Airborne microbial transport limitation to isolated Antarctic soil habitats

Stephen D.J. Archer[1,2], Kevin C. Lee[2], Tancredi Caruso[3], Teruya Maki[4], Charles K. Lee[5], S Craig Cary[5], Don A. Cowan[6], Fernando T. Maestre[7], Stephen B. Pointing[1]

[1] *Yale-NUS College, National University of Singapore, Singapore 138527*

[2] *Institute for Applied Ecology New Zealand, Auckland University of Technology, Auckland 1142, New Zealand*

[3] *School of Biological Sciences and Global Institute for Food Security, Queen's University Belfast, Belfast BT9 7BL, Northern Ireland, UK*

[4] *Department of Chemical Engineering, Kanazawa University, Kanazawa 920-1192, Japan*

[5] *International Centre for Terrestrial Antarctic Research, University of Waikato, Hamilton 3240, New Zealand*

[6] *Centre for Microbial Ecology and Genomics, University of Pretoria, Pretoria 0002, South Africa*

[7] *Departamento de Biologia y Geología, Universidad Rey Juan Carlos, Móstoles, España*

Abstract

Dispersal is a critical yet poorly understood factor underlying macroecological patterns in microbial communities. Airborne microbial transport is assumed to occupy a central role in determining dispersal outcomes and extra-range dispersal has important implications for predicting ecosystem resilience and response to environmental change. One of the most pertinent biomes in this regard is Antarctica, given its geographic isolation and vulnerability to climate change and human disturbance. Here we report the first characterisation of microbial diversity in near-ground and high-altitude air above a typical Antarctic Dry Valley as well as that of underlying soil microbial communities. We found that persistent airborne inputs were unable to fully explain local soil community assembly. Comparison with airborne microbial diversity from non-polar sources suggests that strong selection occurs during atmospheric transport, resulting in regionally isolated airborne inputs and highly specialized soil communities where fungi displayed greater isolation than bacteria from non-polar sources. Overall, microbial communities from this isolated Antarctic ecosystem displayed limited connectivity to the non-polar microbial pool, and alternative sources of recruitment are necessary to explain extant soil diversity. Our findings provide critical insights into the role of airborne transport limitation in determining microbial biogeographical patterns.

Introduction

Dispersal is a key determinant of biogeographic and macroecological patterns in all microbial communities and yet is poorly understood [1]. Airborne microbial transport is assumed to occupy a central role in determining dispersal outcomes [2,3] and extra-range dispersal also has important implications for predicting ecosystem resilience and response to environmental change [4]. Airborne microbial transport on fine particulate matter in air has typically been regarded as ubiquitous due to the small size and survivability of cells [5–7] and so large scale patterns in microbial diversity are viewed as developing largely due to deterministic niche-driven processes [8,9]. Much of the existing evidence for airborne (also known as aeolian) transport of microorganisms, typically viewed as a neutral process [10], is inferred from extant communities at source and sink locations; e.g. [11–13]. Furthermore, direct measurements of airborne microbial taxa have largely focused on indoor or outdoor built environments, e.g. [14–16],rather than across natural environmental gradients, thus limiting our understanding of how microbial transport drives biogeographic patterns. The extent to which the aerosphere is a habitat as opposed to simply a medium for microbial transport is also unresolved and as a result the influence of airborne transport on observed patterns in microbial biogeography has been subject to much speculation supported with little tangible evidence [17–19].

Antarctica is a focus for microbial ecology research due to its geographic isolation, lack of trophic complexity and human influence [20] and vulnerability of endemic biodiversity to climate change [21]. The extent to which airborne immigration may influence isolated Antarctic terrestrial microbial communities, however, is an enduring enigma in microbial ecology [22–25]. Highly specialised microbial communities display strong allopatric signals [26–29], yet microbial dispersal is conventionally viewed

as occurring across inter-continental distances [22,30]. Establishing the extent to which Antarctic communities are connected to the global system via airborne dispersal also has key relevance to predicting potential responses of polar ecosystems to environmental change. Isolated ice-free regions such as the McMurdo Dry Valleys are devoid of vascular plants and dominated by highly specialised soil microbial communities [31] that display adaptations to the extreme environmental conditions [32]. Some taxa, notably cyanobacteria, have been shown to display phylogenetic endemism in Antarctica at the level of rRNA gene-defined diversity [26–29]. Also, lichenised fungi displayed patterns in diversity that suggest they radiated from local refugia rather than exogenous sources outside Antarctica [33]. A global theoretical model for atmospheric aerosols estimated that the rate of airborne microbial exchange to Antarctica may be extremely low, with 90% of aerosols expected to be of local origin [34]. In contrast, empirical studies have claimed circum-polar distribution for some cyanobacteria, chlorophyte algae taxa, and fungi [22,30,35]. Antarctica therefore presents a paradox in microbial biogeography with regard to microbial dispersal.

