal parameters of seasonal patterns. Many taxa are so in tune with predictable seasonal changes that their behaviours are triggered by subtle temperature or moisture changes. For example, millipedes in southern African savannas show these behaviours consistently and there is evidence that the responses are species specific (Dangerfield & Chipfunde 1995, Dangerfield & Kaunda 1994, Dangerfield, Milner & Matthews 1993a, Dangerfield & Telford 1991b).

Drought, flood and fire are usually within these tolerance regimes. Again millipedes are rarely surface-active when rainfall exceeds 40 mm and only emerge when local floods have passed (pers. obs.). The clearing of land for agriculture or the loss of canopy trees from fire, elephants or climate change are mostly outside the tolerance limits. Such disturbances are too rapid to be predictable and are therefore not within the adaptive plasticity of most species. This means that we see dramatic changes in soil fauna assemblages as a result of land clearing, agricultural practices and the felling of canopy trees. We have even seen changes in soil fauna assemblages as a result of elephant impacts on riparian vegetation (J.M. Dangerfield, unpublished data).

The importance of habitat structure as an overall mediator of temperature and moisture conditions in the litter layer and upper soil layers probably overides the geology, soil type and landscape position factors in the general composition of soil fauna assemblages. For example, cockroaches, earwigs, woodlice and crickets are only likely to be present if there is some canopy and herbaceous layer vegetation or woody litter in the habitat. The specific species composition, however, may be strongly influenced by the larger scale and persistent physical parameters such as geology and soil type.

Only recently have studies begun to investigate the more subtle links between the patterns of diversity in the vegetation, especially variation in floristics, and below ground diversity (Haagsma & Rust 1993, Hooper *et al.* 2000, Wolters *et al.* 2000). Whilst there are strong correlations between herbivorous insects and plant diversity it seems likely that patterns in above ground biodiversity will be relatively poor indicators for the diversity of the soil fauna.

The reality for the Four Corners area is that we again know very little about the likely determinants of specific species distributions and subsequent species assemblages of soil fauna, nor on the turnover in composition between habitats. However, we can predict from what we know about the general consequence of global change for soil animals (Smith *et al.* 1998; Young *et al.* 1998), that any recent land use change will have had a significant impact on local composition, perhaps threatening some taxa with local extinction.

#### **11.4 TERMITES**

Throughout Africa the termites are probably the best known of the soil fauna both by local communities and by scientists. Damage to wooden structures, crops and plantations by the ubiquitous fungus growing species costs many millions of dollars and uncountable hours of labour in repair and control. The tangible benefits of termites as a food resource and mounds as a soil amendment seem to pale against these costs. However, the real value of termites in determining soil fertility remains huge but not accounted.

Most savanna environments seem to have a relatively predictable termite assemblage that will include primitive taxa that are mostly wood-feeding and nesting (e.g. *Coptotermes*), numerous fungus-growing taxa (e.g. *Macrotermes, Odontotermes, Microtermes*), some soil-feeding taxa (e.g. *Cubitermes*) and harvesters (e.g. *Amitermes, Nasutitermes*). The open savanna habitats also usually contain the primitive grass harvester species *Hodotermes mossambicus*. While any given habitat within the Four Corners area is likely to contain more than 30 termite species from a dozen genera, there are no definitive inventories within the area. The nearest full description of the termite fauna is for the savanna ecosystem project at Nylsvley in South Africa (Ferrar 1982). A less comprehensive description of termite species that generate distinct surface features was compiled for rangeland and arable habitats in south-east Botswana (Dangerfield et al. 1993b). The distribution and frequency of mounds and soil sheeting varied significantly with land use suggesting that termite activity and composition are likely to be affected if land use intensity changes. Less extensive information is available for other species such as *Cubitermes sankurensis* (Dangerfield 1990b, 1991).

The ecology of the common fungus growing species *Macrotermes michaelseni* has been studied extensively in the Okavango Delta generating information on mound structure and distributions (Schuurman & Dangerfield 1994a, 1996), intraspecific aggression (Schuurman & Dangerfield 1994b) and foraging (Dangerfield & Musogelo 1997, Dangerfield & Schuurman 2000). Further studies have been completed on the consequences of termite activity for decomposition processes in the Okavango Delta (Gregor Schuurman, pers. comm.). The conclusion from these studies is that whilst there are complexities in the behavours and interactions between termite taxa, *M. michaelseni* is clearly a critical organism in the Okavango Delta. As with other *Macrotermes* species in other parts of Africa (e.g. Lepage 1981, Pomeroy 1989), *M. michaelseni* can process more carbon and have a greater overall influence on soils and, indirectly, primary production than the large mammalian herbivores (Buxton 1981).

