Ecology, 99(3), 2018, pp. 583–596

Ecological drivers of soil microbial diversity and soil biological networks in the Southern Hemisphere

Manuel Delgado-Baquerizo,[1,2,3,10] Frank Reith,[4,5] Paul G. Dennis,[6] Kelly Hamonts,[1] Jeff R. Powell,[1] Andrew Young,[7] Brajesh K. Singh,[1,8] and Andrew Bissett[9]

[1]*Hawkesbury Institute for the Environment, Western Sydney University, Penrith, New South Wales 2751 Australia*
[2]*Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, Colorado 80309 USA*
[3]*Departamento de Biología, Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, c/ Tulipán s/n, Móstoles 28933 Spain*
[4]*Department of Molecular and Cellular Biology, School of Biological Sciences, The University of Adelaide, Adelaide, South Australia 5005 Australia*
[5]*Land and Water, Environmental Contaminant Mitigation and Technologies, PMB2, Glen Osmond, South Australia 5064 Australia*
[6]*School of Earth and Environmental Sciences, The University of Queensland, St Lucia Queensland 4072 Australia*
[7]*National Research Collections Australia, CSIRO, Canberra, Australian Capital Territory 2601 Australia*
[8]*Global Centre for Land-Based Innovation, Western Sydney University, Penrith South DC, New South Wales 2751 Australia*
[9]*CSIRO, Oceans and Atmosphere, Hobart, Tasmania 7000 Australia*

Abstract. The ecological drivers of soil biodiversity in the Southern Hemisphere remain underexplored. Here, in a continental survey comprising 647 sites, across 58 degrees of latitude between tropical Australia and Antarctica, we evaluated the major ecological patterns in soil biodiversity and relative abundance of ecological clusters within a co-occurrence network of soil bacteria, archaea and eukaryotes. Six major ecological clusters (modules) of co-occurring soil taxa were identified. These clusters exhibited strong shifts in their relative abundances with increasing distance from the equator. Temperature was the major environmental driver of the relative abundance of ecological clusters when Australia and Antarctica are analyzed together. Temperature, aridity, soil properties and vegetation types were the major drivers of the relative abundance of different ecological clusters within Australia. Our data supports significant reductions in the diversity of bacteria, archaea and eukaryotes in Antarctica vs. Australia linked to strong reductions in temperature. However, we only detected small latitudinal variations in soil biodiversity within Australia. Different environmental drivers regulate the diversity of soil archaea (temperature and soil carbon), bacteria (aridity, vegetation attributes and pH) and eukaryotes (vegetation type and soil carbon) across Australia. Together, our findings provide new insights into the mechanisms driving soil biodiversity in the Southern Hemisphere.

Key words: *Antarctica; archaea; Australia; bacteria; biodiversity; eukaryotes; terrestrial ecosystems.*

Introduction

The inverse relationship between distance from the equator and the diversity of aboveground macro-organisms is a widely recognized global biogeographical pattern (Pianka 1966, MacArthur 1975, Rohde 1992, Gaston 2000, Willig et al. 2003, Currie et al. 2004). Conversely, recent studies evaluating latitudinal patterns in soil biodiversity did not find strong relationships between distance from equator and soil microbial diversity; i.e., of bacteria or fungi (Lawley et al. 2004, Lauber et al. 2009, Chu et al. 2010, Wang et al. 2016). Intriguingly, these studies have mainly been conducted in the Northern Hemisphere, either entirely or including mostly data coming from this Hemisphere, as well as across narrow latitudinal gradients. Short latitudinal gradients might not have enough resolution to test this hypothesis—especially when considering that microbial communities are likely less dispersal limited than plants and animals. Moreover, studies evaluating the diversity-latitude relationship in the Southern Hemisphere are lacking, especially, those covering a wide enough latitudinal range to provide representative conclusions for this important ecological question.

Manuscript received 7 September 2017; revised 8 December 2017; accepted 18 December 2017. Corresponding Editor: Evan L. Preisser.
[10] E-mail: m.delgadobaquerizo@gmail.com

Also lacking are studies identifying the major environmental drivers of soil biodiversity (i.e., archaea, bacteria and micro-eukarya) in the Southern Hemisphere. Compared to the Arctic region, the Antarctic polar region is much poorer in soil organic carbon and microbial diversity (Siciliano et al. 2014). This is in part due to the lack of well-developed vegetation and extremely low temperatures in the southern vs. the northern polar regions. There are no tundra or taiga ecosystems in the high latitudinal regions of the Southern Hemisphere, and temperatures are much lower in the Antarctic vs. the Arctic region (Delgado-Baquerizo et al. 2016*a*). Because of the extreme conditions in the southern polar region, we would expect that, similar to what has been reported for plants and animals (MacArthur 1975, Rohde 1992, Gaston 2000, Currie et al. 2004), soil biodiversity is extremely limited in Antarctica. While an impressive number of studies have suggested that the diversity of bacteria and eukaryotes is indeed extremely limited in Antarctica (Barrett et al. 2004, Adams et al. 2006, Fell et al. 2006, Smith et al. 2006, Yergeau et al. 2007, Aislabie et al. 2008, Niederberger et al. 2008, Pointing et al. 2009, Czechowski et al. 2016), empirical evidence for the Southern Hemisphere is lacking, as none of these studies have explicitly compared the soil biodiversity in Antarctica with that of other southern continents.

