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Diversity of Antarctic terrestrial protozoa

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Heterotrophic protozoa have a global distribution in terrestrial habitats. The functional groups significantly represented are zooflagellates, ciliates, gymnamoebae and testate amoebae. Their range extends into the Antarctic zone, but the species richness of the communities is rarely of the same order of magnitude as those in temperate latitudes. Species diversity is usually very low owing to dominance of the communities by single, or a few, species which are best adapted to the Antarctic terrestrial environment. This is characterized by seasonal, diurnal or unpredictable fluctuations in moisture, temperature and bacterial food supply of high amplitude. The fauna shows pauperization with latitude and climatic severity. Nearly all records of species distribution are consistent with the model that community composition is determined by local conditions. An important exception is the distribution of the testate amoeba genus *Nebela* whose species distribution is influenced by biogeographical factors. Successional changes in community composition in fellfield habitats are characterized by the sequence: pioneer microflagellate colonizers, larger flagellates and small ciliates, and finally testate amoebae. The succession is most closely correlated with the accumulation of organic matter. A model of the strategies of dominant microflagellate species can be constructed by ordinating them on a two-dimensional habitat template of **A–r–K** selection continuum. The globally ubiquitous microflagellate *Heteromita globosa* emerges as the most strongly A–selected and K–selected. The occurrence of terrestrial protozoa near their latitudinal limits of distribution can serve as sensitive indicators of the biological effects of climatic change. Having short generation times and effective means of cyst dispersal, changes in the gross distribution can provide rapid warning of critical changes in thermal regimes.

Keywords: protozoa; species richness; populations; biogeography, succession; adaptations and strategies; bio-indicators.

Introduction

The Antarctic zone may be defined as that lying south of the sub-Antarctic convergence and includes maritime Antarctic islands such as the South Orkneys and South Shetlands, together with the Antarctic Peninsula and the continental landmass of Greater Antarctica. Ground which is free of snow in Summer is potentially available for colonization by terrestrial biota (Wynn-Williams, 1990). Habitats have evolved which may collectively be termed Antarctic tundra. These vary widely in texture, organic content, pH and the extent of vegetation cover. Descriptions and classifications of these have been given by Allen and Heal (1970), Smith (1978) and Claridge and Campbell (1985). The most commonly occurring types and their associated vegetation are shown in Fig. 1. It is clear that the Antarctic provides a range of habitats for terrestrial microbiota broadly comparable to those in arcto-alpine zones with the significant differences that the Antarctic lacks trees and flowering plants are rare. The Antarctic terrestrial environment is characterized by extreme fluctuations of microclimatic variables (Walton, 1984). In particular, seasonal diurnal or irregular fluctuations in ground temperature and moisture impose exceptional stresses on terrestrial organisms. The biota therefore essentially consists of those species which have physiological adaptations and life-history strategies that enable them, not only to survive, but to grow and reproduce under environmental regimes which are only intermittently favourable.

Species – riches of the protozoan fauna

Protozoa are the most diverse and abundant eukaryotes on the Earth. Their diversity lies not in the length of the list of described species (some 40 000 free-living species) in which they are outnumbered by the arthropods by at least two orders of magnitude, but in their highly polyphyletic nature as revealed by 18s ribosomal RNA sequencing studies (Schlegel, 1991). Together with the algae and Oomycota, it becomes necessary to envisage some 45 protistan Phyla (Corliss, 1984) and possibly eight protistan Kingdoms (Cavalier-Smith, 1991). The traditional designation 'Protozoa' defies definition as a single taxon (Vickeman, 1992).

For the purposes of this paper 'protozoa' will be held to include those eukaryotic heterotrophs which are neither animals nor fungi, but to exclude the autotrophs and mixotrophs. Four groups may be distinguished as constituting the great majority of the terrestrial species: zooflagellates; gymnamoebae; testate amoebae; and ciliates. All these,

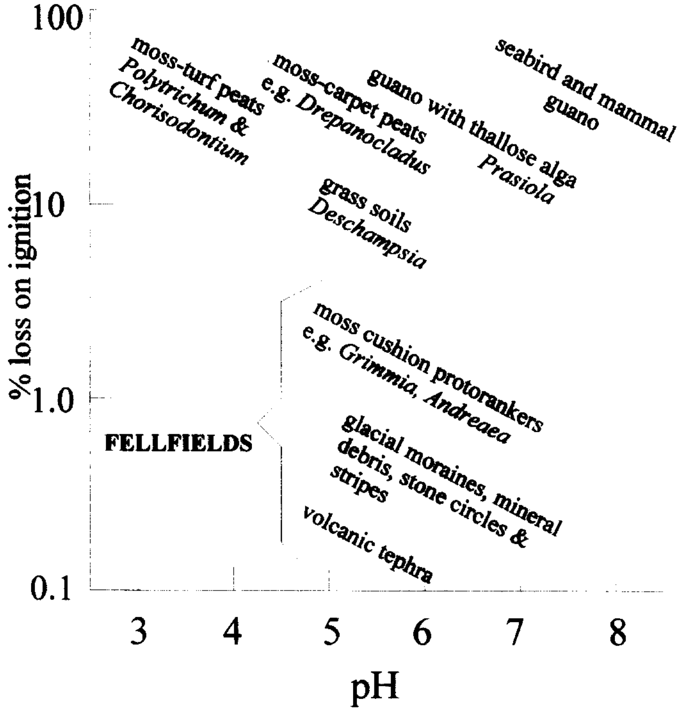

Figure 1. An ordination of the diversity of terrestrial habitats in the Antarctic.

