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SHORT NOTE

Sun exposure drives Antarctic cryptoendolithic community structure and composition

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Abstract

The harsh environmental conditions of the ice-free regions of Continental Antarctica are considered one of the closest Martian analogues on Earth. There, rocks play a pivotal role as substratum for life and endolithism represents a primary habitat for microorganisms when external environmental conditions become incompatible with active life on rock surfaces, allowing life to spread throughout these regions with extreme temperatures and low water availability. Previous research concluded that altitude and distance from sea do not play as driving factors in shaping microbial abundance and diversity, while sun exposure was hypothesized as significant parameter influencing endolithic settlement and development. With this in mind, eight localities were visited in the Victoria Land along an altitudinal transect from 834 to 3100 m a.s.l. and 48 differently sun-exposed rocks were collected. We explored our hypothesis that changes in sun exposure translate to shifts in community composition and abundances of main biological compartments (fungi, algae and bacteria) using Denaturing Gel Gradient Electrophoresis and quantitative PCR techniques. Major changes in community composition and abundance occurred between north and south sun-exposed samples. As Antarctic endolithic ecosystems are extremely adapted and specialized but scarcely resilient to external perturbation, any shifts in community structure may serve as early-alarm systems of climate change; our findings will be of wide interest for microbial ecologists of extreme environments such as arid and hyper-arid area.

Keywords Antarctica · Cryptoendolithic communities · Sun exposure · DGGE · qPCR

Introduction

The rate of warming due to increased levels of greenhouse gases in the atmosphere is amplified with elevation and at high latitudes due to the polar amplification phenomenon that predicts the greatest warming will occur at the Polar regions (Bekryaev et al. 2010). The impact of climate change is, therefore, particularly intense at the Poles and in mountain environments, nowadays known as the Third Pole (Yao et al. 2012; Yang et al. 2014). As a consequence of warming, range-restricted species have already shown severe contractions and been the first groups in which entire species have gone extinct (Parmesan 2006; Descamps et al. 2017; Bhatta et al. 2018).

The Arctic regions are melting faster than the Antarctic and, if the heating trend continues, studies forecast an ice-free North Pole in summer by mid-century. Strong evidence of warming in Antarctica is also documented; the British Antarctic Survey reports a warming trend up to 2.5 °C since the 1940s in the Antarctic Peninsula and Maritime Antarctica, the most rapid changes in mean air temperatures on Earth (e.g. Turner et al. 2005, 2007). Others showed an apparent contrast between strong warming of the Antarctic Peninsula and slight cooling of the Antarctic continental interior, and there is now evidence that significant warming extends well beyond the Antarctic Peninsula and covers most of West Antarctica with a warming exceeding 0.1 °C per decade over the past 50 years (Steig et al. 2009).

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Progression of this warming trend will influence Antarctica's biodiversity by the introduction of allochthonous, competitive species and the consequent extinction of highly specialized and less competitive autochthonous ones (Farrell et al. 2011; Olech and Chwedorzewska 2011; Selbmann et al. 2012), which will have impacts on the ecosystem functions of glaciers, freshwater systems and atmosphere. Thus, it is urgent to develop a strong base of knowledge for Antarctic terrestrial ecosystems and to use this to identify ecosystem changes (NAS 2011).

Endolithism is a specialized colonization of microbes dwelling inside airspaces of rocks. This lifestyle represents adaptation at the edge inhabitable conditions. Airspaces within rocks offer microbiota a protected and buffered microenvironment, allowing life to expand into different extreme conditions, i.e. hot and cold deserts or geothermal environments (Friedmann and Ocampo 1976; Friedmann 1982; Bell 1993; Walker et al. 2005). Rocks are the prevailing substratum for life in the ice-free areas of Antarctica, supporting the highest standing biomass in the Antarctic ice-free desert and mountain tops emerging from the Polar Plateau (Cowan and Tow 2004; Cary et al. 2010; Cowan et al. 2014; Selbmann et al. 2017). The harsh conditions are considered among the closest terrestrial Martian analogue (Quintal et al., 2018). Endolithic microbial life represents the predominant recorded life-form in these areas (Nienow and Friedmann 1993).