Evidence for airborne microorganisms in Antarctica is scarce: two early studies on the Antarctic Peninsula (the west continental edge of Antarctica proximal to South America) identified tentative evidence for airborne bacteria from individual samples without characterisation beyond a low diversity of common taxa and human- and penguin- associated bacteria [36,37]. We recently observed that in the relatively isolated ice-free McMurdo Dry Valleys soil region of East Antarctica airborne bacteria were recoverable from bulk air and may harbour far greater diversity than previously envisaged [38]. These studies were generally inconclusive as to the origin and relationship to local habitats due to methodological constraints (Online Supplementary Material). Here we report diversity of airborne and soil microbial communities in a typical

Antarctic Dry Valley and test the null hypotheses that air and soil communities are a random sample of the regional and global pools. We targeted Bacteria and Fungi since these domains are the most abundant microorganisms in the McMurdo Dry Valleys [31]. We acquired massive bulk-air samples and estimated microbial diversity in near-ground air and underlying soil for low and high elevation sites, as well as polar air above the boundary layer for surface interactions and non-polar sources.

Results and Discussion

The incoming air mass to our study site in the McMurdo Dry Valleys largely transited above the Antarctic Plateau during the maximum predicted residence time for bacteria and fungi in air [34] , while the most distant air mass had a non-polar origin above the coastal shelf of New Zealand (Fig. 1a). Transport was exclusively from the Polar Plateau and across the Trans-Antarctic Mountains during the average residence time for microorganisms in air (Fig. 1a). We thus envisage that severe selection pressure should occur during airborne transit in an air mass with freezing temperatures and high UV exposure at mean altitudes of 2769m (3 day transit) and 3034m (15 day transit).

In general terms, we found that alpha diversity metrics for air and high altitude soil samples were distinct from those observed in valley soils (Fig. 1b,c). Taxa richness was more variable in valley soils than air and high altitude soil, highlighting the more heterogenous nature of soil as a habitat compared with bulk phase air or high altitude soil where conditions are generally unfavourable to colonisation. The elevated mineral soil sites may therefore be representative of near-term airborne deposition to this system. Bacterial taxa richness was similar among all samples although slightly higher in air and elevated soil (Fig. 1b). Conversely, the richness of fungal taxa was highest in

valley soils, and lower in air and elevated soils (Fig. 1c). Soils also displayed greater evenness and lower richness values than air samples, tentatively indicated that airborne fungi are under strong selective pressure. Ordination of weighted UniFrac distances for bacteria and fungi supported these trends in alpha diversity. Valley soil bacterial communities separated clearly from air and elevated soil bacterial diversity (Fig. 1b). A similar although less pronounced pattern was observed for fungi (Fig. 1c).

Taxonomic assignment of bacteria and fungi revealed further complexity. Airborne phylum level diversity was dominated by Proteobacteria, Bacteroidetes and Firmicutes (Fig. 1d, Online Supplementary Information Fig. S2). Phyla with high relative abundance comprised spore-formers and taxa with known UV and/or desiccation tolerant traits viewed as advantageous during atmospheric transport [17] as well as survival in Antarctic soil [32]. The airborne bacterial samples supported relatively high levels of taxa associated with marine influence [7] suggesting recruitment during transit over the Southern Ocean (Online Supplementary Information, Fig. S2). Soil communities supported greater abundance of Actinobacteria and other arid soil taxa [8]. Near-ground air supported 3-5 fold more habitat-specific taxa than high-altitude air and samples from this habitat were most similar to their underlying soil communities. Valley soils supported 56.4% soil-specific taxa compared with only 15.8% in high altitude soils. Valley soils shared very few taxa with the total air sample pool (4.5%) whilst different air habitats (valley, elevated and high-altitude) shared approximately half the taxa encountered in each habitat. The most abundant fungal taxa in air were basidiomycetous yeasts (Fig. 1e, Online Supplementary Information Fig. S2) whereas soils were dominated by unclassified fungi also including yeasts. The yeasts are thought to be well-adapted to Antarctic soil habitats [39]. Ascomycetes were also commonly encountered but Chytrids were encountered only in valley soil and air. Valley soil

supported 48.3% habitat-specific taxa while elevated sites and high-altitude air showed the lowest number of habitat-specific taxa (4.9-8.7%). The different air habitats shared approximately half the taxa encountered in each habitat. Fungi have well-established adaptations to conditions anticipated during atmospheric transport due to the production of resistant spores and UV-protective compounds. Local recruitment may, however, be limited to asexual states since teleomorph fruiting structures are not known from Antarctic fungi [40].