Recent studies suggest that soil organisms strongly co-occur and form well-defined ecological clusters of exclusive taxa, often called modules (Menezes et al. 2015). These modules are expected to include multiple interactions within these clusters, such as those from prey-predator, parasite-host and plant-microbial (symbiosis and pathogenesis) relationships. Thus, ecological clusters of soil taxa are expected to have multiple implications for the maintenance of soil fertility, decomposition and plant productivity in terrestrial environments (Hooper et al. 2000, Wardle et al. 2004, van der Heijden et al. 2008). Unlike the often reported beta-diversity patterns in microbial communities, ecological clusters represent important ecological units that provide the opportunity to identify the environmental preferences of highly connected and identifiable taxa by integrating highly dimensional data into predictable ecological clusters (Menezes et al. 2015, Shi et al. 2016). Despite the importance of these interactions for ecosystem functioning, the relationship between latitude and the relative abundance of ecological clusters of soil microbial taxa has not been previously investigated. As expected for soil biodiversity generally, latitudinal patterns may result in significant changes in the correlation network of soil organisms (bacteria, archaea and eukaryotes), however, empirical evidence for such assumptions is currently lacking. Moreover, despite the importance of ecological networks for ecosystem functioning (Menezes et al. 2015, Shi et al. 2016), our current knowledge of the major environmental drivers of soil ecological networks lags behind that reported for plants and animals.

Here, we identify the major environmental drivers of soil biodiversity in Australia and Antarctica. Compared to continental Australia, Antarctica is likely to promote strong reductions in soil biodiversity and to shift the interaction networks of soil microbes indirectly via extreme reductions in resource availability and temperature. These may include soil organic carbon – a common proxy of organic matter, temperature, i.e., physiological constraints (Currie et al. 2004, Menezes et al. 2015) and changes in biotic attributes, i.e., vegetation types and aboveground diversity, in Antarctica. For instance, strong reductions in temperatures from the tropics to Antarctica may directly reduce the diversity of soil organisms by reducing the number of organisms that are able to live under such physiological constraints (Rohde 1992, Currie et al. 2004). Temperature and resource availability have been recently highlighted as being strongly associated with the diversity of soil bacteria, some fungi and soil microinvertebrates (Santruckova et al. 2003, Fierer et al. 2009, Delgado-Baquerizo et al. 2016*a*, Newsham et al. 2016, Zhou et al. 2016). In addition, a recent study demonstrated that temperature is an important driver controlling the latitudinal patterns in soil bacterial diversity in cold forests from North America (Zhou et al. 2016). Terrestrial ecosystems with higher temperatures often support higher primary productivity, provided that water is also available, resulting in unique vegetation types, e.g., forest vs. grasslands vs. bare surface and lack of vascular vegetation (Santruckova et al. 2003, Currie et al. 2004). Similarly, sites with higher temperatures often support higher litter and organic matter decomposition rates, resulting in higher resource availability (Santruckova et al. 2003, Currie et al. 2004). These factors may ultimately control the number of species that co-exist at a particular location (Currie and Paquin 1987, Turner 1987, Currie et al. 2004). For example, reductions in temperature might also affect ecological interactions such as parasite-host or plant-pathogens interactions (e.g., Sabburg et al. 2015). In addition to these extreme physiological effects of temperature when comparing Australia with Antarctica, multiple direct and indirect effects on soil biodiversity and the abundance of ecological clusters are expected; such as changes in resource availability, aboveground diversity and changes in ecosystem types across continental Australia. The importance of ecosystem type as a driver of microbial communities have been recently highlighted by Szoboszlay et al. (2017) and Terrat et al. (2017), who found strong changes in the diversity and community composition of soil bacteria across different land uses. Much less is known on the role of ecosystem type in driving the biodiversity and ecological clusters of soil taxa within Australia.

We posit that in the Southern Hemisphere, soil microbial diversity at multiple trophic levels is extremely reduced in Antarctica vs. Australia as a consequence of the extreme environmental conditions in Antarctica. On the contrary, and similar to results reported for the Northern Hemisphere, we do not expect large latitudinal variations in soil biodiversity across continental Australia (Lawley et al. 2004, Lauber et al. 2009, Chu et al. 2010, Delgado-Baquerizo et al. 2016*a*, Wang et al. 2016). Ecological clusters of soil taxa are expected to be driven by various environmental drivers, as it is well-known that different soil species have different niche preferences (e.g., biotic attributes, climate and soil properties). To test these hypotheses, we used a continental survey, the Biomes of Australian Soil Environments (BASE) project (Bissett et al. 2016), which includes 647 sites across 58 degrees of latitude between the Australian tropics and Antarctica. The comparison between Australia and Antarctica is especially interesting as both continents were joined together until 45 million years ago (recently in geological terms). Hence, they share a common "Gondwanaland" past in terms of geology, paleontology, vegetation and soil development. Given that soil biodiversity is an important regulator of key ecosystem services such as primary production, nutrient cycling and climate (Bardgett and van der Putten 2014), advancing our understanding on the global patterns of soil biodiversity, and its likely response to changing climate, is of paramount importance.

Material and Methods

Study sites

Our study includes soil samples from 647 locations in the Southern Hemisphere, from Australia (541) to Antarctica (106), which were collected by the Biomes of Australia Soil Environments (BASE) project (Bissett et al. 2016, Appendix S1: Fig. S1). The sites included in this study have information available on the diversity of bacteria, archaea and/or eukaryotes. Field information was collected between 2011 and 2014 from 25 × 25 m plots. Composite soil samples from nine discrete sites within the 25 × 25 m plots were collected from the top 0–0.1 m as described in Bissett et al. (2016).