Various typologies have been observed for the microbial composition and the most complex and widespread are the lichen-dominated communities (Nienow and Friedmann 1993), mainly composed of algae, lichenized and free-living fungi and bacteria, many of which are endemic species to the regions (Nienow and Friedmann 1993; Selbmann et al. 2005, 2008; Egidi et al. 2014). The high degree of adaptation and specialization in exploiting such ultimate niches makes these communities very susceptible to physical and climatic alteration (Selbmann et al. 2017) and any shift in community composition may serve as early-alarm system of environmental perturbation. Based on a substantial sampling of different typologies (volcanic and sedimentary) of colonized rocks in the Victoria Land, Antarctica, sandstone was determined to be the most suitable substratum for microbial endoliths, allowing them to spread and persist under stronger pressure (Zucconi et al. 2016; Selbmann et al. 2017). To assess the future effects of climate change on these unique ecosystems, the response of endolithic communities to increasing environmental pressure, due to altitude (from sea level to 3600 m a.s.l.) and sea distance (up to 100 km) was recently investigated. The results suggested that these two parameters alone do not play a significant role in shaping community diversity and composition, and the need to consider additional variables to elucidate how, in the long run, future changes will impact these unique communities (Coleine et al. 2018a).

With this in mind, a sampling campaign (2015–2016, XXXI Italian Antarctic Expedition) of sandstones was performed in the Victoria Land (Antarctica) in the frame of the Italian National Program for Antarctic Research (PNRA), along an altitudinal gradient from 834 to 3100 m a.s.l., adding sun exposure as a new parameter to investigate its influence on endolithic settlement and development. Recently, Coleine and colleagues analysed a selection of samples collected during the above-mentioned sampling Campaign to test the effects of sun exposures on shaping community composition, taxon abundance, and distribution of functional groups of fungi in endolithic communities, using a metabarcoding approach targeting the internal transcribed spacer region 1 (ITS1). Based on previous studies (Selbmann et al. 2017), it has been also suggested that sampling strategy and environmental parameters considered may have important consequences on a proper and exhaustive biodiversity description. Thus, before proceeding with metabarcoding and metagenomics experiments to develop a detailed picture of biodiversity and functionality, we have performed more rapid and cheaper approaches (i.e. Denaturing Gradient Gel Electrophoresis and quantitative PCR) on forty-eight differently sun-exposed samples collected from eight localities to test hypothesis that changes in sun exposure impact community composition and abundances of primary biological assemblages (fungi, algae and bacteria).

Materials and methods

Study area

Eight localities were sampled in the Victoria Land (Continental Antarctica) during the XXXI Italian Antarctic Campaign (Dec. 2015–Jan. 2016). North and south exposed sandstones were collected along a latitudinal transect from 74° 10′ 44.0″ S 162° 30′ 53.0″ E (Mt. New Zealand) to 77° 54′ 43.6″ S 161° 34′ 39.3″ E (Knobhead), ranging from 834 to 3100 m a.s.l. (Fig. 1, Online Resource 1). All rocks were excised aseptically, posed in sterile plastic bags, preserved at − 20 °C immediately upon collection to avoid contamination and transported to University of Tuscia, Italy and stored -20°. Rocks were sampled in triplicate, C.

Environmental DNA extraction and denaturing gel gradient electrophoresis

DNA was extracted from 0.3 g of crushed and homogenized rocks using NucleoSpin® Plant II Kit (Macherey–Nagel, Germany) and quantified by Quant-iT dsDNA HS assay kit

