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LETTER

Not poles apart: Antarctic soil fungal communities show similarities to those of the distant Arctic

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Abstract

Antarctica's extreme environment and geographical isolation offers a useful platform for testing the relative roles of environmental selection and dispersal barriers influencing fungal communities. The former process should lead to convergence in community composition with other cold environments, such as those in the Arctic. Alternatively, dispersal limitations should minimise similarity between Antarctica and distant northern landmasses. Using high-throughput sequencing, we show that Antarctica shares significantly more fungi with the Arctic, and more fungi display a bipolar distribution, than would be expected in the absence of environmental filtering. In contrast to temperate and tropical regions, there is relatively little endemism, and a strongly bimodal distribution of range sizes. Increasing southerly latitude is associated with lower endemism and communities increasingly dominated by fungi with widespread ranges. These results suggest that micro-organisms with well-developed dispersal capabilities can inhabit opposite poles of the Earth, and dominate extreme environments over specialised local species.

Keywords

Biogeography, dispersal, environmental filtering, polar environments, soil fungi.

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INTRODUCTION

There is increasing evidence that the diversity and composition of soil microbial communities can affect a number of pivotal ecosystem processes, such as decomposition, nutrient cycling, productivity and CO_2 efflux (Vogelsang *et al.* 2006; Maherali & Klironomos 2007; Strickland *et al.* 2009). Therefore, understanding microbial biogeography is essential for predicting how such processes may change in the future. Despite their ubiquity and importance, uncertainties remain over the factors influencing the diversity and biogeography of fungi at the global scale (Hanson *et al.* 2012). Until recently, it was widely believed that the distribution of micro-organisms was largely determined by environmental selection, with most microbes having potentially limitless geographic ranges but being constrained to particular habitats because of the presence of certain environmental conditions. Considerable evidence has now been found to suggest that the distributions of many microbes are in fact limited by dispersal constraints, which may influence the composition of communities to a greater degree than environmental filtering, particularly at larger spatial scales (Taylor *et al.* 2006; Peay *et al.* 2010; Adams *et al.* 2013; Talbot *et al.* 2014). Indeed, a typical working framework is that microbial communities are primarily controlled by dispersal limitation acting at the largest spatial scales, followed by environmental filtering, niche differentiation and competition at increasingly local scales (Mittelbach & Schemske 2015). However, disentangling the relative roles of dispersal limitation and environmental selection can be difficult at the largest spatial scales because increasing distance between sites is usually correlated with increasing environmental dissimilarity.

Recent studies have encompassed sampling over large geographic areas and in-depth molecular analysis of soils to investigate the mechanisms governing fungal community composition, richness and the turnover of species between communities (Talbot *et al.* 2014; Tedersoo *et al.* 2014; Treseder *et al.* 2014; Davison *et al.* 2015). However, such studies have not extended to some of the most isolated and extreme parts of the planet, where the limits of species' abilities to disperse and survive may become more apparent. Studying the fungal communities of Antarctica should offer insights into processes that may influence fungal communities at global scales. In particular, the environmental similarity of the polar regions, but the vast geographical distance separating them, provides an opportunity to test for the effects of environmental filtering and dispersal constraints. The former should lead to a convergence in community similarity and result in fungal species with 'bipolar' distributions (Ricklefs 2004), while the latter should minimise the similarity of fungal communities occurring at the poles (Morlon *et al.* 2008). While these alternative processes of dispersal constraints and habitat filtering are unlikely to operate entirely independently of one another (Martiny *et al.* 2006), they provide a useful basis from which to

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test the relative drivers of soil fungal community composition in the Antarctic.

While the fungal communities of Antarctica boast a long history of description through collections and culturing, knowledge is largely limited to those fungi that produce conspicuous fruit bodies or are readily culturable (Bridge & Spooner 2012). In this study, we use pyrosequencing to characterise the soil fungal communities of three Antarctic islands lying on a latitudinal gradient. We also compile a database of ~ 32 000 fungi from studies of soil fungal communities around the world and use this to produce a null model, designed to simulate a process in which Antarctic sites were colonised by fungi based purely on their frequency of occurrence across global sites, with no environmental selection or dispersal limits. By comparing observations with expectations from this null model, we test for patterns in support of the following opposing hypotheses: if Antarctic soil fungal communities are structured primarily by dispersal limitation, then similarity to Antarctic communities should decrease with increasing distance northwards out of Antarctica; if they are structured primarily by environmental filtering, then similarity should decrease towards the equator, and increase again towards the Arctic. To gain further insight into how these processes act, we also investigate the make-up of Antarctic communities – the endemic fungi, and those that are shared with other sites around the world. In particular, we look at fungal range sizes, testing whether the ranges of Antarctic fungi are larger than expected, as would be predicted if many show preferences for polar environments and have few limits to dispersal; and whether they conform to Rapoport's rule (Stevens 1989) – that is, increasing range size with increasing latitude – a pattern previously tested primarily in the northern hemisphere. In doing so, we demonstrate how the composition and characteristics of Antarctic soil fungal communities provide evidence for the primacy of environmental selection in their formation.