except the ciliates, are polyphyletic and cannot have the status of taxa; for practical purposes, however, they can be regarded as functional ecological groupings.

The exact species composition of the global (let alone Antarctic) terrestrial protozoan fauna is still very imperfectly known. Our ignorance is owing to a combination of factors: inadequacy of surveys, technical problems of isolation and culture, and difficulties and contentions of identification. Comprehensive monographs on the subject include those by Sandon (1927), Bonnet (1964), Stout and Heal (1967), Page (1976, 1988) and Foissner (1987, 1991). From these it may be concluded that there are up to 1000 species of terrestrial protozoa world-wide. The species lists published or reviewed by Sudzuki (1964) and Smith (1978, 1992) suggest that the species-richness of the Antarctic terrestrial fauna may be approximately 200 species, i.e. a substantial fraction of the global fauna. This number includes an estimated 50 zooflagellates, 15 gymnamoebae, 60 testate amoebae and 75 ciliates. Examples of the recorded species-richness of location-specific protozoan communities are shown in Table 1. These numbers almost certainly underestimate the true numbers, but are sufficient to indicate the existence of terrestrial protozoan communities whose species-richness is one order of magnitude less than those of the Arctic, temperate and tropical zones.

Populations and species diversity

Despite some hundreds of terrestrial protozoan species having been recorded at present in the Antarctic, very few of them occur in numbers large enough for their populations to be estimated. This indicates that the communities have very low species diversity, compared with those occurring in lower latitudes, and show a high degree of single or few-species dominance. Estimates of total protozoan abundance or biomass are therefore derived substantially from population determinations of the dominant species. Published records (Smith, 1984; Smith and Tearle, 1985) show that mineral soils (fellfield), devoid of macroscopic vegetation, contain only microflagellates while moss peat and grass soil habitats are dominated by testate amoebae. Despite their numerous species, ciliates never occur in sufficient abundance for population determinations except in marine bird guano. Estimates of peak Summer abundance of dominant species are shown in Table 2. These numbers are only slightly lower than total taxon numbers observed in soils of the northern temperate zone (Cowling, 1994), suggesting that these few species at least are as successfully adapted to terrestrial Antarctic conditions as to other biomes of the Earth. The spectacularly high numbers of testate amoebae in soils with the grass *Deschampsia antarctica* may be seen as a consequence of the stimulation of microbial activity which occurs in the rhizospheres around flowering plant roots (Zwart *et al.*, 1994) – a phenomenon which is absent or greatly reduced around moss rhizoids.

Pauperization of the fauna with latitude and climatic severity

While the Antarctic forms a distinct zone from the rest of the Earth, it is also highly heterogenous in its local and microclimate structure. Including the sub-Antarctic, it presents latitudinal transects of increasing climatic severity some 5000 km long. The influence of latitude on species richness cannot be known with certainty for most protozoan taxa owing to incompleteness of records. However the testate amoebae are sufficiently well recorded to reveal a clear trend (Smith, 1982). The regression of species

Table 1. Recorded species richness of terrestrial protozoan communities.

Location	Enderby Land, Langhovde & Ongul Island	South Shetland Islands, Elephant Island (23 sites)	South Orkney Islands, Signy Island (6 sites)	South Orkney Islands, (15 sites)	South Shetland Islands, Deception Island (6 sites)	South Orkney Islands, Signey Island (12 sites)
Habitats	*Bryum* moss-water	Moss-peat, Grass soil, Glacial moraines,	*Polytrichum-Chorisodontium* moss-peat	*Drepanocladus* moss-carpet	Volcanic tephra (with and without vegetation)	Fellfields (with and without vegetation)
Number of species						
zooflagellates	9	17	16	11	11	11
gymnamoebae	5	4	0	4	2	0
testate amoebae	12	15	17	9	4	4
ciliates	24	18	17	16	19	9

Table 2. Recorded summer abundances of dominant terrestrial protozoan species.