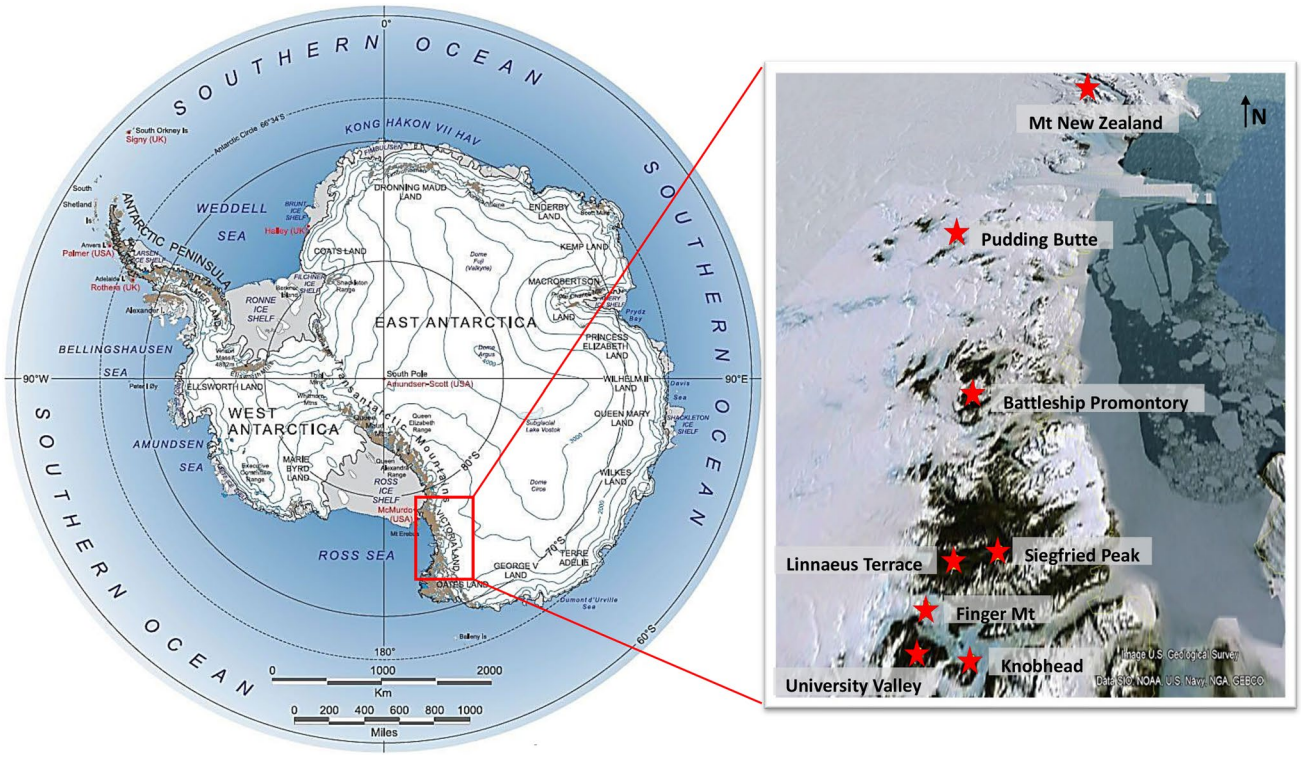


Fig. 1 Map of Antarctica and sampling site in the Victoria Land (Continental Antarctica)

(Invitrogen, Oregon, USA). Microbial diversity was screened by Denaturing Gel Gradient Electrophoresis (DGGE). A semi-nested PCR was performed using primers with a GC-clamp (Muyzer et al. 1993); fungal ITS rRNA was amplified with primers ITS1F (CTTGGTCATTTAGAGGAAGTAA) and ITS2 (GCTGCGTTCTTCATCGATGC) (Gardes and Bruns 1993; White et al. 1990); algal ITS rRNA using LSU0012 (AGTTCAGCGGGTGGTCTTG) and AL1500BF (GATGCATTCAACGAGCCTA) primers (Piercey-Normore e De Priest 2001; Helms et al. 2001); while 341F (GCACGGGGGGCCTACGGGAGGC) and 518R (ATTACCGCGGCTGCTGG) primers (Muyzer et al. 1993) were utilized for 16S rRNA amplification (Valášková and Baldrian 2009).

