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Using Captain Scott's Discovery specimens to unlock the past: has Antarctic cyanobacterial diversity changed over the last 100 years?

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Evidence of climate-driven environmental change is increasing in Antarctica, and with it comes concern that this will propagate to impacts on biological communities. Recognition and prediction of change needs to incorporate the extent and timescales over which communities vary under extant conditions. However, few observations of Antarctic microbial communities, which dominate inland habitats, allow this. We therefore carried out the first molecular comparison of Cyanobacteria in historic herbarium microbial mats from freshwater ecosystems on Ross Island and the McMurdo Ice Shelf, collected by Captain R.F. Scott's 'Discovery' Expedition (1902–1903), with modern samples from those areas. Using 16S rRNA gene surveys, we found that modern and historic cyanobacteria assemblages showed some variation in community structure but were dominated by the same genotypes. Modern communities had a higher richness, including genotypes not found in historic samples, but they had the highest similarity to other cyanobacteria sequences from Antarctica. The results imply slow cyanobacterial 16S rRNA gene genotype turnover and considerable community stability within Antarctic microbial mats. We suggest that this relates to Antarctic freshwater 'organisms requiring a capacity to withstand diverse stresses, and that this could also provide a degree of resistance and resilience to future climatic-driven environmental change in Antarctica.

1. Background

Climate models predict that the Polar Regions will warm faster than other parts of the globe, a scenario that frequently raises concerns over threats to the integrity of their biological communities. In the Arctic this tendency is already well developed, but while substantial warming has been seen in the Western Antarctic Peninsula since the 1950s [1,2], in Continental Antarctica warming trends are slight due to offset by changes to the Southern Annular Mode of atmospheric circulation, linked to ozone depletion [3,4]. However, some evidence of change on the continent is emerging and, as the ozone hole fills, widespread warming of the continent is expected to accelerate [5]. To recognize and forecast biological responses to warming in continental Antarctica, it is important to understand natural population drift and the extent and timescales over which changes in diversity, community structure, and ecosystem processes occur. However, inland Antarctica is dominated by microbial ecosystems, and the absence of suitable records through time of their composition limits an assessment of their temporal stability to date.

In inland Antarctica, aquatic ecosystems such as lakes, streams, and meltwater ponds are recognized as hotspots and refugia for biological productivity and diversity, and within these cyanobacterial mat communities represent the most prominent biology [6–8]. Previous work on the diversity of community composition in these mats has mostly concentrated on establishing relationships between composition, current environment, and geography [9–12]. No assessments along a

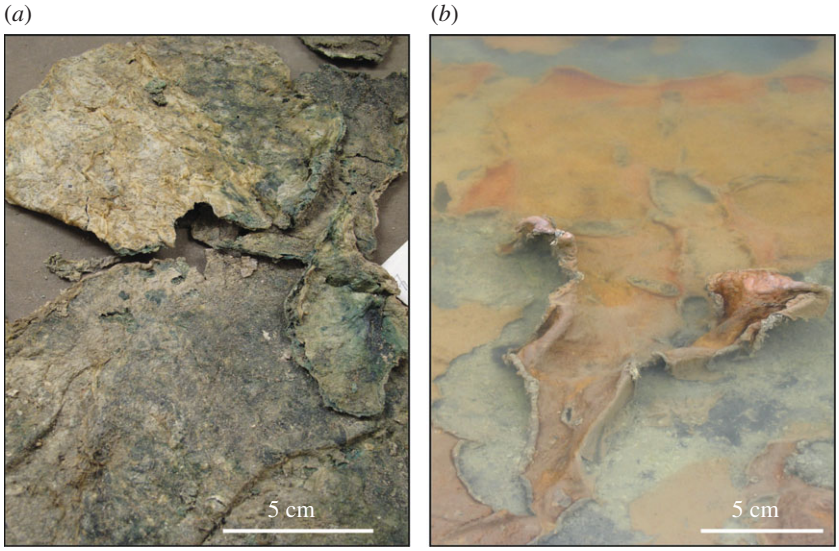

Figure 1. Antarctic cyanobacterial communities in (*a*) a herbarium specimen collected in 1902–1903 during Captain Scott's Discovery Expedition, and (*b*) modern communities growing in a meltwater pond on the McMurdo Ice Shelf, Antarctica.

temporal axis have been carried out in Antarctica. Archived samples of microbial communities do, however, exist that potentially allow for comparison with modern samples using molecular techniques if DNA can be extracted from them, and sufficient metadata is present to identify sampling locations. Dried herbarium specimens of cyanobacterial mats from meltwater ponds on Ross Island and the McMurdo Ice Shelf were collected during the 1902–1903 National Antarctic Expedition, also called the Discovery Expedition, led by Captain Robert Falcon Scott [13]. The careful collection, preservation, and documentation of these samples offers a unique possibility to compare modern and century-old microbial mat communities. Such a comparison would allow the turnover of taxa to be examined and may indicate whether exotic taxa from outside of Antarctica have appeared in these ponds that could be associated with human presence over the last century.