Species	Habitat	Population cm^{-2} in 0–3cm horizon
zooflagellates[a]		
Heteromita globosa Stein	Fellfield fines	1 200–13 800
	Fellfield coarse	300–5 400
	Andreaea moss-cushion	1 100–18 200
	Moss-turf peat	2 000–2 900
Tetramitus rostratus Perty	Chinstrap penguin guano	70–280
Testate amoebae[b]		
Corythion dubium Taranek	*Andreaea* moss cushion	800–1 400
	Grimmia moss cushion	680–1 180
	Moss-carpet peat	3 500–110 400
	Moss-turf peat	3 300–6 800
Cyclopyxis eurystoma Deflandre	*Prasiola* alga	300–5 100
	Grimmia moss-cushion	100–900
	Moss-carpet peat	7 300–10 500
	Moss-turf peat	900–3 300
	Grass soil	47 100–116 000
Arcella arenaria Greeff	*Bryum* moss cushion	530–2 900
Ciliates[a]		
Vorticella microstoma Ehrenberg	Chinstrap penguin guano	540–990

[a] Populations of zooflagellates and ciliates were determined by dilution–culture methods.
[b] Populations of testate amoebae were determined by the filtration direct-count method.

richness on latitude indicates faunal pauperization at a linear rate of −1.2 spp °S^{-1} ($r = -0.881$), reaching a notional zero at 81 °S. Northwards extrapolation of the same trend predicts 98 spp at the equator: a figure close to the 94 spp observed in tropical South America by Bonnet (1996). Evidence that this pauperization is associated with increasing climatic severity is shown by the significant correlations of species richness with mean January temperature ($r = 0.879$) (Fig. 2). The regression line indicates a loss of 3.3 spp for every 1°C drop in temperature (Smith, 1987).

Biogeographical effects on species richness

Soil microbiologists classically subscribed to Becking's dictum: 'Everything is everywhere; the environment selects' (Nicol, 1955), implying that all parts of the Earth have a dispersed reservoir of microbial propagules sufficient to ensure that species occurrences anywhere are determined by local conditions alone. There is evidence, however, that this dictum does not entirely hold true for the larger (>100 μm), heavier (>500 ng) species of protozoa such as the testate amoeba genus *Nebela* Leidy (Smith and Wilkinson, 1987). This large genus contains at least 18 species restricted to Gondwanaland continents and 14 species or varieties endemic to single locations. The species richness of the genus shows a similar pauperization with latitude and January temperatures to that of the testate amoeba fauna as a whole, indicating the importance of local environment in

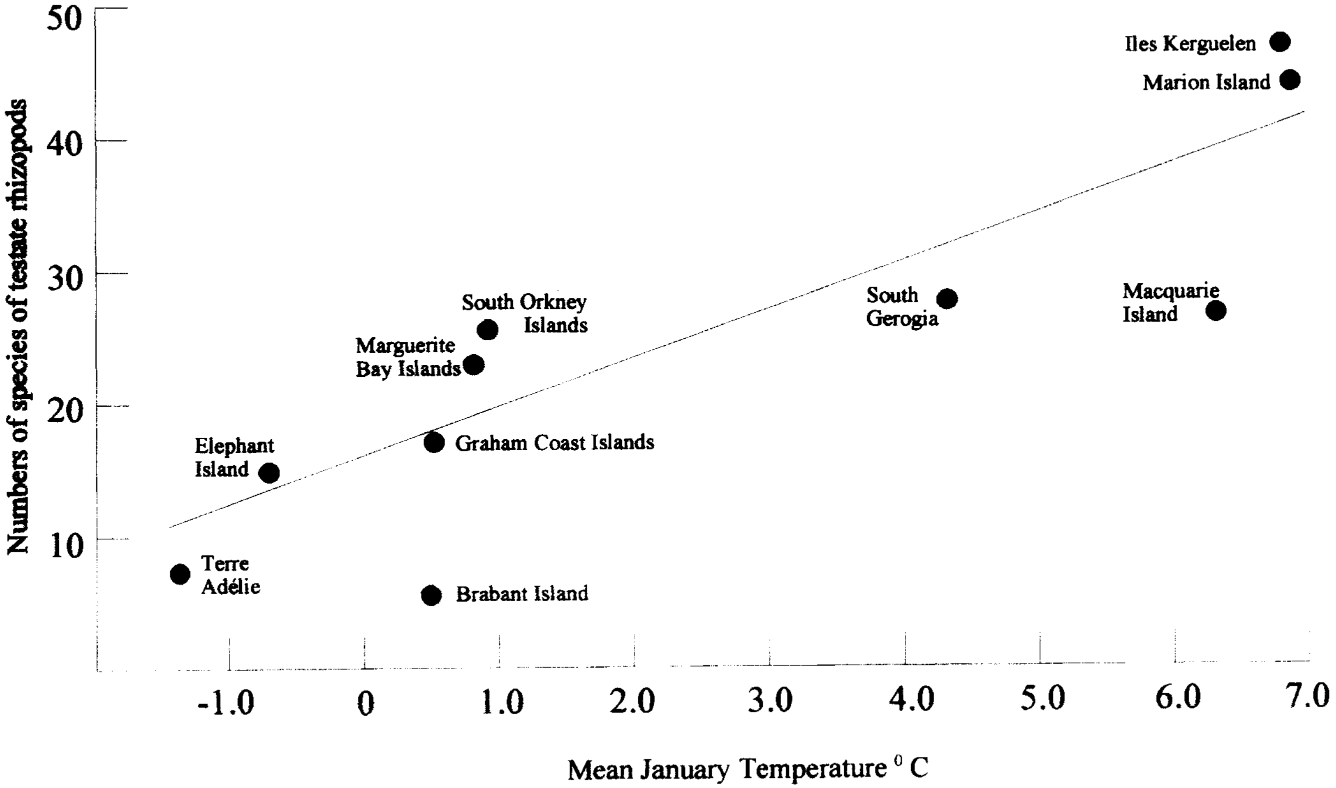

Figure 2. The pauperization of testate rhizopod fauna with climatic severity.

