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ECOLOGY OF DESERT ENVIRONMENTS

(A Festschrift for Prof. J.L. Cloudsley-Thompson on his 80th Birthday)

Editor

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**INVERTEBRATES : THEIR EFFECTS ON THE
PROPERTIES AND PROCESSES OF DESERT
ECOSYSTEMS**

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Invertebrates: their effects on the properties and processes of desert ecosystems

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In 1969 I was a neophyte desert biologist with less than 5 years of experience in a desert region. My work up to that point in time had focused exclusively on the physiological and behavioral adaptations of vertebrates, especially amphibians and reptiles, to life in the desert. In summer of 1969, Professor John Cloudsley-Thompson, his wife Anne, and their sons stayed with us in Las Cruces, New Mexico for a short visit. Conversations and field excursions with John opened my eyes to the endless opportunities for meaningful research on desert invertebrates. His unbounded enthusiasm and interest in the diverse invertebrate fauna was infectious. To this inspiring teacher, John Cloudsley-Thompson, I owe immense gratitude for encouraging me to expand my research on desert biota to invertebrates and to focus on the importance of these animals in deserts. Without his inspiration, this chapter would not have been possible.

Deserts are, by definition, water limited regions. Life in deserts is dependent upon water availability and soil resources (chemical nutrients). Because of limited rainfall and patterns of redistribution of water across desert landscapes, vegetation is patchy. An important component of the diversity of life in arid regions is the patchiness of soil properties and the resulting diversity of the flora of the patches. Patches differ in their characteristics as a result of interactions between flora, fauna, and the abiotic environment. While there is a large literature on heterogeneity and vegetation patterns in arid lands, there is a paucity of literature on the interactions of the fauna, climate, and soils and their effects on heterogeneity. Understanding how desert ecosystems function requires an understanding of feedbacks and indirect effects of fauna on structural properties of ecosystems and on ecosystem processes.

Many of the ways in which animals affect ecosystem properties and processes have been referred to as engineering (Lawton 1994). "A critical characteristic of ecosystem engineering is that it must change the availability (quality, quantity, distribution) of resources utilized by other taxa, excluding the biomass provided directly by the population of allogenic engineers." (Lawton 1994). Although animals make up but a small fraction of the living biomass of desert systems, they may play critical roles in ecosystem processes or as modifiers of ecosystem properties (Chew, 1974, Jones et al. 1994).

The invertebrate faunas of desert regions are composed of representatives of a large number of phyla. Phyla represented in deserts include: Protozoa, Rotifera, Nematoda, Oligochaeta, Mollusca, and Arthropoda. Arthropods are the most conspicuous components of the fauna in most desert areas and have been the focus of much of the research on desert invertebrates. Information on many groups of desert-dwelling arthropods is limited to inclusion on faunal lists with little or no information available on their natural history and ecology. There is, however, a growing literature on the roles of some invertebrate taxa in ecosystems and their effects on ecosystem properties and processes. This review focuses on the role of invertebrates as key players in decomposition and nutrient cycling processes and their roles as engineers that change resource availability for other species and/or contribute to the structure and dynamics of patches that make up different parts of desert landscapes.

Decomposition and Nutrient Cycling

In deserts dead plant materials on the soil surface are decomposed by abiotic processes (heat and ultraviolet light) (MacKay et al. 1987, Moorhead and Reynolds, 1989) or are consumed by invertebrate detritivores and decomposed in their guts by the symbiotic microflora and microfauna (Crawford 1988). Several groups of surface active macroarthropods are included in the desert detritivores: isopods, camel crickets, millipedes, and tenebrionid beetles. The gut symbionts of these detritivores include bacteria, fungi, protozoans and nematodes (Crawford 1988). The gut symbionts allow relatively high assimilation efficiencies (30-70%) even when the animals consume dead plant materials that are primarily cellulose and lignin. Another group of macroarthropods that is widely distributed in deserts are cockroaches (Dictyoptera, Polyphagidae). These arthropods feed on decaying leaves and roots of desert shrubs (Hawke and Farley 1973). The temporal activity patterns of detritivorous macroarthropods vary considerably among the different taxa. The variation in amount of time spent feeding and seeking preferred microclimates is probably a function of the spatial distribution of detritus in the environment and the quality of that material. For example, tenebrionid beetles in the hyperarid Namib, spend much of their time on the surface where their high body temperatures are only slightly below lethal. Hamilton (1973) proposed that 'maxithermy' allowed the animals to increase their fitness by remaining at the warmest sublethal temperatures possible for as long as they can. In hyperarid environments, patches of detritus are widely scattered requiring detritivores to spend considerable search time to locate food sources. Also, 'maxithermy' may be required for the gut microflora to efficiently decompose the detritus. The relative importance of detritivorous macroarthropods as

agents of decomposition and nutrient cycling cannot be assessed from the available data in the literature.

In deserts where leaf cutting Attine ants occur, an unknown fraction of the dead plant material may be transported to the nests and broken down by the fungi cultured by these invertebrate gardeners (Gamboa, 1975). Desert Attine ants collect senesced leaves and senesced floral part (petals and sepals). However there are no quantitative data on the rates of leaf and litter collection that can be extrapolated over a year to estimate fraction of litter processed by these ants.

In most deserts, termites appear to process a large fraction of the total litter input. Because termites are social insects, their numbers and biomass far exceeds that of other detritivorous macroarthropods in most deserts. High biomass of subterranean and epigeic termites have been reported for semi-arid savanna in southern Africa (Ferrari 1982) and large populations have been reported from Saudi Arabia (Badawi et al. 1984). Johnson and Wood (1980) report on a number of species of termites that occur in the arid regions of Africa and the Arabian Peninsula. Their summary of the feeding habits of the species shows that in most of these regions, dead roots and above-ground herbaceous and woody vegetation are utilized by one or more of the species. I have observed large numbers of harvester termites (*Hodotermes mossambicus*) cutting stems of dead grasses or collecting stems and leaves of grasses in the Kalahari Desert and in parts of the Karoo Desert in South Africa. The abundance of soil mounds and foraging entrances in these areas suggest that termites probably process a large fraction of the standing dead grass and detritus in these deserts.

In the Sahel, termites (*Microtermes* spp. and *Ondontotermes* spp.) were responsible for up to 80% of litter mass loss in one year (Mando & Brussaard 1999). In the savanna region of Nigeria, termites were reported to remove approximately 60% of the annual input of dead wood (Collins 1981). Mando and Brussaard 1999) suggested that the dominant termite species in the Sahel may contribute nitrogen rich patches in the soil associated with their combs which are constructed from fecal pellets. They reported that the combs stimulate microbial metabolism, increase nitrogen mineralization rates and are higher in both soil carbon and soil nitrogen than the surrounding soil. In the arid region of northern Kenya, several species of termites combined to remove approximately 50% of the annual production of grass and 4% of the annual input of wood litter (Bagnine 1989).

