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What shapes edaphic communities in mineral and ornithogenic soils of Cierva Point, Antarctic Peninsula?

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Abstract

Three mineral soil and four ornithogenic soil sites were sampled during summer 2006 at Cierva Point (Antarctic Peninsula) to study their bacterial, microalgal and faunal communities in relation to abiotic and biotic features.

Soil moisture, pH, conductivity, organic matter and nutrient contents were consistently lower and more homogeneous in mineral soils. Ornithogenic soils supported larger and more variable bacterial abundances than mineral ones. Algal communities from mineral soils were more diverse than those from ornithogenic soils, although chlorophyll-*a* concentrations were significantly higher in the latter. This parameter and bacterial abundance were correlated with nutrient and organic matter contents. The meiofauna obtained from mineral soils was homogeneous, with one nematode species dominating all samples. The fauna of ornithogenic soils varied widely in composition and abundance. Tardigrades and rotifers dominated the meiofauna at eutrophic O2, where they supported a large population of the predatory nematode *Coomansus gerlachei*. At site O3, high bacterial abundance was consistent with high densities of the bacterivorous nematodes *Plectus* spp.

This study provides evidence that Antarctic soils are complex and diverse systems, and suggests that biotic interactions (e.g. competition and predation) may have a stronger and more direct influence on community variability in space and time than previously thought.

Keywords: Edaphic communities; Biotic interactions; Antarctica

1. Introduction

Although constituting only 0.3% of the surface of the Antarctic continent, ice-free and in particular coastal landscapes are of prime ecological importance (Convey and Stevens, 2007), since soil formation provides a range of opportunities for plant and animal communities to develop. Succesful colonisation and establishment of

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new species in such environments depends on the ability of organisms (or their propagules) to survive during transport as well as finding an "opportunity window" of suitable environmental conditions on arrival (Ellis-Evans and Walton, 1990; Hughes et al., 2006). Indeed, Fermani et al. (2007) observed that microalgal communities from recently disturbed soils on volcanic Deception Island (South Shetland Islands) were less diverse than those from more stable habitats on the same island, and composed mainly of a few "ubiquitous" species.

Wynn-Williams (1990) proposed a model for the colonisation of newly exposed mineral soils, pioneered by the establishment of photosynthetic microalgae. Later, he observed changes in the colonisation process under physical conditions simulating those of the predicted regional climate change (Wynn-Williams, 1996), including increases in both temperature and liquid precipitation. Hughes et al. (2006) noted that changes in atmospheric patterns on the Antarctic Peninsula could also increase the frequency of arrival of allochtonous microbiota, with unpredictable consequences depending on their competitive ability.

Apart from changes in environmental conditions experienced by terrestrial Antarctic ecosystems, continuation of current rates of deglaciation will result in the expansion of ice-free areas in the Antarctic Peninsula (Convey, 2006; Cook et al., 2005). It is therefore necessary to address the consequences of these many aspects of climatic change for terrestrial ecosystems. This requires more detailed knowledge of their structure and biotic interactions, Adams et al. (2006), Bergstrom et al. (2006), and Convey and McInnes (2005), recognised that even extremely simple Antarctic soil communities contain autotrophic, consumer and predatory levels. Their responses may therefore be modulated by biotic interactions, even though these are currently generally assumed to be of minor importance compared to physical constraints, although this view has rarely been the subject of detailed autecological study (Hogg et al., 2006).

During the last decade, soils from Cierva Point have been characterised from an edaphologic context (Godagnone, 2002), and some factors influencing the abundance and diversity of edaphic microalgal communities from Cierva Point have been studied. Mataloni et al. (2000) analysed algal communities colonising discrete polygons of mineral soil in the context of the Theory of Island Biogeography (MacArthur and Wilson, 1967). Mataloni and Tell (2002) found that the diversity of microalgal communities from ornithogenic soils decreased with increasing trophic status, as was also recorded for freshwater microalgal communities. Nevertheless, the unusually high biodiversity of Cierva Point, as with many other Antarctic protected areas, is still far from thoroughly surveyed and consequently understood. Convey and Quintana (1997) found the microarthropod fauna of this site to be representative of the Maritime Antarctica region, although they considered that richness would probably increase with further sampling.

This study compared mineral and ornithogenic soils from Cierva Point by integrated examination of abiotic features and edaphic communities (bacteria, microalgae, meio- and mesofauna) during a single sampling season, in order to analyse changes in abundance, composition and structure of communities, and to identify possible abiotic and biotic drivers of changes in their biological properties.

2. Materials and methods

2.1. Study area

Cierva Point (64°10′S, 60°57′W) is characterised by a mild microclimate and an irregular relief resulting in large microenvironmental heterogeneity, which has allowed the existence of an unusually diverse biota (Agraz et al., 1994). On account of this, it has been designated as Antarctic Specially Protected Area (ASPA) No. 134. During the austral summer 2005/06, seven sites representative of ornithogenic (O1–O4) and mineral soils (M1–M3) at Cierva Point (northwest Antarctic Peninsula, Fig. 1) were sampled on four occasions: 9 and 21 January 2006, 2 and 15 February 2006. Mineral soil sampling sites were located along the broad ridge line connecting Mojón and Escombrera peaks, while ornithogenic sites were located in rookeries of *Pygoscelis papua* (O2, O3), or in resting areas along the paths to the sea used by these penguins (O1, O4). Fig. 2 illustrates two sites representing these different soil types.

2.2. Soil sampling

The geographical position of each sampling site was established with a Garmin Etrex GPS (Garmin International, Inc., Olathe, KS, USA). Slope was measured and its orientation established with a clinometer. Temperature at the time of sampling was measured 1 cm below the surface using a Hanna HI 991301 (Hanna Instruments Ltd., Leighton Buzzard, UK) sensor. At each site, four composite samples (each made up of three small cores from the top centimeter of the soil profile) were used to determine (a) soil

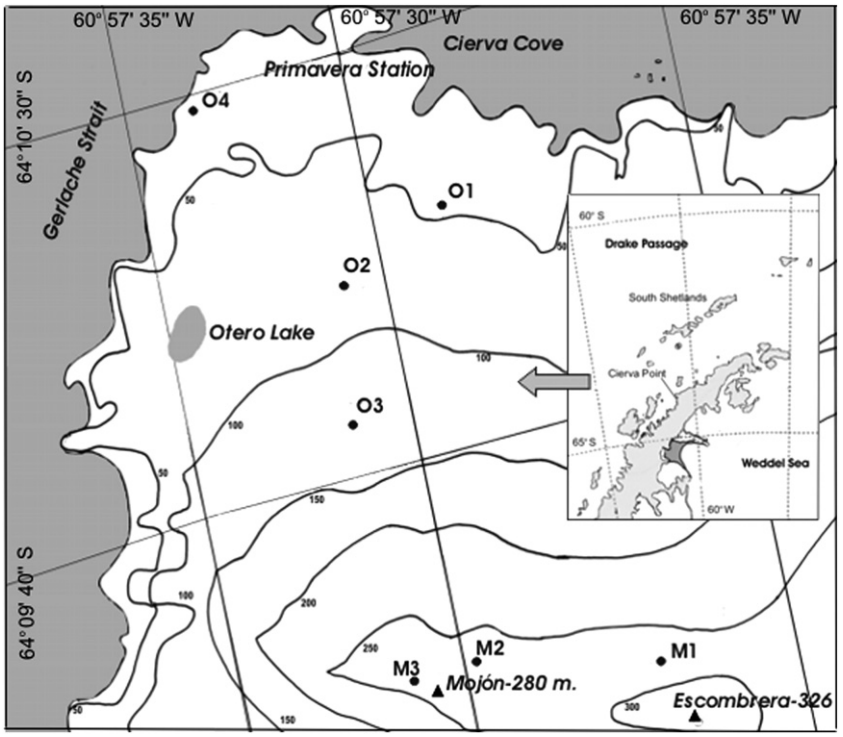

Fig. 1. Map of Cierva Point (Antarctic Peninsula) showing all sampling sites.