MATERIALS AND METHODS

Between October and November 2011, soil samples were collected from Bird Island (54.0089° S, 38.0662° W), Signy Island (60.7107° S, 45.5849° W) and Léonie Island (67.5984° S, 68.3561° W) in the sub-Antarctic, low maritime and high maritime Antarctic respectively. Soil was collected under populations of *Colobanthus quitensis* (Kunth) Bartl. and *Deschampsia antarctica* Desv., the only two native vascular plant species that occur in Antarctica. On each island, 50 mL sterile centrifuge tubes (Corning Inc, Corning, NY, USA) were used to collect samples by hammering them directly into the vertical walls of three soil pits at three depths (2, 4 and 8 cm). Thus, a total of 27 soil samples were collected from across the three islands. The three pits were a maximum of 1 km apart on each island, with an average distance of 311 m separating them. Soil was stored at −80 °C within 5 h of collection and was later freeze-dried to preserve fungal nucleotides. Total DNA was extracted from the soil and the primers ITS1F and ITS4 used to amplify fungal DNA for 454 pyrosequencing (Supplementary Methods). Processing of the resultant sequences was carried out using the QIIME pipeline (Caporaso *et al*. 2010), and involved extraction of high quality ITS2 regions and clustering into operational taxonomic units (OTUs) at 97% sequence similarity (Supplementary Methods). Sequences are deposited in the NCBI Sequence Read Archive (study accession SRP068654).

Collation of data from other studies

Studies in which the full ITS or the ITS2 region had been sequenced were targeted for analysis. Searches were made in Google Scholar for studies focused on fungi occurring in soil (not root- or plant-associated), and in which sequencing had been carried out at a depth of at least 1000 sequences per site. In most cases, studies employed next generation sequencing, but occasionally a combination of cloning and Sanger sequencing had been used (see Table S1 in Supporting Information). Sites within individual studies were grouped unless any site was more than 30 km from another site in the same study. In this case all sites were split. In instances where sites could not be split because of missing information, that study was excluded from the analysis. Any individual sites split within a study with fewer than 1000 sequences were also excluded. In total, 14 studies carried out over 394 sites were included (Fig. S1) (Jumpponen *et al*. 2010; Mello *et al*. 2011; Arfi *et al*. 2012; Ihrmark *et al*. 2012; Orgiazzi *et al*. 2012; Blaalid *et al*. 2013; Clemmensen *et al*. 2013; Monard *et al*. 2013; De Beeck *et al*. 2014; Geml *et al*. 2014; Kadowaki *et al*. 2014; Taylor *et al*. 2014; Tedersoo *et al*. 2014; Timling *et al*. 2014). Data from different studies were available in different forms, thereby necessitating individual downstream processing (Table S1). The ITS2 region of sequences from all studies was extracted and clustered at 97% similarity using USEARCH 6.1 (Edgar 2010), as implemented in QIIME. Resultant OTU tables from each study were rarefied without replacement to 1000 sequences per site using the function rrarefy in the Vegan package (Oksanen *et al*. 2013), R (R Core Team 2015), to minimise effects of differential sampling intensity between studies.

The blast OTU picker (Altschul *et al*. 1990) in QIIME was used to determine the number of fungi that each site shared with Antarctica, using the Antarctic OTUs as a reference database and a 97% similarity cut-off. Some of the statistical analyses required permutation of a global OTU matrix – in this case, OTUs were clustered using the USEARCH function in QIIME.

Statistical analyses

Antarctic communities were compared to a global meta-analysis of soil fungi to investigate the factors driving community formation. If dispersal limitation is the major determinant of Antarctic fungal community composition, then one would expect the Antarctic communities to share most species with sites from nearby non-polar land masses, and share progressively fewer species with sites more distant from Antarctica. If 'everything is everywhere, but the environment selects' (Baas-Becking 1934), then one would expect Antarctic communities to share species with sites from geographically distant, but environmentally similar sites, such as those in the Arctic.

