The importance of the biodiversity of soil biota in arid ecosystems

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The importance of soil biota in maintaining ecosytem integrity is examined by a review of studies of soil processes and soil biota in arid ecosystems. In decomposition and mineralization processes, there is a temporal succession of microarthropod and nematode species. Tydeid mites are keystone species in the early stages of decomposition. Soil pore neck size variation affects the spatial distribution of soil biota and requires that species differ in size to provide efficient processing of organic matter. In arid ecosystems, the sub-set of soil biota that is active at any point in time is determined by the soil water potential and soil temperature. The structure of soil microarthropod assemblages is similar in several arid regions of the world and abundance and diversity are directly related to quantity of litter accumulations and soil organic matter. The unique life histories and behavioural characteristics of desert soil macrofauna (termites and ants) determine the effects of these organisms on soil properties and soil formation. The soil biota, by affecting the spatial and temporal distribution of essential resources (water and nutrients), are essential to the maintenance of the ecosystem integrity of arid ecosystems.

Keywords: diversity; functional groups; keystone species; microarthropods; nematodes; protozoans; termites; ants

Introduction

The important ecosystem processes of energy flow, nutrient cycling, water infiltration and storage in soil are mediated by the soil biota. That biota includes the microflora (bacteria, algae and fungi) plus a complex fauna: protozoans, nematodes, annelids and arthropods (Wallwork, 1976). Soils of arid ecosystems support representatives of all of these groups with the exception of annelids (Wallwork, 1982). It is hypothesized that soil stability and long term productivity are dependent upon the integrity of the soil biota. In an assessment of the role of biodiversity of soil biota in ecosystem function, it is necessary to determine if each species is incrementally important in that function or if there is functional redundancy, i.e. all species are not essential for the system to function. It has been argued by some authors that biological communities are composed of a few functional groups or guilds and that the species that make up the functional groups are ecologically equivalent (Walker, 1992). The argument that communities of soil biota are composed of functionally redundant species is difficult to counter since most studies have focused on a few species in laboratory microcosms or species grouped at the family level or higher taxonomic unit in field studies. Models of community stability show no increase in stability with increased species diversity and food web complexity (May, 1973). While it may not be possible to

provide unequivocal tests of the applicability of the redundancy hypothesis to soil biota, there are other aspects of biodiversity that can be addressed. The keystone species concept can be expanded to include guilds or functional groups of species (Simberloff and Dayan, 1991). By expanding the keystone concept, it is possible to address the question: are there keystone species or guilds within the soil biota? In this paper, the data on the functional roles of the soil biota in arid ecosystems are reviewed and these data are used to examine attributes of biodiversity such as redundancy and keystone taxa.

Abiotic factors

In arid ecosystems the functional importance of species of soil organisms is directly related to their physiological characteristics. Because of the high degree of unpredictability of climate, especially rainfall, in arid and semi-arid regions of the world, soil water potentials vary over a wide range through time and are temporally unpredictable. The guilds or species of soil organisms that are active at a particular time in arid and semi-arid ecosystems are determined by abiotic factors (Whitford, 1989). For example, most protozoans in a desert sandy soil were encysted at a soil water potential of -0.4 MPa but less than 50% of the soil nematode population was inactive (anhydrobiotic) at the same water potential (Whitford, 1989). There are species differences in resistance to desiccation, rapidity of reproduction when water is available, and the threshold for encystment or entry into a cryptobiotic state in the desert soil fauna. The fraction of the soil biota that is active at any point in time is a function of the immediate past weather conditions. In protozoans, whole functional groups may be similarly affected by changes in soil moisture, but in microarthropods it appears that individual species vary considerably in their ability to enter cryptobiosis and/or with respect to the time constant for the recovery from the cryptobiotic state (MacKay *et al.*, 1986). Some key species of microarthropods remain active in very dry soils (soil water potentials >3.0 MPa). Thus the functionally active fraction of the total soil biota varies considerably over time as a function of soil water content and temperature.