In a semiarid grassland in Texas, Bodine and Ueckert (1975) reported that the desert termite, *Gnathamitermes tubiformans*, consumed 55% of the surface litter. In the Chihuahuan Desert of North America where studies have been conducted on quantities of materials consumed by termites, it was estimated that these arthropods processed more than 50% of the annual input of detritus and herbivore dung (Whitford et al. 1982) (Fig. 1). In the Chihuahuan Desert, subterranean termites also consumed large quantities of dead roots. On plots from which termites were excluded, annual mass loss from roots of grasses and herbaceous plants was 15% in comparison to 62% mass loss on plots with termites present (Fig. 2) (Table 1) (Whitford et al. 1988). Studies of the abundance and distribution of subterranean termites in Australia led to the suggestion that these insects may be more important as detritivores in the arid and semi-arid areas of this continent than was estimated in

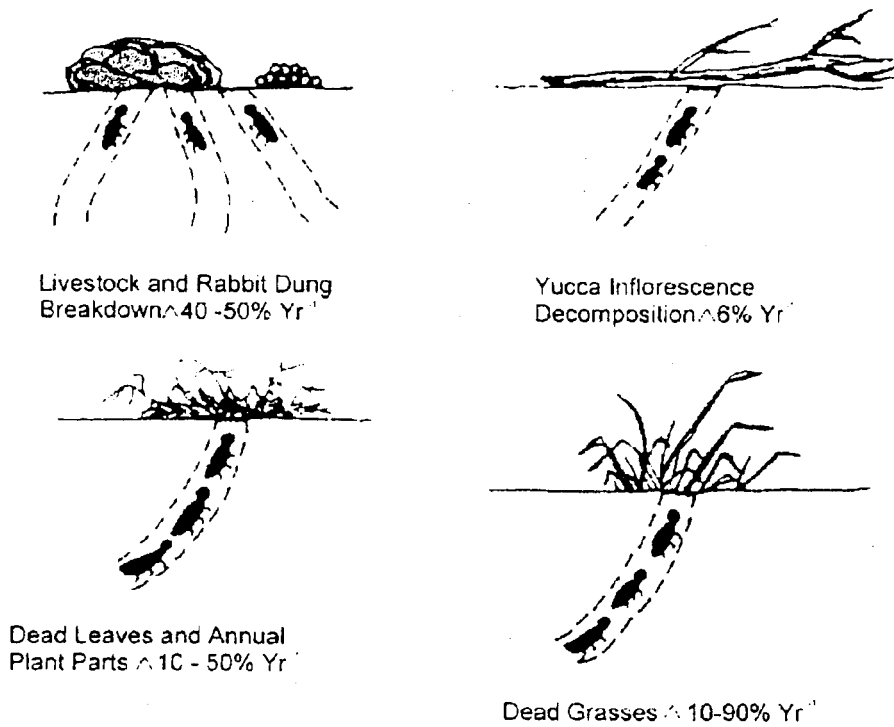


Figure 1. The keystone role of subterranean termites in the decomposition of organic materials in Chihuahuan Desert ecosystems.

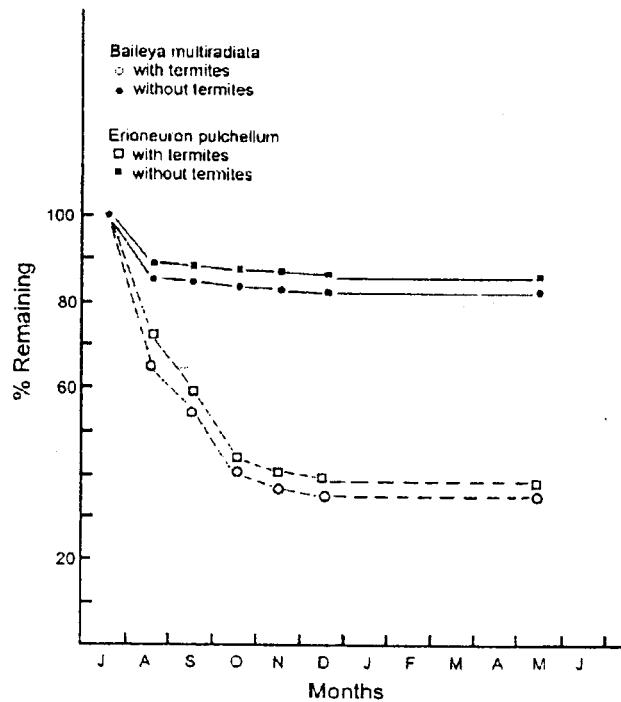


Figure 2. Rates of mass loss of an annual herbaceous plant (*Baileya multiradiata*) and a perennial grass (*Erioneuron pulchellum*) on plots from which termites were chemically excluded and plots with termites present. (From Whitford et al. 1988).

North America (Whitford et al. 1992). In tropical semi-arid grasslands in India, termites were estimated to attack between 73% of the plant debris and up to 100 % of the roots and shoots of some species of grasses (Gupta et al. 1981).

Table 1. Consumption (expressed as percentage of annual standing stock) of dead plant parts and animal dung by subterranean termites in the northern Chihuahuan Desert (After Whitford, 1991). ^a variation in consumption of shrub leaves by subterranean termites is a function of the availability of other (preferred) dead plant material. ^b termites remove the surface layer of wood softened by fungi.

Material	Consumed
Annual plants (above ground parts)	40-90%
Annual plants (dead roots)	50-70%
Grass tillers and leaves (standing dead)	60-90%
Grass roots (dead)	50-70%
Shrub and tree leaves ^(a)	0-90%
Dead wood ^(b)	<1 - 5%
Livestock dung	60-100%
Rabbit dung	15-50%

The processing of dead plant material by the gut symbionts of termites has important implications for the organic matter content of soils and for the cycling of nutrients. The gut symbionts of some species of termites have the capacity to decompose lignins and other recalcitrant organic molecules (Butler and Buckerfield (1979). Thus termites produce only small quantities of feces. Termite feces contain very little recalcitrant carbon to contribute to the soil organic matter pool. The patterns of soil organic matter content on a Chihuahuan Desert watershed were shown to be negatively correlated with the abundance/activity of subterranean termites ($r = 0.97$) (Nash and Whitford, 1995). Jones (1989) based on data from a semi-arid region of Africa suggested that the low soil organic contents of soils in subtropical, semi-arid regions is probably largely the result of termite activity. Since the rates of processes such as nitrogen mineralization are directly related to the soil organic matter content (Whitford et al. 1987), termites can indirectly affect the availability of essential nutrients for plant growth.

There are other characteristics of termites that contribute directly to nutrient cycling processes. Many species of termites have been shown to fix atmospheric nitrogen via hindgut symbionts (Beneman 1973, Bentley 1984, Schaefer & Whitford 1981) which allows termites to utilize foods with high carbon-nitrogen ratios. This nitrogen enters the nitrogen cycle in desert ecosystems primarily through the many predators that feed on termites (Schaefer and Whitford 1981) (Fig. 1). Termites also contribute significantly to cycling of other soil nutrients such as phosphorus and sulfur via this same pathway (Schaefer and Whitford 1981). Mound building termites have been shown to affect soil fertility and nutrient cycling by the concentration of nutrients in the mound soils. The mounds erode when the colonies die and the area of eroded mound soils has higher nutrient contents than the surrounding soils (Coventry et al. 1988). Soil eroded from termite mounds has higher organic carbon and nitrogen content plus enhanced concentrations of some cations such as P, Ca, and Mg (Malaka

1977, Arshad 1982, Pomeroy 1983, Wood et al. 1983). The soil surrounding the mounds is enriched by this eroded material and supports higher biomass production and a different suite of plant species than the surrounding soils (Arshad 1982). Termites that build epigeic mounds thereby contribute to patch heterogeneity in the arid and semi-arid regions in which they occur. The materials used to construct sheeting over potential food materials are also enriched with nutrients such as calcium and potassium (Bagine, 1984).

The high nutrient content of termites and high rates of population growth by some species led to a proposal that termites be harvested to provide high protein supplement for chickens or other domestic stock (French 1982 and personal communication). French proposed that termites could be attracted into baits that could be removed from epigeic mounds or collected from the soil surface. The termites could be emptied from the bait containers into the chicken feed trays. French's proposal could become an important component of food production in arid regions where only a small fraction of the net primary production can be converted into consumable biomass by domesticated animal species. Utilizing termites to feed chickens or other domesticated animals can provide a mechanism for harvesting a larger fraction of the net primary production and convert unuseable cellulose into food for human consumption.

Although termites and other macroinvertebrates are the primary processors of dead plant materials that remain on the soil surface, the decomposition of roots and litter that is buried occurs through the interactions of a complex of soil micro- and mesofauna and the microflora. Plant materials trapped in animal produced pits may be buried by wind-blown soil or by run-off water sediment (Steinberger and Whitford 1983). The decomposition and nutrient mineralization of buried materials and dead roots differs greatly from the processing of plant materials retained on the soil surface.