The unusual patterns of water movement, climate and geology of the Okavango Delta have allowed *M. michaelseni* to extend obvious local influences on soil properties around mounds into large scale ecosystem engineering that sets in motion processes that define, to a considerable extent, the landscape structure of the whole system (Dangerfield *et al.* 1998; Ellery *et al.* 1998, 2000, McCarthy, Ellery & Dangerfield 1998). Mounds provide establishment sites for woody plants that otherwise would not survive annual inundation by floodwaters. These safe sites are the foci of woody plant diversity in the permanently flooded panhandle and, in the south, grow progressively to create islands in the floodplains so typical of seasonal swamps.

There is an extensive literature on termites from Africa and it is difficult to do justice to this body of knowledge here. Many reviews have been published on the importance of termites in nutrient movements, especially as they relate to soil properties (Holt 1990, Jones 1990, Lee & Wood 1971, Lobry de Bruyn & Conacher 1990, Pomeroy 1983) Clearly, the ecological importance of this group is very high and perhaps the most significant of all the soil animal groups in the Four Corners area, but there are probably rather few significant conservation

concerns in terms of vulnerable or threatened species. A few local endemics may be present and vulnerable to land use change, especially the clearing of miombo woodland for charcoal production, but the inventory information is so poor that we will remain ignorant of this for some time. What is needed is continued expression of the beneficial ecological role of termites in soil processes and carbon cycling to balance the traditional image of termites as a pest.

# 11.5 STATE OF KNOWLEDGE FROM ECOLOGICAL AND CONSERVATION PERSPECTIVES

As the bulk of this review has already shown the ecological roles and general biology of soil fauna in the drier tropical savannas of Africa is reasonably well known. Termites are the dominant group and are often critical for many soil processes (Lee & Wood 1971). Ants, beetle larvae, collembola and mites are ubiquitous and also contribute significantly to carbon flows and soil processes. Locally other taxa such as millipedes can become very numerous with high biomass and contribute significantly to the ecosystem (Dangerfield & Telford 1996). So in savannas, just as in other habitats, productivity, stability and sustainability are often mediated, and in some cases buffered, by the activities of soil animals (Dangerfield 1993).

This knowledge has accumulated from individual research projects as well as international initiatives such as the TSBF program (Woomer & Swift 1994) and research is now entering a new phase that tries to implement this knowledge on ecological roles for better environmental management. This implementation is ongoing despite a glaring lack of specific taxonomic knowledge. Detailed inventory data for any of the soil fauna groups is absent and unlikely to come about using traditional taxonomic methods in the foreseeable future. Expertise, will and funds are all lacking. This knowledge gap does not limit the implementation of management or sustainability, but does drastically limit efforts to understand conservation status and planning for conservation of soil fauna.

We know that soil fauna assemblages are impacted upon by global change, especially habitat clearing for agriculture and land management practices such as grazing that alter vegetation structure (Lavelle 1988, Lavelle & Pashanasi 1989). It is also reasonably clear that these changes can be detrimental to key ecosystem processes, particularly if key taxa are lost. We are hampered, however, by not knowing the levels of redundancy offered by the high diversity of soil animals and therefore not knowing the amount of change that can be tolerated before an ecological process is impaired. In an experiment that removed colonies of *Macrotermes michaelseni* from natural savanna habitat in the Okavango delta, foraging by other termite species appeared to compensate and maintain levels of woody litter removal (Dangerfield & Schuurman 2000). This was a targeted removal, however, and not quite the same as a change in habitat as a result of land management.

Conservation status of soil fauna may be less affected by the consequences of sustained climate change, although this remains equivocal. The combination of drier conditions punctuated by more extreme rainfall events predicted for the region may have a negative impact on some species. Negative consequences will be more likely when there is the added stress of habitat loss and fragmentation. Again, without knowledge of endemism and biogeography at meaningful taxonomic levels (genus and below) the significance of these global changes are difficult to predict.