To test these hypotheses, we compared observed patterns against null expectation patterns, derived from randomly assembled Antarctic communities. A thousand null communities were generated, in which the 73 non-endemic fungi were randomly assigned from the global dataset of 32 376 available OTUs. Fungi were picked, without replacement, based on a probability derived from the proportion of sites where the OTU was found – thus more widespread fungi were more likely to be assigned to the null communities. This was designed to simulate a process whereby Antarctic sites were colonised by fungi at random based on their global abundance, with no environmental selection. As we investigated patterns of shared fungal presence, and endemic fungi are, by definition, not shared with any other sites, the number of endemics was kept constant. From the 1000 generated communities, we built a null expectation of the number of fungi shared (using the UCLUST algorithm) between Antarctic sites and sites within a series of eight latitudinal ranges: > 50° south, 30°–50° south, 10°–30° south, 10° south–10° north, 10°–30° north, 30°–50° north, 50°–70° north and > 70° north. The calculated expected values differed between latitudinal bands based on the sampling intensity within each range. By comparing the distributions to the observed values, we calculated *P*-values estimating the likelihood of the observed value under the null expectation. The number of fungi shared with a latitudinal range was considered significantly more than expected by chance if less than 2.5% of the randomisations had more shared fungi; and significantly less than expected by chance if less than 2.5% of the randomisations had fewer shared fungi. All analyses were carried out using R version 3.13 (R Core team, 2015).

We further investigated the distribution of Antarctic fungi shared with other locations by counting the number of Antarctic fungi that occurred at 50°–60° north, 60°–70° north and > 70° north, but did not occur between 50° north and 50° south. The observed count of these 'bipolar' fungi was compared to counts from the 1000 null communities, and significance tested as previously described. Any putative bipolar fungi were also searched against an un-rarefied dataset, to see whether any matches (97% or greater sequence similarity) occurred at low abundances at lower latitudes.

Multiple regression was used to test for the effects of temperature and latitude on similarity to Antarctic fungal communities. Temperature was defined as the mean annual temperature of the coldest quarter, in order to take into account tolerance to cold temperatures. Climate data for each site was downloaded from the WorldClim database, using the summarised Bioclim variables at a resolution of 30 arc-seconds (Hijmans *et al*. 2005). Linear and quadratic terms for latitude were included in the model, to take into account an expected non-linear response. The relative strength of temperature and latitude as predictors of the number of fungi shared with Antarctic communities was assessed by removing predictors from the full model and comparing Akaike information criterion scores. It is possible that the use of different PCR primers in different studies could influence community composition (Tedersoo *et al*. 2015). If sites at particular latitudes used the same primer combination as that used to survey Antarctica in this study (ITS1F/ITS4), this could lead to a higher proportion of fungi at those sites/latitudes being shared with Antarctica. Therefore, as well as testing for an overall effect of primer pair on the proportion of shared fungi at each latitude, we tested whether sites from studies using the ITS1F/ITS4 primer pair had a higher, or lower, proportion of shared fungi than other sites at a similar latitude, using the same latitudinal ranges as in the permutation analyses above.

To test Rapoport's rule, the average latitudinal range size of fungi at each site was calculated. Fungi with a range size of zero were excluded from calculation of the site average, although including them had little qualitative effect on the results. Linear regression was used to test whether the average range size increased with distance from the equator. To test whether Antarctic fungi had a higher range size than expected by chance, we calculated the average range size for the three Antarctic sites combined. We then repeated this calculation for 1000 permutations, in which the locations of the 397 study sites were randomised. This was designed to simulate a scenario where the frequency of OTU occurrence at different sites was maintained, but OTU locations were random. By comparing the generated distribution to the observed value we calculated a *P*-value estimating the likelihood of the observed value under the null expectation, as described previously.

To derive an approximate indication of endemism levels, while taking into account differing sampling intensities around the globe, we calculated the proportion of endemic fungi at each site and multiplied it by a measure of local sampling intensity (the sum of the inverse distances to other sites). Thus, endemism scores would be raised if there was intense local sampling, and down-weighted if few nearby sites were sampled.

RESULTS

Across the three Antarctic islands, we obtained a total of 932 024 DNA sequences with a mean sequence length of 523 bp. After quality filtering and ITS2 extraction, our dataset consisted of 853 156 sequences that were used in downstream analyses. Species level clustering resulted in 988 OTUs, of which 94 were represented by a single sequence and were subsequently removed from the analysis. The number of sequences obtained varied between locations, with Bird Island having 323 647, Signy Island 225 927 and Léonie Island 303 582. From these sequences, Bird Island had 458 OTUs, Signy Island 357 OTUs and Léonie Island 335 OTUs (Table S2). After rarefaction to 1000 sequences per island for comparison with global studies, Bird Island had 87 OTUs, Signy Island 95 OTUs and Léonie Island 74 OTUs (Table S2). This rarefied dataset was compared to a global dataset of 394 additional sites that we compiled from other studies, each rarefied to 1000 sequences, with an average richness of 229 OTUs (95% range: 136–325 OTUs).