Importance of soil biota in decomposition

Much of the information on the role of diversity of microbiota in decomposition processes is based on changes in decomposition rates and taxonomic composition of the soil biota that follow the use of chemical inhibitors to eliminate all organisms of a taxon or some fraction of a taxon (Curry, 1969; Macauley, 1975; Vossbrinck *et al.*, 1979; Santos *et al.*, 1981; Santos and Whitford, 1981). Some insights into the relative importance of different groups of soil biota in decomposition processes in a Chihuahuan Desert ecosystem were provided by eliminating arthropods or fungi by treating plant litter with insecticide or fungicide (Santos and Whitford, 1981) (Fig. 1). Despite the importance of fungi as primary decomposers, decomposition rates were reduced less by fungicide than by insecticide. Mycelial density was reduced in fungicide-treated plant litter in comparison with controls but fungi of the genera *Alternaria*, *Rhizopus* and *Cunninghamella* were isolated from the treated litter. These genera of fungi account for only a small fraction of the soil fungi in untreated Chihuahuan Desert soils but they were capable of decomposing plant material at a rate higher than expected based on their proportion of the species pool in the untreated litter (Stantos and Whitford, 1981). The apparent recovery of decomposition
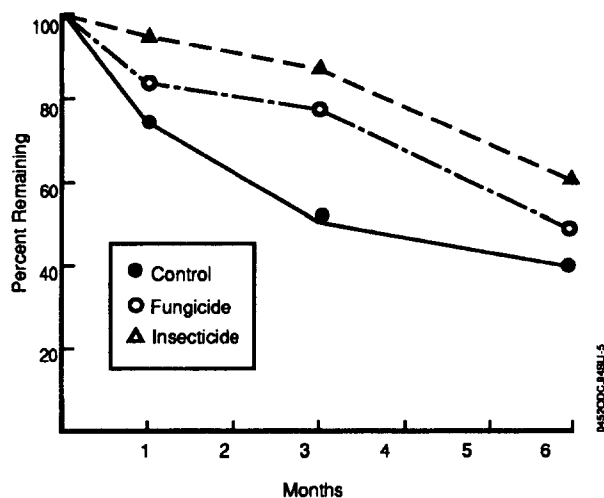
Figure 1. The effects of fungicide and insecticide on the decomposition of buried leaf litter in the northern Chihuahuan Desert (based on data in Santos and Whitford, 1981).

rates after 3 months was attributed to the leaching of fungicide from the treated litter and recolonization of the litter by other taxa of fungi during the later months of the experiment. These results are difficult to evaluate because it is not known if the surviving species in the treated litter belong to the same functional group(s) as those in the untreated litter. Given this caution, it does appear that a more complete assemblage of fungi is necessary for efficient decomposition in the initial stages of decomposition of litter in desert soils. This suggests that complete species assemblages are necessary for the efficient decomposition processes in arid ecosystems but are not essential for the process to occur.

Evidence of the importance of individual species of soil organisms in decomposition processes was provided by Santos *et al.* (1981) and Santos and Whitford (1981). In a desert soil during the early stages of decomposition, rates of mass loss were regulated by small tydeid mites that preyed upon bacteriophagous nematodes (Santos *et al.*, 1981). Predation by these mites regulated the numbers of nematodes. When mites were eliminated, the numbers of bacteria-feeding nematodes increased exponentially and overgrazed the bacteria, thus reducing the rate of decomposition. The small tydeid mites are 'keystone' species, i.e. species whose direct or indirect effects on the survival of other species is disproportionately large in relation to their abundance (Westman, 1990). Their importance in the early stages of decomposition of buried litter and roots contributes to the cycling of essential nutrients. This effect on an essential ecosystem process may well affect the composition and productivity of the ecosystem as suggested by Gutierrez and Whitford (1987a, b).