There is no doubt that land management practices designed to encourage beneficial soil fauna will be useful, economically sensible and likely to be adopted. In the medium-term this will be

beneficial to soil fauna conservation. Greater care in the application and type of insecticide use against pests, such as the planned tsetse fly eradication programs, will also ensure that these kinds of external pressures should be minimized. They are also likely to be more closely monitored (Grant 1988). What will be difficult to judge is the extent of species loss as a result of inevitable land clearing, agriculture and fuelwood practices that are a strong pressure on habitats within the Four Corners area, or losses as a result of the kinds of dramatic land use change that may result from tsetse fly removal.

The knowledge of levels of endemism and biogeography are so scant that any of the traditional conservation measures of reserves, management of hotspots, gap analyses, landscape management for corridors or meaningful mosaics seem inappropriate or impossible to design for soil fauna. Add to this the fact that some of the meso- and microfaunal groups remain almost completely unknown for the region and the task of conservation planning at local scales is indeed daunting.

#### **11.6 PRIORITY ISSUES FOR CONSERVATION**

In the traditional conservation view the obvious priority for soil fauna conservation would be to establish some more detailed inventories at reasonably fine taxonomic ranks and to include some estimates of the levels of endemism. This would provide more reliable measures of species losses and the pressures put on soil fauna assemblages by different natural resource management practices. This is, however, an unrealistic priority given the available expertise, resources and the magnitude of the task. The absence of such data for everywhere else in the world, with the possible exception of the somewhat depauperate continental Europe, also suggests this is unrealistic.

It may be possible to complete some inventories for the better known taxa. Termites would be an obvious choice. Even here, however, the expertise is limited and the majority of voucher specimens are housed outside the region. An inventory of selected groups at the species level would, however, provide invaluable knowledge that would enable at least some extrapolation to levels of species richness and potential species losses.

The most practical priorities would be to focus on an understanding of the pressures put on soil fauna assemblages by different natural resource management practices. This is the pressurestate-response approach to conservation promoted and used successfully in Australia. Natural resource managers, conservation biologists and ecologists identify the most likely pressures on soil animals at different scales from local habitats to landscapes. Likely pressures are changes to land use involving clearing, burning, soil disturbance and vegetation structure, together with introductions of alien weeds, pathogens and pest insects. Reduced elephant disturbance in many areas and increased elephant disturbance in a few others, such as the Chobe riverfront, are also major pressures as feeding by elephants changes vegetation structure and increases woody litter. There are also the inevitable changes to rainfall amounts and distributions brought about by climate change. Measurement of the current state of soil fauna requires a suite of benchmark monitoring sites that cover several land management practices, landscapes and regions. These sites must be selected based on their representation of general habitat patterns and their likelihood of being affected by significant land use or climate change. Regular monitoring of these sites, compared against benchmarks that are in reserves or relatively undisturbed areas, would provide information on the response.

The impediment of taxonomy could be overcome with a morphospecies or rapid biodiversity assessment (RBA) approach (Bachmann 1998, Beattie & Oliver 1994, Oliver & Beattie 1996)

which has been shown to work very successfully for soil fauna (Pik *et al.* 2002b, Pik, Oliver & Beattie 1999). Rapid biodiversity assessment employs the use of morphospecies as effective surrogates for true species in surveys. A morphospecies is distinguished amongst a limited set of specimens from a locality based on physical appearance, a process similar to formal taxonomy but simplified to be fast and efficient for fauna that are poorly known or where taxonomic expertise is in short supply.

Clearly the basic constraint on conservation remains our ignorance of the likely consequences of global change within the Four Corners. We know enough to be concerned as soil fauna assemblages are very likely to change significantly locally and perhaps regionally, yet the setting of practical priorities is difficult. One solution is in a new approach to monitoring described below, that in turning around the idea of cataloguing or conserving biodiversity into using biodiversity as a signature of environmental performance indirectly generates exactly the kinds of data needed to more adequately address conservation concerns and priorities.

Unlike for many of the large mammals, conservation of soil animals will happen in the landscape and not in reserves. Farming, wood use and water use practices that maintain significant numbers of small pockets of mature vegetation throughout the landscape will provide sources of many of the soil animal populations. Tillage, burning and crop residue management are also critical in maintaining the soil organic matter levels that promote soil animal activity. Care in these practices will have the dual benefit of improving both productivity and conservation.