Since we achieved near-asymptote status in diversity estimations for all samples (Online Supplementary Information, Supplementary Methods) we further interrogated the phylogenetic diversity of air and soil by generating heatmaps of distribution by habitat for the 1,000 most abundant taxa. This analysis captured 91% of total bacterial and 96% of total fungal diversity in the libraries (Fig. 2a,b). We also incorporated diversity data from air originating at the nearest non-polar land mass into this analysis. A striking pattern emerged, where soil bacterial and fungal assemblages in the McMurdo Dry Valleys were only partially recruited from local air taxa and could not be further explained by airborne recruitment from exogenously sourced aerosols. These findings support the notion of a system operating in stark contrast with the long-held assumption that microbial dispersal is ubiquitous and deterministic niche processes are the primary driver of community assembly in terrestrial surfaces [1,10].

We therefore further interrogated this association using Ecological Network Analysis (Fig. 2c). Overall, non-polar air displayed least connectivity to all other Antarctic habitats as observed by the weak associations and greater Bray-Curtis distances (Fig. 2c). Bacterial communities clustered by habitat type, a result which is likely to be indicative of selection pressures due to local environmental filtering, which could combine a mixture of biotic and abiotic factors. Conversely, Fungal communities

associated by geographic distance and were thus more likely to be influenced by dispersal limitation. No significant distance-decay relationships were observed for airborne or soil communities between valley and elevated sites (air bacteria $R^2 = 0.009$, soil bacteria $R^2 = 0.006$, air fungi $R^2 = 0.016$, soil fungi $R^2 = 0.024$), suggesting that dispersal within the Dry Valleys may be limited. We suggest that this may reflect the associated steep environmental gradients present in this region. These findings provide the first empirical support to theoretical models of emission and transport for biological particles in the atmosphere that predict very low exchange between Antarctic and non-polar air as well as relatively reduced residence time in air for fungi compared to bacteria due to allometric considerations [34].

We further interrogated the potential strength of this association by performing a Nestedness Analysis and Net Relatedness Index analysis for bacteria and fungi to reveal the extent to which taxonomic and phylogenetic structuring reflected the likelihood of exogenous recruitment (Fig. 3). Strong patterns of nestedness are the classical expectation for a network of highly isolated sites (e.g., distant islands) where passive sampling from regional pools and ordered sequences of extinctions play the major role in structuring local communities [41,42]. Strong or perfect nestedness means that species-poor local communities are a proper subset of richer communities. We used one of the most widely applied and recommended metric of nestedness (NODF: [42–44]) and applied it to the occurrence of the first 1000 most abundant OTUs, both for Bacteria and Fungi. The employed metric NODF (range from 0, no nestedness, to 100, perfect nestedness) comprises both a compositional effect (i.e., species poor communities consist of species that are a subset of richer communities; NODFc) and an incidence effect (i.e., less frequent species always occur in site with widespread species; NODFr). Null models of these metrics showed that communities of both Bacteria and

Fungi were significantly anti-nested, with NODF metrics usually around 30 or below. This general result implies that passive sampling from the regional pool alone is not sufficient to explain the structure of local Antarctic communities. Both Fungi and Prokaryotes, however, were significantly nested for taxanomic composition under the hypothesis that nestedness can be maximised by ordering sites from the most connected to the least connected to a global species pool. This suggests that species poor assemblages of the least connected sites are a proper subset of richer, more connected, sites. Fungi were much more nested (NODFc = 62) than Prokaryotes (NODFc = 18), suggesting a potential major role of dispersal limitation for this group.