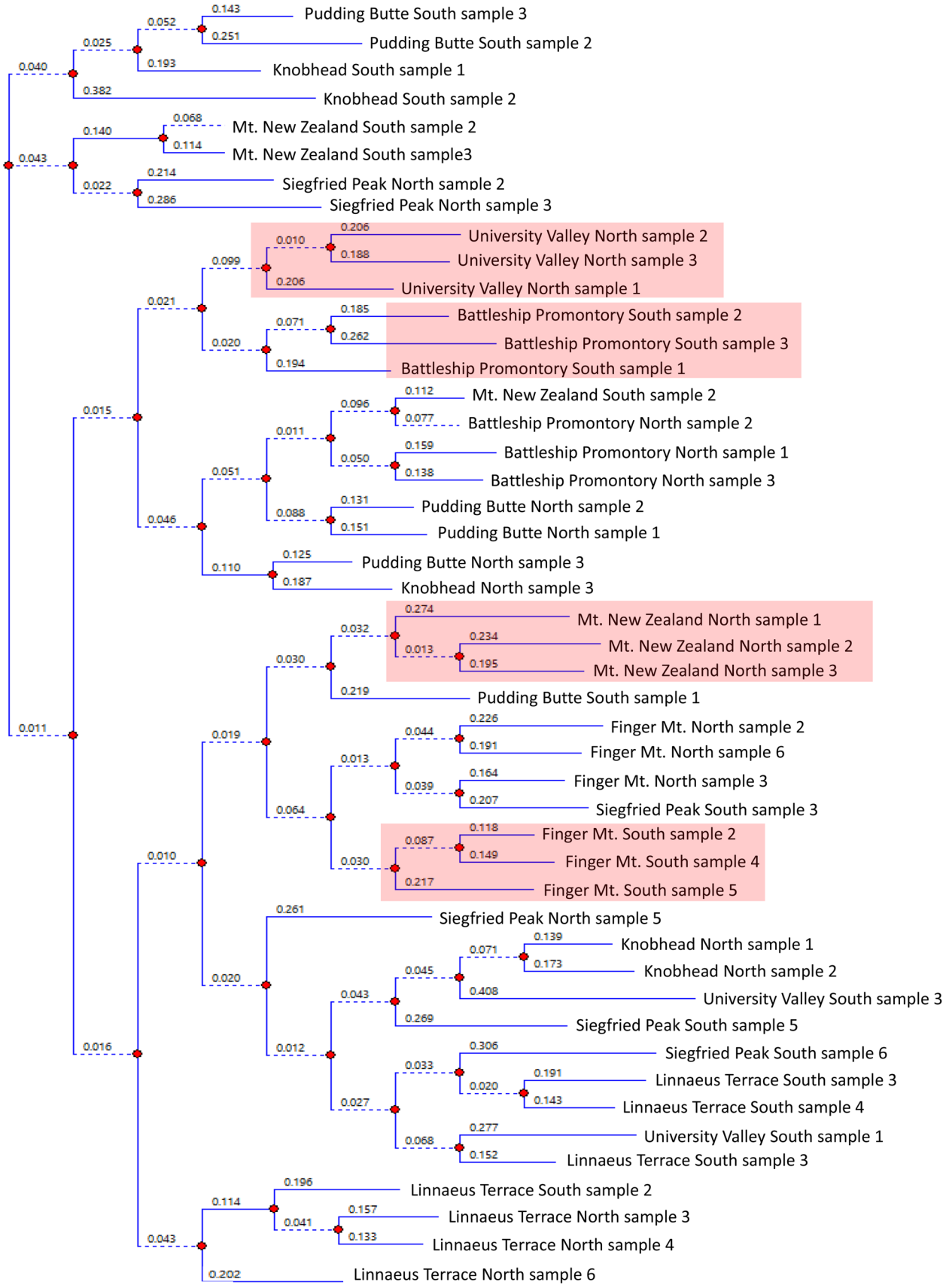
Amplicons were purified using NucleoSpin®Gel and PCR Clean-up (Macherey–Nagel, Germany); 100 ng of DNA were loaded into each well and runs were performed on DGGE Electrophoresis System (C.B.S. Scientific, Del Mar, California, USA). Gels at 7.5% polyacrylamide (37.5:1 acrylamide:bisacrylamide) were mixed in a gradient maker using two different concentrations: 0–70% for eukaryotes (5 h) and 0–60% for bacteria (3.5 h) in 1 × TAE at 60 °C and 200 V.

Bands were visualized by staining for 40 min with GelRed solution (Biutium, Inc, CA, USA) (1.34 g NaCl, 66.7 pi GelRed and 200 mL dw) and then on UV transilluminator (Chemidoc, Bio-Rad). Scanned gels were analysed with TotalLab Quant Software (Cleaver Scientific Ltd; United Kingdom): bands were assigned and matched automatically and then checked manually. Profile similarity was calculated by determining Dice's coefficient (presence/absence) for the total number of lane patterns and was used to used to generate dendrograms Unweighted Pair Group Method with Arithmetic mean (UPGMA).

Triplicates were processed and analysed independently.

NMDS ordination plots

Multivariate statistical analyses were performed to determine the effects of sun exposure using PAST (PAleontological Statistics) v2.17. Changes in community composition were displayed using with Non-Metric Multidimensional Scaling (NMDS) based both on abundance (bands intensity, Bray–Curtis index) and incidence data (Jaccard distance) (Clarke 1993). Abundance data were square-root transformed and analyses were carried out with 999 permutations. NMDS were plotted using the combined occurrence and abundance data of the three replicates from each site. Permutational multivariate analyses of variance (PERMANOVA, $p < 0.05$) based on the Euclidean distance were utilized to establish differences in the two differently sun-exposed rock-inhabiting communities.


