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Density and Diversity of Protozoa in Some Arid Australian Soils

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ABSTRACT. This is the first extensive study of soil protozoa of arid lands. Twenty-six samples from litters, soils, termitaria, and a cyanobacterial crust, collected from central and south Australian arid lands, were analyzed for numbers and species of gymnamoebae, ciliates, and testacea. Amoebae ranged from 1,000–5,000/g of material, and were two orders of magnitude more abundant than ciliates. Both groups increased in abundance and species richness from bare soils through spinifex to mulga to chenopod vegetations. Testacea ranged 900–5,000/g with similar species richness throughout vegetations, but reached 11,900/g with a doubling of species in a refugium in Kings Canyon. The most prevalent species of amoebae, ciliates, and testacea were taxa associated with ephemeral and disturbed habitats (r-selection). The cyanobacterial crust might be considered a micro-refugium because it contained a number of non-encysting protozoa, including *Thecamoeba* sp. and *Nassula picta*, feeding on cyanobacterial filaments. The numbers and species richness of protozoa under shrubs were greater than in bare soils, supporting the resource island hypothesis that desert plants create soil heterogeneity by localizing soil fertility under their canopies.

Key Words. Amoebae, arid lands, ciliates, nutrient recycling, resource island hypothesis, terrestrial ecology, testacea.

ARID lands, like all terrestrial ecosystems, depend upon nutrient recycling by bacteria and protozoa. Protozoa increase the mineralization of organic matter through consumption of bacteria and excrete about 60% of their ingested nutrients directly into the soil system to furnish nutrients for plant uptake and further microbial growth (Griffiths 1994). To be complete, inventories of desert biodiversity (or biota) need to include soil protozoa (and other soil fauna) with the aboveground floras and faunas. This paper on Australian arid lands is a first contribution to providing inventories of desert protozoa.

Seventy percent of the Australian continent is covered by arid lands, which are characterized by irregular precipitation (van Ootserzee 1991). For example, in the century preceeding 1980 in central Australia, (recorded) droughts lasted one to seven years, sometimes separated by only a single wet year. In 40 of those years, no rain fell at some weather stations (King 1986).

Three distinct vegetation systems have evolved in the Australian arid lands (Fig. 1). 1) Open ''mulga'' shrublands, dominated by *Acacia aneura* (''mulga''), with communities of *Allocasaurina* and understory of *Eremophila*, *Senna*, and smaller acacias, grow on well-drained soils that enable even moderate rains to promote plant growth and recharge ground water. 2) Spinifex (primarily *Triodia* and *Plectrachne*) grasslands grow on skeletal and sandy soils that dry rapidly after rainfall. 3) Succulent chenopod shrubs (principally *Atriplex* and *Chenopodium*) colonize clay and stony (''gibber desert'') soils that yield little water to plants. The high proportion of cellulose and lignin in the first two ecosystems favor termites, furnishing an important component to these ecosystems (van Oosterzee 1991), hence several termitaria were collected.

These three ecosystems intergrade with each other. *Acacia* shrubs (and Eucalyptus trees in northern Australia) appear in spinifex communities, while spinifex and chenopods may furnish ground story plants in mulga shrublands. Interspersed in these ecosystems are ecological islands or refugia, such as springs, seepage areas, and topographic features like crevices and canyons, which funnel and concentrate water to form more or less moist habitats (van Oosterzee 1991).

MATERIALS AND METHODS

The study area was an 800 × 100 km elliptical area bounded by Glendambo in the south and Alice Springs, Ormiston Gorge, and Kata Tjuta (the Olgas) in the north. (Fig. 1). Twenty-six samples were collected in July 1996 from pure stands of spinifex, mulga, and chenopod vegetations in the three ecosystems. Soils were collected under spinifex hummocks, litters and soils from under plants in the other two ecosystems, and a soil under a cycad in a refugium, Kings Canyon (E 129° 48′, S 24° 26′). Termite mounds and their underlying soils were collected from spinifex and mulga ecosystems, and a bare soil was collected from between plants in each of the three ecosystems (Table 1). A twenty-seventh sample was collected from a cyanobacterial crust under a spinifex hummock and examined separately. The sampling trowel was disinfected with 70% ethanol before each use, and samples were transported to the laboratory in sterile 100-cc capacity vials.