texture (b) moisture and organic matter content, (c) chemical parameters (pH, conductivity, PO_4-P, NO_3-N and NH_4-N concentrations) and (d) chlorophyll-*a* concentration, respectively.

Samples used for bacterial culture consisted of c. 100 g of fresh soil and were taken with a sterile spoon from the upper 2.5 cm of the soil profile and placed in whirlpack bags. At the Station laboratory, these were air-dried and kept refrigerated during storage and transport to Kiel University.

Samples for the taxonomic study of the microalgal community were taken in small sterile Petri dishes. After microscopic examination at the laboratory of Primavera Station, these were frozen and subsequently used for the inoculation of cultures at the University of Buenos Aires. Sets of three replicate cores were also taken with 13 mm diameter sterile syringes for the estimation of algal diversity. These were stored frozen until studied at the University of Buenos Aires.

To assess soil meiofauna (Nematoda, Rotifera, Tardigrada), on each sampling occasion three replicate samples were taken at each site using a larger corer (2.5 cm diameter) from the upper 2.5 cm of the soil profile, and extracted into 2.5% formaldehyde (final concentration) using a Baermann funnel approach. A further replicate set of soil samples for enumerating arthropods (Acari, Collembola, Diptera) was extracted into 99% ethanol using a Tullgren dry extraction.

2.3. Sample treatment

Physico-chemical parameters were measured at the University of Buenos Aires, including:

(a) The percentage of the coarse soil fraction (>2 mm) was calculated by weighing the samples before and after passing through a sieve. Soil texture was then analysed using a standard gravimetric method (Lamotte Chemical Products Co., USA).
(b) Water content was measured by weighing fresh soil samples, drying at 70 °C to constant mass (DW) and reweighing. Samples were then placed in a furnace at 440 °C for two hours and reweighed (AFDW) to calculate the organic matter content (Frenot, 2002). Both values were expressed as percentages of dry mass.
(c) Composite samples were extracted in 50 ml distilled-deionised water by agitation in cold (4 °C), dark conditions over a 24 h period. Extracts were filtered through pre-weighed Whatman GF/C

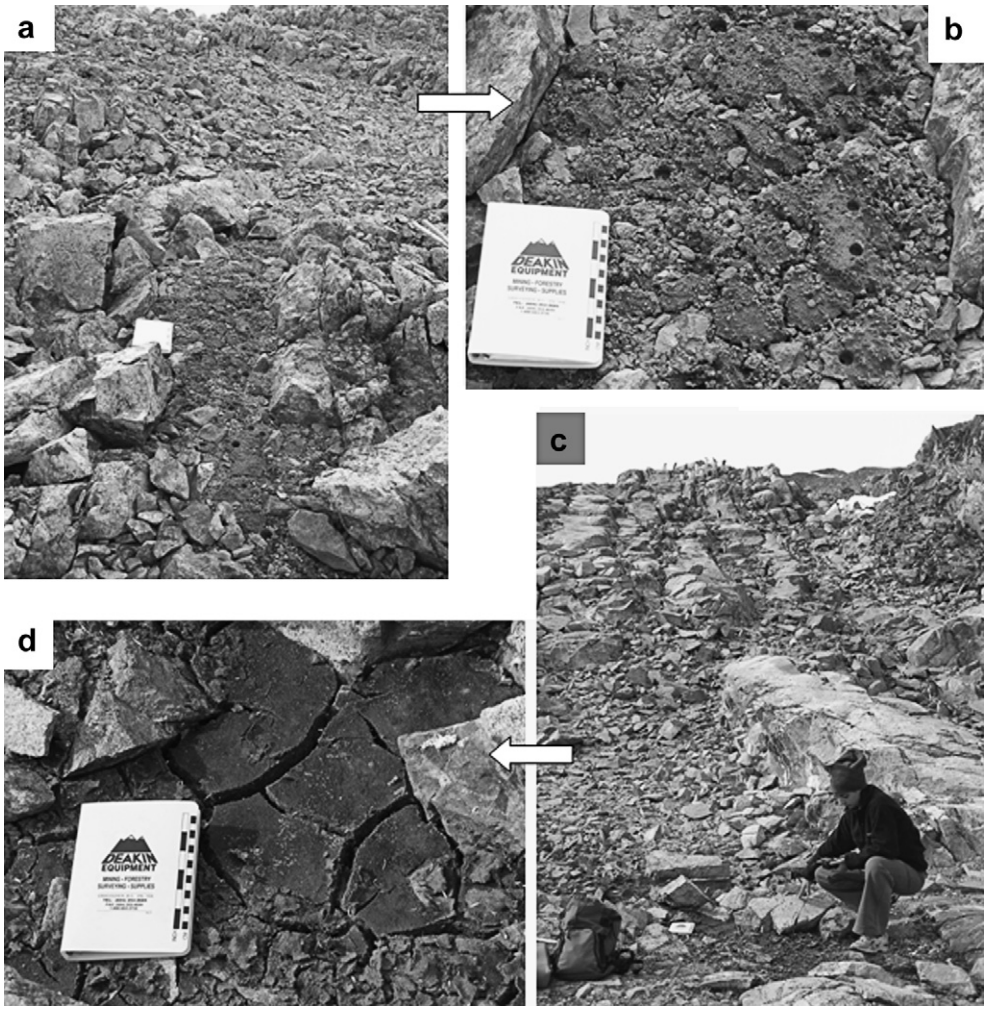

Fig. 2. (a) general view and (b) close up of site M1, an example of a typical mineral soil. (c) general view and (d) close up of site O4. In (c) note the penguins on top of the ridge.

filters. Conductivity and pH of the extracts were measured with Altronix electronic meters (SAEN SRL, Argentina). Nutrient (PO_4-P, NO_3-N and NH_4-N) concentrations were then measured by appropriate colorimetric standardised methods using a Hach DR-890 colorimeter (Hach Company, USA). Filtered soil samples were dried to constant mass and results therefore expressed as µg/g dry soil.

(d) Chlorophyll-*a* was extracted in hot (65 °C) dimethyl sulfoxide (DMSO) for 1 h, followed by centrifugation at 4000 rpm. This solvent was selected in preference to ethanol on account of its higher extraction efficiency for soil samples (Hawkes and Fletchner, 2002). Pheophytin-free pigment concentration of the supernatant was spectrophotometrically determined by measuring absorbance at 665 and 750 nm before and after acidification with 1 N HCl, using the equations given by Hawkes and Fletchner (2002).