Pudding Butte South sample 3
Pudding Butte South sample 2
Knobhead South sample 1
Knobhead South sample 2
Mt. New Zealand South sample 2
Mt. New Zealand South sample3
Siegfried Peak North sample 2
Siegfried Peak North sample 3
University Valley North sample 2
University Valley North sample 3
University Valley North sample 1
Battleship Promontory South sample 2
Battleship Promontory South sample 3
Battleship Promontory South sample 1
Mt. New Zealand South sample 2
Battleship Promontory North sample 2
Battleship Promontory North sample 1
Battleship Promontory North sample 3
Pudding Butte North sample 2
Pudding Butte North sample 1
Pudding Butte North sample 3
Knobhead North sample 3
Mt. New Zealand North sample 1
Mt. New Zealand North sample 2
Mt. New Zealand North sample 3
Pudding Butte South sample 1
Finger Mt. North sample 2
Finger Mt. North sample 6
Finger Mt. North sample 3
Siegfried Peak South sample 3
Finger Mt. South sample 2
Finger Mt. South sample 4
Finger Mt. South sample 5
Siegfried Peak North sample 5
Knobhead North sample 1
Knobhead North sample 2
University Valley South sample 3
Siegfried Peak South sample 5
Siegfried Peak South sample 6
Linnaeus Terrace South sample 3
Linnaeus Terrace South sample 4
University Valley South sample 1
Linnaeus Terrace South sample 3
Linnaeus Terrace South sample 2
Linnaeus Terrace North sample 3
Linnaeus Terrace North sample 4
Linnaeus Terrace North sample 6

◂**Fig. 2** Dendrogram obtained by Unweighted Pair Group Method using Arithmetic average (UPGMA) based on the DGGE profiles of the fungal component of the endolithic communities. The relationships among samples are based on similarity, evaluated by the Dice coefficient. Triplicate samples were analysed

Quantitative PCR

Fungal and bacterial abundances were measured for all samples by quantitative PCR (qPCR) using NS91F (5′-GTCCCTGCCCTTTGTACACAC-3′) and ITS51R (5′-ACCTTGTTACGACTTTTACTTCCTC-3′) for fungi and Eub338 (5′-ACTCCTACGGGAGGCAGCAG-3′) and Eub518 (5′-ATTACCGCGGCTGCTGG-3′) for bacteria (Fierer et al. 2005). To determine relative gene copies abundances, standard curves were generated using a tenfold serial dilution of a plasmid containing a copy of *Cryomyces antarcticus* ITS rRNA gene for fungi and *Escherichia coli* 16S rRNA gene for bacteria. Amplicons were generated in 100 µL reactions, containing 50 µL of 2 × PCR BioMix™ (Bioline, London, UK), 5 pmol of both forward and reverse primers, 43 µL of DEPC water and 5 µL template of DNA. For fungi, amplification was carried out as follows: 95 °C for 3 min and the 35 cycles of 95 °C 40 s, 55 °C 30 s, and final extension at 72 °C 40 s; while bacterial 16S region as follows: 95 °C for 3 min and the 35 cycles of 95 °C 40 s, 53 °C 30 s, and final extension at 72 °C 40 s. PCR products were then purified using the NucleoSpin® PCR Clean-up kit, quantified with Qubit and cloned using the pGEM®-T Easy Vector Systems (Promega, Madison, Wisconsin, US). Plasmids were isolated using the NucleoSpin Plasmid kit (Macherey–Nagel).

Five standards were utilized in series from 10^7 to 10^3 copies.

The 25 µL qPCR reactions contained 12.5 µL iQ™ SYBR® Green Supermix (Bio-Rad, Hercules, California, US), 1 µL of each forward and reverse primers, 0.3 ng of environmental DNA or standard and 9.5 µL nuclease-free water. The reactions were carried out on Quantitative real-time BioRad CFX96™ (Bio-Rad, Hercules, California, US). Primers and amplification protocols are mentioned before. Melting curves were generated to confirm that the amplified products were of the appropriate size. Gene copy numbers were generated using a regression equation for each assay relating the cycle threshold (C_t) value to the known number of copies in the standards, included no-template controls.

All reactions were run in triplicate.

