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Polar endoliths – an anti-correlation of climatic extremes and microbial biodiversity

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Abstract: We examined the environmental stresses experienced by cyanobacteria living in endolithic gneissic habitats in the Haughton impact structure, Devon Island, Canadian High Arctic (75° N) and compared them with the endolithic habitat at the opposite latitude in the Dry Valleys of Antarctica (76° S). In the Arctic during the summer, there is a period for growth of approximately 2.5 months when temperatures rise above freezing. During this period, freeze–thaw can occur during the diurnal cycle, but freeze–thaw excursions are rare within higher-frequency temperature changes on the scale of minutes, in contrast with the Antarctic Dry Valleys. In the Arctic location rainfall of approximately 3 mm can occur in a single day and provides moisture for endolithic organisms for several days afterwards. This rainfall is an order of magnitude higher than that received in the Dry Valleys over 1 year. In the Dry Valleys, endolithic communities may potentially receive higher levels of ultraviolet radiation than the Arctic location because ozone depletion is more extreme. The less extreme environmental stresses experienced in the Arctic are confirmed by the presence of substantial epilithic growth, in contrast to the Dry Valleys. Despite the more extreme conditions experienced in the Antarctic location, the diversity of organisms within the endolithic habitat, which includes lichen and eukaryotic algal components, is higher than observed at the Arctic location, where genera of cyanobacteria dominate. The lower biodiversity in the Arctic may reflect the higher water flow through the rocks caused by precipitation and the more heterogeneous physical structure of the substrate. The data illustrate an instance in which extreme climate is anti-correlated with microbial biological diversity.

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Introduction

In extreme hot and cold deserts the macro-climatic regimens often impose physical conditions close to the limits of life. High winds, aridity, exposure to high light and ultraviolet (UV) radiation, extremes of absolute temperatures and extreme temperature variations synergistically create conditions hostile to the maintenance of life (Potts & Friedmann 1981; Meyer *et al.* 1988; Friedmann & Ocampo-Friedmann 1984; Wynn-Williams 1994). This is reflected in the low abundance of epilithic (rock surface-dwelling) biota in these environments. The biological diversity of microbial communities is roughly correlated with climatic extremes. In Antarctica, for instance, a reduction in biological diversity occurs from the maritime Antarctica to the extreme environment of the continental interior (Convey 2001). Similar observations are made in the Arctic, even on the scale of metres in glacial streams (Elster *et al.* 1997).

One way to cope with extreme environmental conditions is to retreat inside rocks, either within macroscopic cracks as 'chasmoendoliths', or within the subsurface pore spaces of the rock as 'cryptoendoliths'. The micro-environmental conditions inside the rock are very different from the macro-climatic regimen and allow life to maintain itself and grow under macro-climatic conditions that are apparently hostile to life, albeit at slow rates of growth (Vestal 1988; Johnston & Vestal 1991; Sun & Friedmann 1999). The use of the clement micro-environment associated with the inside of rocks as a refugia is probably an ancient innovation and may even date back to the latter part of the Precambrian (Campbell 1982).

As well as inhabiting sedimentary rocks that have sufficient porosity to allow subsurface invasion and lateral growth, particularly sandstones and limestones (Friedmann & Ocampo 1976; Saiz-Jimenez *et al.* 1990; Wessels & Büdel 1995; Weber *et al.* 1996), microorganisms can also inhabit crystalline rocks that have been altered and made more porous. One mechanism by which this can occur is by shock metamorphism caused by the collision of an asteroid or comet with the target rock. Under such circumstances shock volatilization of target minerals can make rocks more porous and

in some instances, increase translucence. This is the case with the impact-shocked gneiss of the Haughton impact structure, Devon Island, Canada, which is host to cryptoendolithic communities in significantly greater abundance than unshocked gneiss (Cockell *et al.* 2002).

Biological diversity within these communities can be influenced by the climatic regime (Friedmann 1980). In hot deserts, where temperatures often exceed 40 °C, eukaryotic components have difficulty surviving. Thus, hot desert cryptoendolithic communities are dominated by prokaryotic components.

We characterize the physical micro-environment of cryptoendolithic communities living in shocked gneiss in the Haughton impact structure, Devon Island (75° N). We compare these conditions with those experienced by the cryptoendolithic communities in the Antarctic at almost the exactly opposite latitude (76° S). We discuss this data in the context of lower cryptoendolithic biodiversity observed in the Arctic location and we speculate on the implications for the cryptoendolithic response to climate change.