The Net Relatedness Index (NRI) added phylogenetic support to the findings of our Network and Nestedness Analysis. NRI analyses demonstrated that local Antarctic communities were not a random sample of the species pool. Antarctic samples of bacteria displayed greater and highly significant phylogenetic clustering than the non-polar samples, which were almost randomly structured and in some case overdispersed (Fig. 4). Although the pattern itself cannot prove any specific process, the results clearly demonstrate that Antarctic bacterial communities, both in soil and air, must have been selected non-randomly, which is consistent with both the taxonomic and phylogenetic composition of our air and soil communities. This result is congruent with other studies on soils in the Dry Valleys region [31,45–47]. Fungi, too, were always significantly clustered, but bacterial communities were always much more clustered than fungi at any given airborne or soil location. The fungal data should, however, be interpreted with care given current issues with phylogenetic reconstruction based on ITS and despite our efforts to correct for this (Online Supplementary Information: Supplementary Methods). Nonetheless even a cautious interpretation of the data suggests a limited extent of input from fungal taxa not present locally, presumably due to long range transport. This

interpretation concurs with other lines of evidence presented here as well as with studies on fungal dispersal from other biomes [48].

Contrary to the view that "everything is everywhere" in terms of airborne microbial transport, our data indicate that the aerosphere is a strongly selective habitat that limits dispersal, although the extent may vary between taxonomic groups and spatial scales. We conclude that inter-continental microbial connectivity to the McMurdo Dry Valleys of East Antarctica is limited, and this supports the hypothesis that the Hadley Cell circulation acts as a dispersal barrier to the poles [17] even during the austral summer when the Polar Vortex is annually at its weakest [49]. The Antarctic continent supports other smaller ice-free soil regions and whilst we are unable to directly extrapolate our data to these, it is reasonable to expect similar patterns given what is known of air circulation to the continent; that is, that other Antarctic ice-free areas may also be somewhat decoupled from global microbial reservoirs. An exception may be the peninsula in West Antarctica, due to its proximity to the South American continent. Comparisons of our soil biodiversity estimates with those for other Dry Valleys locations suggest there is a common core diversity throughout the Antarctic Dry Valleys [39,45–47,50], and that our data are broadly applicable to this region. The low level of airborne immigration from exogenous sources may represent an inherently low flux for Antarctica, despite supplementation from pulsed inputs of diversity from stochastic events, and this may help explain the unique microbial composition of Antarctic soil compared to others globally [51].

Overall our multiple triangulated lines of evidence refute the null hypothesis that local air and soil microorganisms are a random sample of phylogenetic diversity in the regional/global pools. Sources of recruitment other than persistent airborne transport are therefore necessary to fully explain extant Antarctic soil microbial diversity. One

potential explanation is stochastic storm events where particulate matter supporting biological propagules is thought to be transported on local scales within the Dry Valleys [52], although we did not encounter any such events during our sampling expeditions. A further source may be local dispersal from geothermal refugia since they have been demonstrated as important reservoirs for radiative dispersal of animal, plant and lichen taxa [21]. The periodicity from which dispersal from such reservoirs occurs is unknown. An additional reservoir may be the moisture-sufficient soil around lakes where microbial mats are known to persist over inter-annual periods [53]. Local refugia may be important in facilitating resilience at the landscape scale where severe extinction pressure within local scales occurs, due to stochasticity and steep environmental gradients for abiotic variables [54].

Challenges remain in deciphering the relationship of diversity patterns to biomass and ecosystem function [32,55], but the revelation that airborne connectivity is largely localised rather than being an inter-continental scale process emphasises the conservation value of the McMurdo Dry Valleys as a unique ecosystem. This is particularly pertinent in light of a predicted increase in stochasticity for atmospheric air circulation as a result of climate change [56], since increased flux of invasive taxa may arise.

Methods

Air mass at near-surface (1.5m above ground) and underlying ultra-oligotrophic soil was sampled from 11 to 23 January 2017 at eight representative valley and elevated locations throughout the Wright Valley, McMurdo Dry Valleys, Antarctica (77.518633 S, 161.768783 E, Supplementary Information Fig. S1). Air mass above the boundary layer for surface influence was achieved by mounting the apparatus in a

helicopter with an external sampling port (flightpath: 2,000m AMSL, 77.440836 S, 162.657553 E to 77.524583 S, 161.690917 E). Air sampling was also conducted at the only significant non-polar terrestrial landmass (New Zealand) on the projected back trajectory for incoming air mass. High volume liquid impinger pumps were used to collect airborne microorganisms directly into RNA*later* nucleic acid preservation solution. Extensive use of controls and apparatus sterilisation ensured high fidelity of the sampling for the ultra-low biomass habitats. Overall, biotic data was retrieved for 30 massive bulk-phase air samples with a total sampled volume of 2,160,000 L and massive air volumes were collected for each discreet air sample (72,000 L). A detailed sampling rationale and methodology is described in the Supplementary Methods (Online Supplementary Information).