In support of a primary role for environmental selection, we found a U-shaped relationship between the number of fungi shared with Antarctic sites, and the latitude of comparison sites (Fig. 1a). The observed number of fungi shared between Antarctica and sites from latitudes greater than 50° north was significantly higher than expected ($P < 0.05$, Fig. 1b, Table S3). In addition, the observed number of fungi shared

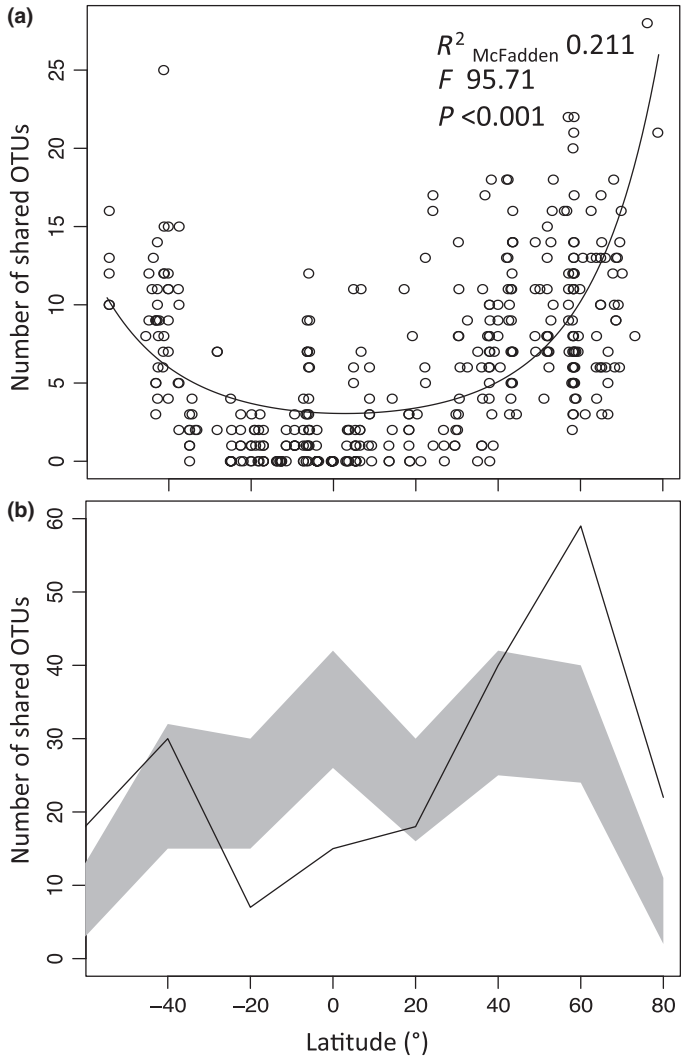

Figure 1 Fungal operational taxonomic units (OTUs) shared between Antarctica and comparison sites across different latitudes. Negative values on the *x*-axis denote latitudes south of the equator. (a) The relationship between the number of fungal OTUs shared with the Antarctic sites and latitude of comparison sites. (b) The observed (black line) and expected number of fungal OTUs shared with Antarctic sites at different latitudinal ranges (see Table S3). The shaded area shows the 95% confidence set of shared fungi from a distribution of 1000 randomly assembled Antarctic communities. The scales of the y-axes differ between the two plots as (a) shows the number of fungi shared with individual sites, and (b) shows the total number of fungi shared with all sites within a latitudinal range.

between Antarctic fungal communities and sites from latitudes between 10° north and 30° south was significantly less than expected ($P < 0.05$, Fig. 1b, Table S3). We also detected a higher than expected number of bipolar fungi – that is, fungi that occur at both poles, but do not occur at intermediate latitudes (Table S4, Table S5). Almost half of the 20 observed bipolar fungi belonged to the class Leotiomycetes, but other Ascomycetes in the classes Eurotiomycetes and Sordariomycetes and Basidiomycetes in the classes Agaricomycetes, Microbotryomycetes and Tremellomycetes, also showed bipolar distributions (Table S5). By searching for the potentially bipolar fungi in a non-rarefied dataset, we found that six of these 20 fungi occurred at low abundances at latitudes between 50° N and 50° S (Table S5). After exclusion of these fungi, there were still significantly more bipolar fungi than expected at latitudes greater than 60° N and 70° N (Table S4).

According to regression analysis, both latitude (R^2 McFadden 0.211, $P < 0.001$, Fig. 1a) and temperature (R^2 McFadden 0.285, $P < 0.001$, Fig. S2) were significant predictors of the number of fungi across the globe that were shared with Antarctica. While environmental selection is predicted to produce similarities between the polar regions, dispersal constraints should limit the similarities between two such distant landmasses. However, considering the southern hemisphere in isolation, both processes may produce the same observed pattern – that is, fewer fungi shared with Antarctica as distance from the continent increases. Temperature was shown to explain more of the variation in the number of fungal sequences shared with the Antarctic communities (Table S6), suggesting that the presence of fungi shared with Antarctica is more likely to be due to similar environmental conditions, rather than geographic proximity. When accounting for latitudinal differences, primer pair was not a significant predictor of shared fungi at the global scale ($F = 1.64$, $P = 0.111$). Sites from studies that used the same primer combination as used for sampling Antarctic soils (ITS1F and ITS4) did not appear to have a higher number of fungi shared with Antarctica than other studies from similar latitudes (Table S7).