Desert soils are characterized by high faunal diversity. Most of the micro- and mesofauna live in water films surrounding soil particles. Protozoans and nematodes encyst or enter an anhydrobiotic state when soil water potentials fall below the critical threshold for that species (Whitford 1989). Most of the soil-dwelling collembola also enter an anhydrobiotic state when soils dry (Poinsot-Balaguer, 1984) and some species of soil mites may enter a cryptobiotic state in dry soils (MacKay et al. 1986).

When soil water potentials in desert soils are above the activity threshold for most of the micro- and mesofauna, decomposition and nutrient mineralization result from the complex food web of the soil biota (Figs. 3,4). In desert soil much of the soil biota is inactive most of the time. Soil water potentials of desert soils remain at -3.0 to -6.0 MPa except for periods following rain. In Chihuahuan Desert soils approximately 50% of the soil protozoan population encysted at a soil water potential of -0.1 MPa and the entire protozoan population was estimated to be inactive at -0.4 MPa (Whitford, 1989). Half of the soil nematode population entered anhydrobiosis at -0.4 MPa and 99% of the soil nematodes were anhydrobiotic at soil water potentials between -3.0 and -5.0 MPa (Freckman et al. 1987). It is apparent that decomposition and mineralization is regulated by the activities of fungi that are capable of growing in dry soils and by those species of soil acari that remain active in dry soils (Whitford, 1989).

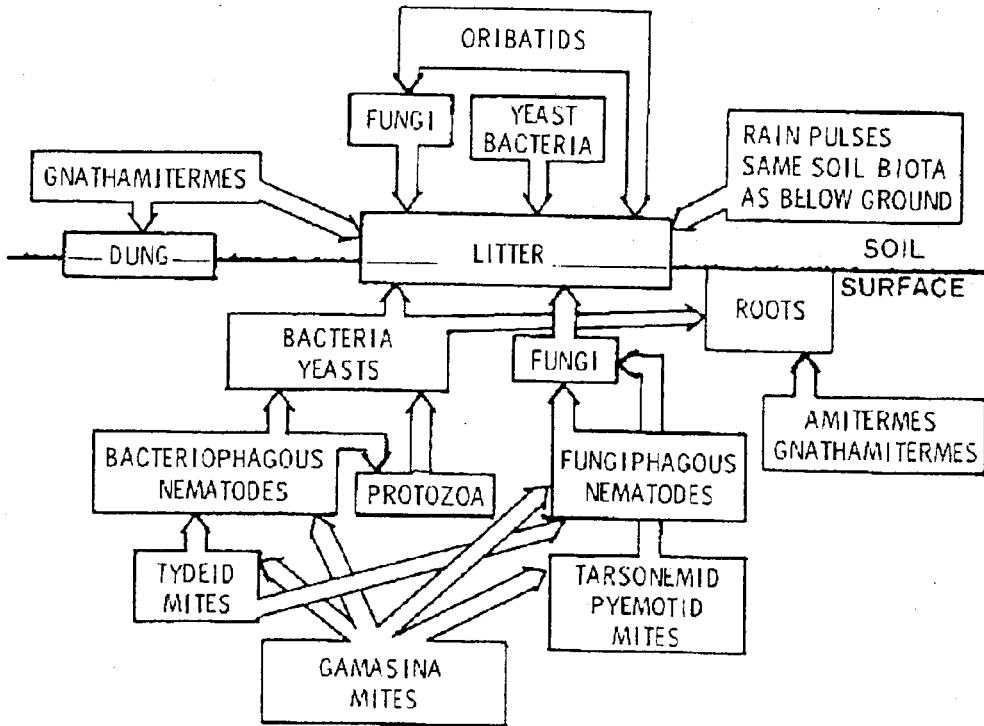


Figure 3. The biota involved in the decomposition of plant litter and dung on the soil surface and the decomposition of roots and buried litter in a Chihuahuan Desert ecosystem. *Amitermes* and *Gnathamitermes* are termite genera. Arrows indicate feeding relationships

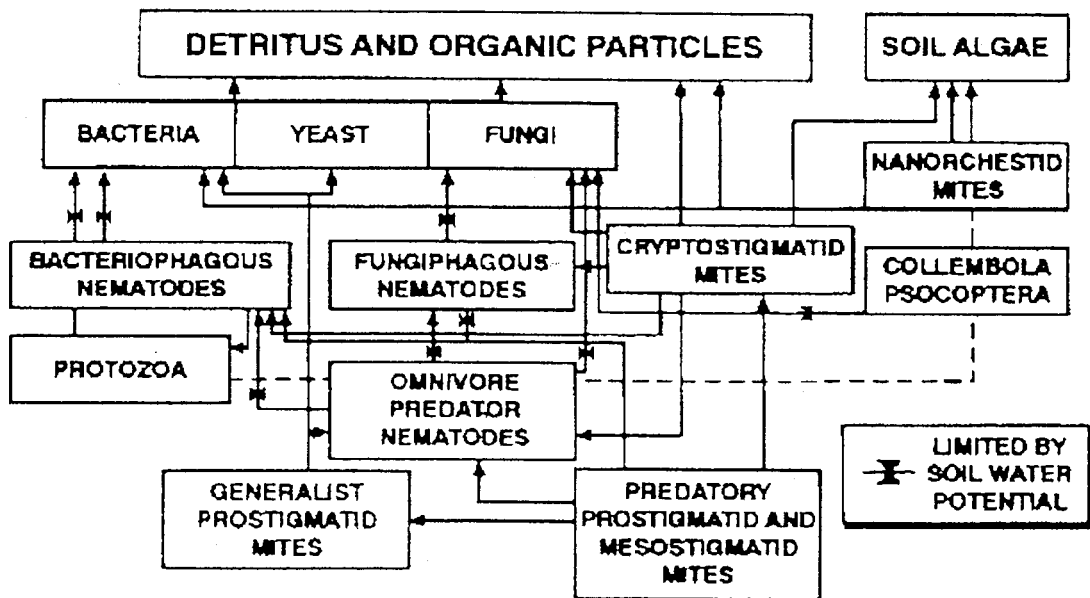


Figure 4. The effect of soil water potential on the structure of the belowground food web involved in decomposition of plant materials in the Chihuahuan Desert (after Whitford 1989).

The initial stage of decomposition of below-ground litter is primarily via soil bacteria. The bacteria are grazed by protozoans, primarily naked amoebae, and by bacteriophagous nematodes. The numbers of protozoans and nematodes are regulated by several species of omnivorous microarthropods (Acarina) that prey on the nematodes (Santos et al. (1981). When microarthropods were eliminated from buried litter by a broad-spectrum insecticide, bacteriophagous nematode numbers increased dramatically. The large numbers of nematodes overgrazed the bacteria thus reducing the rate of decomposition. In mesic ecosystems, microarthropods affect decomposition and mineralization processes by masticating the litter and passing it through their gut. This increases the surface area and inoculates the litter with microflora from the gut of the arthropods. The dominant soil acari in mesic systems are cryptostigmatid (oribatid mites) which make up only a small fraction of the soil acari community in arid and semi-arid ecosystems (Wallwork 1982, Wallwork et al. 1985, Nobel et al 1994). Thus, in arid and semi-arid regions, the role of microarthropods as regulators of the rate of decomposition is indirect via predation rather than direct via consumption of dead plant material.