determining geographical distribution. However, the faunas of some locations deviate from the general trend. Those of the western parts of the Antarctic and southern temperate zones being more species rich, suggesting that biogeographical factors are also influential. These observations led Smith and Wilkinson (1987) to construct a model proposing wide speciation of *Nebela* in the Neotropical realm during the Mesozoic and invoking the influence of continental drift upon secular distribution. This implied that cysts of *Nebela* spp survived the Pleistocene on glacial refugia in order to act as local colonizing propagules in the Holocene. Further analyses of the data (Wilkinson, 1990a, 1994) have refuted the idea of glacial refugia and suggest that Holocene colonization originated from South America. This is supported by the observation of a rich fauna of *Nebela* spp, including sub-specific endemism, on Marion Island – a volcanic island only 500 000 years old. It may be concluded that the secular faunal composition is indeed limited by biogeographical dispersal factors (such as atmospheric circulation) but that continental drift is not involved.

Successional changes in community composition

Attempts to determine terrestrial protozoan succession in Antarctic habitats have been done as part of research on microbial colonization processes in Antarctic fellfields (Wynn-Williams, 1990).

Direct observation of changes of over time are usually not feasible owing to fellfield communities being already long established. However pyroclastic eruptions on Deception Island, South Shetland Islands, in 1967, 1969 and 1970 provided a rare opportunity to monitor the colonization process in newly created sterile tephra. Thirteen protozoan species were recorded in early studies (Smith, 1974). These suggested that after a lag phase of about 10 months, newly deposited tephra acquired protozoan colonists at a rate of 1.37 spp per year (Fig. 3) during the first 4 years. The main pioneer colonists included the microflagellates *Spumella elongata* Belcher, *Heteromita globosa* Stein, and *Cercomonas longicauda* Stein. The rate of colonization was correlated with the organic content ($r = 0.802$) and its accumulation was accelerated in tephra which became colonized by bryophyte vegetation. Ten years later (Smith, 1985), 23 species of protozoa (five flagellates, two gymnamoebae, four testate amoebae and 12 ciliates) were observed in addition to the 13 species recorded previously. It was concluded that the processes of microbial colonization of sterile tephra had been initiated within 1 year of deposition, with the first protozoan species appearing after 10 months.

The rate of increase in numbers of protozoan species in tephra devoid of macroscopic vegetation was most directly associated with the rate of accumulation of organic matter, although there was also evidence that species numbers showed some increase with the passage of time without any increase in organic content. After 12 years, the protozoan fauna of unvegetated tephra had attained a richness (five to seven species) comparable to that in tephra more than 150 years old. Tephra containing macroscopic bryophyte or thallose alga vegetation had markedly lower pH and higher moisture, organic content and species numbers than unvegetated tephra regardless of age. The fauna of some 12-year-old tephra samples showed a species richness (9 to 14 species) approaching that of similarly vegetated tephra more than 150 years old (15 to 17 species). The pioneer protozoa of unvegetated tephra (microflagellates) from different sites were similar, but the protozoa from older tephra with vegetation (flagellates, amoebae, ciliates) showed greater