Soil pH was measured in the field using a CSIRO soil pH kit (Inculo Laboratories, Melbourne, Australia). This method uses a universal indicator solution, a few drops of which are used to mix the soil sample into a paste on a tile. A neutral powder is then added to the sample surface to help in visualizing the indicator color, which is compared to a reference chart to indicate pH within 0.5 unit.

Total ciliates were estimated by the microtiter plate method of Bamforth (1991). Testacean numbers were counted from stained slides (two for each site) prepared by the Korgonova and Geltzer method (1977). Densities of gymnamoebae were estimated by the plaque count method employed by the Australian Water Quality Centre. A subsample prepared for the ciliate count was used to prepare a series of 4-fold dilutions. The diluent was a quarter-strength frog Ringer's solution containing 1 ml of an *E. coli* suspension per 3 ml of diluent. At each dilution, eight 1-ml aliquots were plated on non-nutrient agar in 90-mm plates. When the liquid had been absorbed by the agar, the plates were separated into two sets and incubated at 42 °C and 30 °C for detection of thermophilic and mesophilic amoebae, respectively. The plates were examined daily, the plaques counted, and indivdual amoebae identified by the criteria of Page (1988).

Species richness of all four protist groups was determined using the packed Petri dish method of Foissner (1987). To find more flagellates, two squares of lens paper overlain with coverslips were placed on top of the material in the Petri dish, examined after one day, and the procedure repeated the second day. Most amoebae were found by placing approximately one gram of material into 1 × 4 rectangular wells cut into non-nutrient agar plates spread with *E. coli* and incubated at 30 °C. The Korgonova and Geltzer slides revealed some small testacean species not seen in the packed Petri dishes. Colpodid/Polyhymenophoran (C/P) ratios (Luftenegger, Foissner, and Adam 1985) were determined on each ciliate species assemblage to determine proportions of r/K selection ratios. The cyanobacter-

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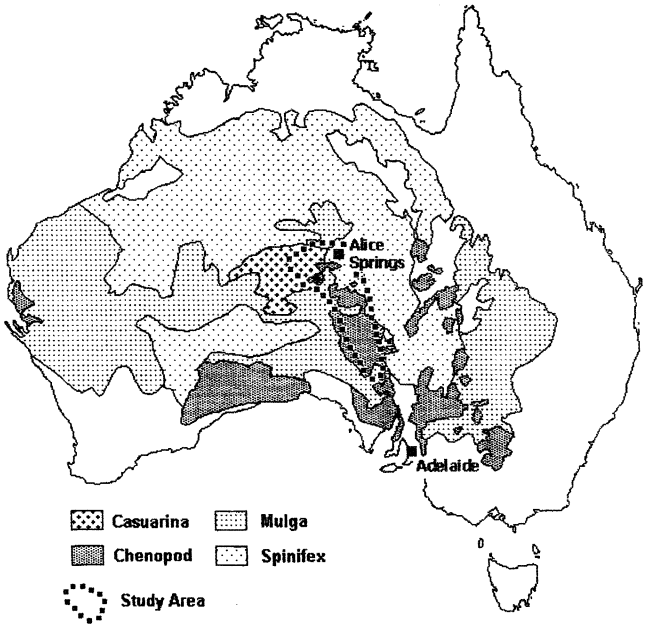

Fig. **1**. Distribution of the principal vegetation types and the study area, (After White 1994).

ial crust was placed in a 90-mm Petri dish and flooded with 25% frog Ringer's solution to find protozoa.

All identifications were made using light microscopy. *Acanthamoeba* are reported on the basis of cyst type, since more precise identification requires DNA techniques (Byers, Bogler, and Burianek 1993). With the exception of the single *Naegleria*, identified by flagellation test, vahlkampfids are identified only by family, since again, DNA techniques must be employed for proper species identifications (Brown and DeJonckheere 1999).

RESULTS

Most of the soils ranged from pH 7–10 (Table 1).

Forty-two types of flagellates were discerned, using size, shape, number, and position of flagella, and speed and mode of locomotion. Nine species could definitely be identified by morphological criteria: *Anisonema* sp., *Cercomonas longicauda*, *Heteromita globosa*, *Oikomonas termo*, *Petalomonas* sp., *Bodo saltans*, *Bodo caudatus*, *Sainouran mikoteron*, and *Spumella* (*Monas*) sp. A small (10 μm) choanoflagellate was found in an *Acacia* litter sample and in soil under a cycad in Kings Canyon. In view of the large number of heteroflagellates of uncertain description and taxonomic identification (Patterson and Larsen 1991) identification of the remaining species could not be carried out precisely under limited light microscopy conditions. Species ranged from 4–12 μm in size.