The later stages of decomposition and mineralization in dry soils are regulated by some of the same species of omnivorous mites feeding on fungi. Fungi replace bacteria as the primary microfloral decomposers in dry soils (Fig 3) (Parker et al. 1984). Experiments in which microarthropods were removed showed that rates of nitrogen mineralization were significantly reduced compared to the rates measured when microarthropods were present. Elimination of fungivorous and omnivorous mites resulted in a large increase in fungal biomass. Mineral nitrogen from soil surrounding dead roots or buried litter is incorporated into fungal biomass. The fungi use the carbon in litter or roots as energy sources but scavenge nitrogen from the surrounding soil in order to produce fungal biomass. The nitrogen incorporated into fungal biomass is considered immobilized, i.e. not available to be absorbed by plant roots. Soil microarthropods that graze on fungal hyphae, release immobilized nitrogen as mineral nitrogen in the form of excretory products. These experiments demonstrate that mineralization of nitrogen in desert ecosystems requires the activities of soil microarthropods.

Pedogenesis

Soil formation theory while recognizing the biochemical contributions of soil biota to soil formation has overlooked biomechanical processes (Johnson and Hole 1994). Invertebrates contribute to soil formation via both biochemical and biomechanical processes. One of the most important contributions of invertebrates to ecosystem function is that of soil formation and turnover. Pulmonate snails (Mollusca: Pulmonata) have been found to be important contributors to pedogenesis in the Negev Desert. Two species of snail, *Euchondrus albulus* and *E. desertorum*, actually eat the endolithic lichens that grow under the surface of limestone rocks in the Negev (Schachak et al. 1987). They estimated that these snails contribute between 0.7 to 1.1 metric tons (0.6 to 1.0 m³) of finely ground limestone per hectare per year. A different species of snail (*Sphincterochila zonata*) contributes to soil formation in a different way. *S. zonata* feeds exclusively on the algae that grow on the soil surface following rain (Shachak and Steinberger 1980). They reported that a considerable amount of

soil was ingested with the algae and calculated that the snails removed approximately 142 kilograms per hectare of soil crust in the year of their study. The snails have assimilation efficiencies of around 10% resulting in considerable organic matter that is mixed with the ingested soil and egested as feces. Shachak and Steinberger (1980) suggest that not all of the ingested algae are killed in the passage through the snail gut and that the live algae in the egesta serve as sources of colonizers of new patches of soil crust. Another invertebrate that feeds on algal crusts and contributes to soil turnover in the Negev is the desert isopod (*Hemilepistus reaumuri*) (Schachak et al. 1976). It was estimated that a single isopod family excavated a volume of 62.3 cm³ during the construction of a burrow system (Schachak 1980). With minimum densities of burrow systems estimated between 0.14 and 1.2 m⁻² at the beginning of the reproductive season in these animals, it is obvious that considerable volumes of sub-soil are transported to the surface in a single year (minimum of 8.7 to 74.8 cm³). Thus in approximately 130-200 years, isopods in this system would transport sufficient subsurface soil to the surface to cover the surface with 1 cm of subsoil. The materials transported to the surface by isopods are disaggregated soil particles (low aggregate stability) that are easily removed by low energy overland flow during storms (Yair and Shachak, 1982). This process affects the soil moisture regime of the ecosystems in the region.

Termites contribute to pedogenesis by the construction of above ground nest mounds, the construction of runway sheeting and foraging sheeting and galleries around potential food items. Mound building termites may be responsible for the horizon development of some soils in regions where mound-building termites are abundant. For example, Holt et al. (1980) estimated densities of termite mounds at 283 ha⁻¹ in the semi-arid woodland near Charters Towers in northern Queensland, Australia. They estimated that if the soil accumulated in the termite mounds were spread evenly over the surface, it would form a layer 1.25 mm thick. Holt et al. (1980) also estimated the amount of soil reworked by termites in the construction and maintenance of mounds (replacing mound materials lost by erosion during intense rains). Using the most conservative estimates of quantities of soil materials used in this process, they estimated that the 20 cm thick sandy-loam A horizons of both the yellow and red earths of the region may have accumulated from the erosional degradation of termite mounds over the past 8000 years.

Their studies corroborate the estimates provided by Lee and Wood (1971). Lee and Wood (1971) concluded that "rates of accretion are slow, but are sufficient to be a significant factor in soil formation, since....the material most commonly used for mound construction is fine particle size fractions from deep soil horizons, so that mound building and subsequent mound erosion result in inversion of soil profiles and burial of coarser particle size fractions".

The bulk density of the mound material of most termite mounds that have been studied is higher than that of surrounding soil (Malaka, 1977, Holt et al. 1980). There is some evidence that mound building termites select materials from several sub-surface horizons and use that material in the mound construction and this may affect the chemical properties of the mound soil (Holt et al. 1980, Okwakol, 1987). The soils of termite mounds are modified by the addition of excreta and/or saliva. This results in higher concentrations of some soil nutrients (organic matter, N, P, Ca and

Mg) in the mound soils than in the surrounding unmodified soils (Malaka 1977a, Arshad 1981, 1982, Pomeroy 1983, Wood et al. 1983). Soil eroded from termite mounds produces a halo of nutrient rich soil around the base of the mounds. This soil halo supports higher quality, high biomass vegetation than the surrounding soil. Termitaria of harvester termites appear to be the origin of the earth mounds (heuweltjies) that are characteristic of the arid regions of southern Africa (Moore and Picker, 1991). These large mounds (up to 25m in diameter and 2.5 m in height) occupy between 14% and 25% of the land surface. The fine texture of the mound soils and the nutrients that are concentrated in the heuweltjie soils are only part of the evidence suggesting that these structures are the result of long-term occupation by termites. Radiocarbon dating of the calcrete in some of the mounds showed that some of the mounds were over 4000 years old (Moore and Picker, 1991).

Many species of subterranean termites construct runway and foraging gallery sheeting. Quantities of soil materials translocated to the surface in the construction of sheeting and galleries may be quite large. Bagnine (1984) estimated that two species of *Odontotermes* translocated soil at a rate of approximately 1060 kg of soil per hectare per year. At that rate of soil translocation, the surface would be covered with 1 cm depth of sheeting in six years (assuming a bulk density of 1.5). Foraging galleries of *Drepanotermes tamminensis* and *Amitermes neogermanus* in the semiarid region of Western Australia had significantly higher clay contents, increased organic carbon and lower pH than the surface soil (Lobry de Bruyn & Conacher 1995). The materials from foraging galleries and soil sheetings covering food sources are washed to the soil surface within a year and contribute to modification of the texture and chemistry of the surface soil horizon.

Ants have been shown to be agents of soil formation in several studies in mesic environments (Baxter and Hole, 1967; Mandel and Sorenson 1982). These authors list the following as ways in which ants modify soils: depositing subsoil on the surface, reducing soil bulk density, increasing concentration of organic matter, influencing nutrient cycling, and disrupting soil horizon development through the process of subsoil transport to the surface. In a humid savanna environment, one abundant ant species, *Paltothyreus tarsatus* was estimated to transport approximately $30 \text{ g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ of sand particles and soil aggregates (Levieux, 1976). This ant species increased the concentration of clay, carbon, iron oxides, and coarse sand in the A horizon (Levieux 1976). Ants play a similar role in soil formation in arid regions. Briesse (1982) reported that the estimated annual soil turnover by ants in an *Atriplex vesicaria* shrubland in the semi-arid region of Australia was $350 - 420 \text{ kg ha}^{-1} \text{ y}^{-1}$. Plant and animal material ejected from the nest mixed with the excavated soil resulting in an increase in carbon, nitrogen and phosphorus in the soils adjacent to the nest. However, Briesse (1982) did not determine the depth from which soil was transported to the surface nor was the textural composition reported.

Hydrology

In deserts, invertebrates directly affect the hydrological properties of soils by producing macropores. They also affect water infiltration and water storage by their effects on organic matter content of the soils. The production of macropores may be

the most important contribution of invertebrates to ecosystem function especially in areas with fine textured soils. Soil scientists and hydrologists have rediscovered the importance of soil macropores as avenues for water infiltration (Phillips et al., 1989). Macropores are continuous tubes or spaces (voids) in the soil with diameters larger than spaces in which capillary water movement occurs. Water is transported to deeper parts of the soil profile more rapidly than predicted by infiltration models of various particle-size distributions. Infiltration models predict water movement via capillary networks in soils. Water movement into soil via macropores is referred to as bulk flow. Bulk flow can occur in any small tunnel or burrow that is open at the surface. Subsurface structures may also contribute to water percolation. The numbers of macropores per unit area need not be large in order for the macropores to have an impact on water infiltration and storage. Several arthropod taxa have been shown to be important producers of macropores. These taxa include in order of relative importance: termites, ants, isopods, burrowing spiders, cicadas, and beetles.