Materials and methods

Description of the Arctic endolithic communities

Impact-shocked gneiss is found within the Haughton impact structure, a well-preserved complex crater located on Devon Island, Nunavut, Canadian High Arctic, at 75° 22′ N, 89° 41′ W (Grieve 1988). The structure was formed 23.4 ± 1.0 Ma near to the Oligocene–Miocene boundary (Jessberger 1988) and has a diameter of about 24 km (Pohl *et al.* 1988; Scott & Hajnal 1988). The crater is filled with grey-weathering carbonatitic (i.e. carbonate-rich) impact melt rocks (Osinski & Spray 2001) that contain outcrops of the shocked gneiss. The presence of the gneiss in the melt rocks indicates that the excavation depth was greater than 1750 m as the gneiss were originally part of the Precambrian basement rocks. Overlain on the basement are Lower Paleozoic sedimentary rocks comprising mostly carbonates (dolomite and limestone).

In the eastern part of the crater, impact melt rocks are found as discrete outcrops separated from the main deposits in the central part of the crater by a complex system of broad (up to ∼1 km wide) alluvial terraces associated with meanders of the Haughton River.

Like other places on Devon Island, the soils of the Haughton region are primarily dolomitic and nutrient poor (e.g. Walker & Peters 1977; Bliss *et al.* 1994; Lévesque & Svoboda 1995). The low biological productivity is further exacerbated by the climatic conditions; Devon Island experiences frigid winters with 24 h of darkness and short, cool summers. Most of the crater shows polar desert characteristics with vegetation cover on the melt rocks of less than 5% (Cockell *et al.* 2001).

The samples of shocked gneiss used in this study were obtained from an isolated hill of impact melt rocks at 75° 24.53′ N, 89° 49.76′ W. At this location, only gneiss that was shocked to pressures greater than ∼10 GPa was found.
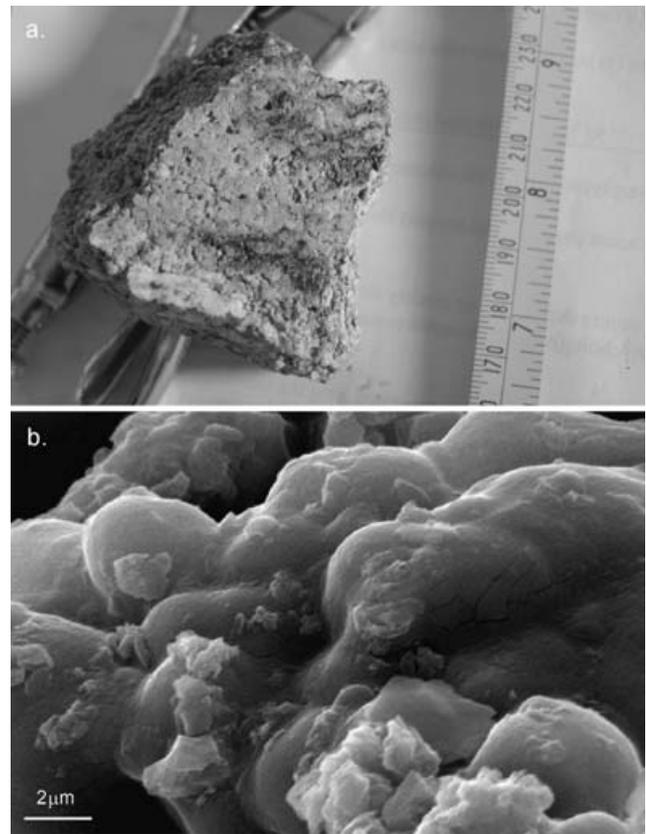

Fig. 1. (a) Impact-shocked gneiss from the Haughton impact structure showing pumice-like texture of rock and irregularity of substrate for microbial colonization. (b) Colony of cyanobacterial cells visualized by scanning electron microscopy growing along the surface of an impact-induced micro-fracture.

The cyanobacteria within these rocks are found both as chasmoendolithic and cryptoendolithic communities inhabiting the subsurface of the gneiss (Cockell *et al.* 2002). The colonization of the shocked gneiss, in contrast with low or unshocked gneiss, is made possible by both an increase in porosity and translucence caused by shock metamorphism (Fig. 1).