(e) Bacterial communities were analysed by epifluorescence microscopy (acridine orange stain, image analysis with a Leica Q500MC) for total number and biomass (Bölter et al., 2006).

At Primavera Station, soil samples were wetted with sterile water and coverslips placed on the surface for 48 h. These were then removed and attached algae observed under an Olympus BX-31 light microscope fitted with a *camera lucida*. The remaining material was inoculated into both solid and liquid BBM (Chantanachat and Bold, 1962) and BG-11 (Stanier and Cohen-Bazire, 1977) media under controlled conditions (50 µmol photons cm^{-1}, 12:12 light:dark

cycles, 15 °C). Cultures were observed after 15 and 30 days, and rare species identified following isolation. A range of literature sources was employed for taxonomic identification, the primary sources being those of Ettl and Gärtner (1995) and Komárek and Anagnostidis (1999, 2005).

For the estimation of diversity, sterile coverslips were placed on top of soil cores previously wetted with sterile water, incubated for 48 h and removed with the attached algae. For every sample, 200 organisms were counted in each of the three replicates, and relative frequencies used to calculate diversity according to the Shannon–Weaver index (Mataloni and Tell, 2002). Species were grouped for further analysis according to growth form, as: sarcinoids (SA), flagellates (FG), filaments (FM), diatom unicells (DU), coccoid unicells (CU) and mucillaginous colonies (MC).

Extracted arthropod taxa were indentified and counted in the three replicates from each sample separately, and their mean density per cm^2 of soil surface calculated. A limited number of microarthropod species were obtained from these sampling locations, not presenting taxonomic challenges. Meiofauna were recorded at group level (Rotifera, Tardigrada) or identified to family or genus (Nematoda); following Andrássy (1998) and Maslen (1979a,b). Densities of meiofauna (nematodes, rotifers and tardigrades) varied widely between samples. Thus, the following ordinal scale rank was established: 0 (absent), 1 (1–5 inds), 2 (6–10 inds), 3 (11–50 inds) 4 (>50 inds), and an average rank obtained for each sample. In order to permit combined analysis, arthopod densities were expressed using the same scale.

2.4. Data analyses

Variation of each abiotic feature over time at each sampling location was examined. *t*- Tests were used to examine differences between soil types. In order to compare maximum potential exposure to solar radiation, geographical orientations were transformed (scaled) into values and these multiplied by the slope. Correlation analyses were performed between all abiotic features studied and a PCA performed to ordinate all samples according to those shown to be independent (Digby and Kempton, 1987).

A general correlation matrix included all abiotic parameters plus descriptors of the bacterial community (TBN = Total bacterial number, BBM = bacterial biomass, MCV/MBS = mean cell volume/mean bacterial surface), microalgae (density, chlorophyll-*a* concentration, species richness, equitability, diversity, and abundance), and the fauna (abundance ranks of rotifers, tardigrades and all identified taxa of nematodes and arthropods). Abundances of virtually all organisms did not show normal distributions even when transformed, a typical feature of many soil ecosystems. Therefore, non-parametric Spearman's rank correlations were calculated.

Samples were grouped through a cluster analysis performed on the basis of the ranked abundances of meio-and microfauna, using the $(1 - \text{Pearson } r)$ distance and the WPGMA linking method (Sokal and Sneath, 1963). The same technique was applied to the main microalgal species obtained (defined as those with a relative frequency >10% at least in one sample).

3. Results

3.1. Environmental features

The two soil types differed widely in most abiotic features. Mineral soils consistently experienced lower temperatures on account of their higher altitude, and had a finer texture (sandy loam) than ornithogenic soils. Neither this parameter nor the proportion of larger stones was related to the slope at the study sites used (Table 1). Average values of abiotic features (pH, conductivity, water content, organic matter and nutrient concentrations) were consistently lower and less variable in mineral soils. Variation in soil moisture followed the same trend at all sites, diminishing towards the third sampling date and increasing after a rainy period (Mataloni, personal observation). Concentrations of NH_4-N related to this pattern ($r = 0.74$) (Fig. 3).

Results of the PCA performed on the basis of abiotic features ordinated the samples as shown in Fig. 4. Variance explained by the two first axes was 61.74%. Features with highest eigenvectors on the first axis (41.61% of variance) were NO_3-N (−0.51), pH (−0.46) and moisture (−0.45). Samples from the organically enriched and wetter sites (O3 and O4) were located on the left of the diagram, while O1 and O2 were located at the center and all samples from mineral soils in a narrow range along the horizontal axis. Axis 2 (20.13% of variance) was mainly influenced by the exposure (0.67), percentage of coarse particles (0.48) and temperature (0.48) at each site. Samples from O1 clearly differed from all other ornithogenic sites based on these features, and those from the three mineral soil sites were also separated along this axis.

Table 1
Abiotic variables recorded at each study site.

	M1	M2	M3	O1	O2	O3	O4
Height (m.a.s.l)	309	273	276	65	81	137	41
Slope (degrees)	2	13	7	22	8	11	0
Slope orientation	ENE	NE	NNE	NNE	ESE	NNW	
% Coarse fraction	14.69	47.3	24.35	41.19	41.9	25.18	29.68
Texture	Sandy loam	Sandy loam	Sandy loam	Loamy sand	Loamy sand	Loamy sand	Sandy
Temperature (°C)	7.3 (5.8–10.2)	8.8 (6.6–12.3)	8.6 (6.8–10.8)	12.3 (8.2–17.7)	9.1 (7.6–12.1)	10.7 (7.6–13.1)	10.7 (7.4–-13.2)
pH	2.9 (2.75–-3)	3.3 (3.1–-3.6)	3.1 (3.1–-3.17)	4.3 (3.3–-6.63)	4.1 (3.4–-5.9)	7.61 (7.35–-7.73)	6.13 (4.78–-6.7)
Conductivity (µS/cm)	675 (482–922)	280 (173–471)	393 (330–455)	204 (138–250)	255 (176–343)	788 (703–952)	209 (189–225)
Moisture (% DW)	14.04 (7.17–20.84)	15.55 (7.8–22.26)	18.27 (14.86–22.68)	16.4 (7.05–41.4)	49.48 (16.12–79.38)	104 (29.46–191)	190 (97.52–326)
Organic matter (% DW)	2.36 (1.88–2.67)	3.6 (3.16–3.86)	4.16 (3.64–4.48)	10.75 (5.87–14.23)	14.55 (10.44–20.62)	37.52 (29.97–44.74)	48.05 (41.53–54.1)
NO3-N (µg/g DW)	0.55 (0.19–1.32)	0.41 (0.14–0.73)	0.28 (0.16–0.54)	51.2 (42.59–65.78)	57.97 (51.06–71.04)	99.45 (48.17–187)	168 (94.2–247)
NH4-N (µg/g DW)	1.13 (0.19–1.61)	0.47 (0.09–0.77)	0.39 (0–0.76)	195.00 (0–532)	173 (0–505)	1350 (1161–1580)	616 (141–1318)
PO4-P (µg/g DW)	3.16 (2.12–5.77)	1.09 (0.38–1.66)	1.43 (0.48–2.52)	211 (84.17–298)	451 (266–730)	6751 (1686–18692)	869 (330–1918)

For those measured on each sampling date, mean values are given, with minimum and maximum values in parentheses.