Our goals were to determine: whether DNA can be extracted from dried mat material sufficient to determine how communities of cyanobacteria have changed over a 100-year period; whether cyanobacteria dominant in the past have been replaced with different dominate taxa in modern samples; and whether taxa that are present now but not in historic samples have an origin outside of Antarctica. To this end, we carried out the first high-throughput sequencing analysis of herbarium specimens collected from Antarctica by the 'Heroic Age' expeditions. We compared these with present-day cyanobacterial mats from geographical locations as similar as possible to those sampled at the beginning of human presence, on the McMurdo Ice Shelf and Ross Island, Antarctica. The latter is a location that currently experiences one of the highest levels of human activity in East Antarctica, and perhaps most vulnerable to the introduction of human-vectored invasive taxa [14].

2. Material and methods

(a) Study sites and samples

Cyanobacterial mat samples were studied from the Ross Island and McMurdo Ice Shelf in Southern Victoria Land Antarctica (electronic supplementary material, figure S1, tables S1 and S2). Seven cyanobacterial mat samples were collected from ponds and ice eskers during the 'Discovery' National Antarctic Expedition led by Captain Robert Falcon Scott between February 1902 and December 1903 (figure 1). Six samples were from the McMurdo Ice Shelf and one from close to winter quarters on Ross Island near Hut Point. McMurdo Ice Shelf samples were from an area approximately half way between Brown and Black Peninsula [13]. The Scott's Discovery samples were compared with present-day cyanobacteria from microbial mats collected from freshwater meltwater ponds on the McMurdo Ice Shelf, Cape Royds and Cape Evans on Ross Island in January 2011, and Hut Point, Ross Island near the Discovery Hut in January 2012 (electronic supplementary material, figure S1 and table S2).

(b) DNA extraction, PCR, PCR-product purification, and pyrosequencing

All molecular biological work for Scott's Discovery and present-day samples were carried out in different laboratory spaces using separate pipettes and reagents to prevent cross contamination of samples. DNA from Scott's Discovery samples were extracted under a UV and ethanol-sterilized laminar flow cabinet. Two to four DNA extractions were required for the Scott samples, and pooled at equal amounts prior to PCR as previously done in 16S rRNA gene surveys of cyanobacteria in benthic microbial mats [15–17]. Present-day samples were also extracted in duplicate and pooled to overcome patchy distribution. All DNA extractions were carried out using the MoBio Biofilm DNA kit (Carlsbad, CA, USA) according to the manufacturer's instructions.

Cyanobacterial 16S rRNA genes were amplified using Platinum High Fidelity Taq Polymerase (Invitrogen) in triplicate using cyanobacterial specific primers 16S378F and 16S781R modified from Taton *et al.* [18]. These primers provide a broad coverage across the phylum cyanobacteria [18]. PCR products were pooled per sample and purified using Qiagen gel-purification (Qiagen, Hilden, Germany) according to the manufacturer's instructions, and quantified in duplicate by Qubit. Approximately 450 bp long reads were generated by Junior 454-pyrosequencing (Roche). For detailed methods, see electronic supplementary material and methods.

(c) Sequencing and statistical analysis

The 454 sequencing data were analysed using QIIME v. 1.8.0 [16]. Split library.py was used to demultiplex the samples, apply Q25 quality control, and remove all sequences less than