Temperatures in the endolithic habitat

Temperatures within a gneissic endolithic habitat were measured from 17 to 26 July, 2002. Temperatures were measured using copper-constantan thermocouples attached to a Campbell CR-10X datalogger (Campbell Scientific Inc., Logan UT) set to read at 20 s intervals and using a CR10TCF internal temperature reference. Temperatures were measured at 1 m above the ground (air temperatures), directly on the surface of a rock of dimensions $6 \times 6 \times 7$ cm³ and at a depth of 2 mm in the rock in the endolithic zone. A 1 mm diameter hole was drilled into the side of the rock, at a depth of 2 mm and parallel to the surface. The length of the hole was 1.5 cm. The hole was sealed with petroleum grease (Vaseline) after emplacement of the thermocouple. Direct solar heating of the exposed thermocouples was assumed to be negligible.
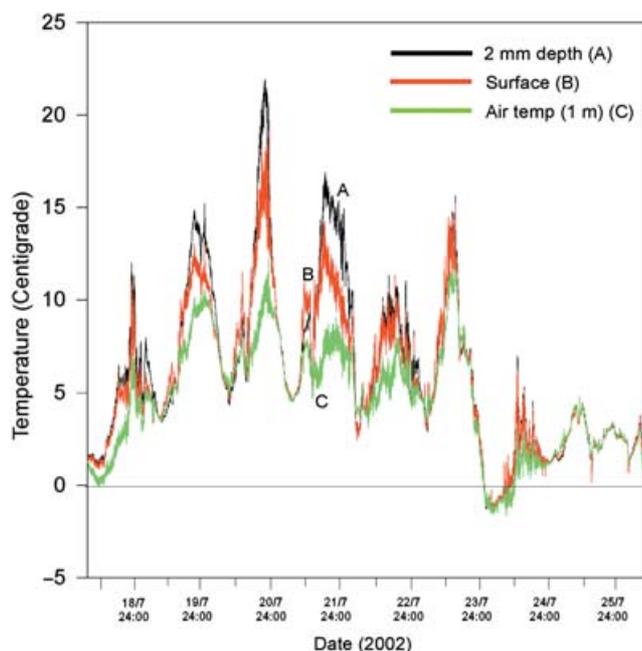
Fig. 2. Temperature data from 06:00 on 18 July to 09:00 on 26 July, 2002. The horizontal line in the graph denotes 0 °C.

Measurements of ground temperatures over a 1 yr period were obtained using a Hobo™ data logger (Onset Computers, Bourne, MA) and an external thermistor (Hobo™ TMC6-HB temperature sensor). The thermistor was attached to the surface of a rock at the field site and left to record at 2 h intervals from 14 August, 2001 to 10 July, 2002.

Moisture in the endolithic habitat

Two pieces of shocked gneiss with different mass (a, 207.2 g, b 68.9 g) were selected from the melt rock outcrop. The two rocks were placed next to the rock used for temperature measurements. They were weighed at 4 h intervals over 8 days from 17 to 25 July, 2002. At the beginning of the experiment the rocks were immersed in a pan of water for 3 h to simulate immersion in snowmelt. After the experiment the rocks were returned to Cambridge and their dry mass was determined after heating the rocks at 105 °C for 48 h in a thermally controlled laboratory oven (Heraeus, Hanau, Germany). This value was subtracted from the field measurements to determine the moisture content of the rocks over time in grams.

During the experiment relative humidity (%) was measured using a Hobo™ data logger with a built-in relative humidity sensor. Measurements were recorded every 1.5 min.

Porosity of the endolithic gneiss

The porosity of the shocked gneiss was determined by measuring the density of four rocks as described previously (Cockell *et al.* 2002). The pore space of the four samples was determined by mercury intrusion porosity as an intrusion volume per gram of material (MCA Services, Meldreth, Cambridge). Using the density of the samples, the porosity was expressed as the percentage of the rock that is air space.
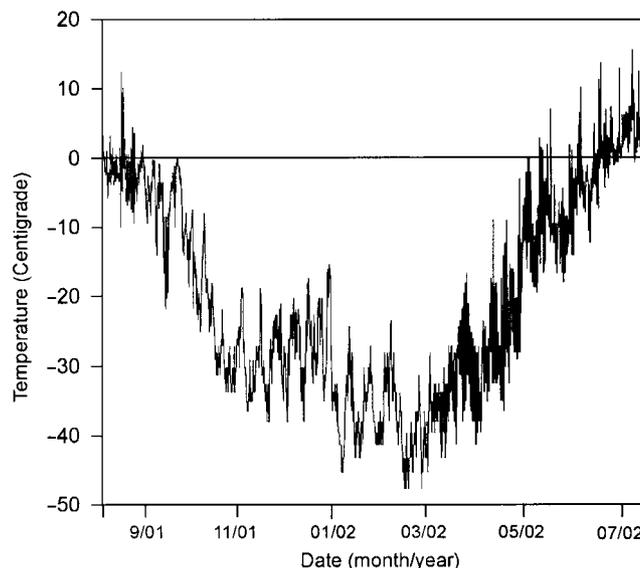

Fig. 3. Rock surface temperature from 16:00 on 14 August, 2001 to 10:00 on 10 July, 2002. The horizontal line in the graph denotes 0 °C.