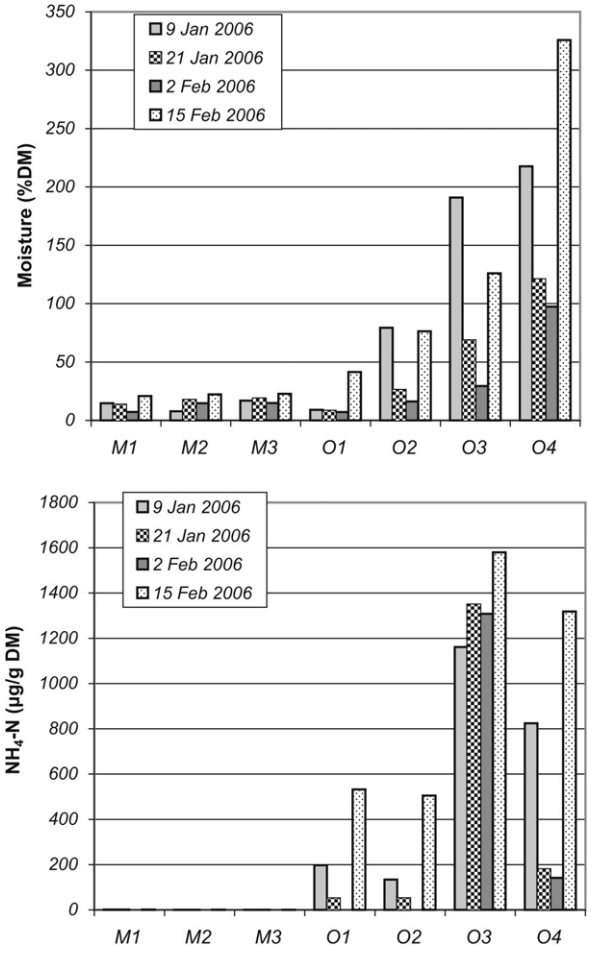

Fig. 3. Soil water (expressed as % of the dry mass) and NH_4-N contents (µg/g dry mass) at the different study sites over the sampling period.

3.2. Bacteria

Table 2 shows the main features of bacterial communities. Total bacterial number (TBN) and bacterial biomass (BBM) were highly correlated ($p < 0.05$, $r = 0.98$) and showed very similar variations in time and space. Fig. 5 shows that ornithogenic soils supported larger and more variable bacterial abundances than mineral soils ($p = 0.006$). TBN was highly correlated ($p < 0.05$ in all cases) with nitrate-N concentration ($r = 0.83$) and organic matter ($r = 0.77$), and also with chlorophyll-*a* concentration ($r = 0.64$) and water content ($r = 0.61$).

The quotient between the mean cell volume (MCV) and the mean bacterial surface (MBS) indicates cell size, as it increases when the community is dominated by large cells, e.g. rods. Mineral soils showed significantly

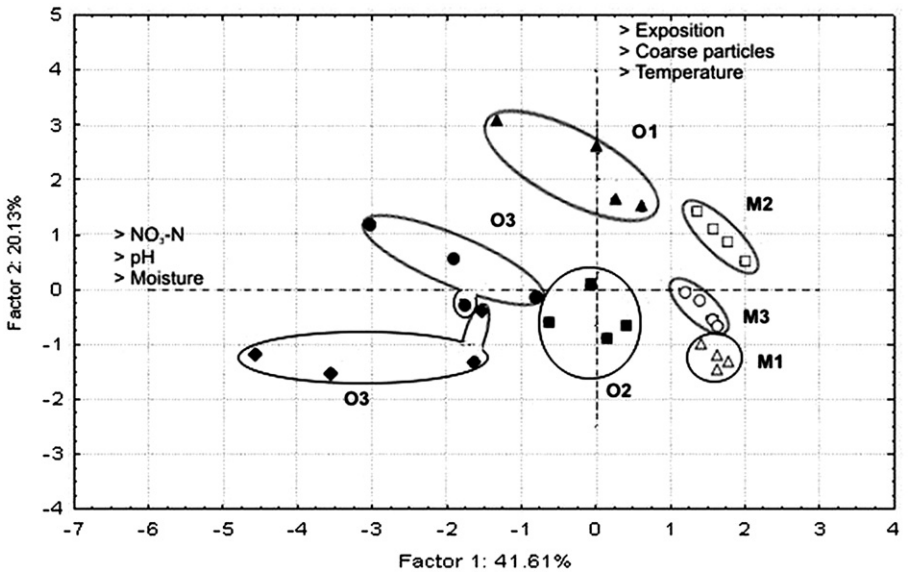

Fig. 4. Ordination of samples by PCA based on abiotic features.

Table 2
The main descriptors of the bacterial community at each sampling location.

Site	Date	TBN	BBM	MCV/MBS [μm]	Cocci %
		Total bacterial number (inds. 109/g DW)	Bacterial biomass (μg C/g DW)		
M1	09 Jan	0.110	0.200	0.053	62.54
	21 Jan	0.077	0.098	0.047	69.86
	02 Feb	0.094	0.108	0.045	76.02
	15 Feb	0.132	0.216	0.051	71.73
M2	09 Jan	0.052	0.074	0.049	71.94
	21 Jan	0.084	0.102	-	78.2
	02 Feb	0.087	0.094	0.045	80.97
	15 Feb	0.078	0.067	0.042	86.47
M3	09 Jan	0.133	0.142	0.045	81.07
	21 Jan	0.058	0.052	0.043	80.71
	02 Feb	0.147	0.136	0.043	86.21
	15 Feb	0.090	0.146	0.051	75.32
O1	09 Jan	0.359	0.420	0.046	81.06
	21 Jan	0.152	0.196	0.048	76.28
	02 Feb	0.118	0.163	0.049	78.21
	15 Feb	0.324	0.600	0.053	62.21
O2	09 Jan	0.735	1,597	0.056	62.76
	21 Jan	0.250	1,310	0.047	79.08
	02 Feb	0.424	0.630	0.050	75.13
	15 Feb	0.191	0.345	0.053	70.93
O3	09 Jan	1,186	2,670	0.056	56.08
	21 Jan	1,263	1,997	0.051	72.45
	02 Feb	1,439	3,807	0.059	50.33
	15 Feb	0.421	0.682	0.051	75.32
O4	09 Jan	2,889	5,777	0.055	62.82
	21 Jan	0.455	1,116	0.058	55.56
	02 Feb	0.344	0.880	0.058	55.69
	15 Feb	0.804	1,879	0.057	58.37

MCV/MBS = mean cell volume/ mean bacterial surface.