The effect of termites on water infiltration varies with the natural history of the termite species in a particular desert area. Species that build above-ground termitaria affect infiltration by the volume of water shed from the nest structure that infiltrates into the soil immediately surrounding the mound. The soil around termite mounds has a high density of termite constructed tunnels that serve as macropores and that reduce the bulk density of the soil (Lee and Wood, 1971 a,b). Subterranean termites affect infiltration by the abundance of foraging tunnels that open to the surface or are within the upper 2-3 cm of the surface soil. Subterranean termites affect infiltration both by the abundance of macropores and by the reduction in bulk density of the soil. In a Chihuahuan Desert shrubland, a study comparing infiltration on plots with subterranean termites with plots from which termites had been eliminated showed that final infiltration rates were considerably higher in the plots with termites (Elkins et al. 1986). Subterranean termites increased cumulative infiltration amounts, final infiltration rates, soil water content and porosity of crusted soils in the African Sahel (Mando et al. 1996, Mando and Miedema 1997). In the arid regions of southeastern Australia, the estimates of small galleries and soil voids produced by termites suggested that these animals were important agents of soil modification that enhanced infiltration. Whitford et al. (1992) estimated 138 voids and tunnels m^{-2} to a depth of 20 cm. These types of voids and tunnels were responsible for enhanced infiltration and storage of water in soils where subterranean termites were concentrated (Figs. 5 & 6) (Tongway et al. 1989). Additional evidence for the impact of subterranean termites on infiltration was provided by Greene et al (1990) who found high infiltration rates in soils with preferential flow paths that were produced by termites. Infiltration rates were dramatically reduced in areas where annual burning resulted in the filling of termite produced channels by sand and silt. In the Australian arid and semi-arid region, banded or striped vegetation patterns characterize many of the watersheds (Tongway and Ludwig 1990) and termites are important agents in the development and functioning of that vegetation.

Although there have been no direct measurements of the effects of desert isopods on water infiltration, their burrowing behavior produces macropores. Studies of the desert isopod, *Hemilepistus reaumuri*, described the burrow systems in detail

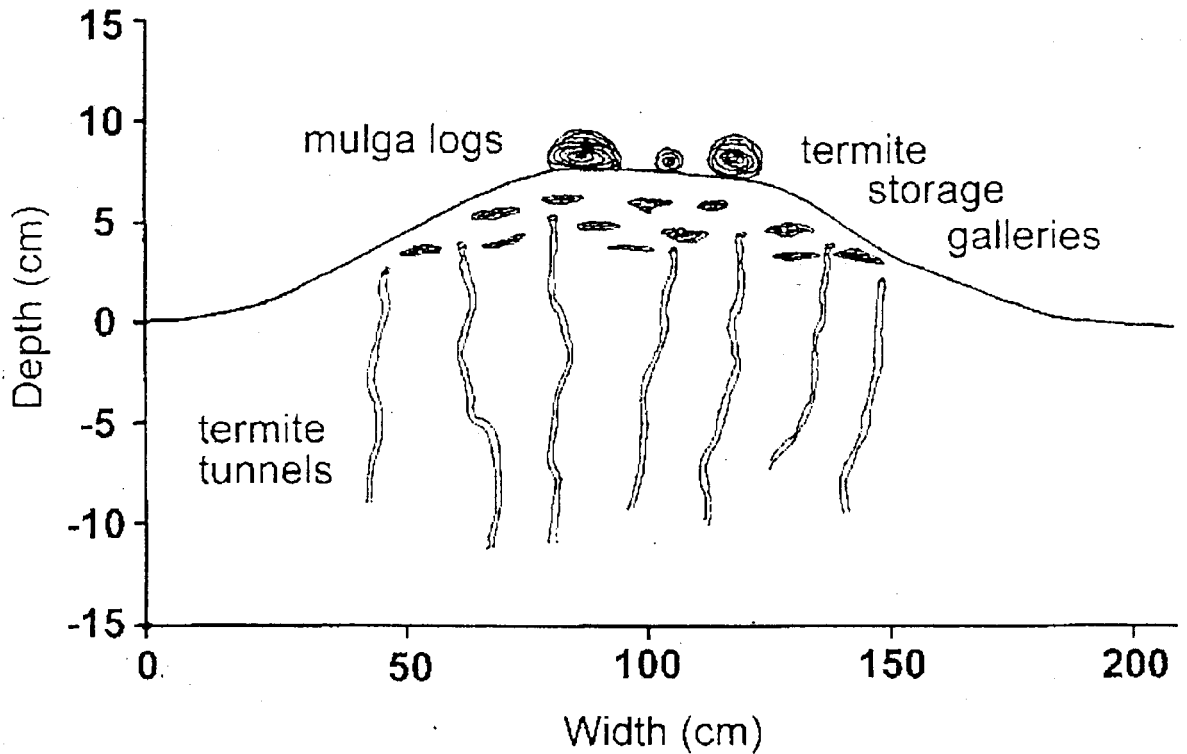


Figure 5. The macropore structure of a log mound on an erosion slope in a banded mulga (*Acacia aneura*) landscape in southeastern Australia.

(Shachak, 1980). During the course of a year, a simple burrow of 10 cm in depth is enlarged to a burrow up to 40 cm in depth with numerous side tunnels and chambers. The density of isopod burrows was estimated to be 0.14 m^{-2} to 1.2 m^{-2} in February which is in the middle of the rain season in the Negev. That density of burrow systems should have a significant effect on water infiltration in the fine texture loess soils of the Negev plains.

Soil nesting ants affect the hydrological characteristics of soils by the effects of the nests on bulk density and by the macropores provided by nest entrances and surficial chambers. Bulk densities of soils with ant nests are generally lower than the bulk densities of soils not associated with ant nests (Lobry de Bruyn and Conacher, 1990). The macropores produced by soil nesting ants affects ponded infiltration but infiltration rates are not significantly different at rainfall intensities that are not sufficiently high to produce ponding (Herrick and Whitford, 1995). Studies of the effects of ant nests on bulk flow in desert soils in Western Australia showed that bulk flow via ant biopores occurred only when the surface layer of soil was saturated and when there was surface ponding (Lobry deBruyn and Conacher 1994). The importance of the contribution of soil-nesting ants to water infiltration varies with the abundance of nest entrances per unit area and with soil texture. In the Australian arid zone there is a high abundance of some species of ants on sandy soils. Funnel ants (*Aphaenogaster barbigula*) occurred at nest densities of up to 37 m^{-2} (Eldridge, 1993). He reported steady-state infiltration rates on soils with nest entrances of 23.3