The taxonomy of fungi from the three Antarctic islands was characterised up to class level where possible (Fig. S3). All three islands had a high proportion of fungi belonging to the Leotiomycetes, although the abundance of this class increased with latitude from Bird Island to Léonie Island. The abundance of fungi in the Microbotryomycetes showed the opposite pattern, with this taxon being one of the most frequently found classes of fungi at Bird Island. The fungal class Agaricomycetes was relatively rare across all three islands (Fig. S3).

If dispersal limitation is the primary determinant of community composition in Antarctica, the isolated nature of the continent might be expected to result in a high number of endemics and communities that most closely resemble those of the nearest landmasses, such as South America. Contrary to this expectation, the proportion of soil fungi found at each of the three Antarctic islands that was shared with other sites around the world increased with increasing southerly latitude, with 65.5, 49.5 and 40.5% of fungi being endemic at Bird Island, Signy Island and Léonie Island respectively (Fig. 2). Overall levels of Antarctic endemism appeared relatively low (Fig. S4), although comparisons of endemism levels with other studies can be complicated by different sampling intensities across the globe.

The taxonomic affiliation of fungal OTUs differed between those fungi that were shared with other sites around the world, and those that were endemic to Antarctica (Fig. 3). The shared fungi were dominated by Leotiomycetes, which made up over 60% of the fungal sequences, with the number of fungi belonging to this class increasing at higher latitudes. Sequences belonging to the Dothideomycetes were also more abundant in the shared vs. endemic fungi. Fungi endemic to Antarctica showed a higher proportion of unidentified fungal

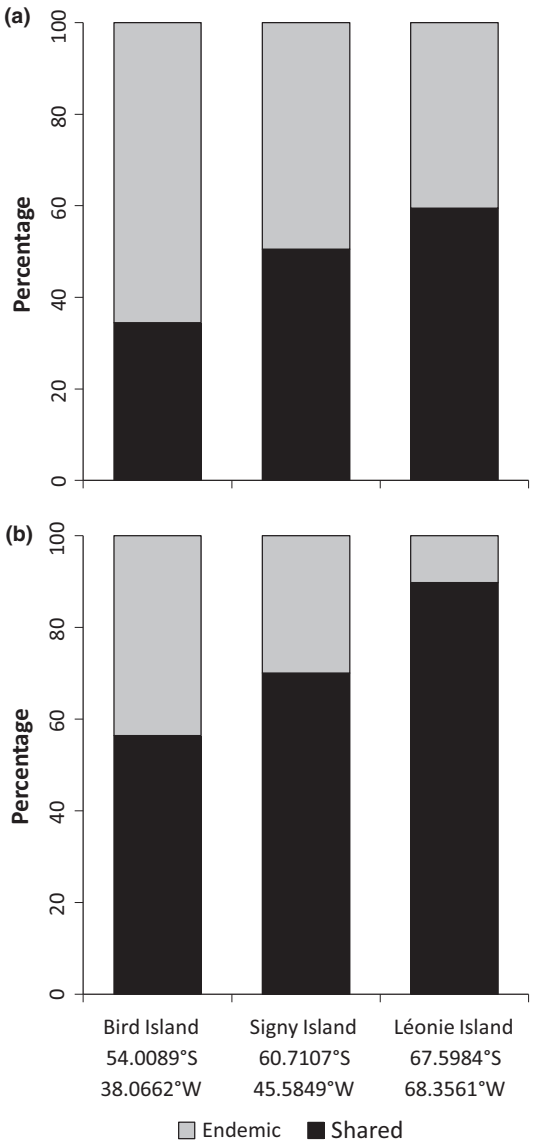

Figure 2 Percentage of Antarctic fungal operational taxonomic units (OTUs) that were endemic to Antarctica or shared with other regions of the world. (a) Percentage richness of Antarctic fungal OTUs (i.e. number of unique taxa) that either matched, at 97% similarity, a sequence found in a data set from another region of the world ('shared'), or were only found in the Antarctic data set ('endemic'). (b) Percentage abundance of Antarctic fungal OTUs (i.e. number of sequences obtained) in each category of shared or endemic.

taxa than shared fungi, and the proportion of endemic sequences that could not be identified below Kingdom level reduced as the latitude of the three islands increased (Fig. 3). A high proportion of endemic fungi belonged to the Eurotiomycetes at Signy and Léonie Islands, with this class representing 40 and 30% of the sequences on these islands respectively.