As the decomposition process proceeded in the study, the microfaunal community became more complex with a succession of taxa joining the soil biotic assemblage involved in the process (Fig. 2). The soil food web responsible for decomposition and mineralization became more complex through time, stabilized and then decreased in complexity as the mass of the undecomposed material remaining approached 10% or less of the original
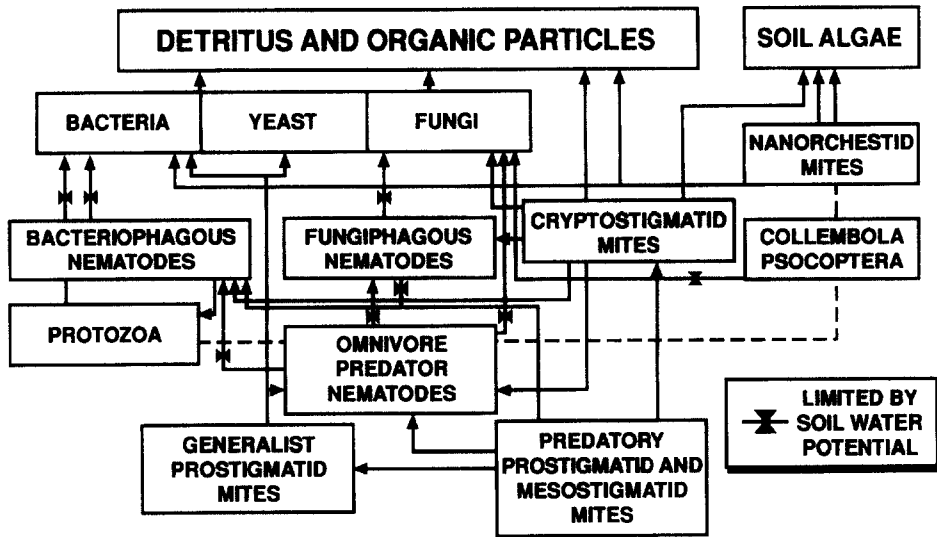
Figure 2. The structure of a desert soil food web based on guilds of soil organisms (based on data in Santos and Whitford (1981) and Parker *et al.* (1984a and 1984b)).

mass (Santos and Whitford, 1981). The soil food web changed from dominance by bacteria-feeding nematodes and tydeid mites in the early stages of decomposition to dominance by fungiphagous nematodes and a variety of mites capable of feeding on fungi and/or nematodes (Santos and Whitford, 1981; Parker *et al.*, 1984b). The shift in numerical dominance from bacteriophagous nematodes to fungiphagous nematodes during decomposition has been documented in a number of studies (Wasilewska *et al.*, 1981; Whitford *et al.*, 1982) and is temporally coincident with shifts in the species of microarthropods. Without such a shift, mineralization processes would probably be adversely affected. The changes in composition of major trophic functional groups and of species of organisms during the decomposition process probably occurs among the protozoans and insect larvae but these changes have not been documented.

The importance of abiotic constraints on the soil fauna and their effect on decomposition and mineralization processes in the Chihuahuan Desert was documented by Parker *et al.* (1984a). They found that small fungiphagous mites were primarily responsible for mineralization of nitrogen that had been immobilized in fungal biomass. In mesic ecosystems, protozoans and nematodes are the most important soil animals mediating nitrogen mineralization (Anderson and Ineson, 1984), but in arid soils these 'grazers' on microbial biomass are encysted or anhydrobiotic for extended periods of time. The small fungiphagous prostigmatid mites remain active even after the water films on soil aggregates have disappeared (Whitford, 1989). This group of mites includes tydeids and other taxa of prostigmatid mites that have been shown to be important regulators of decomposition rates (Santos and Whitford, 1981).