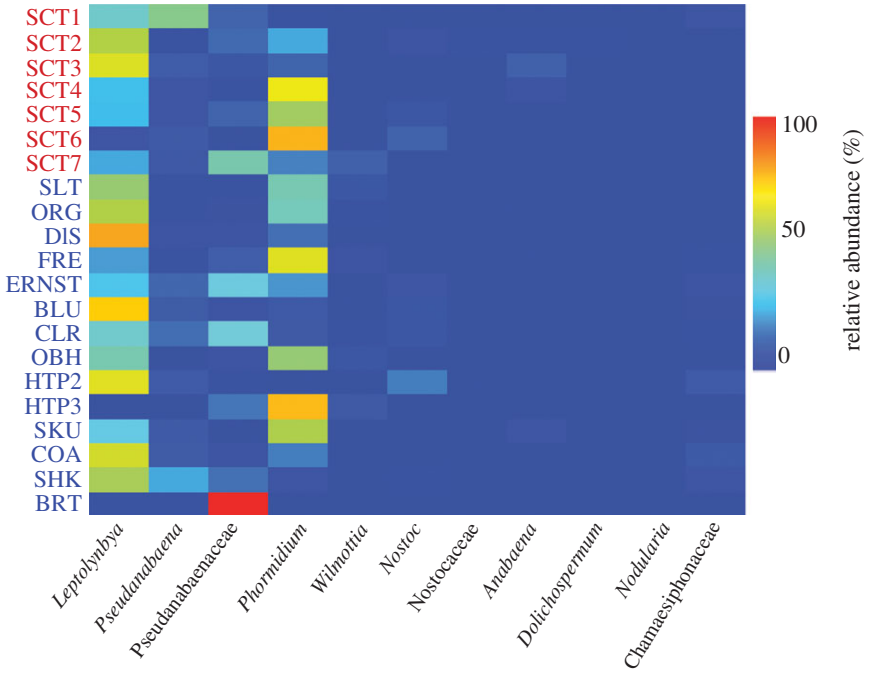

Figure 2. Comparison of relative composition (%) of cyanobacteria genera or lowest assigned taxonomic rank in cyanobacterial mat communities collected as part of Scott's Discovery Expedition in 1903 (red coloured names) and 14 modern samples (blue coloured names) collected in 1911 and 1912 on Ross Island and the McMurdo Ice Shelf, Antarctica.

300 bp long, forward and reverse primers as well as sequences with homopolymers of more than 6 bp. Sequences from the three runs were combined and operational taxonomic units (OTUs) generated using the standard operation protocol for 454 data sequencing by QIIME using 99% sequencing [19].

Chao species richness using 9 999 bootstraps was calculated in PAST [20]. Cyanobacterial communities based on presence/absence and 4th root transformed abundance data were analysed using non-metric multidimensional scaling (2D NMDS) based on Bray–Curtis similarities and results were plotted in two dimensions. ANOSIM was used to test if modern and Scott's Discovery samples are significantly different using PAST [20]. A phylogenetic tree was constructed using maximum likelihood with RAXMLHPC2 on TG [21] as described by Jungblut *et al.* [15].

3. Results

We used cyanobacteria-specific 16S rRNA gene assessment to compare seven cyanobacterial mat specimens from Scott's Discovery Expedition from the McMurdo Ice Shelf and Ross Island with 14 present-day cyanobacteria-based mat communities from the same geographical regions. In total 340 operational taxonomic units (OTUs at 99% similarity), were delineated across all sites and 267 OTUs and 312 OTUs were detected in the historic and modern samples, respectively (electronic supplementary material, tables S1 and S2). The cyanobacterial communities in modern and historic samples were comprised of 16S rRNA gene sequences that grouped within *Leptolynbya*, *Pseudanabaena*, Pseudanabaenaceae, *Phormidium*, Nostocaceae, *Nostoc*, *Nodularia*, *Anabaena*, *Dolichospermum*, and Chamaesiphonaceae (figure 2) based on Greengenes assignment in QIIME. The 10 most abundant 16S rRNA genotypes at 99% OTU-level made up at least 63% of the total diversity in all samples but one (electronic supplementary material, figure S2). They had highest similarity (%) to *Leptolynbya antarctica*, *Phormidium autumnale*, *Phormidium pseudopriestleyi*, and species of *Phormidesmis*, *Pseudophormidium Microcoleus*, and *Pseudanabena* based on BLAST similarity match to GenBank (electronic supplementary material, table S3). In total 29 OTUs with 1.1% relative abundance or less were present only in Discovery microbial mats, while 72 were found only in the modern samples. Modern-only OTUs were present at up to 26.36% relative abundance, although the majority had less than 2.5% relative abundance. The phylogenetic analysis showed that all of the OTUs found in modern but not historic samples formed clades with environmental sequences or cyanobacterial isolates from the Antarctic (electronic supplementary material, figure S3).

Comparisons of community composition, based on resemblance matrices from presence/absence and 4th root relative abundance data, showed that for both historic and modern samples, samples from Ross Island and the McMurdo Ice Shelf tended to cluster together (figure 3). There were significant differences between historic and modern samples when tested by one-way ANOSIM using presence/absence ($p = 0.0386$, $R = 0.1917$) and relative abundance data ($p = 0.0406$, $R = 0.1917$).