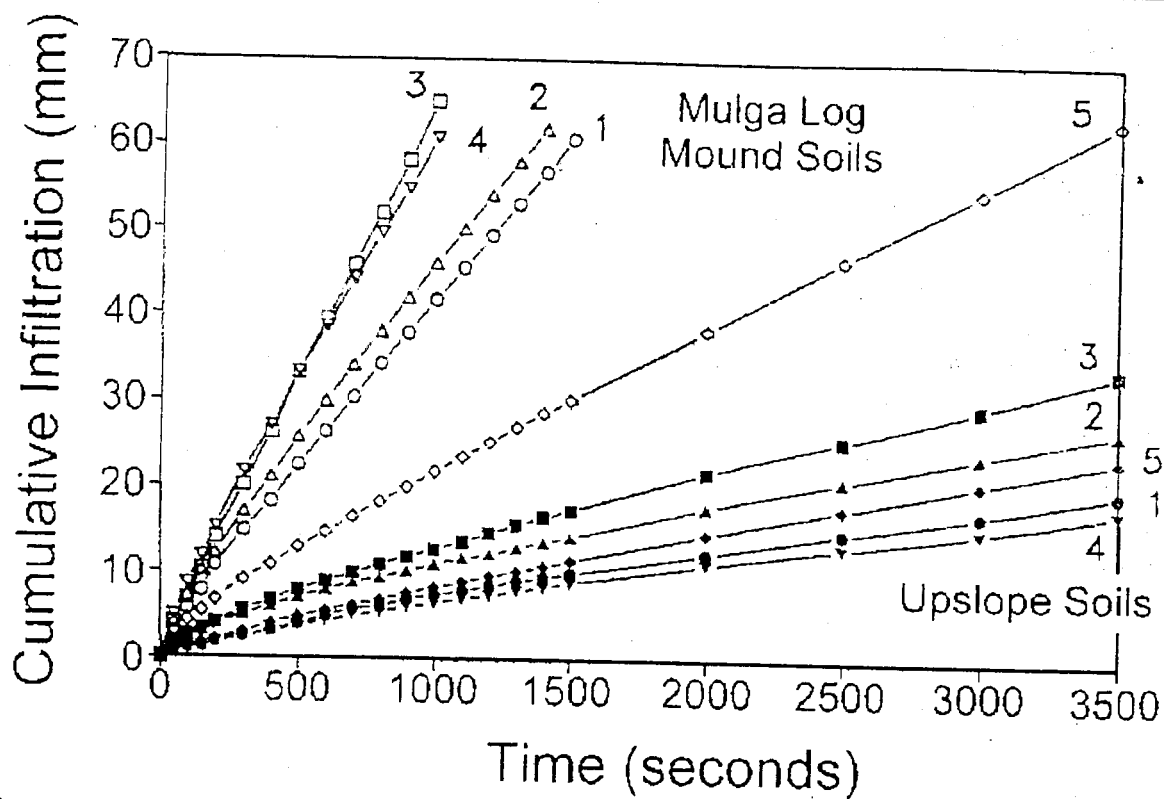


Figure 6. Comparisons of cumulative infiltration rates on mulga log mounds and upslope soils in a banded mulga (*Acacia aneura*) landscape in southeastern Australia (from Tongway et al. 1989).

mm min^{-1} which was significantly higher than the infiltration rates measured on soils not in the proximity of *A. barbigula* nests (5.6 mm min^{-1}).

The effect of bulk flow through the macropores produced by the tunnel systems in ant nests can have an important effect on the distribution of soil water in the profile. Soils associated with harvester ant (*Pogonomyrmex owyheeii*) mounds had higher soil water content at depths between 60 cm and 100 cm than soils not associated with ant nests (Laundre 1990). Laundre reported that the amount of water added to the soil during spring recharge was greater at 20 cm depth in soils at the edge of the nest clearings than nest soils. Soil water recharge in soils under ant mounds was greater at depths 60 cm and the soils between 60 cm and 100 cm received considerably more water than the upper 20 cm of soils away from the influence of the ant nest macropores (Laundre 1990)

Effects on Vegetation

Arthropods indirectly affect increased plant production both by their activities as modifiers of soil fertility and water infiltration and by their effects as consumers. Ants and termites affect both the species composition and biomass production of soils that are modified by their activities (Table 2). Ants that enrich the soil in the immediate vicinity of their nests include seed harvesting ants, leaf-cutting (Attine) ants, and species that transport plant and animal material to the nests. Some species

of ants create chaff-trash piles around the nest perimeter that increase the organic matter content of the soil under the ejected material (Wagner et al. 1997). A corona around the base of epigeic termitaria is generally characterized by higher nutrient concentrations and soil organic matter than soils not associated with mounds (Lee and Wood, 1971 a&b, Coventry et al. 1988, Lobry deBruyn & Conacher, 1995). Nutrient enrichment and modified water infiltration and storage affect both the species composition and the productivity (biomass production) of the vegetation in the vicinity of ant nests (Table 2). However the limited available data on the effects of termites and ants on plant biomass production and species composition must be interpreted with caution. The species of plants that increase in biomass and that are favored by the insect modified soils are not necessarily the same for the same arthropod species on different landscape units within a region (Whitford and DiMarco, 1995). There are also inter-annual differences in the responses of vegetation in the vicinity of ant colonies. These differences are probably the result of time lags in soil processes such as nitrogen immobilization and mineralization (Fisher & Whitford, 1995).

Table 2. *Effects of ants and termites on soils in arid and semi-arid ecosystems.*

Ant Species	Location	Effect on Soil	Reference
<i>Camponotus acvapimensis</i>	Humid savanna Africa	>sand fraction, aggregates, clay, coarse sand, macroporosity, C_{total} .	Levieux (1976)
<i>Paltothyreus tarstus</i>	Humid savanna Africa	>clay, coarse sand, macroporosity, C_{total} ; turnover $30 \text{ g m}^{-2} \cdot \text{y}^{-1}$	Levieux (1976)
<i>Aphaenogaster barbigula</i>	Semi-arid woodland, Australia	>infiltration, soil turnover 3360	Eldridge & Pickard (1994)
<i>Aphaenogaster spp.</i>	Semi-arid woodland, W. Australia	Turnover: $465 \text{ g m}^{-2} \cdot \text{y}^{-1}$ (gray sand loam); $223 \text{ g m}^{-2} \cdot \text{y}^{-1}$ (yellow sand) >clay	Lobry deBruyn & Conacher (1994)
<i>Formica perpilosa</i>	Southwestern U.S.A	>nitrogen mineralization rates > NO_3 , NH_4 , P, H_2O	Wagner (1997)
Ant community	Chihuahuan Desert ecosystems	Soil turnover $21.3 - 85.8 \text{ kg ha}^{-1} \cdot \text{y}^{-1}$	Whitford et al. (1994)
<i>Pogonomyrmex rugosus</i>	Chihuahuan Desert, U.S.A	>cover four species of annuals > NO_3 , N_{total} , Ca, Mg	Whitford & DiMarco (1995)
<i>Pogonomyrmex occidentalis</i> & <i>P. owyheeii</i>	Great Basin Desert, Oregon, U.S.A	>biomass of herbaceous plants	Sneva (1979)
<i>Pogonomyrmex occidentalis</i>	Great Basin Utah, U.S.A.	>microbial biomass, & vesicular- arbuscular micorrhizae	Friese & Allen (1993)
<i>Pogonomyrmex rugosus</i> & <i>Veromessor pergandei</i>	Sonoran Desert Arizona, U.S.A	>density and cover six species of annual plants	Rissing (1986)
<i>Veromessor andrei</i>	California -USA annual grassland	<abundance of two dominant plants, >abundance two alien annuals	Hobbs (1985)
Ant community	<i>Atriplex vesicaria</i> shrubland, Australia	Soil turnover: $350-420 \text{ kg ha}^{-1} \cdot \text{y}^{-1}$ > C_{total} , N_{total} , P_{total}	Briese (1982)
<i>Pogonomyrmex rugosus</i>	Burro-grass Chih- uahuan Desert	> N_{total} , Organic matter, biomass, average mass per plant (<i>Erodium texanum</i>)	Whitford (1988)