Soil pore neck size and diversity

The diversity of soil biota and their importance in ecosystem processes are related to the physical structure of the soil as it affects the ability of various species of soil organisms to move through the soil (Elliot *et al.*, 1980). Many of the smallest organisms (protozoans and nematodes) are dependent upon water films and can move through very small pores in the soil. Flagellates and small amoebae are the most numerous protozoans because they can occupy all pore spaces down to 8 μm diameter (Bamforth, 1988). Small naked amoebae are the most abundant protozoans in desert soils (Parker *et al.*, 1984b). Pore neck size is more critical for the microarthropods which vary greatly in size and cannot pass through pore neck diameters smaller than the diameter of their bodies. Some of the largest Mesostigmata may be ten times larger than the smallest Prostigmata and hence are restricted to only the largest pore spaces. The varying pore sizes in the soil provide refugia for smaller microbial feeding forms from the larger predators. The distribution of pore sizes thus affects the relative abundance and species composition of the microarthropod fauna which is the active fraction of the soil fauna during dry periods.

The total size spectrum of soil fauna may not be apparent because of the limitations of the techniques used to extract animals from the soil. In a recent study, Andre *et al.* (1994), using a new flotation method for extraction, recorded 31 species of microarthropods from coastal sand dunes. Most of these species were undescribed mites and were smaller than 200 μm in diameter. These mites were significantly smaller than those previously described from this habitat. This new technique revealed densities of microarthropods varying between 175 000 and 1 400 000 individuals per square metre, three to ten times higher than densities usually reported in soils. While one can only speculate as to the functional significance of this group of extremely small body size microarthropods, their small size suggests that they may play an important role in decomposition and/or mineralization processes in soils because of their access to the small pore spaces and because they are probably active in dry soils.

Diversity of desert soil microarthropods

Although not as numerous as soil protozoans or nematodes, there have been more studies of the species assemblages of soil microarthropods in arid and semi-arid regions than of these more numerous groups. The microarthropod fauna of desert soils can be very diverse. A list of 133 species was compiled during a study of decomposition and the associated soil microarthropod fauna on a Chihuanhuan Desert watershed (Cepeda-Pizarro and Whitford, 1989). This list included 114 species of Acari, ten species of Collembola and nine species of other insects (Psocoptera, Coleoptera and Diptera). However only 28 species accounted for 85% of the microarthropods collected and only nine species occurred at frequencies greater than 2%. These included the prostigmatid mites, *Speleorchestes* sp., *Tarsonemus* sp., *Siteroptes* sp., *Tydeus* sp., *Paratriophtydeus* sp. and *Bakerdamia* sp.; the cryptostigmatid mite, *Joshuella striata* and the collembolans, *Brachystomella arida* and *Isotoma* sp. (Cepeda-Pizarro and Whitford, 1989). Most of the abundant species were those found to be important regulators of decomposition and mineralization processes (Santos *et al.*, 1981; Santos and Whitford, 1981; Elkins and Whitford, 1982; Parker *et al.*, 1984b) primarily as a result of grazing on fungi and preying on nematodes. The cryptostigmatid, *J. striata*, is a well adapted desert mite that is widely

distributed in North American deserts and is probably phytophagous or fungiphagous. As with most soil animals, the feeding behaviours and trophic relationships of these species are inferred from a few laboratory studies (Walter, 1987; Moore *et al.*, 1988).

The composition and diversity of desert microarthropod faunas appears to differ primarily in relation to the presence, absence and depth of the litter layers under plants and of the chemical/physical characteristics of that litter (Santos *et al.*, 1978). For example, the microarthropod community found in soils under creosote bush, *Larrea tridentata*, in the Mojave Desert in Nevada (Franco *et al.*, 1979) was similar to that found in soils under creosote bush in the Chihuahuan Desert (Cepeda-Pizarro and Whitford, 1989), despite the large differences in average rainfall and seasonality of rainfall in these deserts. The average rainfall in the northern Chihuahuan Desert is 250 mm with 60% of that in the months of July–September and the average rainfall in the Mojave Desert is less than 100 mm mostly coming in the winter months November–March.