Soil fungi in Antarctica were found to have a significantly larger range size (mean of 98.7°) than expected under a null model in which the global occurrences of Antarctic soil fungi were randomised ($P = 0.01$, 95% of average range sizes were between 96.3° and 68.5°), and fungi on the three Antarctic Islands have the highest mean range size of all the fungal communities included in this study (Fig. 4a). The latitudinal range sizes of Antarctic fungal OTUs show a strongly bimodal distribution, with fungi either having a small geographic range size, or a much larger distribution spanning global latitudes (Fig. 4b). In contrast, the distribution of latitudinal range sizes for fungi in the global dataset shows most fungi with a relatively small range, and a sharply decreasing proportion of fungi with larger range sizes (Fig. 4c).

DISCUSSION

In this study, we found a higher than expected number of fungi shared between soils in Antarctica and those at high northern latitudes, as well as fungi that display apparently bipolar distributions. These findings have implications for microbial biogeography, suggesting that in such extreme and isolated environments, environmental selection may be a more important determinant of community composition than dispersal constraints. Previous studies have noted similarities between the fungi isolated from Antarctic soils with those collected in the Arctic (Pegler *et al.* 1980; Bridge & Newsham 2009; Timling *et al.* 2014), suggesting that some fungal taxa may exhibit bipolar distributions. However, because of the absence of sufficient molecular data, it has not previously been possible to test rigorously the extent to which the same fungal taxa occur at high latitudes in both the northern and southern hemispheres. In addition, it has not previously been feasible to investigate whether potentially bipolar fungi occur just as frequently at lower latitudes, or if they display reduced abundance towards the equator. Our analyses indicate that the low temperatures of polar environments lead to the observed community similarities, although it should be noted that it is not possible to rule out the role of other, unmeasured environmental variables, and that dispersal constraints may be acting at a smaller geographic scale than tested here.

The meta-analysis conducted in this study allowed for a comparison of Antarctic fungi with other soil fungal communities across the globe, but analyses carried out across such a diverse range of studies need to be treated with some caution. Selection of studies was carried out in order to include only those that examined soil fungal communities (rather than plant- or root-associated communities), but the spatial scale of individual study sites and samples was not held constant, which could influence the diversity and composition of the fungal species recovered. Furthermore, the use of different PCR primers is known to have a strong influence on the fungal community recovered (Tedersoo *et al.* 2015). Our analysis of the effects of primers on shared fungi was designed to see whether primer choice may bias our analysis of the proportion of fungi shared with Antarctica – not to test whether primer choice influences overall community composition. It is possible that no effect of primer pair was seen because only 14 comparison sites used the same primer combination as in our study, or because the model response in this test is similarity to a particular community rather than global community similarities. We cannot exclude the possibility that primer choice and sampling design will influence the composition of fungi recorded at the global sites with which we made com-