#### 11.7 MONITORING

There is now an established rationale and several case studies for the use of insects in the monitoring of environmental change (Andersen 1990, Beattie *et al.* 1993, di Castri *et al.* 1992, Hilty & Merenlender 2000, Kremen 1992, Lawton *et al.* 1998, McGeoch 1998). Many of these are soil fauna groups (Andersen 1990, Desender & Baert 1995, Pik *et al.* 2002b, Wheater, Cullen & Bell 2000, Whitford *et al.* 1998) because these taxa show all the critical characteristics need for reliable environmental monitoring, especially sensitivity, measurable responses and generality across landscapes.

The Key Centre for Biodiversity and Bioresources at Macquarie University in Australia has taken this idea of invertebrate assemblages as a signal of environmental status and developed tools to rapidly measure these biological signatures (Oliver, Dangerfield & York 1999, Oliver et al. 2000, Pik, Beattie & Dangerfield 2002a). These ideas and technologies have been brought together into a system called biotrack<sup>®</sup> (Pik et al. 2002a, Pik et al. 2002b). This system was designed to handle a large volume of biological material quickly and efficiently, so that it is possible to process 100,000 specimens from a survey in only a few weeks. Previously this would have taken years. Such an approach opens up the scope of assessment projects to include ecosystem scale problems or problems that require repeated sampling to provide monitoring information. It also allows unique flexibility in the design of surveys to compensate for patchiness and complexity of real systems, which increases statistical power and the reliability of data interpretations. A system like biotrack that draws on a simplified taxonomy (morphospecies), involves parataxonomists and achieves efficiency through information technology solutions is the most likely way that serious understanding of soil fauna conservation will happen in areas such as the Four Corners. More importantly, however, use of such tools will provide input for adaptive management that will have real outcomes for rural people.

The most effective approach for evaluation and monitoring is to select a series of sites on a range of land uses within a landscape and to include in those sites at least one reserve or intact

vegetation remnant as a local benchmark against which to compare other land uses. Each cluster of sites should be within a distinct catchment and several clusters should form the monitoring program. A site can be characterised by a series of ten pitfall trap and/or soil core samples from which ants, beetles and selected minor taxa are identified using RBA methods. A termite survey may also be beneficial.

The core advantage of localized site clusters is that sites can be selected to cover a wide range of land uses and can include sites which have undergone remediation or managed for improvements in overall system health. The use of systems such as bio**track** in the hands of local scientists and labour enables large numbers of sites to be sampled at minimal cost. The comparative approach that is possible because of many sites is a powerful way to understand the consequences of global change for conservation and also provides knowledge for effective adaptive management of production practices.

Soil fauna assemblages are powerful indicators of habitat and long-term ecological change. This alone is enough to suggest a monitoring program for soil fauna would be fruitful. Although our current knowledge is scant for the Four Corners area there is enough to suggest that these animals should be a target for both management and conservation given their pivotal role in maintaining ecosystem processes.

#### **11.8 REFERENCES**

Andersen, A.N. (1990). The use of ant communities to evaluate changes in Australian terrestrial ecosystems: a review and recipe. *Proc. Ecol. Soc. Aust.* **16**: 347-357.

Anderson, J.M. & Ingram, J.S.S. (1989). *Tropical Soil Biology and Fertility: A Handbook of Methods*. CAB International, Wallingford.

Andre, H.M., Noti, M.-I. & Lebrun, P. (1994). The soil fauna: the other last biotic frontier. *Biodiv. & Cons.* **3**: 45-56.

Bachmann, K. (1998). Species as units of diversity: an outdated concept. *Theory in Biosciences* **117**: 213-230.

Beattie, A.J. & Oliver, I. (1994). Taxonomic minimalism. Trends Ecol. & Evol. 9: 448-490.

Buxton, R.D. (1981). Termites and the turnover of dead wood in an arid environment. *Oecologia* **51**: 379-384.

Dangerfield, J.M. (1990a). Abundance, biomass and diversity of soil macrofauna in savanna woodland and associated managed habitats. *Pedobiologia* **34**: 141-151.

Dangerfield, J.M. (1990b). The distribution and abundance of *Cubitermes sankurensis* (Wassmann)(Isoptera; Termitidae) within a Miombo woodland site in Zimbabwe. *Afr. J. Ecol.* **28**: 15-20.