Diversity assessments for bacteria and fungi, the two most abundant microbial groups in the Dry Valleys, were made using Illumina MiSeq sequencing of rRNA loci. A total of 3636 bacterial amplicon sequence variants (ASVs) and 5525 fungal operational taxonomic units (OTUs) were identified (Online Supplementary Information: Supplementary Methods). Bacterial 16S rRNA-defined ASVs were delineated using the DADA2 method for exact sample sequence inference [57] and fungal ITS-defined OTUs using 97% sequence similarity clustering approach [58] (Online Supplementary Information: Supplementary Methods). We achieved near-asymptote in diversity estimation for all samples (Online Supplementary Information: Supplementary Methods). All sequence data generated by this study has been submitted to the EMBL European Nucleotide Archive (ENL) under BioProject PRJEB27416 with accession numbers ERS3573837 to ERS3573946. All diversity metrics and alpha/beta diversity estimates were made using R [59] (all packages employed listed in Online Supplementary Information, Supplementary Methods). We employed Network Analysis, Nestedness

Analysis and Net Relatedness Index to test the null hypothesis that local air and soil microorganisms are a random sample of phylogenetic diversity in the regional/global pools (Online Supplementary Information: Supplementary Methods).

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Author contributions

S.D.J.A. and S.B.P. conceived the study; S.D.J.A and C.K.L. conducted fieldwork; T.M. developed and validated the helicopter sampling method; S.D.J.A. performed laboratory experiments; S.D.J.A., K.C.L., T.C., and S.B.P. performed data analysis and interpretation; D.A.C., F.M. and S.B.P. critically assessed and interpreted the findings; S.B.P. wrote the manuscript with input from all authors.

Materials & Correspondence

Correspondence and requests for materials should be addressed to S.B.P. Email: stephen.pointing@yale-nus.edu.sg.

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Display Items (3 Figures)

Fig. 1. Antarctic air and soil habitats support distinct bacterial and fungal diversity. a) Average minimum and maximum estimated residence time for microorganisms in air based on HYSPLIT back trajectory analyses. Back trajectories indicate distance travelled for sampled air mass at 3 d (598 - 2581 km distance, average altitude of 2769 m, maximum altitude of 5174 m A.M.S.L.) and 15 d (4673 - 11216 km distance average altitude 3034m, maximum altitude 6886 km)**. b) and c)** Alpha diversity estimates (Chao1 richness and Pielou's relative evenness) and visualisation of community dissimilarity using Principal Co-ordinate Analysis of weighted UniFrac distance by habitat for **b)** Bacteria and **c)** Fungi. Boxplot whiskers represent 1.5 times the interquartile range from the first to the third quartiles or the maximum/minimum data point within the range. **d) and e)** Distribution and relative abundance of **d)** Bacteria and **e)** Fungi in Antarctic air and soil. Each stack bar represents data from three pooled replicates for each substrate location. Diversity is shown at phylum level since this is the highest taxonomic rank at which between-substrate differences are noticeable. Venn diagrams show ASVs and OTUs count and percentage occurrence within and between each habitat. The high altitude samples, i.e., those without underlying soil, do not have corresponding soil samples. Sampling locations: valley (soil and 1.5m above ground), elevated (soil and 1.5m above ground at higher altitude locations at Bull Pass and valley ridges), 2000m (helicopter samples). Interactive graphics identifying taxonomic composition to lower taxonomic ranks within each sample are presented in the Online Supplementary Information (Fig. S2). Comparison with non-polar samples is given in the Online Supplementary Information Fig. S2.