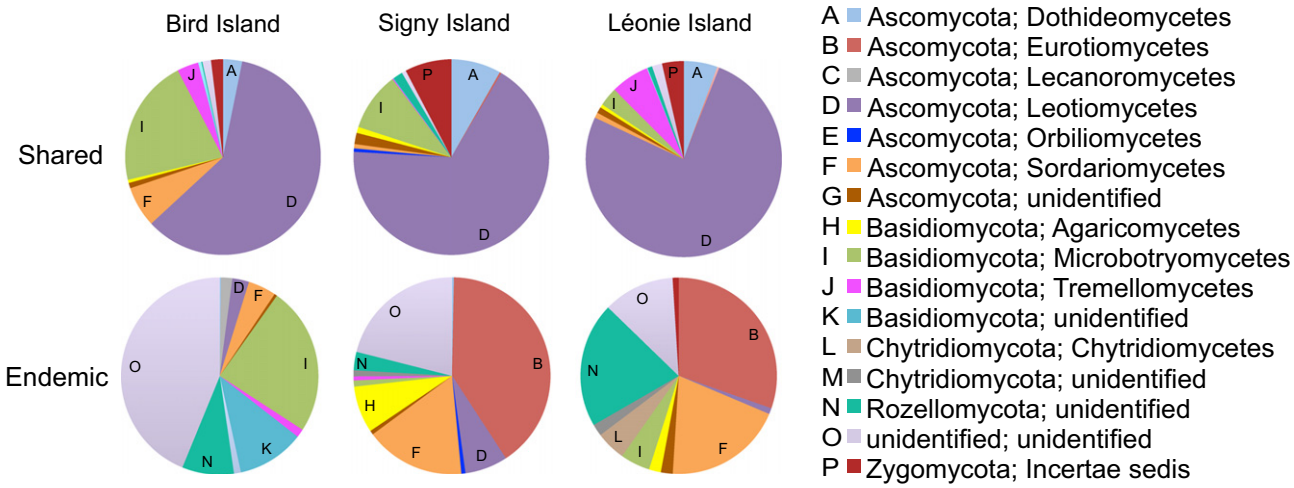

Figure 3 Percentage abundances of 1000 sequences that fell into different taxonomic classes across three Antarctic islands. The top row represents the abundance of Antarctic operational taxonomic units (OTUs) that matched at 97% similarity, sequences in datasets from other parts of the world ('shared'), while the bottom row represents the abundance of those OTUs that were only present in the Antarctic dataset ('endemic'). Segments representing more than 2.5% of the total are labelled with a letter to aid identification.

parisons. Nevertheless, it is unlikely that these factors would affect our hypothesis testing by favouring similarity or dissimilarity to Antarctic fungal communities at particular latitudes.

An additional factor to consider in a meta-analysis of sequencing studies is the quantity of target DNA. The fraction of the true species' pool that is sampled will be affected by the amount of DNA template, and the depth of sequencing. If the polar communities were quantitatively smaller, then they would be sampled to a greater depth than temperate communities, and so some putatively bipolar fungi may occur at intermediate latitudes but would be removed by rarefying each sample to a common sequence depth. Likewise, it is possible that rarefaction of the Antarctic dataset may remove additional bipolar fungi. We attempted to address the former scenario by searching a non-rarefied database for the putatively bipolar fungi, and it was notable that the most extreme bipolar fungi – those that only occurred in Antarctica and at latitudes greater than 60° N or 70° N – tended to still be absent from intermediate latitudes.

While Agaricomycetes are present in Antarctic soils, they represent an infrequent taxon making up at most 3% of fungal sequences on Signy Island, and less than this on the other two islands studied. In contrast, Agaricomycetes are a dominant fungal taxon found in most soils of the world, constituting an average of 50% of recorded sequences in soil (Tedersoo *et al.* 2014), and being one of the most OTU rich fungal taxa (Meiser *et al.* 2014; Tedersoo *et al.* 2014). The absence from Antarctic soils of woody plant roots, which often form ectomycorrhizas with members of the Agaricomycetes at lower latitudes, is likely to explain the much lower abundance of this class of fungi in the Antarctic. Alternatively, the reproductive biology of many Agaricomycetes, which often requires co-dispersal of compatible mating types, may make long-distance dispersal unlikely. The non-endemic fungi in Antarctica include a high proportion of fungi in the Leotiomycetes and Dothideomycetes. Some members of these fungal classes have been observed to disperse to Antarctica from more northern landmasses via birds such as skuas, which may act as vectors for the transport of fungi such as *Pseudogymnoascus* species (Marshall 1998).

Comparatively reduced levels of fungal endemism in polar regions has previously been suggested in a study of Arctic fungal communities, which found that of the common fungi present in Arctic soils, only one appeared to be endemic to the region (Timling *et al.* 2014). In contrast, fungal endemism at lower latitudes appears to be considerably higher. For example, Talbot *et al.* (2014) estimated that approximately 85% of soil fungi were endemic to different bioregions of North America. Large range sizes may be responsible for the relatively low levels of endemism seen in Antarctica – where relatively high levels of endemism are seen across broad geographic scales, most soil fungi have restricted ranges (Talbot *et al.* 2014). It is possible that the large range sizes found in Antarctic soil fungal communities are driven in part by the geographic isolation of the islands, restricting colonisation by fungal species with small dispersal ranges. However, the high similarity to communities in the Arctic indicates that the large observed range sizes may reflect habitat filtering by the extreme environment of Antarctica, such that fungi able to colonise the region are those with strong dispersal capabilities but also the ability to survive in hostile polar environments.

The observed high mean range size of fungi in Antarctic soil communities, together with the increasing dominance of widespread fungi as distance from the equator increases, provides evidence in support of Rapoport's Rule (Stevens 1989; Gaston *et al.* 1998), which states that organisms' latitudinal range sizes increase at higher latitudes. Support for this theory was recently reported in a global study of fungal biogeography, which found that the latitudinal range size of fungi increased towards the poles (Tedersoo *et al.* 2014). Rapoport's rule is generally understudied in the high latitudes of the southern hemisphere, and it has previously been argued that the rule's applicability might be restricted to the northern hemisphere, because of less land cover and narrower temperature ranges in the southern hemisphere (Gaston & Chown 1999; Lundmark