Dangerfield, J.M. (1991). Soil modification by *Cubitermes sankurensis* (Wassmann) (Isoptera; Termitidae) within a Miombo woodland site in Zimbabwe. *Afr. J. Ecol.* **29**: 267-269.

Dangerfield, J.M. (1993). Soil animals and soil fertility: A critical component of woodland productivity? In: *The Ecology and Management of Indigenous Forests in Southern Africa* (edited by G.D. Piearce & D.J. Gumbo), pp. 209-215. Zimbabwe Forestry Commission and SAREC, Harare.

Dangerfield, J.M. (1997). Abundance and diversity of soil macrofauna in northern Botswana. J. *Trop. Ecol.* 13: 527-538.

Dangerfield, J.M. & Chipfunde, L. (1995). Stress tolerance and burrowing behaviour in the southern African millipede *Alloporus uncinatus* (Attems). *J. Zool.* **235**: 17-27.

Dangerfield, J.M. & Kaunda, S.K. (1994). Millipede behaviour in a savanna woodland habitat in south-east Botswana. *Afr. J. Ecol.* **32**: 337-341.

Dangerfield, J.M., McCarthy, T.S. & Ellery, W.N. (1998). The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. *J. Trop. Ecol.* **14**: 507-520.

Dangerfield, J.M., Milner, A.E. & Matthews, R. (1993a). Seasonal activity patterns and behaviour of juliform millipedes in south-eastern Botswana. *J. Trop. Ecol.* **8**: 451-464.

Dangerfield, J.M. & Musogelo, D.K. (1997). Termite foraging on toilet roll baits in semi-arid savanna, south-east Botswana. *Sociobiology* **30**: 133-143.

Dangerfield, J.M. & Schuurman, G. (2000). Foraging by fungus growing termites (Isoptera: Macrotermitinae) in the Okavango Delta, Botswana. *J. Trop. Ecol.* **16**: 717-732.

Dangerfield, J.M. & Telford, S.R. (1991a). Distribution patterns of *Aphiloscia maculicornis* Budde-Lund (Crustacea, Oniscidae) in a moist tropical forest above Victoria Falls, Zimbabwe. In: *Third International Symposium on the Biology of Terrestrial Isopods* (edited by P. Juchault & J.P. Mocquard), pp. 57-63. Vol. III, Poitiers, France.

Dangerfield, J.M. & Telford, S.R. (1991b). Seasonal activity patterns of Julid millipedes in Zimbabwe. J. Trop. Ecol. 7: 281-285.

Dangerfield, J.M. & Telford, S.R. (1995). Tactics of reproduction and reproductive allocation in woodlice from southern Africa. *J. Trop. Ecol.* **11**: 1-9.

Dangerfield, J.M. & Telford, S.R. (1996). The ecology of savanna millipedes in southern Africa. In: *Acta Myriapodologica* (edited by J.-J. Geoffroy, J.-P. Mauriès & M. Nguyen Duy - Jacquemin), Vol. 169, pp. 617-625. Mémoirs Museum natural Histoire nationale, Paris.

Dangerfield, J.M., Veenendaal, E., Riddoch, B. & Black, H. (1993b). Termites and land use in south-east Botswana: Variety and abundance of termite surface features. *Botswana Notes & Records* 24: 165-180.

David, J.F., Ponge, J.F. & Delecour, F. (1993). The saprophagous macrofauna of different types of humus in beech forests of the Ardenne (Belgium). *Pedobiologia* **37**: 49-56.

Dempster, J.P. (1989). Insect introductions: natural dispersal and population persistence in insects. *Entomologist* **108**: 5-13.

Desender, K. & Baert, L. (1995). Carabid beetles as bio-indicators in Belgian coastal dunes: a long term monitoring experiment. *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Entomologie* **65**: 35-54.

di Castri, F., Robertson Vernhes, J. & Younes, T. (1992). Inventorying and monitoring biodiversity. Biology International, Special Issue 27, pp. 1-28.

Eggleton, P., Williams, P.H. & Gaston, K.J. (1994). Explaining global termite diversity: productivity or history. *Biodiv. & Cons.* **3**: 318-330.

Ehrlich, P.R. & Murphy, D.D. (1987). Conservation lessons from long term studies of checkerspot butterflies. *Cons. Biol.* 1:122-131.