Sampling at these locations was conducted at different times throughout the year and in different years. Diversity patterns in this dataset are, therefore, integrated across

different seasons thus, we do not expect any impact of seasonality on our conclusions (i.e., data from different latitudes always include information from multiple seasons). Please note: for statistical analyses, we used climatic parameters averaged at the annual level, as explained below.

Molecular analyses

Illumina MiSeq was used for sequencing as described in Bissett et al. (2016). Briefly, amplicons targeting the bacterial 16S rRNA gene (27F–519R; Lane 1991), archaeal 16S rRNA gene (A2F–519R; Lane et al. 1985) and Eukaryotic 18S rRNA gene (Euk_1391f–EukBr) were prepared and sequenced (Appendix S2). In all cases, Operational Taxonomic Units (OTUs) were built at 97% sequence similarity. OTU abundance tables were rarefied at 14,237 (16S rRNA gene), 3,000 (archaeal 16S rRNA gene) and 4,866 (Eukaryotic 18S rRNA gene) sequences/sample to ensure equal sampling effort across samples. The Shannon diversity index of each microbial group was calculated on these rarefied OTU tables (Appendix S2). From the 647 samples, 570 samples of archaea, 637 samples of bacteria, and 602 samples of eukaryotes were included in further analyses due to DNA amplification problems.

Environmental and physicochemical analyses

Mean annual temperature (MAT) and Aridity Index (AI; mean annual precipitation/potential evapotranspiration) and soil pH and total organic carbon were determined as explained in Appendix S2. Aboveground diversity (Shannon) was obtained from each location from the Atlas of Living Australia (ALA) spatial portal (http://spatial.ala.org.au; 10 km grid). For clarity, we used aridity [maximum AI value in the dataset–AI] instead of the aridity index (Appendix S2).

Correlation network analyses

To identify clusters (modules) of strongly associated soil taxa including unique soil phylotypes, a correlation network, i.e., co-occurrence network, was established. We conducted these analyses with 529 samples for which we have matching information for archaea, bacteria and eukaryotes. To produce a practicable correlation network, we kept those taxa that accounted for more than 80% of the relative abundance of bacteria, archaea and eukaryotes, performed independently for archaea, bacteria and eukaryotes. These bacterial, archaeal and eukaryotic taxa were then merged into a single abundance table. This resulted in a dataset with 6,792 taxa including 5,085 bacteria, 46 archaea and 1,661 eukaryote phylotypes. We then calculated all pairwise Spearman's rank correlations (ρ) between all soil taxa. We focused exclusively on positive correlations as they provide information on microbial taxa that may respond similarly to environmental conditions (Barberán et al. 2014). We considered a co-occurrence to be robust if the Spearman's correlation coefficient was >0.50 and $P < 0.01$ (see Barberán et al. 2014 for a similar approach). Note that this cut-off has a mathematical meaning, because variables that are highly correlated to each other (e.g., Spearman rank coefficients > 0.5) often suffer from multi-co-linearity indicating a strong mathematical link between two variables. It also has a biological meaning, because we only focus on organisms that are strongly co-occurring with each other, and therefore are more likely to interact with each other within the food web. The network was visualized with the interactive platform gephi (Bastian et al. 2009). Finally, we used default parameters from the interactive platform gephi to identify modules of soil taxa strongly interacting with each other. We then computed the relative abundance of each module by averaging the standardized relative abundances (z-score) of the taxa that belong to each module. By standardizing our data, we ruled out any effect of merging data from different soil groups: bacteria, archaea and eukaryotes. Information on functional traits for fungal taxa within each module was obtained from the online application FUNGuild described in Nguyen et al. (2016). Note that, given the large spatial scale of our study, the ecological modules in these studies likely resemble real ecological functional units that are also present on other continents. However, the phylotypes within each ecological cluster might slightly vary, as some species of archaea, bacteria or eukaryotes might be endemic from the Southern Hemisphere, Australia or Antarctica, and may potentially not be present elsewhere.

Statistical analyses

Statistical analyses were conducted for Australia only and for Australia and Antarctica together. The analyses were performed in this way, because it can be argued that latitudinal patterns that may appear in the Southern Hemisphere are the consequence of comparing such disparate (geographically remote, environmentally distinct) sites (Australia with Antarctica) at the extremes of the latitudinal gradient studied, and that such patterns would not occur in across a more contiguous gradient (e.g., Australia only). Note that latitudinal gradients of our samples are not wide enough in Antarctica to conduct these analyses in Antarctica only. When analyzing data from Australia and Antarctica together, our latitudinal gradient is not continuous. Therefore, here we used multiple non-parametric approaches, which work well with discrete variables and included correlation networks (Spearman), PERMANOVA, Random Forest, Spearman correlations and bootstrapped Structural Equation Modeling to support the conclusions in this study.

ANOVA analyses and modeling of the shape of the relationship between latitude and microbial attributes

We first evaluated the correlation (Spearman; a non-parametric approach) between absolute latitude and microbial attributes in Australia and Antarctica together, and in Australia only. Moreover, we tested for differences in soil diversity and relative abundance of soil modules of strongly co-occurring taxa among different latitudes, i.e., for the study low latitudes are defined as [<23° S], middle latitudes [23–66° S] and high latitudes [>66° S]; Marsh and Kaufman 2013) using one-way PERMANOVA (non-parametric MANOVA), with geographical region as a fixed factor (Anderson 2001). By grouping our data by geographical regions, we are not treating our data as continuous, which given the distance between Australia and Antarctica would have been problematic.