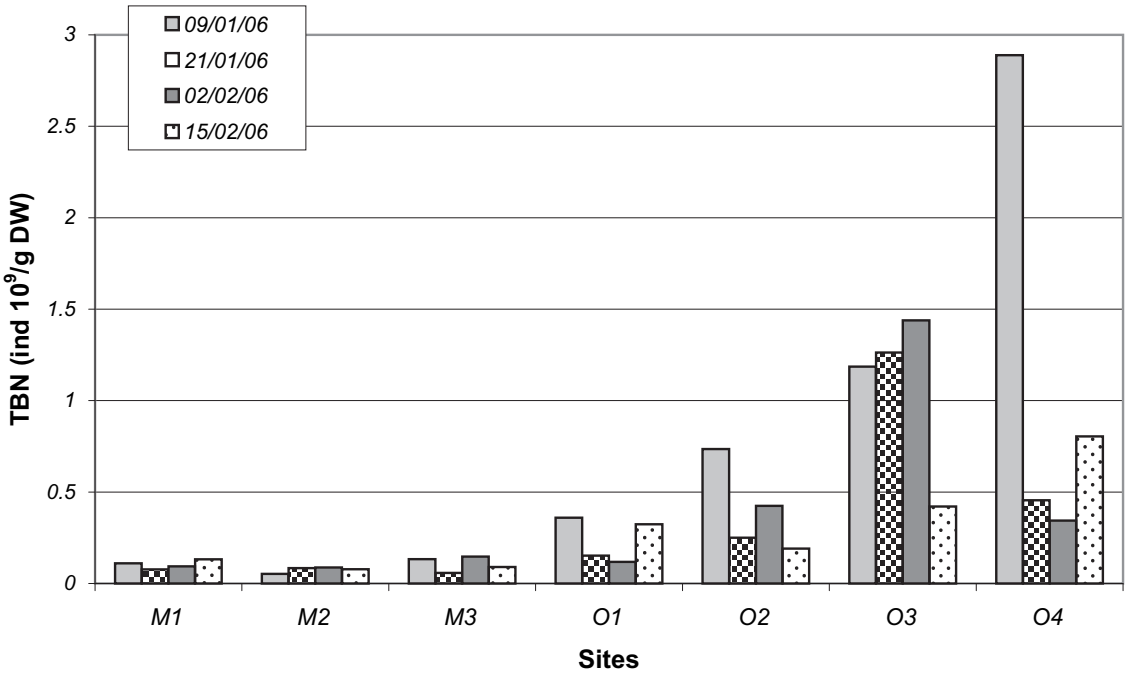

Fig. 5. Changes over time in bacterial abundance (total bacterial number) at each sampling site.

smaller values for this quotient ($p < 0.001$), and a larger percentage of small cocci, than ornithogenic soils (76.75% vs. 67.02%, respectively, $p = 0.008$). Coincidently, MCV/MBS was positively correlated with organic matter ($p < 0.05$, $r = 0.63$). Bacterial communities from ornithogenic soils were therefore both more abundant and made up of larger cells.

3.3. Microalgae

Total species richness at the different sites varied between 14 taxa at O3 and 73 at M3, with most taxa belonging to the Chlorophyceae. A detailed description of the microalgal communities is given elsewhere (González Garraza et al., com. pers.). Values of the Shannon–Weaver diversity index (Magurran, 2004) were highly correlated ($p < 0.05$) with species richness ($r = 0.94$), and also correlated with equitability ($r = 0.67$). Mineral soils were more diverse than ornithogenic soils ($p < 0.001$). In contrast, algal biomass as estimated from chlorophyll-*a* concentration, was significantly higher in ornithogenic soils ($p < 0.001$) and showed significant correlations with nitrate-N and phosphate-P concentrations, organic matter and pH ($p < 0.05$, all r between 0.74 and 0.77). As illustrated in Fig. 6, changes in algal biomass and diversity with progression through the season showed different trends for all sites, although mineral soils were less variable.

Abundances of the different forms of microalgae are shown in Fig. 7. In mineral soils, the community was composed mostly of diatoms. These were accompanied by filamentous taxa (mainly Cyanobacteria) and, at M1, also by green coccoid unicells. Total algal abundance at M1 and M3 showed a diminishing trend over the first three sampling dates, which reflects changes in soil humidity, but this was not seen at site M2, located on a solifuction stripe. Although more diverse in terms of species number, mineral sites were more homogeneous in growth forms than ornithogenic ones.

Algal abundances of ornithogenic soils were lowest at O1, where the dominance of the algal community over the sampling period shifted from filaments of the eutrophilous chlorophyte *Prasiola crispa* to coccoid chlorophytes. Diversity values were low both at this site and at O3, highly dominated by filaments of the cyanobacteria *Phormidium attenuatum*. This dominance accounted for the abundance of filaments being highly correlated with NH_4-N concentration ($r = 0.72$) and total abundance ($r = 0.62$).

The most diverse and dynamic community amongst samples of this soil type was that of O4, the only site in which all microalgal life forms were present together on at least one sampling date. The positive correlation ($p < 0.05$) between the rarest growth forms (flagellates and mucillaginous colonies, $r = 0.99$) is explained by

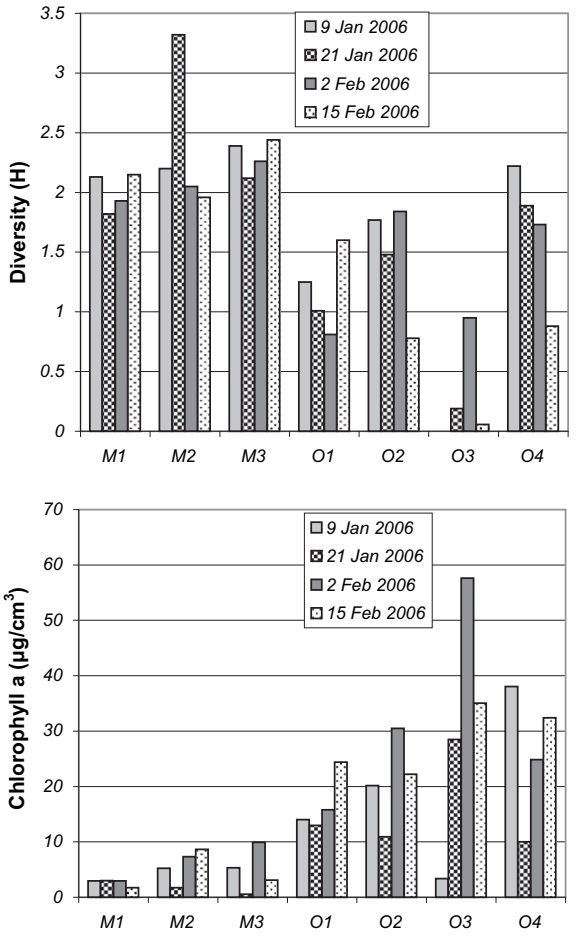

Fig. 6. Variation of the diversity of the microalgal community as measured by the Shannon–Weaver index (H), and photoautotrophic biomass expressed as chlorophyll-*a* content of the soil at each sampling site.

their common presence at this site. Sarcinoid cyanobacteria were correlated with both these growth forms ($r = 0.56$) and TBN ($r = 0.61$).