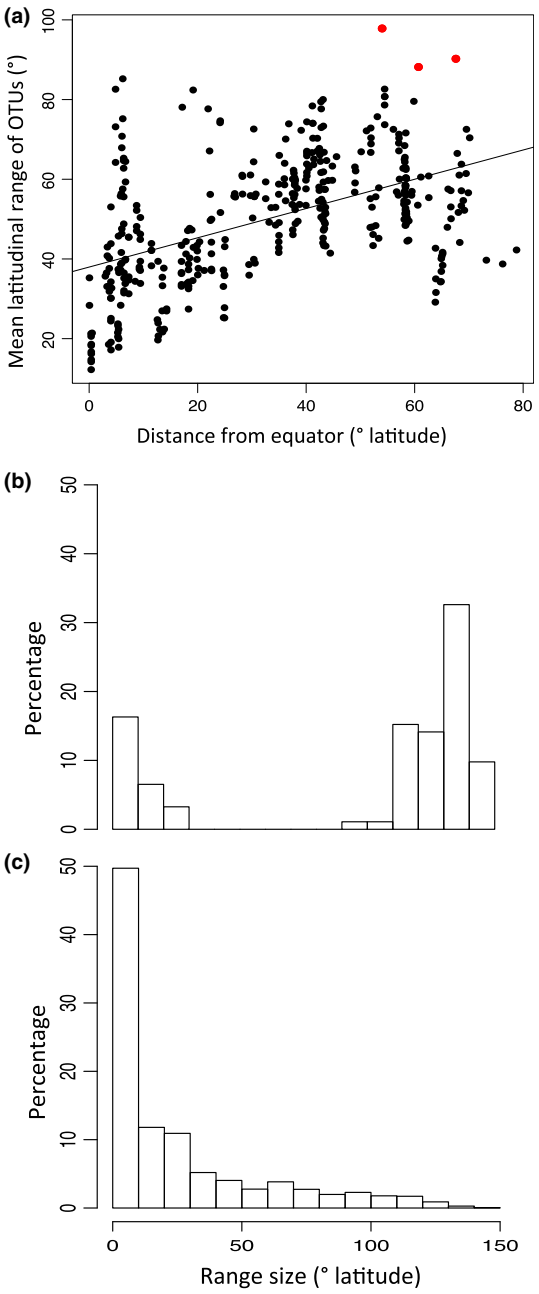

Figure 4 Characteristics of latitudinal range sizes of Antarctic fungal operational taxonomic units (OTUs). (a) Relationship between the mean latitudinal range of OTUs found at each site against the distance of the site from the equator. Points representing the three Antarctic islands are coloured in red. (b, c) Distribution of latitudinal range sizes of (b) Antarctic OTUs and (c) all fungal OTUs from worldwide geographic locations. Bin sizes are 10° latitude.

2006; Veter *et al.* 2013). However, a recent study of global marine bacterial communities (Amend *et al.* 2013), found that bacterial OTUs in the southern hemisphere had range sizes approximately twice those of OTUs found in the northern hemisphere.

Many lichens are also known to display bipolar distributions, and a recent population genetics study found evidence that the bipolar lichen *Cetraria aculeata* colonised Antarctica via South America during the Pleistocene (Fernández-Mendoza & Printzen 2013). With the data currently available, it is not possible to discount alternative hypotheses for the establishment of bipolar distributions in fungi, such as trans-tropical migrations during the Pleistocene, and ancient vicariance (Donoghue 2011). Future studies could seek to investigate further genetic similarities and gene flow of bipolar microbes using isolates from different populations. Genetic studies below the ITS level may provide insight into the frequency of dispersal events, and the length of time that different populations have been separated. Indeed, the results in this study must be interpreted in the light of the single cut-off used to cluster fungal OTUs (97%), which may fail to differentiate some taxa with narrower geographic ranges. In addition, much of the fungal diversity of Antarctica remains unsampled, with this study focusing solely on soil habitats on three islands.

Debate has continued for many years over the validity of the Baas-Becking (1934) view of microbial biogeography, that 'everything is everywhere, but the environment selects'. In recent years, many studies have used molecular techniques to demonstrate that dispersal barriers exist for some fungi and other soil microbes. We show that Antarctic communities share fungi with those from the opposite pole, and that environmental constraints, such as low temperatures, may determine similarities between the communities in these extreme habitats. Since Antarctic soil fungal communities are dominated by fungi with large range sizes, our results are consistent with a scenario in which many polar fungi have the potential to be globally ubiquitous, but their presence in specific environments is limited by factors including environmental selection.

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AUTHORSHIP

C.H.R., K.K.N, J.A.J. and R.B. secured funding for this work and supervised the project. F.C., C.H.R. and K.K.N carried out the fieldwork. F.C. conducted lab work, conceived research question, carried out analysis and wrote the initial draft of the manuscript. All authors contributed to final manuscript preparation.

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