Ellery, W.N., McCarthy, T.S. & Dangerfield, J.M. (1998). Biotic factors in mima mound development: Evidence from floodplains of the Okavango Delta, Botswana. *Inter. J. Ecol. & Environ. Sci.* 24: 293-313.

Ellery, W.N., McCarthy, T.S. & Dangerfield, J.M. (2000). Floristic diversity in the Okavango Delta, Botswana as an endogenous product of biological activity. In: *Biodiversity in Wetlands* (edited by B. Gopal, W.J. Junk & J.A. Davis), pp. 195-226. Backhuys, Leiden, Netherlands.

Ferrar, P. (1982). Termites of a South African savanna I. List of species and subhabitat preferences. *Oecologia* **52**: 125-132.

Giller, P.S. (1996). The diversity of soil communities, the "poor man's tropical rainforest". *Biodiv. & Cons.* **5**: 135-168.

Grant, I.F. (1988). Appropriate technology for monitoring environmental effects of insecticides in the tropics. In: *Field Methods for the Study of the Environmental Effects of Pesticides* (edited by M.P. Greaves, B.D. Smith & P.W. Greig-Smith), pp. 147-156. BCPC, Thornton Heath.

Haagsma, K.A. & Rust, M.K. (1993). Two marking dyes useful for monitoring field populations of *Reticulitermes hesperus* (Isoptera: Rhinotermitidae). *Sociobiology* **23**: 155-164.

Hendrix, P.F. (1996). Nearctic earthworm fauna in the southern USA: biodiversity and effects on ecosystem processes. *Biodiv. & Cons.* **5**: 223-234.

Hilty, J. & Merenlender, A. (2000). Faunal indicator taxa selection for monitoring ecosystem health. *Biol. Cons.* **92**: 185-197.

Holt, J.A. (1990). Carbon mineralization in semi-arid tropical Australia: the role of mound building termites. PhD thesis, University of Queensland, Townsville.

Hooper, D.U., Dangerfield, J.M., Brussaard, L., Wall, D., Wardle, D., Bignell, D.E., Brown, V.K., Coleman, D., Giller, K., van der Koppel, J., Lavelle, P., van der Putten, W.H., de Ruiter, P., Rusek, J., Sala, O., Silver, W., Tiedje, J., van Veen, J.A. & Walters, V. (2000). Interactions between above and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. *BioScience* **50**: 1049-1061.

Jepson, P.C., Efe, E. & Wiles, J.A. (1995). The Toxicity of Dimethoate to predatory Coleoptera: Developing an approach to risk analysis for broad-spectrum pesticides. *Archives of Environ. Contamin. & Toxicology* **28**: 500-507.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* 69: 373-386.

Jones, J.A. (1990). Termites, soil fertility and carbon cycling in dry tropical Africa: a hypothesis. *J. Trop. Ecol.* **6**: 291-305.

Kovach, J., Petzoldt, C., Degni, J. & Tette, J. (1992). A method to measure the environmental impact of pesticides. *New York's Food & Life Sci. Bull.* **139**: 1-8.

Kremen, C. (1992). Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Applic.* **33**: 203-217.

Lavelle, P. (1988). Assessing the abundance and role of invertebrate communities in tropical soils: Aims and methods. *J. Afr. Zool.* **102**: 275-283.

Lavelle, P., Dangerfield, J.M., Fragoso, C., Lopez-Hernandez, D., Eschenbrenner, V., Brussard, L. & Pashanasi, B. (1994). The relationship between soil macrofauna and tropical soil fertility. In: *The Biological Management of Tropical Soil Fertility* (edited by P.L. Woomer & M.J. Swift), pp. 137-169. John Wiley & Sons, Chichester.

Lavelle, P. & Pashanasi, B. (1989). Soil macrofauna and land management in Peruvian Amazonia (Yurimaguas, Loreto). *Pedobiologia* **33**: 283-291.

Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holts, R.D., Srivastava, D.S. & Watt, D.A. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* **391**: 72-75.

Lawton, J.H. & Brown, V.K. (1993). Redundancy in ecosystems. In: *Biodiversity and Ecosystem Function* (edited by E.-D. Schulze & H.A. Mooney), pp. 255-270. Springer-Verlag, Frankfurt.