Amoebae were about two orders of magnitude more abundant than ciliates (Table 2, Fig. 2). Inspection of Fig. 2 shows that three groupings could be seen: interspace soils with only 1,000–3,000 amoebae/g (dry weight), spinifex soils with 4,000–13,000 amoebae/g, and chenopod litters with $>$ 75,000 amoebae/g. The mulga, termite, Kings Canyon, and chenopod soils showed a scattered distribution.

Acanthamoeba species were extremely common (Table 3), with Group II (polygonal) and Group III (circular) cyst-forming species occurring together at 80% of the sites. The next three prominent taxa were vahlkampfids, *Hartmanella*, and *Platyamoeba*. The family Thecamoebidae, represented by the genera *Dermamoeba*, *Sapinia*, and *Thecamoeba*, was almost as widespread as *Acanthamoeba*. Other species occurred at only one to four sites. A mesophilic *Naegleria* sp. was found in soil under a termite mound.

Table **1**. Summary of the collections of arid soils from Australia.

Sites	Litter	Soil	Mound	pH
Spinifex		3		6.5–9.5
Mulga:				
Acacia	2	3		5.5–8.0
Allocasaurina	1	1		7.0
Eremophila	1			7.0
Chenopod	3	3		9.5–10.0
Termitaria		2	3	6.0
Cycad, Kings Canyon		1		7.0
Interspace soils		3		6.5–7.0
Totals	7	16	3	

Only a few ciliates were found in interspace soils, compared to 150–400/g in soils under plants and termite mounds. From 500–980/g ciliates inhabited most plant litters and several soils under chenopod shrubs (Table 2, Fig. 2). Species numbered 1–12 in interspace soils, 10–18 in many litters and soils under plants, and $\geq$ 22 in *Acacia* and chenopod litters and chenopod soils. Fifty-seven species, 52 identified to genus or species level, were found (Table 4). *Holosticha* spp. were the most frequent ciliates, but a variety of small bactivores furnished most of the species at each site. The genera *Colpoda* and *Crytolophosis* were always present. C/P ratios of $\leq$ 2.00 in the bare interspace soils and several other sites, and ratios of 1.00–1.89 at most other sites, showed a large proportion of colpodid species. C/P ratios of 0.35–0.88 for two *Acacia* litters and six chenopod litters and soils were due to a large number of spirotrich species. Haptorial ciliates belonging to the genera *Enchelys*, *Eneheluyodon*, *Spathidium*, *Litonotus*, and *Dileptus* were found at 80% of sites.

Testacean numbers averaged 1,033 (900–1,200)/g for interspace soils, but were three times more abundant, 3,400 (1,300–5,000)/g in litters and soils under plants and termitaria. Only about 10% of the tests were occupied. Small acrostomes of the genera *Euglypha*, *Cryptodifflugia*, and *Difflugiella*, and the plagiostome *Trinema* were the most prevalent and furnished over half of the individuals at sites (Table 5). Bare interspace soils averaged 7 (6–8) species per site. Other soils had almost double this diversity, averaging 12 (7–18) species per site. The cycad soil in Kings Canyon, a refugium, had double the numbers (11,900) of individuals and species (27), five of which occurred only there (Tables 2, 5).

The cyanobacterial crust was dominated by *Microcoleus* filaments, some of which were observed being consumed by *Thecamoeba* sp. and the ciliate *Nassula picta*. Also present were a non-encysting *Saccamoeba* sp., the heliozoans *Actinophrys sol* and *Radiophrys* sp., and four other ciliates, *Bursaridum difficile*, *Enchelydium* sp., *Paruroleptus muscorum*, and *Strongylidium muscorum*.

DISCUSSION

A number of desert biochemical studies have led to the development of the resource island hypothesis, which states that shrubs create heterogeneity in soils by localizing soil fertility under their canopies (Schlessinger et al. 1996). In a study of three North American deserts, Schlessinger et al. (1996) found that invasion of arid lands by shrubs created ''islands of fertility'' with greater N, PO_4, and SO_4 than in bare soil between plants. Likewise, Herman et al. (1995) found heterotrophic bac-

Table **2**. Numbers and species of protozoa in litters (L) and soils (S) in arid lands of Australia.