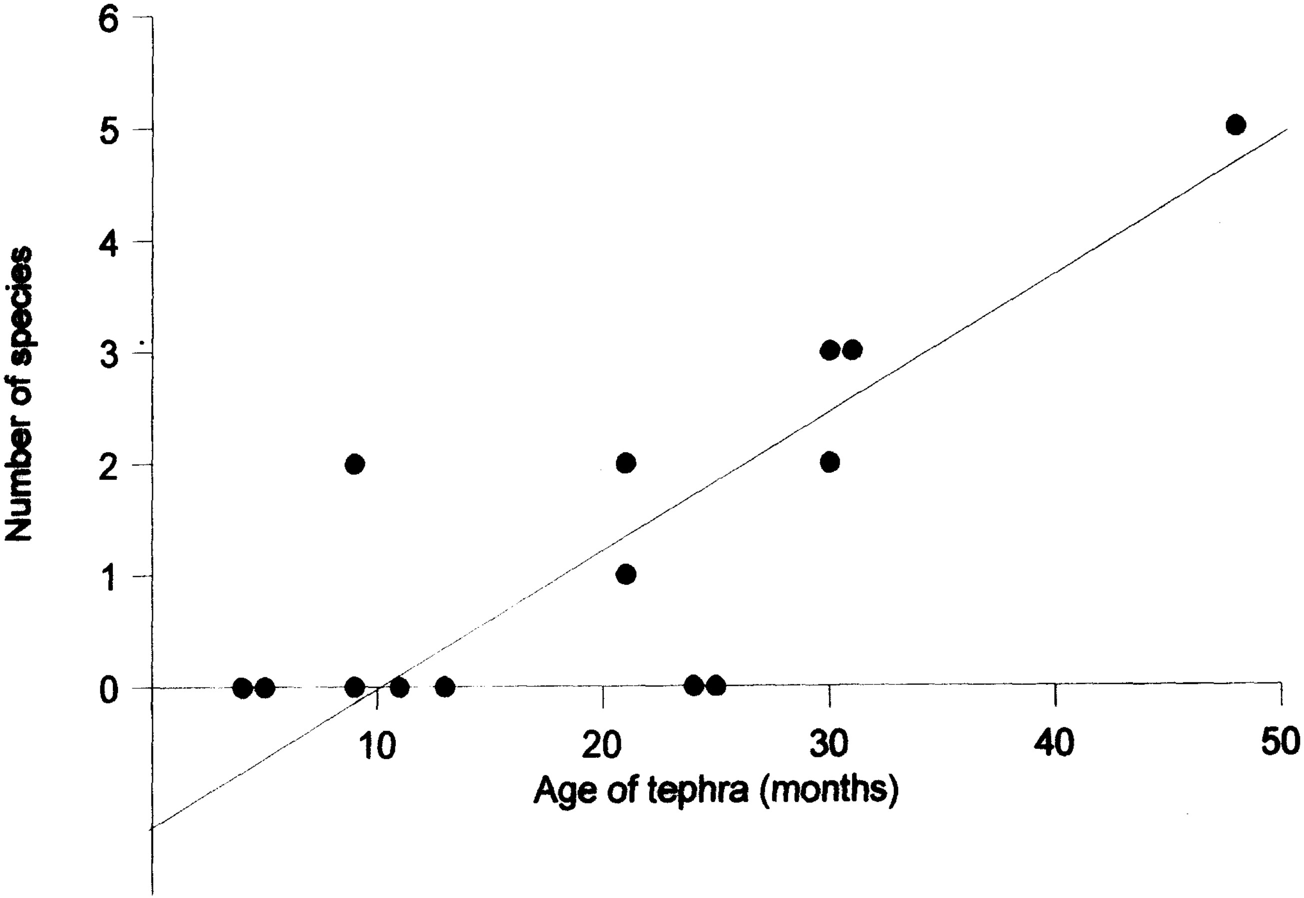

Figure 3. Increase in species richness of protozoan communities in volcanic tephra with age.