SIMPER analysis was performed to determine the contribution of 16S rRNA genotypes to the dissimilarity of the historic and modern communities. One genotype present in the modern samples only was identified to have a contribution of 1.11%, all other genotypes found only in the modern samples contributed less than 0.4% of the difference (electronic supplementary material, table S3).

4. Discussion

With climatic-driven environmental change increasingly evident in continental Antarctica [5], an understanding of the scale of historic community dynamics is essential to predicting the extent to which future environmental changes can be expected to cascade to shifts in diversity, community structure, and ecosystem processes. This is especially true

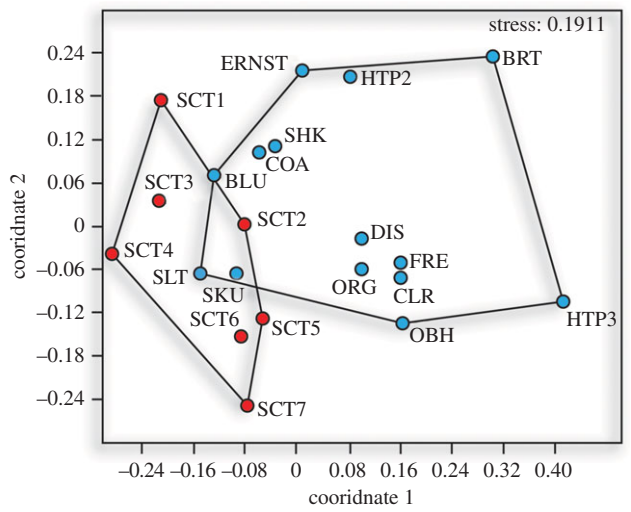

Figure 3. Non-metric dimensional scaling plots (2D) of 16S rRNA gene cyanobacteria mat communities collected as part of Scott's Discovery Expedition in 1903 (red circles) and 14 modern samples collected in 2011 and 2012 on Ross Island and the McMurdo Ice Shelf (blue circles), Antarctica, with convex hulls indicating smallest polygon containing all samples from the Scott and modern samples respectively.

for keystone organisms such as cyanobacteria which form essential habitat and drive food webs and carbon cycling in polar freshwater systems. However, our understanding of microbial diversity and ecology on a genotypic level in Polar Regions is based on a few decades of research of biogeography and the relationship between biodiversity and environmental gradients based non near-synoptic sampling. Our study represents the first comparison of cyanobacteria in Antarctic freshwater ecosystems across the twentieth century by comparing the cyanobacterial 16S rRNA gene communities from microbial mats collected during Captain R.F. Scott's Discovery Expedition in 1902–1903 with recent benthic microbial mat assemblages from 2011 to 2012. The observation that robust DNA-based analyses can be made of such archived material confirms their value as a resource for understanding the dynamics of Antarctic cyanobacterial communities along temporal scales.

Our data showed that similar cyanobacteria dominated the communities with some changes from historic pond samples to modern samples. Some degree of cyanobacterial 16S rRNA genotype turnover is indicated by the presence of genotypes in only the historic (i.e. loss of taxa) or the modern samples (gain of taxa). However, our analysis showed that shifts in relative abundance rather than presence-absence explained most of the changes in community assembly. NMDS analyses suggest that relative-abundance changes are generally small, but the tendency of modern and historic samples to cluster in distinct groups suggest that changes may have been coherent across ponds. This coherent behaviour implies a response to an over-arching environmental variable, rather than pond-specific changes, resulting in a gradual selective shift [22]. If this is a response to the relatively small environmental change that has occurred in the last 100 years, community response to changes in growth conditions may be expected to increase under accelerated climatic-driven environmental change scenarios for continental Antarctic.

The absence of a substantial drift or turnover of dominant species over 100 years is surprising, since microbial communities are often described as tending to change over time [22–24]. Furthermore, turnover of species has been postulated as being favoured by intense disturbance and variable growth conditions, and regular freezing to low, sub-zero temperatures followed by a period of growth under growth conditions that vary from year to year [25] might be expected to favour change. Overlain on annual stress and year-on-year variability of growth conditions have been long-term trends such as increasing UV irradiance in the later part of the twentieth century [26]. Rather than the high stress environment promoting turnover, it may be that the high stress environment has selected, over time, a metapopulation of organisms that tolerate winter freezing, short cold summers as well as salinity and nutrient variability [11,27]. The absolute requirement of such adaptation to allow organisms to persist in this habitat may provide a degree of community resistance and resilience to future climate-driven environmental change in Antarctic terrestrial aquatic ecosystems—so long as extreme stress events continue to dictate composition. In addition, estimates of the rate of cyanobacterial mat community biomass development in similar polar regimes suggest that maximum biomass take many years to be attained, allowing composition to integrate many years of growth conditions which may further add to limited species dynamics [28].