Results

Temperatures within the endolithic habitat

During the 9 d of measurements the mean air temperature was 4.51 °C, the mean rock surface temperature was 5.49 °C and the mean temperature in the endolithic habitat was 5.93 °C (Fig. 2). The highest temperature recorded in the endolithic habitat was 21.78 °C at 13:17 on 20 July. The corresponding air temperature was 10.57 °C and the rock surface temperature was 16.11 °C. The coldest temperature recorded in the endolithic habitat was −1.45 °C at 01:24 on 24 July. The corresponding air temperature was −1.54 °C and the rock surface temperature was −1.39 °C. During this period, the endolithic temperature reached freezing at 23:08 on 23 July and remained below freezing until 07:50 the following morning. During the period of measurement the only other time that the air temperature dropped to below freezing was at 08:04 on 18 July. At this time the endolithic temperature was 1.25 °C and it remained above freezing.

From 14 August 2001 to July 10 2002 the mean ground temperature at the field site was −20.34 °C and the minimum temperature was −45.35 °C (Fig. 3). Of the 331 days during which measurements were made 38 days showed a diurnal freeze–thaw cycle.

Water availability in the endolithic habitat

Relative humidity ranged from a minimum of 31.3 to 100% (Fig. 4). The mean relative humidity over the measurement period was 74.8%.

The rocks could retain water for days after saturation. After artificial immersion in water for 4 h, the larger of the specimens had drawn up 8.4% of its dry mass in water and the smaller specimen 6.1% (Fig. 4). Following exposure to field conditions without rain, the larger specimen had
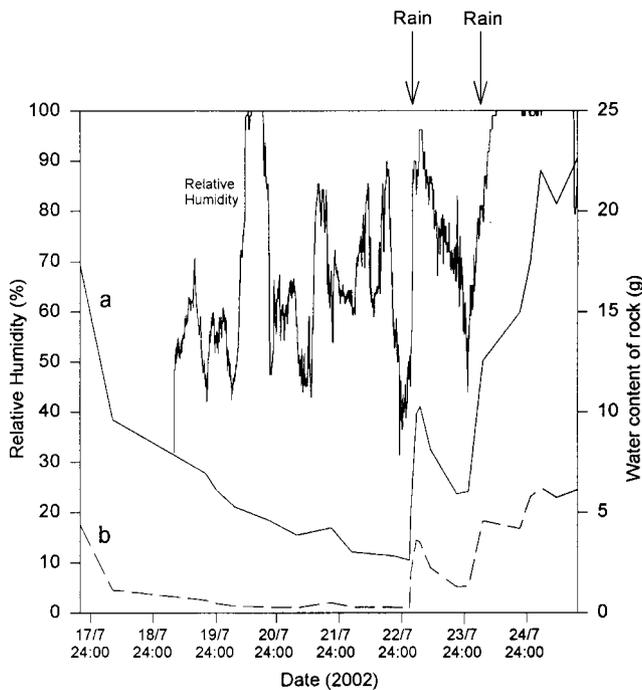
Fig. 4. Relative humidity (left-hand *y*-axis) measured during the rock moisture experiment from 21:00 on 17 July to 23:00 on 25 July. The right *y*-axis shows the mass gained (g) by two rocks, where the control mass was the dry mass. The dry masses were: (a) 207.2 g and (b) 68.9 g. Above the graph are the times at which rain occurred. In the first rain event 1 mm of water was deposited from 13:30 to 14:30 on 23 July. In the second rain event 4 mm of rain was deposited from 13:30 on 24 July to 0900 on 25 July, although light drizzle continued until the end of the experiment, hence the increasing rock mass.

retained 3.3 % of its mass in water after 48 h and 1.4 % after 5 d. The smaller specimen (with a smaller surface area, but a larger surface area to volume ratio) had retained 0.9 % of its mass in water after 48 h and 0.4 % after 5 d. After natural rain events, water uptake was rapid. After the delivery of 1 mm of rain in 1 h (first rain event in Fig. 4), the larger specimen had increased its percentage mass in water from 1.3 % to 4.8 %. The smaller specimen increased its percentage dry mass from 0.3 % to 5.2 %. After the second, more continuous, rain event and at the end of the experiment, the large specimen had 11.2 % of its dry mass in water and the smaller specimen 9.0 %.