In a study of microarthropods associated with three dominant shrubs that line dry stream beds (arroyos), Kamill *et al.* (1985) recorded 32 species and Cryptostigmata were the numerically dominant group. The dominant species in the arroyo habitat were rare or absent in the adjacent uplands (Cepeda-Pizarro and Whitford, 1989) which were dominated by Prostigmata. The arroyo fauna was more similar to that described by Wallwork (1972) from litter and soil under small trees, *Juniperus* sp. in the desert in southern California. The similarities between the faunas described by Wallwork and Kamill *et al.* are correlated with the litter layers and litter characteristics rather than with similarities in climate or soils. These comparisons suggest functional differences at the species level rather than at the functional group level.

In a study of a variety of habitats in the semi-arid zone of eastern Australia, Noble *et al.* (1994) reported on assemblages of soil microarthropods from a number of locations and habitats. In most habitats, the dominant Prostigmata were families of mites that are also numerous in North American desert habitats: Tydeidae, Nanorchestidae and Pygmephoridae. However there were some exceptions, e.g. Ereynetidae that have not been reported from North American Desert soils. At the generic level there were fewer similarities and the most abundant tydeid mite, *Afrotydeus* sp. was rare in North American desert soils. Diversity ranged from 25 species in mulga (*Acacia aneura*) woodland to seven species under Nitre-bush, *Nitraria billardieri*. J.G Cepeda-Pizarro (personal communication) reported that microarthropod communities were similar at the family level but differed at the species level in a comparison of soil microarthropods from the semi-arid zone of central Chile with soil microarthropod assemblages from North American deserts. These comparisons raise the question: are species within these families of mites functionally equivalent? If the species within families of microarthropods have similar physiologies and occur at similar relative abundances, they are probably functionally equivalent in arid ecosystems in different parts of the world.

Diversity of Protozoa and Nematoda

In comparison with the data available on species diversity in desert soil microarthropods, there are no studies of species diversity of nematodes and protozoans. Studies of nematodes and protozoans have assumed that guilds are functional units and reported results by trophic groups or guild categories (Steinberger *et al.*, 1984, Parker *et al.*, 1984b, Freckman and Mankau, 1986, Freckman *et al.*, 1987). These studies document that in

desert soils, Cephalobid (bacteriophagous) nematodes are most numerous in early stages of decomposition and are replaced by the fungivorous and omnivore-predator trophic groups in the later stages of decomposition. Determining trophic status of nematodes in a sample is easier than identifying nematodes to species. This has been the primary reason for assuming that species within a trophic group are functionally equivalent.

There are no data on species assemblages of soil protozoans from arid and semi-arid soils. Few studies of ecosystem processes in these soils have included protozoans in the measurements. These studies have reported protozoan populations as ciliates, flagellates, and amoebae with no attempt at further taxonomic breakdown (Parker *et al.*, 1984b).

Macroarthropods and soil properties

In a recent review of the role of termites and ants in soil modification, Lobry de Bruyn and Conacher (1990) state that research needs to focus on community as distinct from single species effects. Ants and termites affect soil processes by increasing soil porosity and infiltration (Elkins *et al.*, 1986), reducing or increasing bulk density, altering soil erosion by depositing subsoil on the surface, and altering the concentration and spatial distribution of soil nutrients (Lobry de Bruyn and Conacher, 1990). Studies in the Chihuahuan Desert have shown that colonies of some species of ants affect the nutrient concentration in soils around the nest disc (Whitford, 1988; Whitford and DiMarco, 1995) which, in turn, affects the species composition and biomass production of plants in the vicinity of the nest. Similar patterns have been observed in the southern African Karoo Desert (Dean and Yeaton, 1993) and in the desert in Israel (Danin and Yom-Tov, 1990). Soil nutrient enrichment effects are evident only in ant species in which individual nests persist for decades. These species account for less than one quarter of the ant species in Chihuahuan Desert communities (Whitford, 1978). Soil enrichment effects also vary with the soil of the area; ant species that enrich the soil around nests on one part of a watershed may not enrich soils on another part of the watershed (Whitford and DiMarco, 1995).