Statistical analysis were performed using one-way analysis of variance (Anova) and pairwise multiple comparison using SigmaStat 2.0 (Jandel, USA). Differences were calculated by Tukey test ($p < 0.05$).

Fungal-to-bacterial ratio was calculated from log-transformed abundance values.

Results and discussion

Denaturing gradient gel electrophoresis profiles and biodiversity analysis

Antarctic cryptoendolithic communities host among the most resistant microorganisms on Earth, being able to survive under environmental conditions once viewed as incompatible with life (Horowitz et al. 1972).

The lack of consistent microbial diversity patterns along altitudinal and sea distance gradients has suggested that new hypotheses about the driving factor shaping biodiversity must be put forward (Selbmann et al. 2017; Coleine et al. 2018a). Towards this end, the aim of this study was to test the potential effects on the structure and composition of the bacterial, fungal and algal assemblages of a new parameter, namely sun exposure, as a significant variable influencing endolithic settlement and development, using a preliminary molecular screening approach on 48 rocks collected along the Victoria Land (Continental Antarctica).

DNA was efficiently extracted from almost all rock samples, with few exceptions (i.e. Mt New Zealand and Linnaeus Terrace south) where DNA was not detectable, but amplifications were successfully for all samples.

Because results were similar when analysing fungi and algae, only data based on fungi are reported.

Overall, the banding patterns of the replicates showed a high degree of similarity (data not shown), which was also supported by the dendrograms, generating DGGE patterns that grouped together as most similar to each other (Fig. 2, Online Resource 2). A coherent grouping according to sun exposure was generated in the clustering based on profiles, with few scattered exceptions, highlighting an evident relationship between microbial composition and this environmental parameter. In particular, in the clustering generated on fungal profiles, samples were split according to the localities for University Valley, Pudding Butte, Battleship Promontory, Mt. New Zealand and Finger Mt. (Fig. 2). The grouping was also evident in the clustering based on bacterial profiles (Online Resource 2); as for fungi, the splitting was obtained in communities from Pudding Butte (south), Battleship Promontory (south) and Finger Mt. (south), but also for Linnaeus Terrace and Knobhead for both sun expositions.

These findings highlight the effectiveness of sampling strategy applied for the Antarctic Expedition 2015–2016 and did not reflect what was observed by Selbmann et al. (2017). In that study, based on a previous sampling (PNRA, Antarctic Expedition 2010–2011), the largest Antarctic sampling to date of rocks hosting lithic communities, including different rock typologies (i.e. sandstone, granite, dolerite) from 46 different localities in Victoria Land, was investigated. Results indicated a remarkable local variability found even

in rocks from the same site, perhaps due to the size of sampled area in some cases (up to 100 mq^2) and to variability of rock typologies collected.

Non-metric multidimensional scaling analysis and community composition

The observed shift in community composition correlated to sun exposure was also confirmed by Non-Metric Multidimensional scaling (NMDS) analysis, which organizes data into 2-D spatial graphs by reducing dimensionality. NMDS ordination plots were generated both with the only presence-absence matrix using the Jaccard index and with the combined frequency of occurrence using the Bray–Curtis index. Because both approaches produced similar results, we show results based on abundance only.

When stress values are < 0.1, the NMDS plot is considered to be an acceptable representation of the original data; in fact, a stress value below 0.1 indicates a reliable ordination of data, without a real probability of misinterpretation (Clarke 1993). In this analysis, the stress value was 0.09 for fungi and 0.07 for bacteria, fitting with the ideal ordination.

NMDS plots generated from the DGGE profiles of amplified fungal ITS and bacterial 16S rDNA revealed that only small changes occurred among samples collected in the same sun-exposed rock surface ($p > 0.05$) and did not exhibit any changes in endolithic communities by sampled localities (data not shown). On the contrary, a major change (1-way NPMANOVA, $p < 0.05$) occurred between north and south sun-exposed communities, showing a strong structuring of fungal and bacterial communities according to the sun exposure (Fig. 3a, b).