3.4. Fauna

The meiofaunal community was composed of a few species of nematodes, rotifers and tardigrades. As with microalgal growth forms, mineral soils hosted a more homogeneous community. Here, the nematode genus tentatively identified as *Teratocephalus* sp. dominated all samples, and its abundance rank was positively correlated with the abundance of diatoms ($r = 0.74$), the algal group dominating this soil type, and the height above sea level ($r = 0.75$). It was also negatively correlated with abiotic indicators of ornithogenic soils such as PO_4-P ($r = -0.80$), NO_3-N ($r = -0.76$) and chlorophyll-*a* ($r = -0.68$) ($p < 0.05$ in all cases). The bacterivorous nematode *Plectus* spp. occasionally accompanied this species, while small specimens of the family Tylenchidae were recorded only at M2. Tardigrades and rotifers were rare at these sites, except for M3, which also showed the largest total abundances. Very few arthropods were obtained from these mineral soils, and then solely on the first sampling date at M3 (Fig. 8).

The fauna obtained from ornithogenic soils varied widely in both composition and abundance. The less enriched O1 supported a more limited community, mainly composed of rotifers and a few nematodes. Regarding the latter, the predatory nematode *Coomansus gerlachei* was replaced in abundance over time by the bacterivorous *Plectus* spp. No arthropods were recorded at this site. Tardigrades and rotifers dominated the meiofauna at the eutrophic site O2, along with a larger population of *C. gerlachei*. The collembolan *Cryptopygus antarcticus* and the mite *Alaskozetes antarcticus* were very abundant at this site. The dipteran *Belgica antarctica* was also present in small numbers.

At site O3, the very high bacterial numbers supported a large population of *Plectus* spp. in spite of the high NH_4 concentrations. The microbial omnivorous nematode *Eudorylaimus* spp. also appeared to be able to tolerate these conditions. The occurrence of both genera was positively correlated ($r = 0.79$), both with organic matter content ($r = 0.66$ and 0.73, respectively) and bacterial abundance ($r = 0.54$ and 0.64, respectively). O4 was the most diverse site in terms of fauna. Though numerically dominated by the nematodes *Plectus* spp. and *Eudorylaimus* spp., it also showed a typical group composed of the arthropods *A. antarcticus*, *B. antarctica* and *C. antarcticus*, together with rotifers and tardigrades. None of these taxa was correlated with the densities of bacteria, algae or any particular algal growth form.

Fig. 9 depicts the grouping of samples according to their faunal composition. Among the two large groups it illustrates, that composed of all samples from mineral soils is more homogeneous on account of the dominance by the nematode *Teratocephalus* spp. The two samples from M2 where Tylenchidae were found, and the only sample from M3 hosting arthropods are the last to join in this group.

The grouping of ornithogenic soil samples, in turn, is based on the dominance of the nematode *Plectus* spp. at the sites with higher bacterial densities. The absence of arthropods from O1 accounts for its reduced similarity with O3 and O4. Samples from O2, in turn,

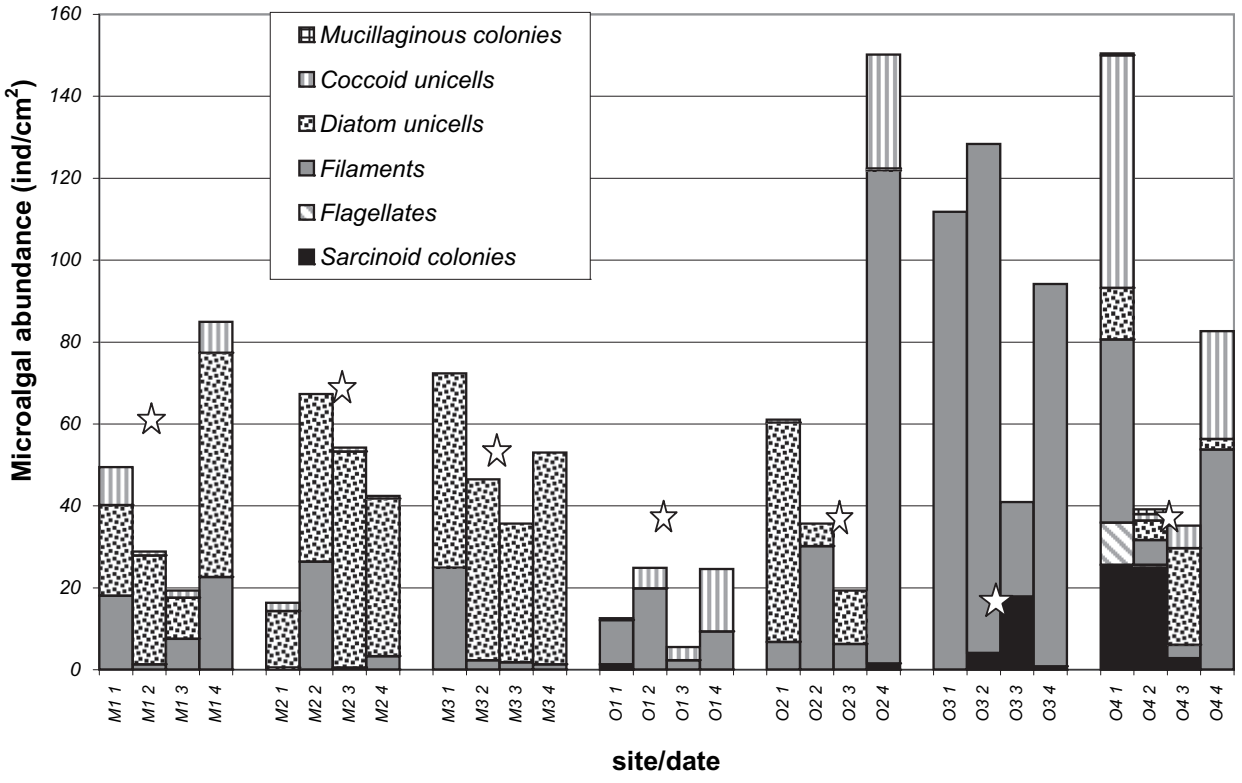

Fig. 7. Total number of microalgal taxa (stars) at each sampling site, and variation of the abundances of different microalgal growth forms over the sampling period (bars). Each label on the horizontal axis represents one sampling date at one sampling site, e.g.: M1 2 = Site M1, second sampling date.

form a separate group due to the high dominance of rotifers, tardigrades and arthropods at this site.

4. Discussion

4.1. Environmental features

Values of the nutrient concentrations obtained in the current study (Table 1) lie within the variation ranges for both soil types observed at Cierva Point and the geographically close (about 100 km) but geologically distinct Deception Island (Fermani et al., 2007; Mataloni et al., 2000; Mataloni and Tell, 2002). As stated by Fermani et al. (2007), our results confirmed that the steep, unstable substrates are not an important stress factor for the communities studied. Ordination of samples using PCA (Fig. 4) showed physical and chemical features of mineral soils to be spatially homogeneous and less variable in time in comparison with those from ornithogenic soils. As observed from the eigenvector values of a number of parameters, the comparatively high environmental diversity of ornithogenic soils was not explained by any of these features alone, but rather by the combination of a wider spectrum of physical settings and microclimatic features.