Leakey, R.J.G. & Proctor, J. (1987). Invertebrates in the litter and soil at a range of altitudes on Gunung Silam, a small ultrabasic mountain in Sabah. *J. Trop. Ecol.* **3**: 119-129.

Lee, K.E. & Wood, T.G. (1971). Termites and Soils. Academic Press, London.

Lepage, M. (1981). L'impacte des populations récoltantes des Macrotermes michaelseni (Sjostedt)(Isoptera: Macrotermitinae) dans une écosystème semi-aride (Kaijaido, Kenya) II. Nourriture récoltée, comparison avec les grands herbivores. *Insectes Sociaux* **28**: 309-319.

Lobry de Bruyn, L.A. & Conacher, A.J. (1990). The role of termites and ants in soil modification: A review. *Aust. J. Soil Res.* 28: 55-93.

Mawdsley, N.A. & Stork, N. (1995). Species extinctions in insects: ecological and biogeographic considerations. In: *Insects in a Changing Environment* (edited by R. Harrington & N. Stork), pp. 321-369. Academic Press, London.

McCarthy, T.S., Ellery, W.N. & Dangerfield, J.M. (1998). The role of soil biota in shaping flood plain morphology on the Okavango alluvial fan, Botswana. *Earth Surface Processes & Landforms* **23**: 291-316.

McGeoch, M.A. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* **73**: 181-201.

Mitchell, B.L. (1980). Report on a survey of the termites of Zimbabwe. Occ. Papers Nat. Mus. & Monum., Ser. B, Nat. Sci. 6: 189-323.

Murphy, C.F., Jepson, P.C. & Croft, B.A. (1994). Database analysis of the toxicity of antilocust pesticides to non-target, beneficial invertebrates. *Crop Protection* **13**: 413-420. New, T.R. & Yen, A.L. (1995). Ecological importance and invertebrate conservation. *Oryx* **29**: 187-191.

Oliver, I. & Beattie, A.J. (1996). Invertebrate morpho-species as surrogates for species: A case study. *Cons. Biol.* **10**: 99-109.

Oliver, I., Dangerfield, J.M. & York, A. (1999). When and how to conduct a biodiversity assessment of terrestrial invertebrates. In: *The Other 99%. The Conservation and Biodiversity of Invertebrates* (edited by W. Ponder & D. Lunney), pp. 8-18. Transactions of the Royal Zoological Society of New South Wales, Sydney, Australia.

Oliver, I., Pik, A., Britton, D., Dangerfield, M.J., Colwell, R.K. & Beattie, A.J. (2000). Virtual Biodiversity assessment systems. *Bioscience* **50**: 441-450.

Pik, A., Beattie, A.J., & Dangerfield, J.M. (2002a). BioTrack simplifies monitoring of invertebrates on restored sites. *Ecological Restoration* **20**: 67-68.

Pik, A.J., Dangerfield, J.M., Bramble, R.A., Angus, C. & Nipperess, D.A. (2002b). The use of invertebrates to detect small-scale habitat heterogeneity and its application to restoration practices. *Environ. Monitoring & Assessment* **75**: 179-199.

Pik, A.J., Oliver, I. & Beattie, A.J. (1999). Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Aust. J. Ecol.* 24: 555-562.

Pomeroy, D.E. (1983). Some effects of mound-building termites on the soils of a semi-arid area of Kenya. J. Soil Sci. 34: 555-570.

Pomeroy, D.E. (1989). Studies on a two species population of termites in Kenya (Isoptera). *Sociobiology* **15**: 219-236.

Samways, M.J. (1993). Insects in biodiversity conservation: some perspectives and directives. *Biodiv. & Cons.* **2**: 258-282.

Samways, M.J. (1996). Insects on the brink of a major discontinuity. *Biodiv. & Cons.* **5**: 1047-1058.

Schaefer, M. (1990). The soil fauna of a beech forest on limestone: trophic structure and energy budget. *Oecologia* **82**: 128-136.

Schaefer, M. & Schauermann, J. (1990). The soil fauna of beech forests: comparison between a mull and a moder soil. *Pedobiologia* **34**: 299-314.

Schuurman, G. & Dangerfield, J.M. (1994a). Abundance, distribution and feeding ecology of fungus growing termites of the genus *Macrotermes* in Moremi Game Reserve, Report No. 2. Dept. Wildlife & National Parks, Gaborone.