Porosity of the gneiss

Of the four samples analysed, the mean mercury intrusion volume was 0.19 ± 0.058 ml g^{-1}. The mean bulk density was 1.17 ± 0.24 g cm^{-3}. The mean porosity of the samples was 22 ± 6.4 %.

Discussion

Endolithic communities in the Antarctic survive at the limits of life. McKay & Friedmann (1985) measured the temperatures associated with endolithic habitats at Linnaeus Terrace in the Ross Desert, Antarctica. Over a 12 d period they

recorded a maximum air temperature of 0.6 °C and a minimum of −15.2 °C. Air temperatures rarely rose above freezing and at the surface of the rock the temperature fluctuated over the 0 °C threshold 13 times during a 45 min measurement period. During this period no freezing was experienced in the endolithic zone, which, because of the thermal inertia of the sandstone, was protected against rapid freeze–thaw.

Although the subsurface endolithic habitat provided protection against freezing, organisms in these Antarctic habitats are at the limits of survival. Friedmann *et al.* (1994) examined a transect of endolithic communities from Battleship Promontory (76° 54′ S) to Horseshoe Mountain (77° 34′ S) over which mean annual temperatures decline. Living communities were found at Battleship Promontory, but at Horseshoe Mountain the leaching patterns of acids from extinct communities and the lack of extant communities suggested that this environment was too extreme for survival. At Mount Fleming, where the mean annual rock surface temperature was −24.2 °C, the presence of extinct and extant communities suggested that communities were at the absolute limits for survival.

In contrast, our data suggest a much more clement environment for the endolithic microorganisms at the almost exact opposite latitude. Like the Antarctic, mean temperatures in the subsurface were higher than the rock surface or air temperatures, but unlike the Antarctic, they did not merely prevent freezing, but provided temperatures often in excess of 10 °C and on one day in excess of 20 °C, when the air temperature was itself only 10 °C.

The water stress experienced by the Arctic communities is less than that experienced by the Antarctic cryptoendoliths. In the Antarctic, snowmelt provides the cryptoendoliths with infrequent moisture and air relative humidity values range from 15 to 75 % (Friedmann & Ocampo-Friedmann 1984), although the communities can only photosynthesize at relative humidities in excess of 70 % (Palmer & Friedmann 1990).

The Arctic endolithic communities not only receive snowmelt during the spring in analogy with the Antarctic communities, but are saturated with rain events throughout the summer. Water within the rock can be retained for many days after wetting and provides moisture for the communities prior to the next rain event. In large rocks, heterotrophs deep within the rocks (see Fike *et al.* 2003) might have moisture supplied throughout the season. We did not obtain a depth profile of the moisture in our rocks, and it is likely that although moisture is retained in the rocks for some time after wetting, the distribution of this moisture will vary. During dry periods, the near-surface endolithic environments will dry out more quickly than the interior of the rock. Conversely, during periods of rainfall, the surface environment will be wetted more quickly than the interior of the rock into which water must slowly percolate through the impact-induced fractures. Nevertheless, the data demonstrate that throughout the light season, well after snowmelt has ceased, rain can supply these endolithic communities with water, in contrast with the arid Dry Valley communities in Antarctica (Friedmann & Ocampo-Friedmann 1984).

Cryptoendolithic communities are well protected from UV radiation. It was previously shown that a 0.8 mm covering of gneiss could reduce the UV-induced inactivation of *Bacillus subtilis* spores by two orders of magnitude (Cockell *et al.* 2002). Similar levels of UV protection in Antarctic crypto-endolithic habitats are suggested by the high attenuation of visible light observed by Nienow *et al.* (1998b). Nevertheless, despite the low absolute exposures, these communities can still be susceptible to high relative changes of UV radiation caused by ozone depletion.