4.2. Bacteria

The high quantity of organic matter in ornithogenic soils, mainly O3 and O4, accounted for the large abundance of bacteria in these sites (Fig. 5), as reported by Bölter et al. (1999) for soils studied along a transect from Cape Horn to the Antarctic Peninsula. Probably as a consequence of their guano degrading activity (Tatur, 1989), bacterial abundance and biomass were also highly correlated with nitrate and phosphate concentrations, which are responsible in turn for high chlorophyll-a concentrations. A similar correlation between bacterial and algal abundance was reported by Bölter (2001) from Arctic soils. Bacterial communities from mineral and ornithogenic soils also differed in their structure – in spite of all being dominated by small cocci, in those from nutrient-deprived mineral soils the level of dominance was greater (Table 2). This lower volume/surface area quotient would permit a faster, more efficient nutrient uptake, as discussed by Bölter et al. (2002).

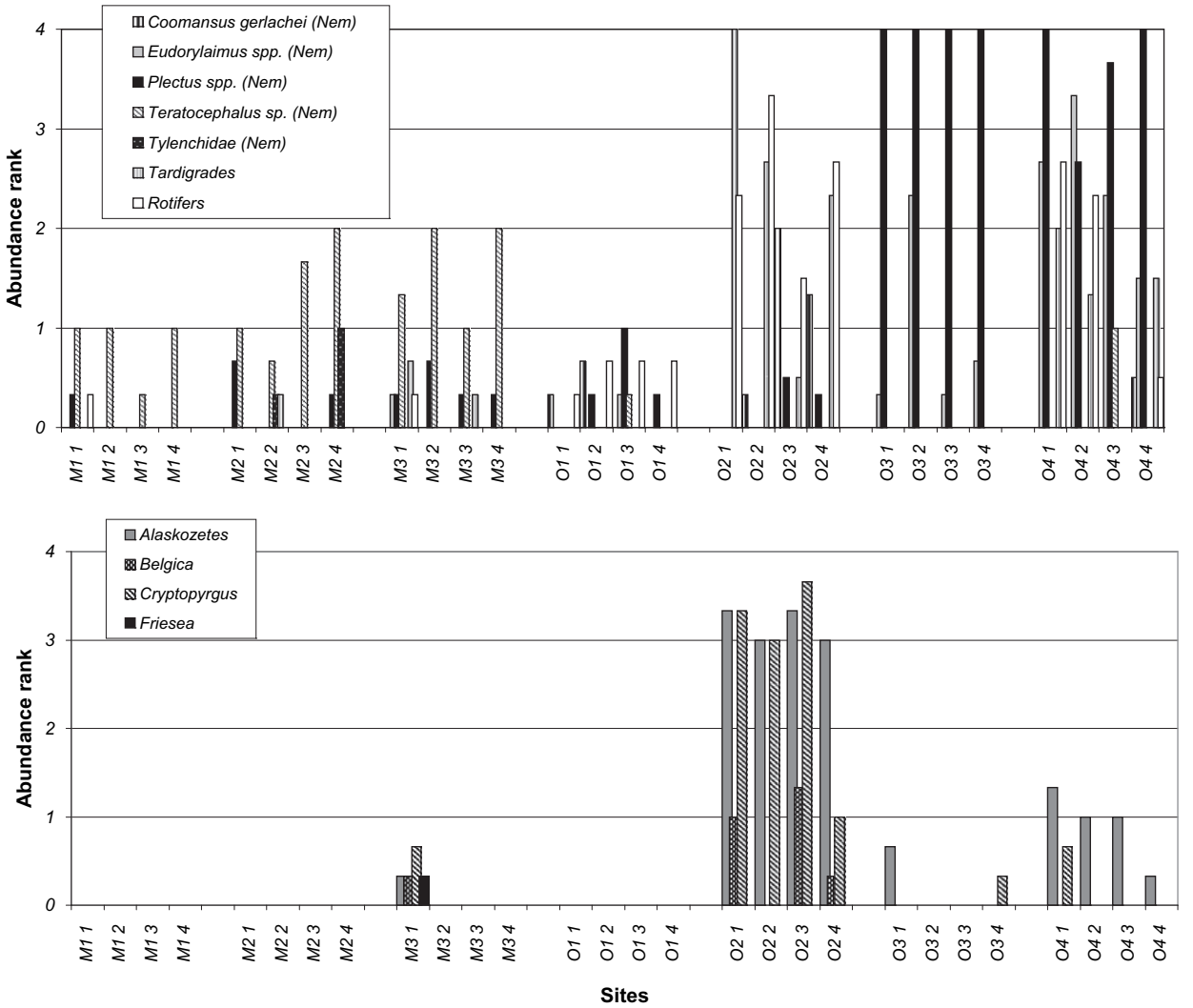

Fig. 8. Ranked abundances of meiofauna (top) and microarthropods (bottom) at all sampling sites over the sampling period. Each label on the horizontal axis represents one sampling date at one sampling site, e.g.: M1 2 = Site M1, second sampling date.

4.3. Microalgae

Diversity of algae, as measured by the Shannon–Weaver index (H) (Fig. 6a), could be atributed to variations in species richness rather than equitability, on account of their different correlation coefficients. Therefore, increases or decreases in the number of taxa contributed most to changing species diversity, except at site O2, where high abundance of the filamentous cyanobacteria *Phormidium murrayi* caused an abrupt diversity decline on the last sampling date. Although mineral soils were clearly more diverse in terms of algal species numbers than ornithogenic ones, their diversity was considerably lower in terms of growth forms (Fig. 7). As these mineral soils were more stable than ornithogenic soils, it could be hypothesised that higher environmental stability accounts for the selection of particular life forms (mainly cyanobacterial filaments and coccoid diatoms), as observed by Wynn-Williams (1990) and Mataloni et al. (2000), and also encourages establishment of a wider range of species with these life forms, even in low numbers. Variation in algal abundance reflected that of soil moisture content, confirming the suggestion of Arnold et al. (2003) that water availability is a crucial limiting factor for microalgae in this type of soils. The exception to this was site M2, located in a drainage area with subsurface water flow, an effect also observed by Fermani et al. (2007) on Deception Island.