Schuurman, G. & Dangerfield, J.M. (1994b). Assessment of intraspecific aggression in *Macrotermes michaelseni* (Isoptera: Macrotermitinae). *Sociobiology* **24**: 1-6.

Schuurman, G. & Dangerfield, J.M. (1996). Mound dimensions, internal structure and potential colony size in the fungus growing termite *Macrotermes michaelseni* (Isoptera: Macrotermitinae). *Sociobiology* **27**: 29-38.

Sherratt, T.N. & Jepson, P.C. (1993). A metapopulation approach to modelling the long term impact of pesticide on invertebrates. *J. Appl. Ecol.* **30**: 696-705.

Smith, P., Andrén, O., Brussaard, L., Dangerfield, J.M., Ekschmitt, K., Lavelle, P. & Tate, K. (1998). Soil biota and global change at the ecosystem level: Describing soil biota in mathematical models. *Global Change Biology* **4**: 703-712.

Stark, J.D., Jepson, P.C. & Thomas, C.F.G. (1995). The effects of pesticides on spiders from the lab to the landscape. *Review Pesticides Toxicol.* **3**: 83-110.

Taiti, S. & Ferrara, F. (1980). The family Philosciidae (Crustacea Oniscoidea) in Africa, south of the Sahara. *Italian J. Zool.* **4**: 53-98.

Theiling, K.M. & Croft, B.A. (1988). Pesticide side-effects on arthropod natural enemies: a database analysis. *Agric. Ecosyst. Environ.* **21**: 191-218.

Tingle, C.C.D. (1995). Some effects of DDT used to control tsetse fly on woodland invertebrates in Zimbabwe. *Acta Zool. Fennica* **196**: 361-363.

Tingle, C.C.D. & Grant, I.F. (1995). Effect of DDT selectively applied for tsetse fly (*Glossina* sp) control on litter decomposition and soil fauna in semi-arid mopane woodland in Zimbabwe. *Acta Zool. Fennica* **196**: 364-368.

Tingle, C.C.D., Lauer, S. & Armstrong, G. (1992). Dry season, epigeal invertebrate fauna of mopane woodland in northwestern Zimbabwe. *J. Arid Environ.* **23**: 397-414.

Vickerman, G.P. (1988). Farm scale evaluation of the long-term effects of different pesticide regimes on the arthropod fauna of winter wheat. In: *Field Methods for the Study of the Environmental Effects of Pesticides* (edited by M.P. Greaves, B.D. Smith & P.W. Greig-Smith), pp. 127-135. BSPS Monograph 40, BCPC, Thornton Heath.

Wheater, C.P., Cullen, W.D. & Bell, J.R. (2000). Spider communities as tools for monitoring reclaimed limestone quarry. *Land. Ecol.* **15**: 401-406.

Whitford, W.G. (1996). The importance of the biodiversity of soil biota in arid ecosystems. *Biodiv. & Cons.* **5**: 185-195.

Whitford, W.G., De Soyza, A.G., Van Zee, J.W., Herrick, J.E. & Havstad, K.M. (1998). Vegetation, soil, and animal indicators of rangeland. *Environ. Monitoring & Assessment* **51**: 179-200.

Wolters, V., Silver, W.E., Bignell, D.E., Coleman, D.C., Hooper, D.U., Lavelle, P., van der Putten, W., de Ruiter, P., Rusek, J., Wall, D., Wardle, D.A., Dangerfield, J.M., Brown, V.K., Giller, K., Sala, O., Tiedje, J. & van Veen, J.A. (2000). Global change effects on above- and belowground biodiversity in terrestrial ecosystems: Interactions and implications for ecosystem functioning. *BioScience* **50**: 1089-1098.

Wood, T.G. & Sands, W.A. (1978). The role of termites in ecosystems. In: *Production Ecology* of *Ants and Termites* (edited by M.V. Brian), pp. 245-292. Cambridge University Press, Cambridge.

Woomer, P.L. & Swift, M.J. [editors] (1994). *The Biological Management of Tropical Soil Fertility*. John Wiley & Sons, Chichester.

Young, I., Blanchart, E., Chenu, C., Dangerfield, J.M., Fragoso, C., Grimaldi, M., Ingram, J.S.S. & Jocteur Monrozier, L. (1998). The interaction of soil biota and soil structure under global change. *Global Change Biology* **4**: 703-712.