We then identified the shape of the relationship between latitude (i.e., absolute latitude or distance from equator) and (1)

the diversity (Shannon) of soil bacteria, archaea and eukaryotes and (2) the relative abundance of major modules of strongly co-occurring soil taxa for both continents together. In particular, we fitted four different functions: linear, quadratic, cubic and logarithmic. We selected the best model fit in each case by following the Akaike Information Criteria (AIC_c; Burnham and Anderson 2002). The lower the AIC_c index the better the model. Here, we consider a $\Delta AIC_c > 2$ threshold to differentiate between two substantially different models and then select the best of those models (Delgado-Baquerizo et al. 2016*b*). When more than two models were similar (i.e., $\Delta AIC_c < 2$) we then selected the most parsimonious model (e.g., quadratic vs. cubic). We repeated these analyses for Australian samples only to examine if similar trends are found when limiting our analyses to one continent only.

Finally, we used Pearson correlations to further evaluate the relationship between distance from the equator and the richness (i.e., number of OTUs) of total bacteria, archaea and eukaryotes and also between distance from the equator and richness of the main groups within archaea, bacteria and eukaryotes.

Links between the diversity of soil organisms across the Southern Hemisphere

We evaluated the relationships between the diversity of archaea, bacteria and eukaryotes using linear regressions. We also assessed the correlation between the richness of main taxa of archaea, bacteria and eukaryotes. We evaluated the correlation between the matrices of distance for archaeal, bacterial and eukaryotic community composition (OTU level) using Bray-Curtis distance and Mantel test correlations.

Random Forest

We then used Random Forest analysis (Breiman 2001), as described in Delgado-Baquerizo et al. (2016*c*), to identify the major significant environmental predictors of soil diversity and of the relative abundance of the main modules within our network on interactions (see Appendix S2).

Structural equation modeling

We used structural equation modeling (SEM; Grace 2006; see Appendix S2 for details) to evaluate the direct and indirect effects of distance from the equator (absolute latitude), aridity, mean annual temperature, soil-C, soil pH and biotic attributes, i.e., aboveground diversity and vegetation types including forests, grasslands and croplands on (1) the Shannon diversity of archaeal, bacterial and eukaryotic communities and (2) the relative abundance of soil modules of strongly co-occurring taxa (a priori model in Appendix S1: Fig. S2) in the Southern Hemisphere (Australia and Antarctica together). We then repeated these analyses for Australia only. Finally, we explored relationships between the richness of main taxa of soil archaeal, bacterial and eukaryotic communities with latitude (absolute), climate, and soil properties using Pearson correlations.

Results

We found that soil microbial taxa grouped into six major ecological clusters (modules), comprised of populations strongly co-occurring with one another (Fig. 1a). All modules

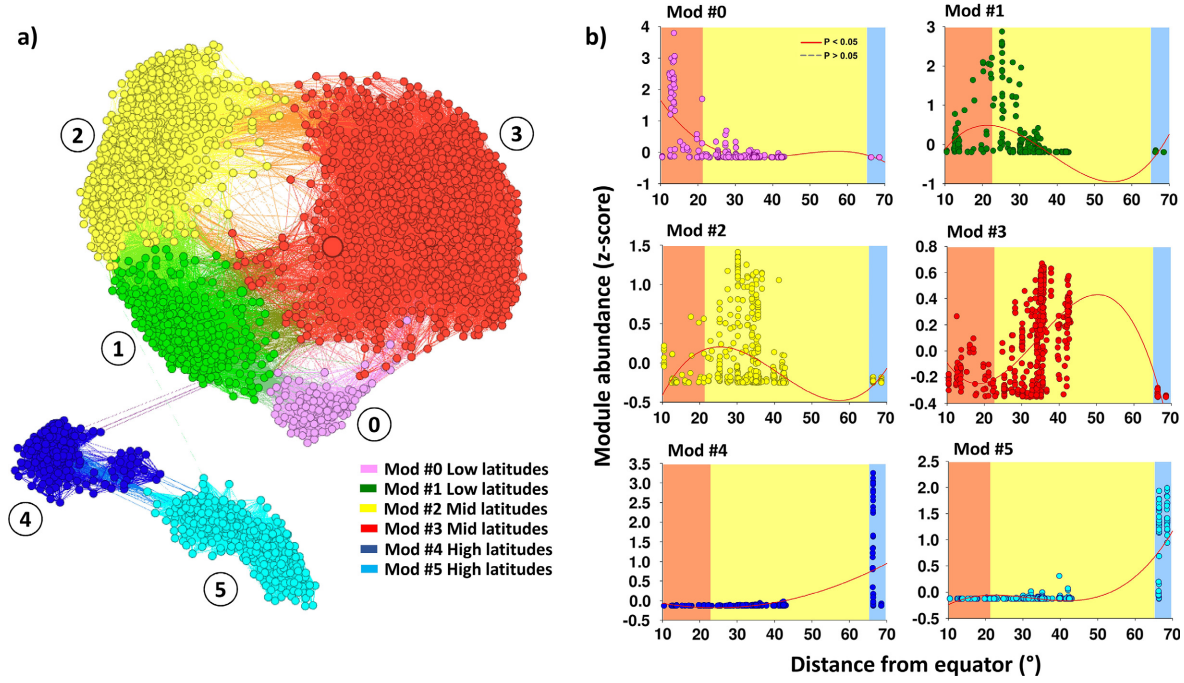

Fig. 1. Soil correlation network. Panel (a) represents a network diagram with nodes (taxa of archaea, bacteria and eukaryotes) colored by each of the major six identified modules in the Southern Hemisphere (Australia and Antarctica). Panel (b) includes the relationships between latitude (absolute) and the relative abundance of each soil module. Model fit statistics and AIC_c index describing the relationship between latitude (absolute) and the relative abundance of Modules#1–6 are available in Data S1.