Microalgae from ornithogenic soils varied widely in abundance, community composition and diversity

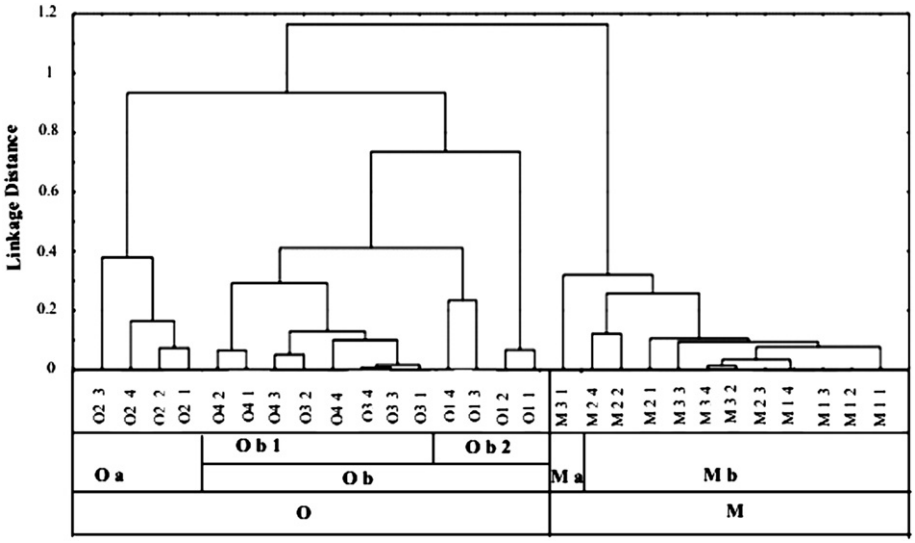

Fig. 9. Dendrogram of samples based on the ranked abundances of meiofauna and microarthropods. The homogeneous group M corresponds to mineral soils, and the heterogeneous O group to ornithogenic soils. For explanation of subgroups, see text.

between sites as well as within each site, reflecting the larger environmental variability. Site O3, located in an active penguin rookery, showed the lowest diversity, consistent with previous studies of microalgal communities in bird colonies (Akiyama et al., 1986; Fermani et al., 2007; Mataloni and Tell, 2002). This is also consistent with the experimental demonstration of the inhibitory effect of guano extracts on algal growth (Akiyama et al., 1986). In contrast, site O4 showed the highest diversity of both species and growth forms, with all the latter being represented, and dominance shifting successively from coccoid Chlorophyceae, sarcinoid cyanobacteria, coccoid diatoms and lastly to filamentous cyanobacteria. This marked temporal pattern suggests that the abundance of nutrients and high microenvironmental variability of this site allows the existence of a large and diverse microalgal propagule bank, whose different components exploit different combinations of environmental conditions. In this context, the role of biotic interactions such as competition could be more relevant than previously thought in shaping these communities (Bergstrom et al., 2006; Hogg et al., 2006).

4.4. Fauna

All mineral soil samples were dominated by a nematode tentatively identified as *Teratocephalus* sp., a bacterivorous genus (Newsham et al., 2004). At sites M2 and M3 this species was accompanied by other bacterivorous nematodes, *Plectus* spp, which can also feed on microalgae (Convey and Wynn-Williams, 2002) (Fig. 8). The virtual absence of microarthropods from mineral soils can be attributed to the importance of water availability and temperature as limiting factors for this group (Convey et al., 2002) as well as to the low autotrophic biomass available in barren soils to support these relatively large organisms. Only in one sample were 1 or 2 individuals of each species found, most probably relating to the presence of small cushions of the moss *Andraeae* sp. in the periphery of the soil polygon, since Convey and Quintana (1997) recorded two of these species on these mosses at Cierva Point.

Amongst the ornithogenic sites, meiofauna was less abundant at O1, while arthropods were absent from this site which experiences combined high temperature and low moisture. The presence of the grass *Deschampsia antarctica* near O2 may have accounted for tardigrades and rotifers dominating the microfauna at this site. Arthropod abundances were highest at this site, mainly those of the mite *A. antarcticus* and the springtail *Cryptopyrgus antarcticus*. According to Worland and Lukesová (2000) both species are algivorous. At Cierva Point, Convey and Quintana (1997) observed that the former was frequently associated with nutrient enrichment by bird colonies. Unlike Petz (1997), we found that nematodes (*Plectus* spp.) dominated the most guano-enriched ornithogenic sites, even under possibly limited soil oxygen conditions due to waterlogging. As with the microalgae, site O4 showed the highest meiofaunal diversity, with all categories except

small Tylenchidae being represented at least on one sampling date. The mite *A. antarcticus* was the only arthropod consistently present at this site.

Cluster analysis of samples according to the relative abundance of the fauna (Fig. 9) showed a high similarity for mineral soils, as observed for microalgal life forms. In contrast, ornithogenic soil sites have marked differences in their faunal and microalgal composition both in space and time, with the exception of O3. Here, extreme values for organic matter and nutrient concentrations appeared to over-ride the effect of any temporal changes in other parameters.

4.5. The sites

Mineral soils showed high environmental similarity, both among sites and over time, as shown by the ordination of samples derived from the PCA. The structure of microalgal communities reflected this, though showing a high species diversity within each site due to the existence of a selective propagule bank favoured by these microclimatic conditions. Bacterial and faunal communities also were similar in space and time, suggesting simple, stable food webs.

Abiotic features at ornithogenic soils, in contrast, varied considerably in both space and time, and biological communities clearly responded to this. Site O1 was the most exposed to solar radiation, a feature that would favor colonisation and growth of autotrophic organisms (Agraz et al., 1994), yet this was not reflected in algal abundance. At this site, higher temperatures and solar radiation combined with low moisture for most of the season, may combine to act as a stress factor for algae, as discussed by Bergstrom et al. (2006). These features can also control chemical release of nutrients (Huiskes et al., 2006). The microalgal community at this site was dominated by filaments of the opportunistic alga *P. crispa* (cf. Davey, 1989), except for the last sampling date, in which coccoid Chlorophyta grew rapidly on account of the combination of increased temperature and soil moisture. Fermani et al. (2007) observed coccoid Chlorophyta to be common components of the soil propagule bank. Although each species was present in low proportions, they grew rapidly in cultures under moist, warmer conditions. As the study of Fermani et al. (2007) was based on single sampling opportunities, they interpreted these organisms as possible components of the soil propagule bank surviving −but not actively growing- under suboptimal conditions. Our results show that these species can utilise an "opportunity window" of favourable conditions in which they replace the filamentous *P. crispa* as the dominant algal growth form, increasing microalgal diversity. The possession of long-surviving propagules is therefore an important life history feature able to influence community structure, as noted by Convey et al. (2006). Site O2 was located near O1, and showed a very similar environmental setting, except for exposure and soil moisture. Nevertheless, these features seem to be important enough to result in the development of a very different, more complex, biota, characterised by a higher abundance and diversity of microalgae and meiofauna, and the presence of arthopods. On the other hand, like O1, site O4 was located on a path created by gentoo penguins accessing to the sea, yet its lower exposure, higher moisture and greater nutrients concentrations allowed for a rich, abundant biotic component, with high correlations among nutrients and the abundances of bacteria, microalgae and their main consumer *Plectus* spp. Comparison between these sites provides an example of the distinct consequences of different microclimates within one geographic site, driving the development of community structure. Due to the complexity of these interactions, multivariate analysis failed to explain the observed variance in community composition.

This study provides evidence that Antarctic soils are more complex and diverse systems than usually believed, as also indicated by the low similarity between communities from ornithogenic soil sites and their variation over time. This shows that biotic interactions (competition and predation) may have a more direct and complex influence on community variability in space and time than previously thought (Bergstrom et al., 2006). A detailed experimental approach based on case studies is needed in order to fully understand the role of biotic interactions in the colonisation and development of Antarctic edaphic habitats. This knowledge is of prime importance in the study of the reaction of these systems to climatic change since, as recognised by Convey (2006), the integration of responses throughout the food web holds the key to the understanding of the ecological impact of this phenomenon.

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