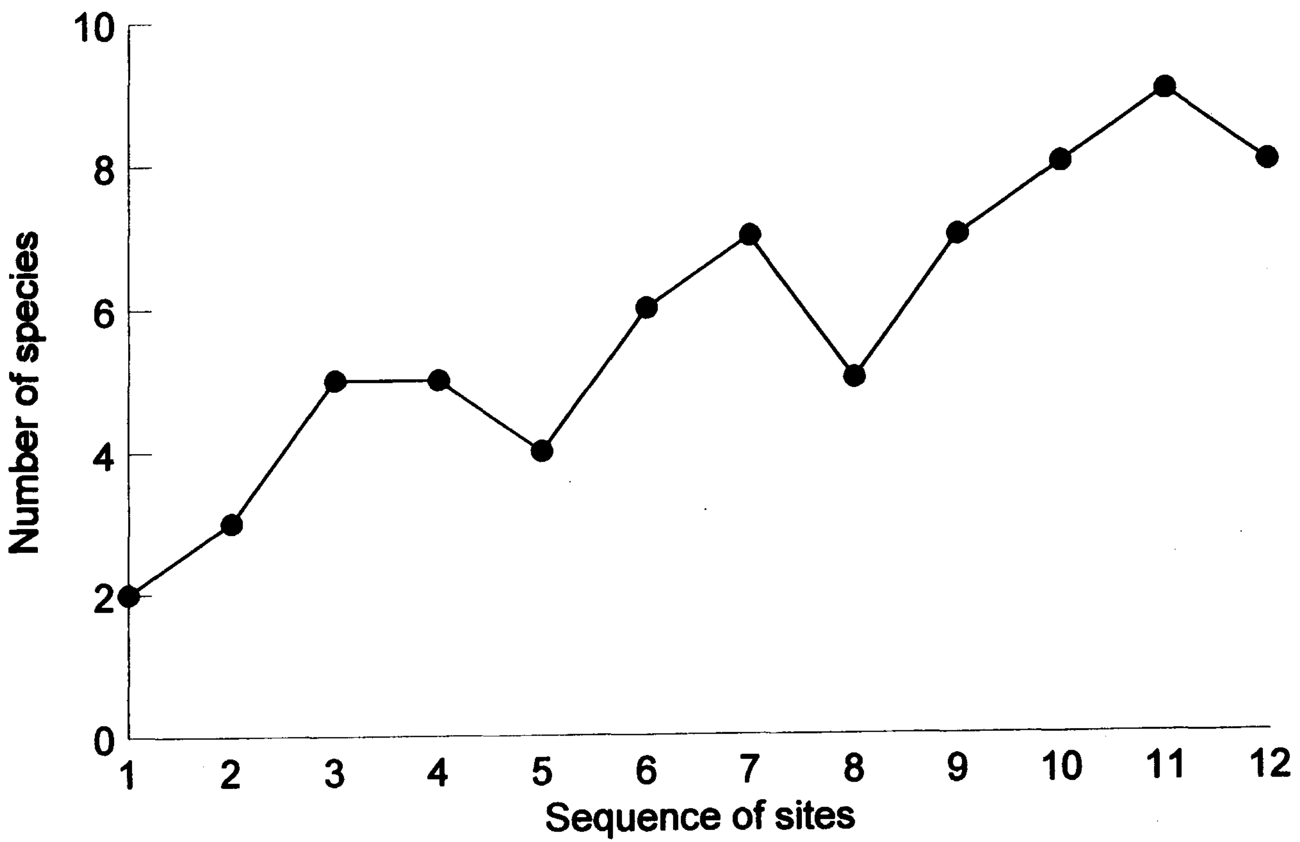

Figure 4. Species richness of protozoan communities in Signy Island fellfields with sites sequenced by cluster analysis.

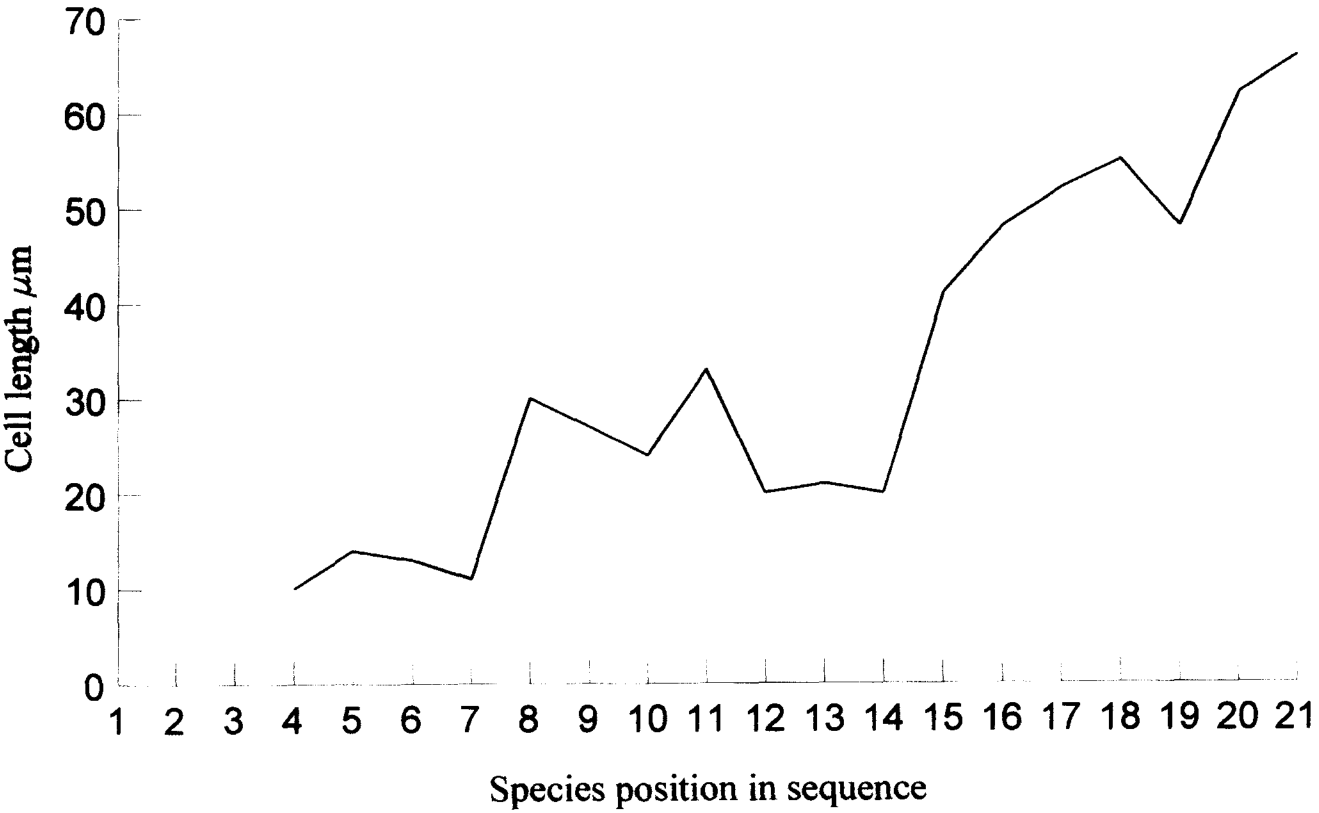

Figure 5. Increase in size of protozoan species in Signy Island fellfields (four-species running mean) with inferred position in colonization sequence.

heterogeneity between sites. Testate amoebae were recorded only from tephra more than 150 years old with bryophytes except for *Corythion dubium*, which was also observed in 12-year-old tephra with *Drepanocladus*, thus confirming the status of this species as the most ubiquitous and successful testate amoeba in the maritime Antarctic (Smith, 1978; Cowling, 1985).