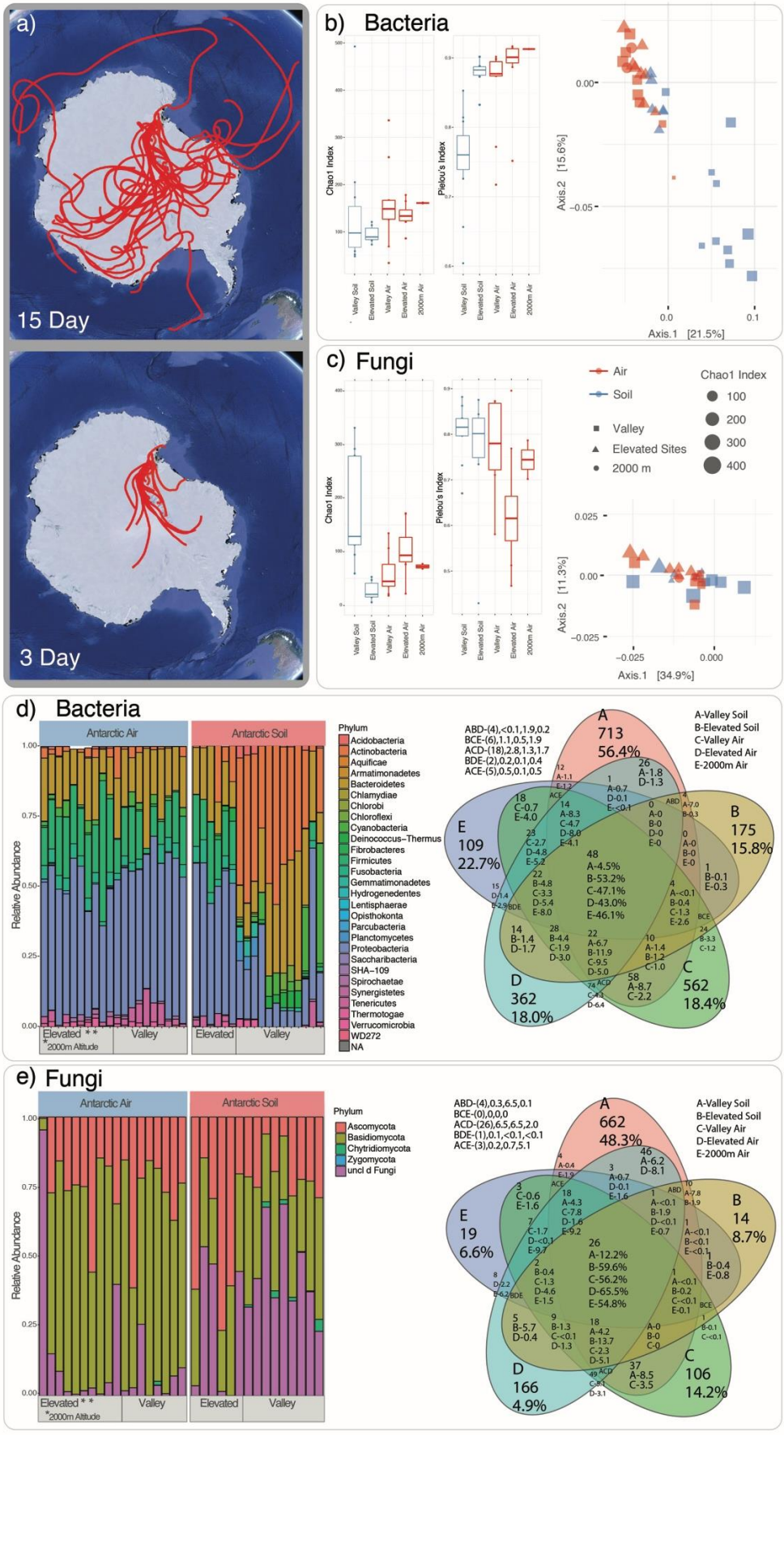

a)
15 Day
3 Day
b) Bacteria
Chao1 Index
Pielou's Index
Valley Soil
Elevated Soil
Valley Air
Elevated Air
2000m Air
Axis.2 [15.6%]
Axis.1 [21.5%]
c) Fungi
Air
Soil
Valley
Elevated Sites
2000 m
Chao1 Index
100
200
300
400
Axis.2 [11.3%]
Axis.1 [34.9%]
d) Bacteria
Antarctic Air
Antarctic Soil
Relative Abundance
Elevated * *
*2000m Altitude
Valley
Phylum
Acidobacteria
Actinobacteria
Aquificae
Armatimonadetes
Bacteroidetes
Chlamydiae
Chlorobi
Chloroflexi
Cyanobacteria
Deinococcus−Thermus
Fibrobacteres
Firmicutes
Fusobacteria
Gemmatimonadetes
Hydrogenedentes
Lentisphaerae
Opisthokonta
Parcubacteria
Planctomycetes
Proteobacteria
Saccharibacteria
SHA−109
Spirochaetae
Synergistetes
Tenericutes
Thermotogae
Verrucomicrobia
WD272
NA
A-Valley Soil
B-Elevated Soil
C-Valley Air
D-Elevated Air
E-2000m Air
A 713 56.4%
B 175 15.8%
C 562 18.4%
D 362 18.0%
E 109 22.7%
e) Fungi
Ascomycota
Basidiomycota
Chytridiomycota
Zygomycota
uncl d Fungi
A 662 48.3%
B 14 8.7%
C 106 14.2%
D 166 4.9%
E 19 6.6%