were formed by multiple soil taxa including archaea, bacteria and eukaryotes (Appendix S1: Fig. S3; Data S1). Similar trends were found when we evaluated the correlation (Spearman) between distance from equator and the relative abundance of Modules#0–5 in (1) Australia and Antarctica and (2) Australia on its own (Appendix S3: Tables S1 and S2). The relative abundances of Modules#0 and #1 increased towards low latitudes (Figs. 1b, 2; Appendix S3: Table S2), while Modules#2 and #3 peaked at mid-latitudes (Figs. 1b, 2; Appendix S3: Table S2). Two modules (Modules#4 and #5; Figs. 1b, 2 and Appendix S3: Table S2) were also identified as being characteristic of Antarctica. The membership of each module is shown in Data S1 and Appendix S1: Fig. S3.

Similar trends were detected when we evaluated the link between distance from equator and the relative abundances of the six modules within Australia only (Appendix S1: Fig. S4 and Appendix S3: Table S1). Module#3 included OTUs from the *Gregarinasina* (a group of Apicomplexan alveolates that parasitise a large number of invertabrates) and multiple invertebrates including members of the *Arthropoda* and *Nematoda* (Appendix S1: Fig. S3; Data S1). Module#4 contained multiple taxa from the phylum *Ciliophora* (Protozoa) which may be important bacterivores in the Antarctic. Modules#0 and #3 included members of the Glomerales (Arbuscular Mycorrhizal fungi). Module#3 also contained ectomycorrhizal *Clavulina cristata* and *Cortinarius* sp. populations (Module#3), the ericoid mycorrhizal *Oidiodendron tenuissimum*, and the animal pathogen *Pseudogymnoascus pannorum var. pannorum*. Module#2 contained fungal phylotypes from the family *Ascobolaceae* (a dung saprotroph; Nguyen et al. 2016). Modules#0–4 decreased toward Antarctica (Figs. 1, 2; Appendix S1: Fig. S4).

The biodiversity of Antarctic soil microbial communities was lower than that of those in continental Australia (Fig. 3).

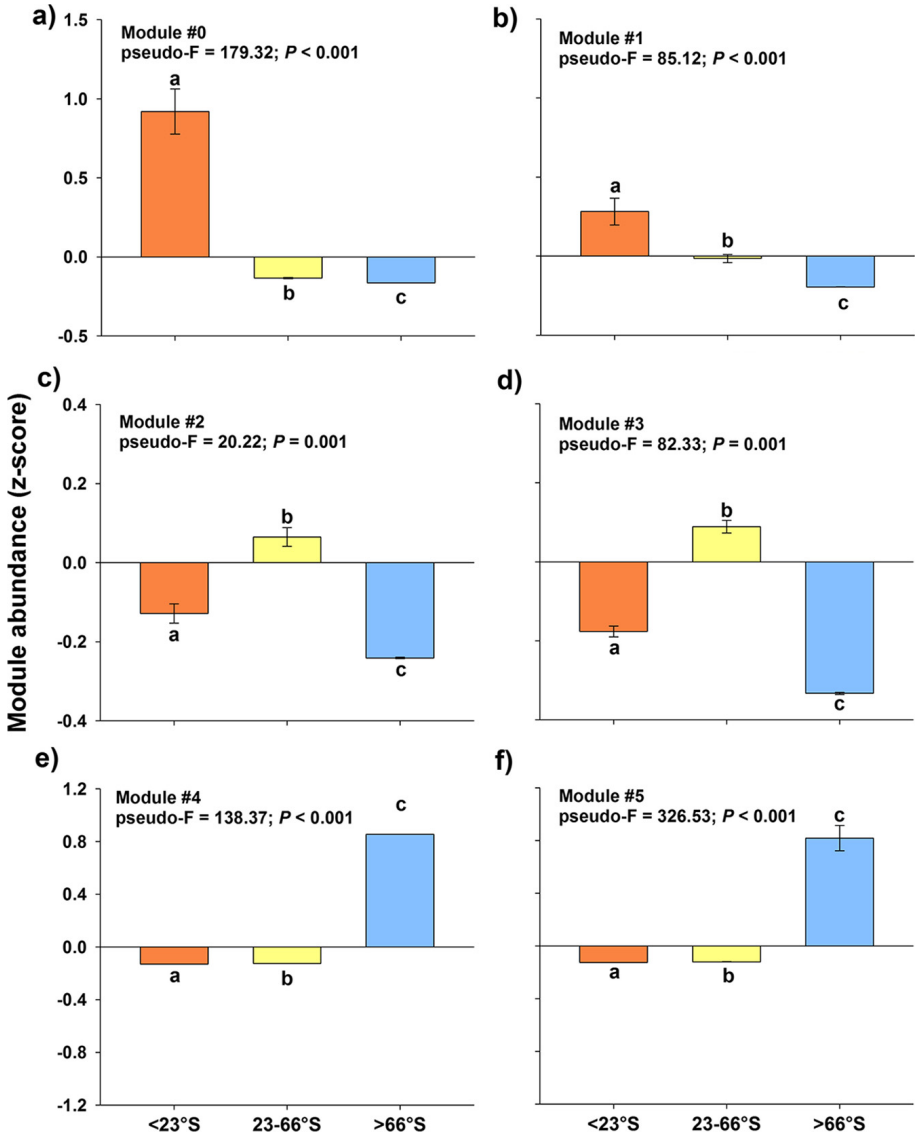

FIG. 2. Mean values (±SE) for the relative abundance of modules #1–6 across three different geographical regions. Geographical regions as follows: low latitudes [23° N to 23° S], middle latitudes [23–66° S] and high latitudes [>66° S] (Marsh and Kaufman 2013). Different letters in this panel indicate significant differences among latitudinal ranges.