The succession of protozoan communities may also be inferred by analysing the species composition of a variety of fellfield materials and determining clusters by the methods of numerical taxonomy. This was used as part of the Fellfield Ecology Research Programme on Signy Island, South Orkney Islands (Smith, 1984; Smith and Tearle, 1985). Despite this being an indirect approach, it yielded results remarkably similar to those from direct observations on Deception Island. The sequence of sites showed a trend of increasing species richness (Fig. 4) which was positively correlated with organic content ($r = 0.860$) and, in materials with very low moisture and organic content, with pH also ($r = 0.762$). The inferred sequence of colonizing species showed a trend of increasing cell dimensions (Fig. 5) from microflagellates, through larger flagellates and small ciliates to the single testate amoeba species *Corythion dubium*.

Diversity of adaptations and strategies of zooflagellates

The dominant heterotrophs in the biotic communities of unvegetated habitats include the zooflagellates *Heteromita globosa* Stein, *Spumella elongata* Belcher, *Bodo saltans* Ehrenberg and *Tetramitus rostratus* Perty. All of them are small (5–20 μm), non-pigmented bacteriophagous heterotrophs which use flagella for feeding and locomotion. Despite their similarities, these species are phylogenetically heterogenous (Cavalier-Smith, 1991) and show physiological differences. From the research of Brent (1954), Smith (1973b), Hughes and Smith (1989), Zwart and Darbyshire (1992) and Smith *et al.* (in press), it is possible to distinguish the characteristics by which these species are adapted to different Antarctic habitats (Fig. 1) or achieve resource partitioning within habitats. These are summarized in Table 3. *Heteromita globosa* is the most abundant and ubiquitous flagellate, not only in the Antarctic, but in soils world-wide. Its success can be attributed to its versatile ability to feed both by flagellar currents and by pseudopodial phagotrophy in both surface grazing and free-swimming modes. Additionally it shows a precise adaptation to freeze-thaw cycles in rapidly encysting with decreasing temperature at +1.5°C and then re-excysting at the same threshold when temperatures rise again. Encystment induced by cold alone is not known to occur in any other flagellate species.

Field observations suggest that *Bodo saltans* is a niche replacement species for *Heteromita* in alkaline habitats (fellfield fines of calcareous origin; penguin guano). There is experimental evidence that *B. saltans* is favoured by high pH at low temperatures only – those most frequently experienced in Antarctic habitats. Encystment has never been observed in this species. It is among the smaller of common soil flagellates and it is possible that it survives sub-zero temperatures as stationary phase trophozoites in supercooled water-filled micro-crevices.

Spumella elongata (= *Oikomonas termo* Ehrenberg) is a less abundant species than the aforementioned and exhibits more free-swimming feeding than the other species, although it can also readily ingest bacteria when it is sessile.

Table 3. Characteristics of terrestrial zooflagellates.

	Heteromita	*Bodo*	*Spumella*	*Tetramitus*
Length	1–10 μm	5–8 μm	4–5 μm	18–24 μm
Flagella	2 Heterodynamic	2 Heterodynamic	1 + short Accessory	4 Homodynamic
Flagellar surface attachment	****	****	*	none
Pseudopodia formation	**	None	*	*****
Feeding: surface grazing	****	***	*	*****
Feeding: free-swimming	***	***	*****	***
Encystment response to dessication/starvation	*****	None	*****	*****
Encystment response to low temperature	*****	None	Unknown	Unknown
Temperature relations				
Optimum temperature	23°C	22°C	>28°C	30°C
Ratkowsky sub-optimal curve coefficient day^{-1}. °C^{-1}	0.041	0.078	0.084	0.048
pH optimum >10°C	Acid	Acid	Acid	Alkaline
<10°C	Acid	Alkaline	Acid	Alkaline

* indicates minimal; ***** indicates maximal.

Tetramitus rostratus is fully an amoebo-flagellate. It is a larger species than the others, but it can feed, grow and multiply in both amoeboid and flagellate phases, depending upon moisture content. It is strictly coprozoic and in the Antarctic its distribution is restricted to seabird and mammal guano.