In addition to effects of environmental change over time, the risk of invasive species to Antarctic biodiversity has been raised during the past 100 years with increased human activity. Biosecurity is a recognized key issue in environmental management in Antarctica [14]. Cyanobacteria are likely invaders; they are inconspicuous, able to tolerate prolonged desiccation and easily spread by wind once introduced. Indeed, previous work has detected the cyanobacterial genus *Cylindrospermum* in this part of Antarctica, which is absent from morphology-based inventories of species from 100 years ago, and is suggested as a recent introduction [29]. However, where we found 'new' genotypes in the modern samples, these had highest similarity to Antarctic environmental sequences and strains, including *Leptolynbya antarctica*, *Phormidium*, and *Pseudanabaena* [11,22]. In addition, these are all filamentous, mat-forming oscillatorian cyanobacteria, similar to the dominant cyanobacteria in all mats described here, and would likely have similar functionalities [11,22]. Therefore, it seems likely that turnover that has occurred in cyanobacterial assemblages will have had limited effect on the functional attributes of the mat communities [23,24]. We suggest that, despite a human presence, cyanobacterial composition in our study locations has not experienced a detectable level of shift in composition due to cyanobacteria from outside of the continent.

This apparent lack of exotic taxa may be due not to an absence of propagules, but perhaps to a failure of potential invaders to establish and thrive due to more stringent environmental conditions in Antarctic ecosystems. There might also be stochastic limitations to colonization of non-native taxa due to already existing high biomass benthic cyanobacterial mat stocks and lack of niche opportunities [30], again suggesting that the microbial mats are naturally resistant to invasion. The absence of distinct alien taxa in our study is no guarantee, that they have not or cannot be introduced. It is therefore essential that current biosecurity protocols designed to limit the introduction of biological material due to human activities remain for Antarctica. There is also the risks of other, more invasive biota reaching Antarctica that allow new trophic levels to colonize these ponds that could disrupt their current biota and food webs, such as macroscopic invertebrates.

Potential problems with our analysis include the storage conditions of the herbarium samples and the limited ability to assign taxonomic units based on the short reads obtained from a single gene. It is not known if different cyanobacteria vary in their susceptibility to degradation during long-term storage at room temperature, and some of the rare taxa absent from the old samples might have been lost due to degradation of the DNA. It can also not be excluded that the lower richness in the historic samples might be due to the long-term storage of the samples, and more in-depth sequencing may have revealed a higher degree of community turnover. Future phylogenetic interference using multiple gene loci would provide a better taxonomic resolution, and in-depth metagenomic sequencing analysis could assist in detecting rare genotypes for future comparisons of modern and historic cyanobacteria in Antarctica.

5. Conclusion

What are the implications for the next 100 years when more substantial climate change is expected to occur in Antarctica [3]? Our data allow us to conclude that environmental change to date has been absorbed with no substantive change in cyanobacterial composition, and that there has been no obvious impact on cyanobacterial 16S rRNA genotype composition from invasive species associated with human presence. We suggest that this ability to accommodate variability in summer growth conditions will allow the composition of cyanobacterial assemblages to retain a considerable level of stability over time, such that existing communities are likely to be resistant to a moderate degree of climate change, as long as the overwhelming stress of winter freezing and short summer growth period continues. However, the risks of other, more invasive cyanobacterial taxa and other biota reaching Antarctica remains, as does the possibility that synergy between climate change and human activity may allow new trophic levels to colonize these ponds and disrupt their current biota and food webs. The importance of continuing biosecurity measures that not only cover animals and plant propagules but also microbial species cannot be overstressed. The work also highlights the potential of molecular analysis of historic microbial specimen collections for Antarctic microbial biodiversity and underutilized resource for temporal assessments of microbial biodiversity and ecology.

Data accessibility. This article has no additional data.

Authors' contributions. A.D.J. conceived the study, A.D.J. and I.H. collected the field data, A.D.J. performed molecular lab and sequence analysis, and both participated in the design of the study and drafted the manuscript. All authors gave final approval for publication.

Competing interests. The authors declare no conflict of interest.

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