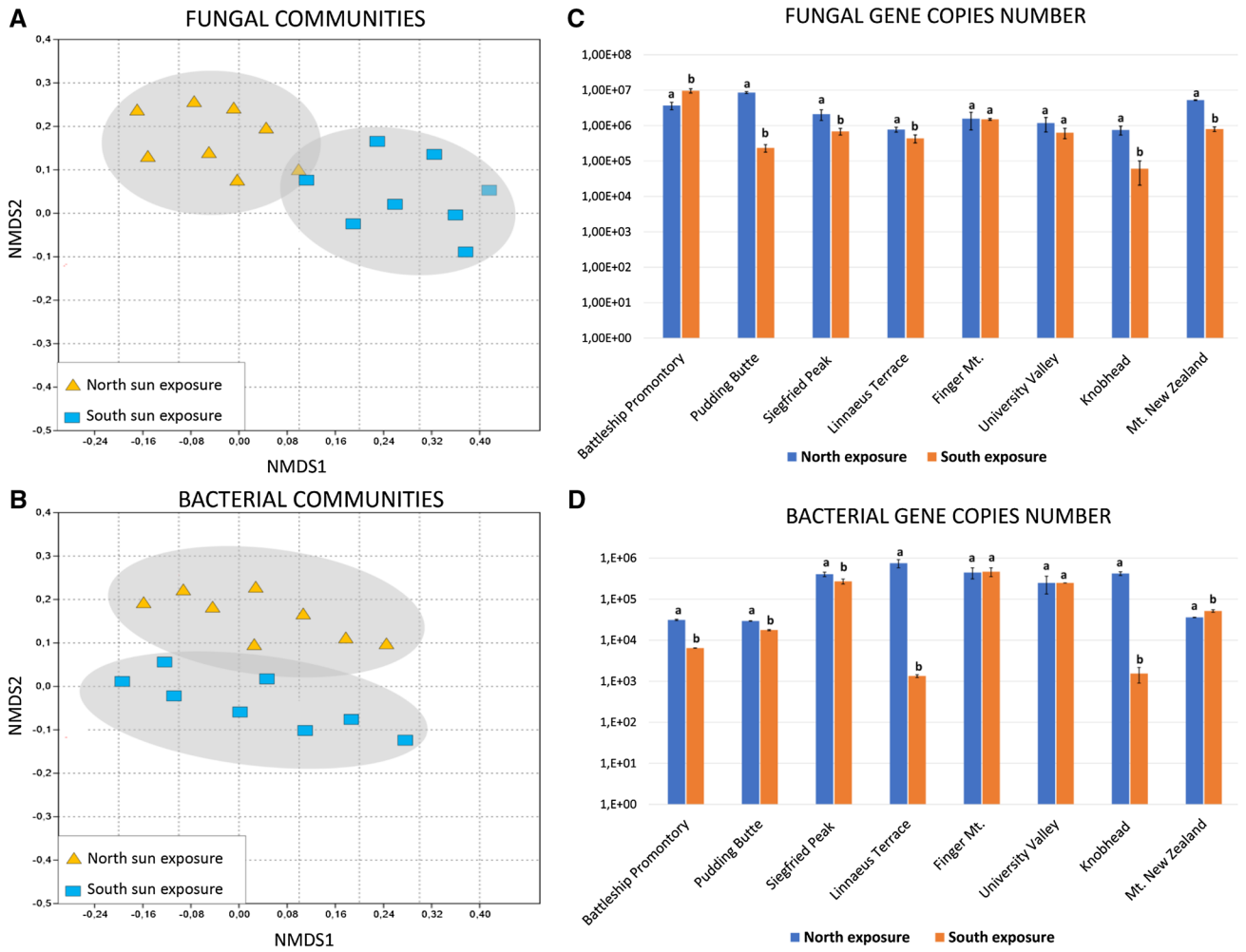


Fig. 3 Non-Metric Multidimensional Scaling (NMDS) ordination plots for fungal (**a**) and bacterial endolithic communities (**b**), calculating the Bray–Curtis index, based on square-root transformed abundance data. Abundances of total fungi (**c**) and bacteria (**d**) in endolithic communities, as estimated using the qPCR assays. Error bars are the standard errors. Significant differences are calculated by Tukey test with p value < 0.05 and indicated by different letters. Stress value (a): 0.09. Stress value (b): 0.07

An apparent gradient in abundance and community composition in response to sun exposure was previously observed in Coleine et al. (2018b), where authors investigated biodiversity and composition of functional groups of fungi in Antarctic endolithic communities and reported the absence of any correlation with altitude, while a remarkable variability was observed considering the sun exposure parameter.