While ant species that occupy nests for short time periods may not significantly affect soil chemistry, they may modify soil physical properties and contribute to soil formation (Lobry de Bruyn and Conacher, 1990). In grasslands of the Chihuahuan Desert, it was found that four species of ants which have relatively short-lived colonies, transported between 21 and 86 kg ha^{-1}yr^{-1} of sub-surface soil to the surface. This sub-surface soil was accumulated in nest craters where it was more susceptible to redistribution by wind and water than was the surface soil with intact microbial crusts. Those species with long-lived colonies contributed virtually no soil transport and other species did not accumulate soil in nest craters around the nest entrances. In a semi-arid ecosystem in Australia, a single species, *Aphenogaster barbigula*, was estimated to transport 33.6 kg ha^{-1}yr^{-1} of subsoil to the surface (Eldridge and Pickard, 1994).

The ant faunas in arid and semi-arid regions generally consist of several species of seed harvesters (*Pogonomyrmex, Messor, Monomorium (Chelaner)* and *Pheidole*), one or more dominant Dolichoderinae, several species of generalists and one or more species that are opportunists (Whitford, 1978; Anderson, 1983; Willis *et al.*, 1992). Species richness in Chihuahuan Desert ant communities ranges from three species to 36 species. There are important life history, behavioural and physiological differences among species within a genus that affect the role that the individual species play in the ecosystem and minimize

competition between species that share food resources (Whitford *et al.,* 1976; Whitford, 1978).

Termites also transport subsoil to the surface. Some species of termites produce fragile surface galleries that are different in composition from the surface soils and that are readily erodible. Production of this erodible material can be very large, (1000–5650 kg ha⁻¹yr⁻¹ in the Chihuahuan Desert) (MacKay and Whitford, 1988). Other termite species produce above ground mounds that are highly resistant to erosion (Lobry de Bruyn and Conacher, 1990), although over time these mounds decay and contribute to soil formation.

Termite species also differ in their symbiotic gut microflora which affects the kinds of organic materials they consume and the breakdown products that are excreted (Breznak, 1984). In some ecosystems, termites process more than 70% of the annual input of plant litter (Whitford, 1991). The partitioning of litterfall among competing colonies and its decomposition in the guts of termites may be so efficient that there is little or no carbon incorporated into the soil (Jones, 1990). In the Chihuahuan Desert it was shown that even in an ecosystem with only three species of termites, concentration and patterns of distribution of soil organic matter were the result of termite activity (Nash and Whitford, 1995). The importance of termite species as decomposers of dung, wood, leaf litter and grass, plus their importance in the maintenance of soil macroporosity and as a food source for other species, has led to the consideration of termites as 'keystone' taxa in desert ecosystems (Whitford, 1991). In some ecosystems, termites are sufficiently diverse and abundant to contribute significantly to atmospheric fluxes of carbon dioxide and methane. These functions further emphasize the keystone role that species of termites may play in arid and semi-arid ecosystems.

This brief review of the limited data on soil modification activities of ants and termites demonstrates that species differ widely in their effects on soils. Assemblages of ants and termites in arid ecosystems range from less than ten species to more than 100 species per hectare. The combined effects of these species assemblages depend on species composition and interactions between the species. These organisms are important determinants of the structure and function of arid ecosystems because of their effects on the spatial and temporal distribution of essential resources: water and nutrients.

Conclusion

This review has focused on the functional roles of soil organisms in arid and semi-arid ecosystems. It should be emphasized that while the soil biota in these systems is diverse, the total diversity of all groups is lower than in mesic ecosystems. The climatic extremes and unpredictability of desert climate are such that many of the species in any taxon will be operating very close to their tolerance limits. The lower diversity and species operating close to tolerance limits affects the composition of the functional fraction of the soil biota. Despite the limitations imposed by the abiotic environment, there are several taxa of soil organisms that are keystone taxa. There may be many more keystone species among the soil biota that have yet to be discovered. Therefore, while the redundancy hypothesis may hold for highly-evolved, high-diversity ecosystems which are environmentally stable and favourable for biological activity, it is less likely to apply to arid and semi-arid ecosystems.

Acknowledgements

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