Termite Species	Location	Effect on Soil	Reference
<i>Macrotermes subhyalinus</i> , & <i>M. michaelseni</i>	Semi-arid savanna, Kenya	Mounds: >CEC, C _{organic} , N, clay *CEC = cation exchange capacity	Arshad (1981)
Subterranean termites	Savanna, Sahel Africa	>porosity, hydraulic conductivity, cumulative infiltration, final infiltration rate, water storage >bulk density	Mando (1997) Mando et al. (1996)
<i>Odontotermes</i> spp.	Arid grassland Brushland, Kenya	Sheeting: rate of formation: 1059 kg. ha ⁻¹ y ⁻¹ , >clay, sand, C _{total} , Ca, K, <silt, pH, CEC, Mg, Na	Bagnine (1984)
Macrotermitinae and others	Semi-arid <i>Acacia</i> brushland, Tanzania	>C _{organic} , N, K, <Ca, Na	Jones (1989)
<i>Trinervitermes trinervoides</i>	Semi-arid grassland, South Africa	>production of grasses (<i>Themeda triandra</i> & <i>Tagus koeleroides</i>), Mg, Ca, N, P, TEC* (*total exchangeable cations) <pH	Smith & Yeaton (1998)
<i>Amitermes vitiosus</i> , <i>Drepanotermes perniger</i> , & <i>Tumulitermes pastinator</i>	Semi-arid woodland, Australia	Turnover 300-400 kg. ha ⁻¹ y ⁻¹ , >(2-7 times reference soil) EC, N _{total} P _{soluble} , C _{organic} Ca, Mg, K, Na	Coventry et al. (1988)
<i>Amitermes</i> , <i>Tumulitermes Drepanotermes</i> , <i>Coptotermes Nausititermes</i> spp.	Arid and semi-arid Australia	Mounds: >clay, silt, C _{organic} , N _{total} Ca, Mg, K, & TEC (total exchange capacity)	Lee & Wood (1971)
<i>Amitermes vitiosus</i> and other species	Semi-arid woodland, Australia	0.025 - 0.50 mm y ⁻¹ soil accumulation	Holt et al. (1980)
<i>Drepanotermes tamminensis</i> & <i>Amitermes obeuntis</i> , <i>A. neogermanus</i>	Semi-arid woodland, Western Australia	Mounds: clay, C _{organic} , pH Sheeting: clay, C _{organic} , pH	Lobry de Bruyn & Conacher (1995)
<i>Amitermes</i> spp. <i>Nasutitermes magnus</i> , <i>Drepanitermes rubiceps</i>	Semi-arid woodland, Northeastern Australia	>biomass production of annual grass and a legume	Okello-Otaga & Spain (1986)
<i>Gnathamitermes tubiformans</i>	Chihuahuan Desert U.S.A	Turnover rate of standing stock of nutrients in upper 10 cm, times per year: N-3.5, P-2.5, S-2.5	Schaefer & Whitford (1981)
<i>Gnathamitermes tubiformans</i>	Chihuahuan Desert U.S.A.	Gallery sheeting: production 1000-5650 kg. ha ⁻¹ y ⁻¹	MacKay & Whitford (1988)
<i>Heterotermes aureus</i> & <i>Gnathamitermes perplexus</i>	Sonoran Desert Arizona	Sheeting: 744 kg. ha ⁻¹ y ⁻¹ , >pH, Ca, Mg, K, Na, C _{organic} , N _{total} , >clay by 21 kg ha ⁻¹ y ⁻¹	Nutting et al. (1987)

The effect of termite mounds on vegetation varies with the age and status of the emounds. For example in semi-arid grassland in South Africa, a grass species preferred by grazing animals (*Themeda triandra*) was dominant in the area around active mounds of *Trinervitermes trinervoides* (Smith and Yeaton, 1998). Chihuahuan Desert subterranean termites affect biomass production of the dominant shrub, cre-

sotebush (*Larrea tridentata*) and the species composition and biomass production of annual plants (Fig. 7) (Gutierrez and Whitford, 1987). The primary effect of termites on annual plants was through their effect on soil organic matter, water infiltration and soil nutrients, especially nitrogen.) The higher biomass production of shrubs on plots with termites present was attributed to both greater water and nutrient availability when compared to plots where termites had been eliminated (Gutierrez and Whitford, 1989).

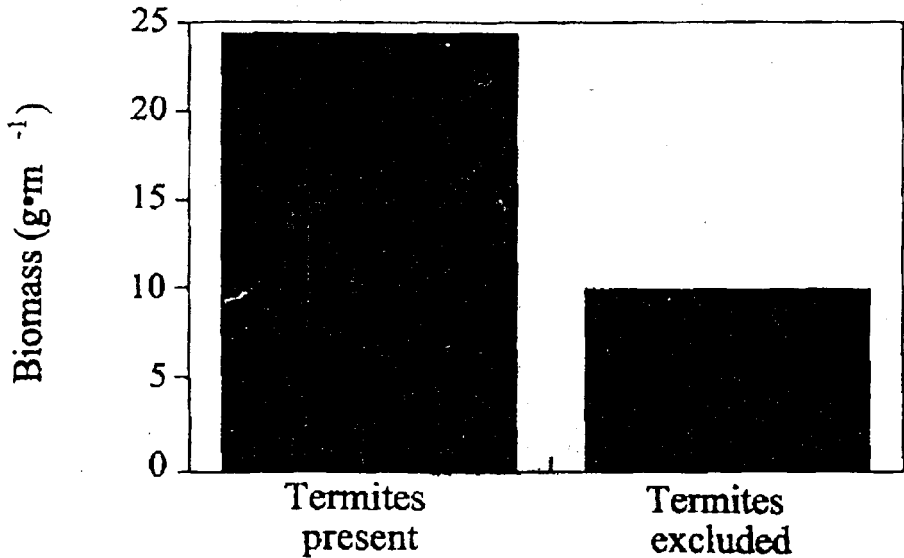


Figure 7. Biomass production of herbaceous plants on plots with no termites (excluded by chemical treatment) and on untreated plots with termites present. (Data from Gutierrez & Whitford 1987).

Arthropods can indirectly affect plant growth by stimulating the activity of the soil microflora or by supplying soluble nitrogen directly to the soil beneath the plant canopies. The most abundant insects on shrubs in deserts are sucking insects (Homoptera and Hemiptera) (Lightfoot & Whitford, 1987, Schowalter, 1996, Schowalter et al. 1999). The frass and honeydew production from these insects fertilizes the litter under the shrub canopies with soluble carbohydrates and nitrogen. This readily available form of carbon and nitrogen stimulates the growth of microflora on the litter (Lightfoot and Whitford, 1987). Rapid growth of soil microflora as a result of inputs of high carbon, low nitrogen substrates results in the immobilization of soil nitrogen in the rapidly growing microbial biomass (Parker et al. 1984). Nitrogen immobilization imposes severe nitrogen limitations on the biomass production of shrubs and of ephemeral and perennial herbaceous species.

Arthropods acting as engineers can produce habitat for other species by their activities. One example of habitat production is the girdling of stems of living trees or shrubs by cerambycid beetles. In the Chihuahuan Desert, a cerambycid beetle (*Oncideres* spp.) girdles a large percentage of the twigs of mesquite (*Prosopis glandulosa*) (up to 40% of the branches with diameters from 0.5 to 2.0 cm) (Ueckert et al. 1971). Stems are girdled at the end of the growing season and the female cerambycid oviposits in the stem above the girdle. Girdling the stem prevents the plant from producing resin to cover the eggs or developing larvae. The girdled stems

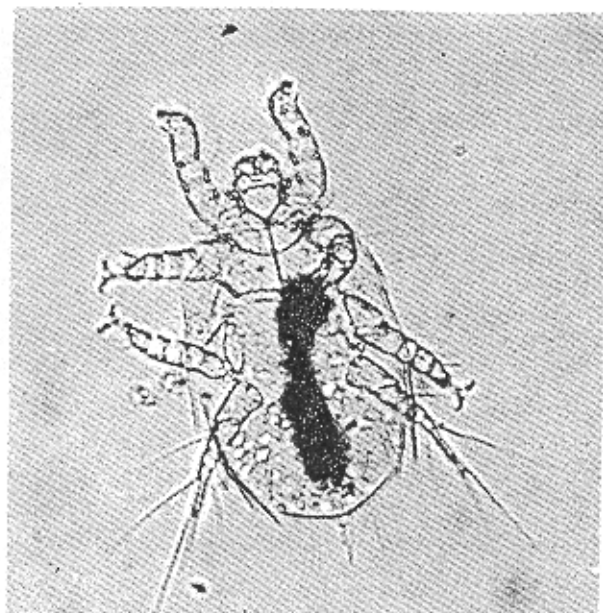


Plate 1. Fugiphagous mite with a bolus of fungal material in the gut.