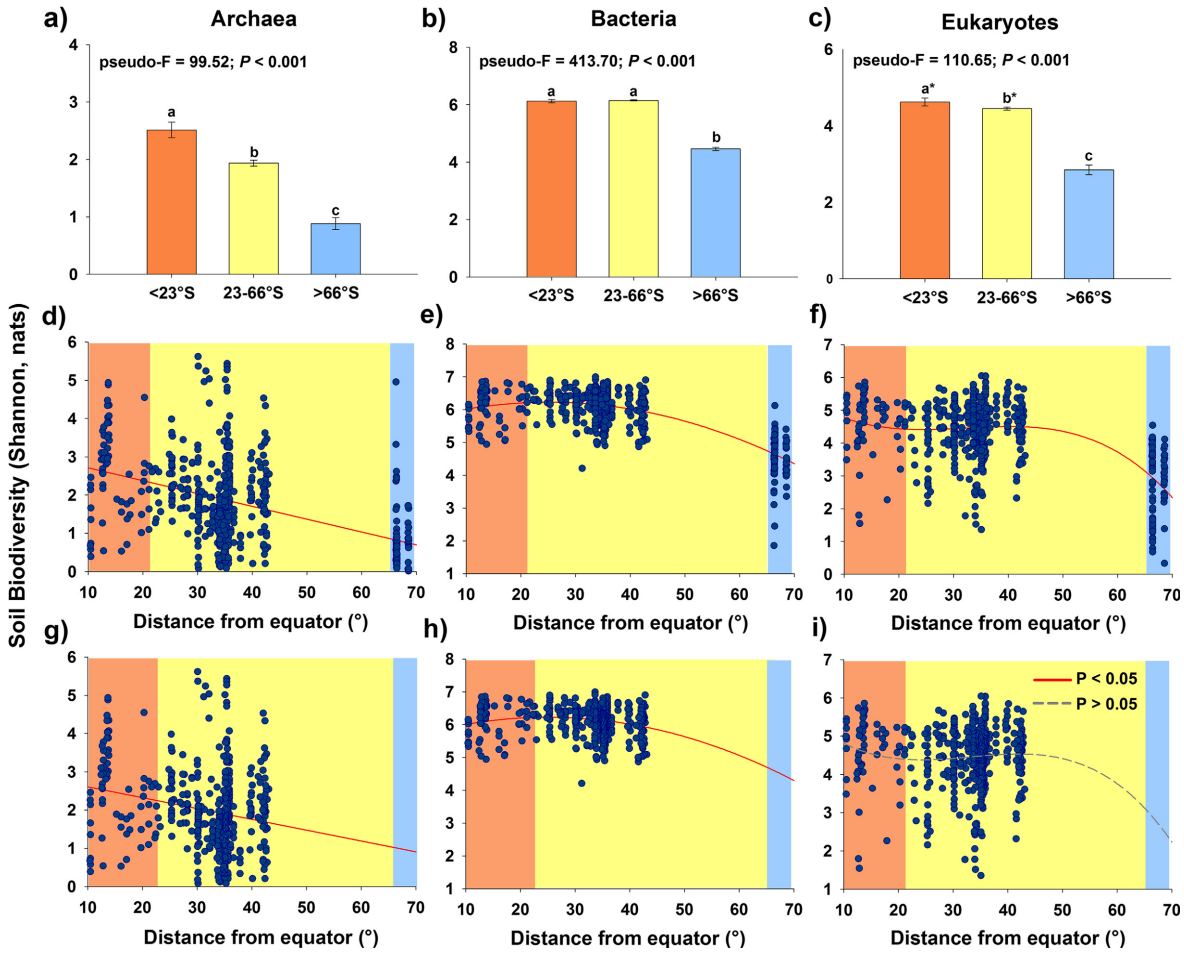

FIG. 3. Shifts in soil biodiversity with distance from the equator in the Southern Hemisphere. Panels (a–c) show mean values (±SE) for the diversity of archaea, bacteria and eukaryotes across three different geographical regions. Geographical regions as follows: low latitudes [23° N to 23° S], middle latitudes [23–66° S] and high latitudes [>66° S] (Marsh and Kaufman 2013). Different letters in this panel indicate significant differences among latitudinal ranges ($P < 0.05$ but $^*P = 0.058$, post-hoc test after PERMANOVA). Panels (d–f) show regressions between distance from the equator and the diversity of archaea, bacteria and eukaryotes in Australia and Antarctica together. Panels (g–i) show regressions between distance from the equator and the diversity of archaea, bacteria and eukaryotes in Australia using the same models in panels (e, f). R^2, P-values and AIC_c index describing the relationship between latitude (absolute) and soil biodiversity (Shannon) are available in Appendix S3: Table S2.