Our findings support the hypothesis that sun radiation not only affects rock surface temperatures, water availability and metabolic activity (Coleine et al. 2019) but also endolithic community biodiversity (Coleine et al. 2018b). It was previously hypothesized that the distribution of endoliths reflects the degree of sunlight in northern-exposed rocks; in northern-exposed rocks, environmental conditions are more favourable than southern exposed faces, and cryptoendolithic colonization is more often observed and favoured (Friedmann 1977; Friedmann and Weed 1987). The capability to maintain biological activity may depend on sufficient insulation of the rock to allow an efficient photosynthetic process; moreover, warmer temperatures will allow metabolic activity and more water due to snow melt (McKay and Friedmann 1985; Deegenaars and Watson 1998).

Relative abundance of fungal and bacterial communities

Community structure was also shaped by north and south exposure when fungal and bacterial abundances were estimated with a qPCR assay. In most localities, fungal (ranging from 6.1×10^4 to 9.8×10^6 gene copies) and bacterial (7.7×10^5 to 1.3×10^3 gene copies) abundances changed significantly according to sun exposure. Overall, both fungal and bacterial abundances varied between the two sun exposures, except in the case of Finger Mt. and University Valley in Dry Valleys (Southern Victoria Land), where abundances of the two major biological compartments was similar (Fig. 3c, d; Online Resource 3). Furthermore, microbial abundance was generally higher in north-exposed rocks, with only a few exceptions: fungi were most abundant in south sun-exposed samples at Battleship Promontory, while bacteria were larger in number at Mt. New Zealand south.

We also calculated the fungal:bacterial (F/B) ratio, a metric to assess environmental impacts and the functional implications of microbial communities (Raeymaekers 2000; Fierer et al. 2005). The fungal-to-bacterial ratio (F/B) (based on log-copy numbers) showed a slightly higher dominance of fungi were significantly different in all samples ($p < 0.05$). In north-exposed rocks F/B was 1.24 ± 0.2 (mean $\pm$ SD), while in south surface, where conditions are much more extreme, it was 1.37 ± 0.31 (data not shown).

We propose that further studies are needed to elucidate the relationship between fungi and bacteria, and to reveal their functions in these ecosystems. Nevertheless, this result is not surprising: extreme environments (i.e. Antarctic desert) are not an only prerogative of archaea and bacteria. Among eukaryotes, fungi (alone or in symbiosis with cyanobacteria or algae forming lichens) are the most versatile and ecologically successful phylogenetic lineage, evolving to survive and proliferate in the extremes (Magan 2007), even in habitats normally precluded to the most (Selbmann et al. 2013). Fungi are, for instance, generally more resistant to desiccation than bacteria with hyphae that may cross air-filled soil pores to access nutrients and water (Gordon et al. 2008; de Vries et al. 2012).

The most remarkable fungal example for stress resistance is the Antarctic cryptoendolithic black fungus *Cryomyces antarcticus*, isolated from the McMurdo Dry Valleys, chosen as the best eukaryotic test organisms for astrobiological investigations for its stunning resistance to temperature cycles (− 20/ + 20 °C), high temperature (+ 90 °C) and saline concentration (up to 25% NaCl) (Onofri et al. 2008; 2012; 2015). It was found resistant to ionizing radiation up to 55.81 kGy (Selbmann et al. 2018), while the bacterium *Deinococcus radiodurans*, widely considered the extremophile par excellence and gold-medalist of radiation resistance (Battista et al. 1997; Venkateswaran et al. 2000), survives up to 20 kGy of gamma radiation.

In conclusion, although the DGGE and qPCR-based approaches did not show individual taxa responses, it is still considered a powerful, rapid and cost-effective method for determining variation in microbial community composition (Zheng et al. 2013; Kovalski-Mitter et al. 2018). This technique gave us the advantage to process a great number of samples for all main assemblages (fungi, algae and bacteria), providing a clear trend of how sun exposure influences Antarctic cryptoendoliths, expanding our knowledge on the relationship between environmental parameters and biodiversity.

The results will inform planning of future Antarctic campaigns to maximize identification of active endolithic communities. Based on this study, we will be able to explore the composition deeply focusing on a targeted selection of rock samples. Such future studies will characterize taxa identity and abundance in rocks hosting endolithic communities, examine the complex community dynamics, their stress-adaptation strategies, and potential functions across an environmental variation gradient.

A detailed picture on how these communities respond to increasing environmental pressures will also give clues for predicting and monitoring the effects of global change on these unique border ecosystems.

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preserving Antarctic rock samples analysed in this study and stored in the Culture Collection of Fungi from Extreme Environments (CCFEE), University of Tuscia, Italy.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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