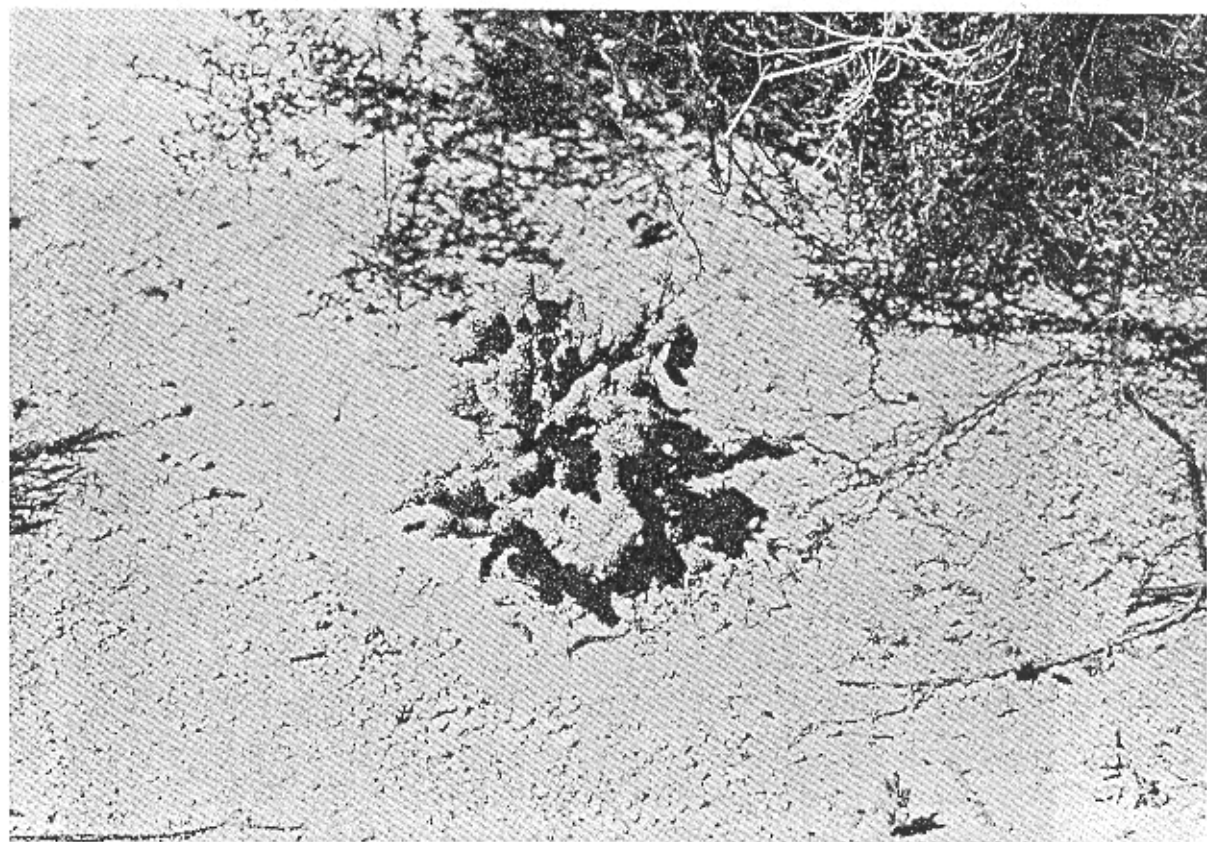


Plate 2. Foraging gallery produced by subterranean termites (*Gnathamitermes tubiformans*) around a dead plant in the Chihuahuan Desert.



Plate 3. The nest cone of honey pot ants (*Myrmecocystus mexicana*) constructed from nodules of calcium carbonate translocated from a depth of 1 meter.

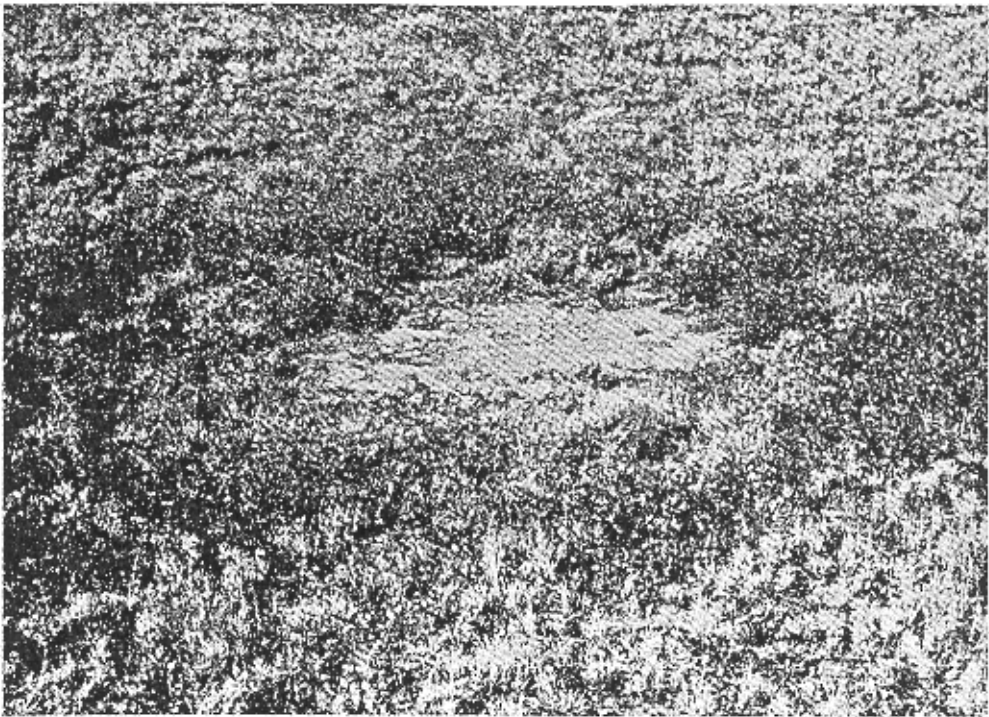


Plate 4. A ring of large herbaceous plants (*Erodium texanum*) around the nest disk of the seed harvester ant (*Pogonomyrmex rugosus*) in a burro-grass (*Scleropogon brevifolia*) community in the Chihuahuan Desert.

(dead wood) are suitable habitat for developing larvae of other wood boring insects. Wood boring insects found in the girdled stems of mesquite included species from several families: Buprestidae, Bostrichidae, Cleridae, and Scolytidae (Riazance & Whitford 1974). Girdling stems of shrubs has the same effect as pruning domesticated fruit trees. Lateral nodes below the girdle take on apical dominance and produce new stems in the following growing season. Frequently several branches will develop below a girdle. The effect of pruning by stem girdling insects is to induce compensatory growth. The compensatory growth of girdled stems on mesquite more than compensates for the lost biomass of the girdled stem and contributes to higher net primary production in the girdled shrubs (Whitford et al. 1978).

This review provides some examples of the contributions of invertebrates to ecosystem properties and processes. These few examples of the diversity of important activities of invertebrates in ecosystems should not be construed to be an exhaustive list or complete review of the contributions of invertebrates. There are many other mechanisms by which invertebrates play crucial roles in the structure and dynamics of arid ecosystems. The complex roles that many taxa of invertebrates need to be elucidated in order to provide clearer understanding of the importance of invertebrate diversity to the maintenance of sustainable ecosystems.

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