Specifically, we found strong negative correlations between distance from equator and the diversity of archaea, bacteria and microeukarya in the Southern Hemisphere (i.e., Australia and Antarctica together; Appendix S3: Tables S1 and S2). In general, Shannon's Diversity Index indicated that soil biodiversity (archaea, bacteria and eukarya) decreased with distance from the equator toward Antarctica (Fig. 3d–f). Archaea followed a linear decrease in Shannon's diversity with distance from the equator, while that of bacterial and eukaryotic communities exhibited quadratic and cubic relationships, respectively (Fig. 3; Appendix S3: Table S2). Furthermore, we found strong negative correlations between distance from the equator and richness (i.e., the observed numbers of OTUs) within major groups of archaea, bacteria and microeukarya for both continents together (Appendix S3: Table S3; community composition available in Fig. 4). When comparing the diversity of archaea, bacteria and eukaryotes across large geographical regions (low, mid and high latitudinal regions of our transect), we found that soil biodiversity was the lowest in Antarctica (Fig. 3a–c). However, when limiting our analyses to Australia only, we only found small latitudinal variations in soil biodiversity across the continent. For example, we found weak, albeit significant, negative significant correlations between the diversity of bacteria and archaea and their distance from the equator (Fig. 3g–i; Appendix S3: Table S1). However, the diversity of soil microeukarya was not significantly correlated with distance from the equator (Appendix S3: Table S1). When comparing the diversity of archaea, bacteria and microeukarya within Australia, small variations were also detected in the diversity of eukaryotes and archaea between low and mid latitudes, but the diversity of bacteria across these two regions was similar (Fig. 3a–c).

We found significant positive relationships between the Shannon diversity of archaea, bacteria and eukarya (Appendix S1: Fig. S5). Similar results were found when we evaluated the correlation between the richness of main taxa of archaea, bacteria and eukaryotes (Appendix S3: Table S4). Most importantly, we observed significant positive relationships between the matrices of dissimilarity of archaea,

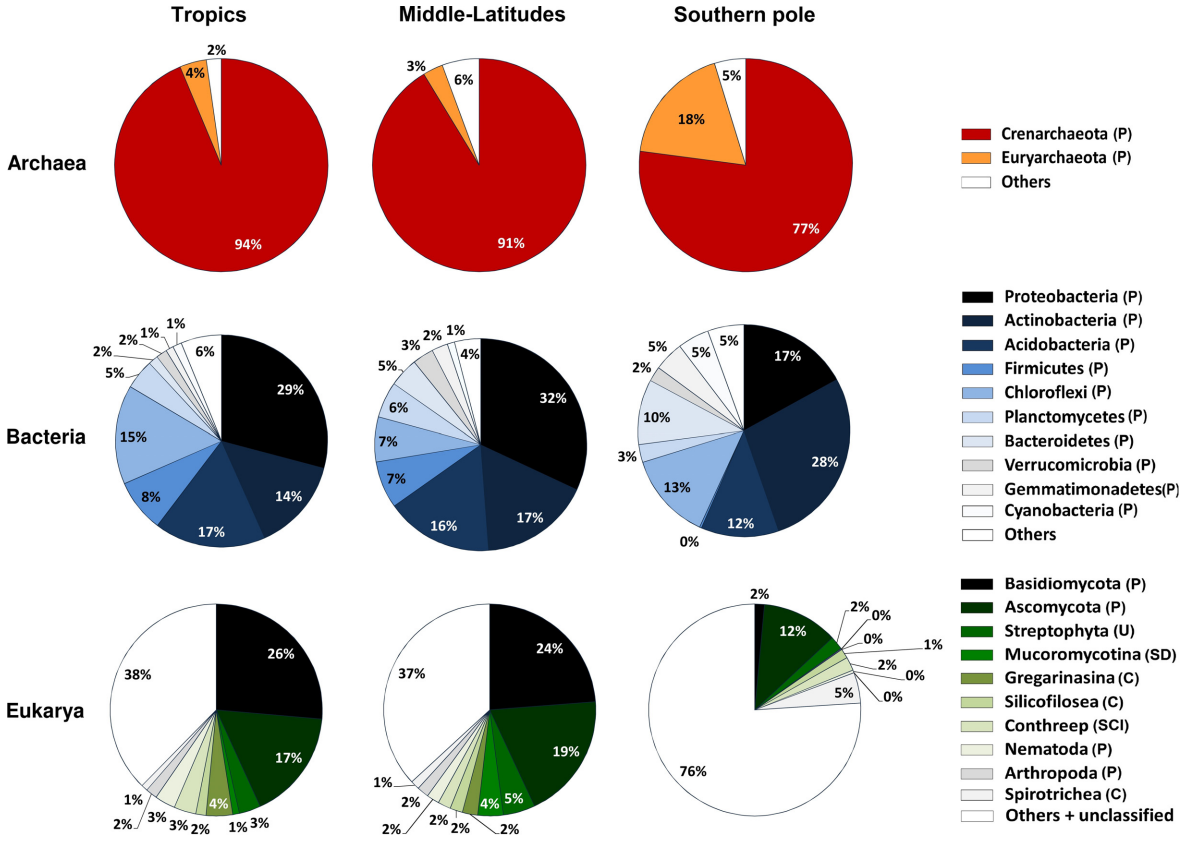

FIG. 4. Relative abundance of main groups of archaea, bacteria and eukaryotes across different latitudinal regions from the Southern Hemisphere. P = Phylum; C = Class; SCl = Super clade; U = Uncladed; SD = Subdivision. Geographical regions as follows: low latitudes [23° N to 23° S], middle latitudes [23–66° S] and high latitudes [>66° S] (Marsh and Kaufman 2013).

bacteria and eukarya (Fig. 5), suggesting commonalities in the processes driving community diversity and composition at the cross-continental scale. Moreover, the diversity of aboveground communities (Shannon) was strongly and positively related to the diversity of bacteria and eukaryotes, but not to that of archaea (Appendix S1: Fig. S5).