In the Antarctic, cryptoendolithic communities are exposed to elevated UV radiation as a result of the depletion of the ozone column during spring (October–November). Depletion can be in excess of 50 %, leading to ozone column abundances below 100 Dobson units and increases in surface DNA-weighted irradiances by up to an order of magnitude (Booth & Madronich 1994). Although ozone depletion occurs in the Arctic, it is less severe because of the more disturbed polar vortex (Dahlback 2002).

The less extreme environmental conditions in the Arctic site compared with the Antarctic are further manifested in the high abundance of epilithic growth. At 75° N there is substantial epilithic growth on exposed rocks (Cockell *et al.* 2002). There are two reasons for this observation. First, there is more precipitation to support epilithic growth. In the Antarctic these communities are rapidly desiccated by high winds. Secondly, as our data indicates, the surfaces of rocks on Devon do not experience the rapid freeze–thaw fluctuations found in the Dry Valleys of the Antarctic (McKay & Friedmann 1985). Although, during the passage of cold fronts, the surface of rocks can freeze (Fig. 2), these events occur over a period of hours and do not subject organisms to rapid and frequent freeze–thaw cycles.

Despite the more extreme environment in Antarctica, the sandstone habitats support much higher microbial biodiversity than the gneissic habitats at the Arctic location. The Antarctic endoliths are characterized by layered zones of microbial growth supporting lichen components and bands of eukaryotic algae (Friedmann *et al.* 1988). In contrast, the Arctic endoliths support low prokaryotic biological diversity, primarily accounted for by *Chroococcidiopsis*-like cyanobacteria and in some chasmoendolithic habitats, species of *Gloeocapsa*. This observation is counter to the observations of a less extreme climatic regimen and it suggests that more than extreme environmental stress regulates microbial biodiversity in the lithic habitat.

In attempting to reconcile the fact that eukaryotic components exist in the Antarctic rocks, but only prokaryotic components exists in the cryptoendolithic habitat of hot deserts such as the Sinai and Negev, Friedmann (1980) suggested that the high temperatures and extreme aridity prevented the maintenance of eukaryotic components in hot desert environments. Whilst this may be the case in hot deserts, it does not explain the low biological diversity and lack of eukaryotic colonization in the Arctic gneiss, where the relative humidity is high and temperatures clement for eukaryotes during the summer growing season.

Another factor of importance in colonization of rocks is the porosity. Lower porosity would be expected to restrict the spread of fungal hyphae and thus endolithic lichens. However, Nienow *et al.* report porosity values for sandstones from the Linnaeus Terrace of between 2.3 and 13.0 %. The mean of the 10 samples they present data for was $9.0 \pm 3.1\%$ (Nienow *et al.* 1988a). These values are half the values we measure for the shocked gneiss and suggest that the pore space for lichen and eukaryotic colonization is available in the gneiss.

One possible explanation for the lower diversity is the higher water flow through the rocks in the Arctic, because of higher precipitation. The frequent flow of water through the rocks might hinder the establishment of well-defined microzones that are found in the Antarctic endolithic communities.

A second explanation may be the irregularity of the pore space distribution in the gneiss. The relatively homogeneous pore space of the Antarctic sandstones allows growth of organisms to occur consistently along the subsurface space, permitting zones of microbial communities to become established at well-defined depths with well-defined vertical light and nutrient gradients, providing the micro-environments for different organisms (Friedmann *et al.* 1988; Nienow *et al.* 1988b). In contrast, the Arctic gneiss is irregular in its porosity, with patches of endolithic growth often no greater than 1 cm in length. This is caused primarily by the uneven shock-processing of the gneiss (Bunch *et al.* 1998), the shock processing giving rise to the endolithic colonization in the first place (Cockell *et al.* 2002). The observation of eukarya within endolithic communities from Eureka, Nunavut Canada (80° N, 85° W) (Omelon, unpublished observations), might support the idea that the physical structure of the substrate has an important influence on colonization and diversity.

The data have implications for the effects of climatic change on cryptoendolithic communities. Potential changes may be more complex than simply community changes induced in response to long-term temperature changes or water availability. The constraints of growth in the endolithic micro-habitat, caused by the nature of the pore space and the stability of the habitat will influence the way in which these communities take advantage of changed environmental conditions. Climate warming in the Arctic may not lead to higher cryptoendolithic biodiversity in the gneiss because this substrate already excludes eukaryotic and even other prokaryotic organisms abundantly represented in the epilithic environment. In the Antarctic, climate warming could even reduce cryptoendolithic biodiversity by increasing precipitation, thus increasing the rate of sandstone weathering and the rate of water flow through the rock, disrupting subsurface colonization.

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