Collection		Protozoa × 10^3/g dry weight			Protozoa taxa		
		Amoebae	Ciliates	Testacea	Amoebae	Ciliates	Testacea
1. Spinifex	S	6.21	0.15	4.90	7	12	20
2. Spinifex	S	12.90	0.15	2.70	5	16	7
3. Spinifex	S	4.29	0.06	2.30	8	22	10
4. *Acacia*	S	29.96	0.27	2.20	6	17	9
5. *Acacia*	L	28.76	0.63	2.20	4	28	11
6. *Acacia*	S	4.00	0.38	4.00	5	24	9
7. *Acacia*	L	24.66	0.57	2.60	6	26	9
8. *Acacia*	S	10.27	0.25	4.10	6	13	13
9. *Allocausarina*	L	17.79	0.50	3.50	12	24	14
10. *Allocausarina*	S	12.36	0.45	2.90	8	17	13
11. *Eremophila*	L	6.79	0.29	2.70	6	9	11
12. Chenopod	L	220.53	0.85	4.10	12	16	14
13. Chenopod	S	31.63	0.96	2.90	11	26	14
14. Chenopod	L	112.81	0.98	5.10	8	22	17
15. Chenopod	S	49.59	0.38	3.40	4	25	12
16. Chenopod	L	76.07	0.89	3.10	10	23	10
17. Chenopod	S	12.54	0.51	4.70	4	22	14
18. Cycad	S	23.92	0.22	11.90	9	21	27
19. Termitaria mound		14.53	0.03	1.90	4	10	10
20. Termitaria mound		12.40	0.15	2.10	6	23	9
21. Termitaria	S	14.43	0.20	1.60	9	25	9
22. Termitaria mound		1.23	0.21	1.30	6	18	8
23. Termitaria	S	15.86	0.44	2.00	6	27	13
24. Interspace soil	S	1.20	0.05	0.90	5	9	6
25. Interspace soil	S	2.04	0.03	1.20	5	12	6
26. Interspace soil	S	3.09	0.01	1.00	3	4	8

teria (including a subset of nitrogen-utilizing organisms) more abundant under desert shrubs than in bare soil spaces between plants. The great difference in numbers of amoebae, ciliates, and testacea in this study show that protozoa are also more abundant under shrubs, with their nutritional sources of bacteria and organic matter (Table 2, Fig. 2). Arthropods and small vertebrates, living under shrub canopies, contribute to the microbial community by adding their excreta to these nutrient islands.

In arid soils, fungi, microarthropods, and termites can extend mineralization beyond the brief wet periods exploited by the bacteria-protozoa-nematode water film community. However, a dramatic increase in decomposition occurs when the wetting of a desert soil triggers rapid increase in microbial population activity (Sarig and Steinberger 1993). Bacteria and flagellates increase immediately, followed by amoebae. The two protist groups track the bacteria decreasing in abundance as protozoan predation releases nutrients to the soil (Clarholm 1994; Griffiths 1994). An interesting plant aid to microbial decomposition in central Australia occurs in the umbrella-shaped canopy of mulga trees, that guide rainwater by stemflow into the ground around the tree base. This increases the soil water content six times over the average amount of precipitation (van Oosterzee 1991).

The rare episodic rainfalls make permeable spinifex soils soggy, and create flood soils under mulga vegetation (van Oosterzee 1991). In experiments on soil flooding, excess water decreases microbial activity but may increase microbe-substrate contact to enhance activity as the soil dries (Bosio and Sokow 1995). Applied to spinifex and mulga ecosystems, episodic rain would initially create anaerobic conditions, but mix the water film community of bacteria and protozoa to enhance subsequent aerobic activity.

Abundance and diversity reflect the recent metabolic history as well as showing the growth potential of the microbial community. The large protozoan populations in litters and soils under shrubs (Table 2, Fig. 2) enable instant exploitation of rapidly increasing bacterial populations following wetting. The biodiversity of ciliates in *Acacia* litters and chenopod litters and soils is comparable to some savannahs and temperate hardwood forests (Bamforth 1995). This increased diversity is due partly to predators, such as haptorids and spirotrichs, that may feed on other protozoa.