Fig. 2. Comparison of bacterial and fungal diversity from Antarctic and non-polar sources. a) Distribution and relative abundance for the 1,000 most abundant bacterial ASVs and fungal OTUs. **b)** Rarefaction curves are shown for Bacteria and Fungi for each Antarctic habitat to illustrate sampling depth to near-asymptote. **c)** Co-occurrence associations derived from Ecological Network Analysis. We enforced maximum Bray-Curtis distance of 0.2 for Bacteria and 0.4 for Fungi to establish connection between nodes (representing communities). The nodes were positioned using the Fruchterman-Reingold method. Sampling locations: valley (soil and 1.5m above ground), elevated (soil and 1.5m above ground at higher altitude locations at Bull Pass and valley ridges), 2000m (helicopter samples) and New Zealand (non-polar).

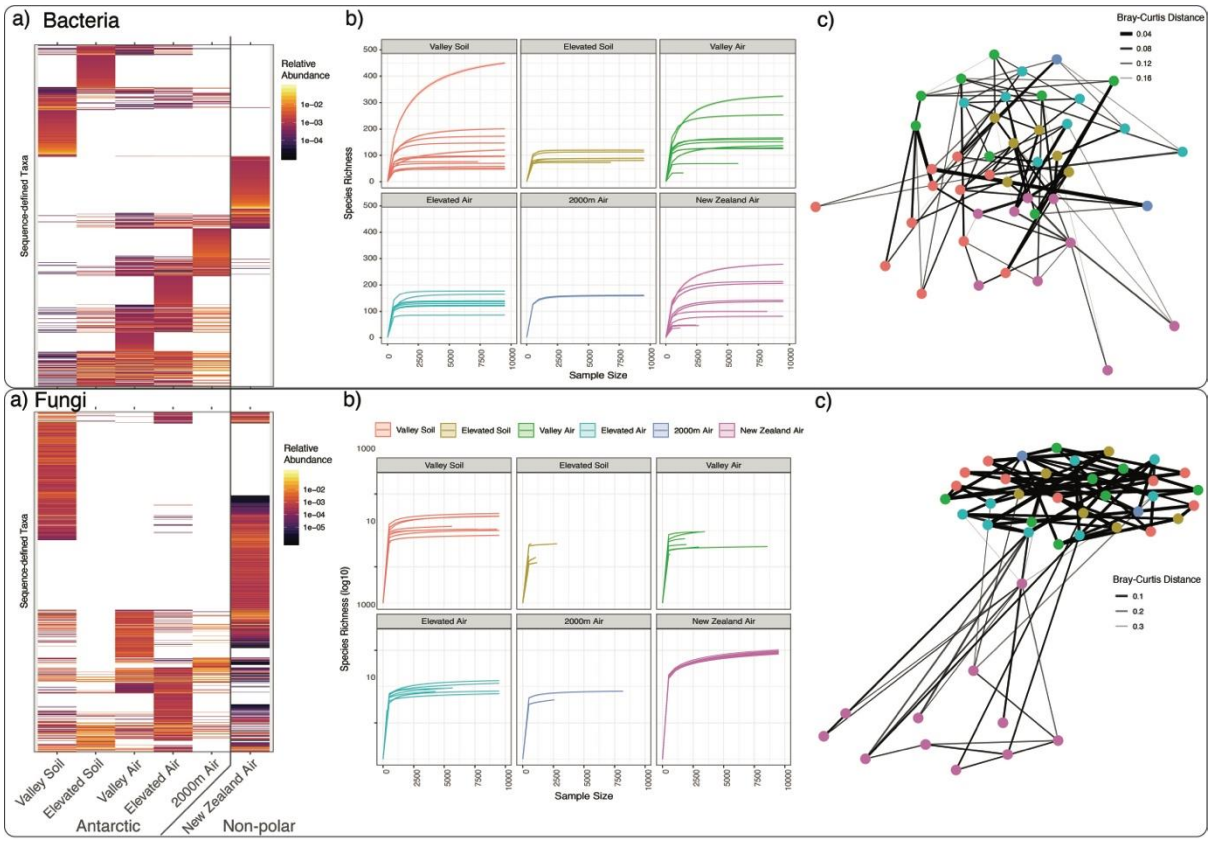
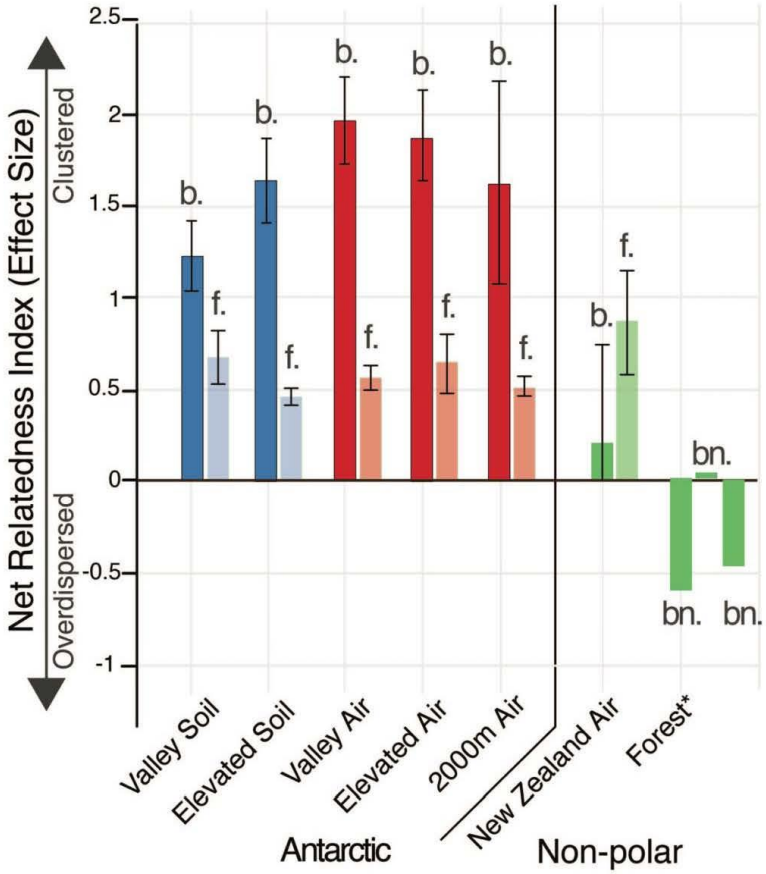