The species' cardinal temperatures are determined by fitting curves to plots of the square root of maximum population specific growth rate against temperature (Ratkowsky *et al.*, 1983). The slopes of the curves at sub-optimal temperatures are a measure of the species' psychrotrophy. The curve coefficients (Table 3) indicate that all the species show psychrotrophy and that *Heteromita* and *Tetramitus* show the greatest degree of facultative psychrophily, maintaining relatively high growth rates even at temperatures below 5°C.

Appraisal of these microflagellates' characteristics suggests that a model of the diversity of their strategies can be proposed using the concepts of **r**– and **K**–selection. These have previously been applied to freshwater ciliates (Luckinbill, 1979) and to soil ciliates (Lüftenegger *et al.*, 1985), but not to terrestrial flagellates. In view of the unpredictable and/or adverse (only rarely and intermittently favourable) nature of Antarctic terrestrial environments, it is thought necessary to utilize a two-dimensional habitat template of **A**–**r**–**K** selection (Greenslade, 1983) rather than a linear **r**–**K** continuum. The three types may be briefly summarized:

A–selection: environment only rarely favourable, highly predictable, low biotic stress, density-independent population regulation.

r –selection: environment variably favourable, unpredictable, low biotic stress, density-independent population regulation.

K–selection: environment favourable, highly predictable, biotic stress high, density-dependent population regulation.

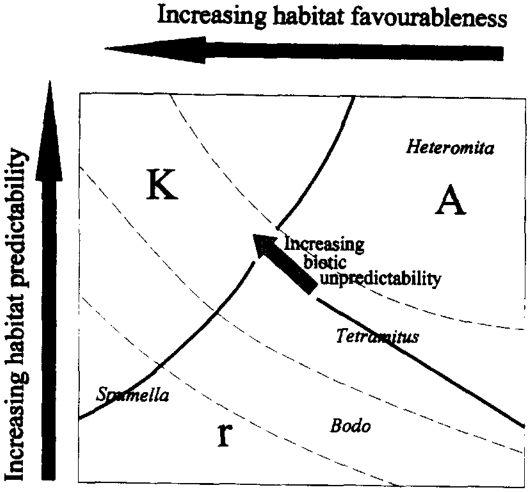

Figure 6. An ordination of microflagellate species on a two-dimensional habitat templet.

The postulated position of the four flagellate species on the **A–r–K** habitat template are shown in Fig. 6. The small size, diversity of feeding modes and encystment/excystment facility of *Heteromita* not only makes it the most successful species under **A**-selecting conditions, but also gives it a highly competitive advantage under **K**-selecting conditions. *Spumella*, by contrast, is the least successful of these four species owing to its greater niche and feeding specialization. *Tetramitus* lacks the advantage of small size, but is compensated by its ability readily to assume either flagellate or amoeboid trophozoite forms. *Bodo* shares some of the advantages of *Heteromita* but critically lacks the encystment/excystment facility. More experimental data on the temperature and feeding relations of these species are needed for the further refinement of this model.

Bio-indicator value of Antarctic terrestrial protozoa

The potential of protozoa as bio-indicators in terrestrial ecosystems is attracting increasing attention. They are seen as uniquely valuable in this respect on account of their short life-cycles, their sensitivity and rapid responses to environmental perturbations and their occurrence in extreme habitats (alpine, polar) devoid of other eukaryotic biota. This topic has been comprehensively reviewed by Foissner (1987, 1994) including consideration of the effects of irrigation, fertilizers and pollution by heavy metals, biocides and radionuclides. Awareness of the need for comprehensive protection of the Antarctic environment, including environmental impact assessment, environmental monitoring and wildlife conservation, has been greatly heightened in the 1990s (SCAR, 1991), and there is potential for terrestrial protozoan studies to make a distinctive contribution in this context. In particular, the occurrence of common species of protozoa near their altitudinal or latitudinal limits of distribution may serve as sensitive indicators of the biological effects of global climatic change. The combination of properties of short generation time and effective means of dispersal in cyst form means changes in their patterns of distribution could provide early warning of critical changes in terrestrial thermal regimes (Smith and Crook, 1995).

The soil ciliate genus *Colpoda* Müller is ubiquitous and almost globally cosmopolitan, but has its southern limit of frequent and ubiquitous distribution at the sub-Antarctic/maritime Antarctic boundary (Smith, 1978). Species of *Colpoda* have indeed been detected south of this boundary, but only as a result of analysis of very large samples and even then they are not present in every sample (Ryan *et al.*, 1989; Foissner, 1996). Experimental and micrometeorological evidence (Smith, 1973c; Smith *et al.*, 1990; Coutts, 1993) suggests that the global distribution of *Colpoda* spp is determined by terrestrial microclimates alone. During the 21st Century, maritime Antarctic islands, such as the South Orkneys and South Shetlands, could begin to experience terrestrial thermal regimes, which at present occur only in the sub-Antarctic, as a result of global warming. If this does occur, then the author predicts that one of the immediate effects of this climatic amelioration will be the ubiquitous establishment of *Colpoda* spp in the terrestrial habitats of the maritime Antarctic. We shall see.

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