A surprising number of soil protozoa can be found in arid lands. This study records 145 species of amoebae, ciliates, and testacea. Varga (1936) listed 36 species of amoebae and 23 species of testacea from desert and high plateau soils in Algeria; Rodrigues-Zaragosa and Garcia (1997) reported 40 species of amoebae from the rhizosphere and soil under a desert cactus. This diversity is due to ubiquitous dispersal (Finlay 2002), but species able to cope with harsh arid land conditions (r selection) provided the most prevalent populations. *Acanthamoeba*, the most widespread soil amoeba (Page 1988), was the most abundant amoeba in this study (Table 3), and was also prominent in the study of Rodriguez-Zaragoa and Garcia (1997). In this study, ten of the thirteen most prevalent ciliate species (Table 4) are characteristic of stressed and ephemeral habitats (Bamforth 2001), and five of the most abundant testacea species (Table 5) are early colonizers (Wodarz et al. 1992).

A refugium is a region that enables certain organisms to persist when the original ecosystem becomes less habitable due to climate change. Kings Canyon provides water sources in shady crevices in which the cycad *Macrozamia macdonneii* and other plants grow (van Oosterzee 1991). Although amoebae and ciliates did not differ in numbers or species from desert sites (Table 2, Fig. 2), the effect of a more stable moisture regime was seen in the slowly growing testacea, which were three times more abundant, with twice as many species.

The cyanobacterial crust under one of the spinifex shrubs contained a distinctive protozoan community. In *Microcoleus* crusts, several filaments occupy a common sheath, and addi-

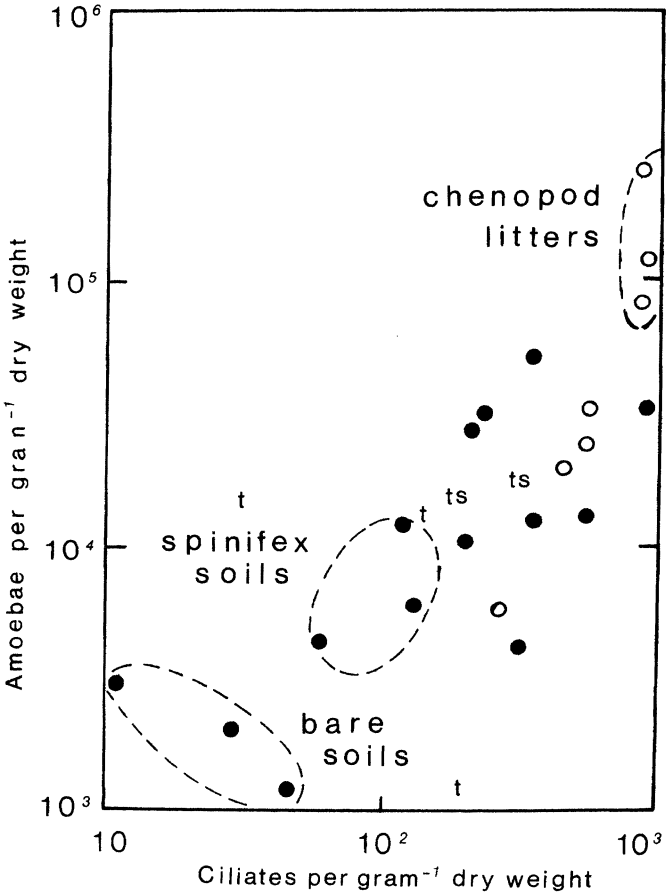

Fig. **2**. Abundances of amoebae and ciliates in litters, soils, and termitaria. Open symbols are litters; solid symbols soils, t, termite mounds; ts, soils under the mounds.

Table **3**. Prevalence of gymnamoebae in collections in arid lands of Australia.

Species	Number out of 26
Acanthamoeba group II (polygonal) cyst	24
Acanthamoeba group III (round) cyst	23
Unidentified Vahlkampfid	21
Hartmanella spp.	16
Dermamoeba sp.	14
Sappinia diploidea	14
Platyamoeba placida	8
Thecamoeba sp., parietal nucleus	7
Filoseans	7
Platyamoeba stenopodia	6
Thecamoeba sp., vesicular nucleus	5
Saccamoeba sp.	4
Balamuthia-like (with pores)	3
Cochliopodium sp.	3
Echinamoeba sp.	3
Comandonia sp.	2
Nuclearia sp.	2
Adelphamoeba sp.	1
Cashia sp.	1
Gocevia sp.	1
Naegleria sp.	1
Protacanthamoeba sp.	1
Willaertia magna	1

Table **4**. Prevalence of ciliates in collections in arid lands of Australia.