a) Bacteria
Relative Abundance
1e−02
1e−03
1e−04
Sequence-defined Taxa
b)
Valley Soil
Elevated Soil
Valley Air
Elevated Air
2000m Air
New Zealand Air
Species Richness
Sample Size
c)
Bray-Curtis Distance
0.04
0.08
0.12
0.16
a) Fungi
Relative Abundance
1e−02
1e−03
1e−04
1e−05
Sequence-defined Taxa
Valley Soil
Elevated Soil
Valley Air
Elevated Air
2000m Air
New Zealand Air
Antarctic
Non-polar
b)
Species Richness (log10)
Sample Size
c)
Bray-Curtis Distance
0.1
0.2
0.3

Fig. 3. Phylogenetic structuring of local and global pools for bacterial and fungal diversity. a) Net Relatedness Index analysis of phylogenetic structure within each sample type for Bacteria (b) and Fungi (f). Error bars show the standard error of the mean for all samples in a given substrate type. Values for highly dispersed non-polar bacterial communities associated with forest soil are given for comparison (bn) and indicated by an asterisk [60]. Sampling locations: valley (soil and 1.5m above ground), elevated (soil and 1.5m above ground at higher altitude locations at Bull Pass and valley ridges), 2000m (helicopter samples) and New Zealand (non-polar). **b)** Nestedness estimates made using the NODF model (where 0 = no nestedness, 100 = perfect nestedness). Fungi were more nested (NODFc = 62) than Bacteria (NODFc = 18). Bacteria and Fungi were significantly nested for taxa composition under the hypothesis that nestedness can be maximised by ordering sites from the most connected to the least connected. Least connected sites are demonstrated as a proper subset of richer, more connected sites.

a)



b)

	Connectivity gradient						Soil Selection Gradient					
	NODF		NODFc		NODFr		NODF		NODFc		NODFr	
	Metric	SES	Metric	SES	Metric	SES	Metric	SES	Metric	SES	Metric	SES
Bacteria	33	**-8**	18	**13**	33	**-8**	33	**-8**	29	**-17**	33	**-8**
Fungi	30	**-24**	62	**12**	30	**-24**	30	**-21**	13	**-16**	30	**-21**