Species	Number out of 26
Holosticha spp.	25
Colpoda steini	22
Cyrtolophosis elongata	20
Cyclidium muscorum	19
Gonostomum affine	18
Parauroleptus sp.	17
Platyophrya vorax	17
Pseudochilodontopsis mutabilis	17
Colpoda edaphani	16
Colpoda inflata	15
Cyrtolophosis mucicola	15
Leptopharynx costatus	15
Sathrophilus muscorum	15
Colpoda cucullus	14
Colpoda maupasi	12
Amphisiella sp.	11
Hemisincirra gellerti	11
Oxytricha setigera	11
Enchlydium longicaudatus	9
Holoticha muscorum	9
Oxytricha sp.	9
Colpoda aspera	8
Enchelydium sp. no. 1	8
Histriculus muscorum	8
Voticella astyliformis	8
Bryometopus pseudochilodon	7
Enchelydium sp. no. 2	7
Microdiaphanosoma arcuata	7
Spathidium spp.	7
Dileptus sp.	6
Hemisincirra sp.	6
Litonotus sp.	5
Pseudocyrtolophosis alpestris	5
Belpharisma hyalinum	4
Bursaridium sp.	4
Enchelydium sp. no. 3	3
Aspidisca sp.	3
Enchelys sp.	3
Euplotes musicola	3
Homalogastra setosa	3
Pseudoholophrya terricola	3
Spathidium longicaudatum	3
Trachelophyllum apuculatum	3
Arcuspathidium muscorum	2
Drepanomonas revoluta	2
Microthoras simulans	2
Rostrophryides australis	2
Tachysoma sp.	2
Tetrahymena rostrata	2
Bresslauides australis	1
Colpoda henneguyi	1
Grossglockneria acuta	1
Nassula picta	1
Nivaliella plana	1
Plagiocampa rouxi	1
Vorticella similis	1

tionally secrete polysaccharides that provide protection against desiccation (Belnap and Gardner 1993). This community can therefore be considered to occupy a micro-refugium, analagous to topographical refugia, such as Kings Canyon, in desert landscapes.

Termites influence the distribution of organic matter in arid environments (Whitford 1996), creating fertility soil islands under their structures and locking organic matter up in their mounds (termitaria). Termitaria are prominent features in spi-

Table **5**. Prevalence of testacea in collections in arid lands of Australia.

Species	Number out of 26
Euglypha rotunda	25
Euglypha laevis	20
Euglypha tuberculata	20
Cryptodifflugia compressa	19
Difflugiella oviformis	19
Euglypha cuspidata	19
Trinema enchelys	19
Phryganella sp.	18
Difflugia lucida	16
Pseudodifflugia fascicularis	11
Tracheleuglypha acolla	11
Microcorycia flava	10
Tracheleuglypha dentata	10
Trinema complanatum	10
Pseudodifflugia senartensis	9
Pharyganella acropodia	5
Euglypha lanceolata	4
Difflugiella oviformis fusca	3
Difflugia acuminata	3
Difflugiella sacculus	3
Euglypha cristata	3
Unidentified (2 species)	3
Chlamydophrys sp.	2
Euglypha strigosa glabra	2
Pseudoawerintzewia calcicola	2
Trinema lineare	2
Trinema plenum	2
*Arcella arenaria**	1
*Cyclopyxis arcelloides**	1
*Euglypha dentata**	1
*Euglypha polylepis**	1
Heleopera humicola	1
*Heleopera sylvatica**	1
Schwabia terricola thomasi	1

* Found only in Kings Canyon.

nifex and mulga ecosystems. Tongway, Ludwig, and Whitford (1989) found increased organic matter and soil permeability in termite galleries under those mulga log mounds that develop under dead trees. The two soils under termite mounds in this study supported protozoan populations similar to the shrub fertile islands (Table 2, Fig. 2). Some of the protozoa extracted from the mounds may have been active, but most probably emerged from cysts that had been cemented in the impenetrable mound walls for decades, waiting for eventual mound abandonment by the insects, when decay would return protozoa to the soil.

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