Random Forest analyses indicated that distance from the equator is a significant predictor of soil biodiversity and the relative abundance of Modules#0–5 in (1) Australia and Antarctica together and (2) Australia alone (Appendix S1: Figs. S6, S7). The only exceptions were Modules#2 and #5 for which distance from equator was not a significant predictor when analyzing samples from Australia only (Appendix S1: Fig. S6). Temperature, soil properties and vegetation attributes were important environmental predictors of soil biodiversity and the biological network of soil microbial communities (Appendix S1: Figs. S6, S7), although the relative importance of these environmental factors was highly taxa and module dependent (Appendix S1: Figs. S6, S7).

Structural equation models explained 30–74% of the variation in Shannon soil indices and relative abundances of soil modules (Figs. 6, 7 and Appendix S1: Figs. S8–S11). In general, mean annual temperature had the largest total standardized effect (sum of direct and indirect effects) on the distribution of Modules#2, #3, #4 and #5 when analyzing Australia and Antarctica together (Fig. 6 and Appendix S1: Fig. S8). The highest negative total standardized effect of temperature was detected on Module#3 (Fig. 6 and Appendix S1: Figs. S8–S10), which contains multiple bacterial taxa with low temperature preferences, these include *Fimbriimonas* spp., *Opitutus* spp., *Candidatus Xiphinematobacter* spp., *Pedosphaera* spp., *Janthinobacterium* spp., *Rhodoplanes* spp., *Phenylobacterium* spp., *Gemmata* spp. and *Pedobacter* spp (Oliverio et al. 2016). Distance from the equator and soil pH both had total negative effects on the relative abundance of Module#0 in Australia and Antarctica together and Australia only (Fig. 6 and Appendix S1: Figs. S8–S10). Module#1 was mainly driven by aridity in Australia and Antarctica together and Australia only (Fig. 6 and Appendix S1: Figs. S8–S10). Remarkably, multiple phenotypes of the dryland bacteria *Geodermatophilus obscurus* and *Rubrobacter* spp. were included in this module (Appendix S3: Table S1). Soil properties, aridity, aboveground diversity and cropping were also major drivers of the relative abundance of different ecological clusters when Australia and Antarctica are analyzed together, however the relative importance of these environmental factors was highly module dependent (Appendix S1: Fig. S10). The importance of temperature as a driver of the relative abundance of modules was much more limited in Australia only (Appendix S1: Fig. S10).

Distance from the equator showed the largest negative total standardized effect (sum of direct and indirect effects) on the diversity of soil archaea, bacteria and eukaryota (Fig. 7), when analyzing data from Australia and Antarctica

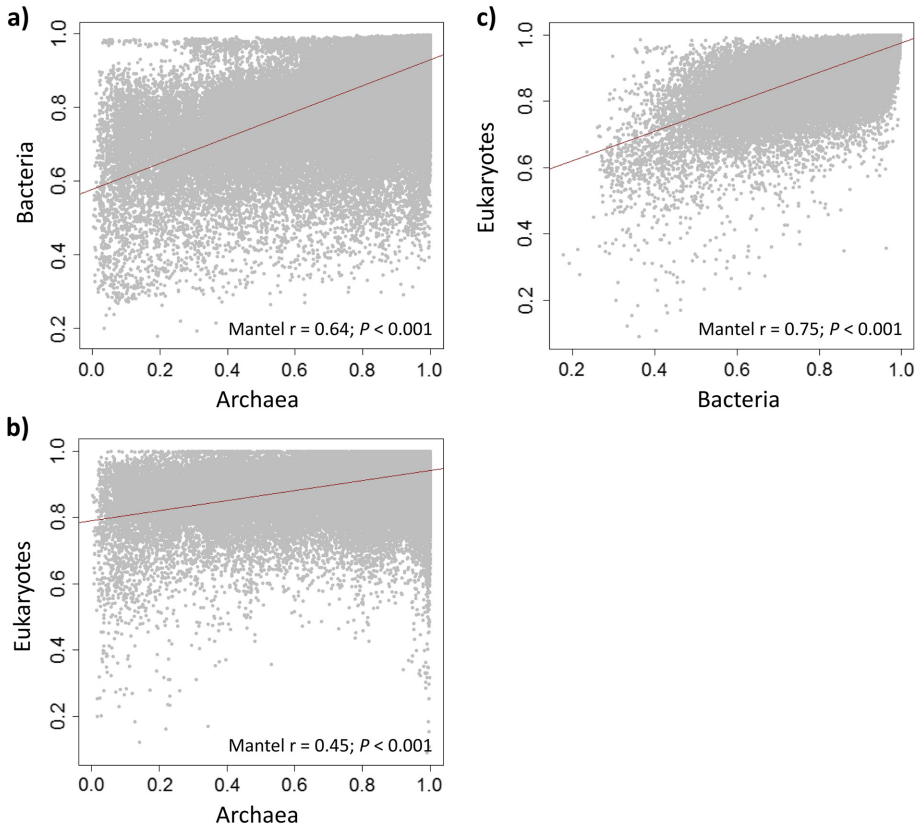

FIG. 5. Relationship between β-diversity (community dissimilarity) based on Bray-Curtis distance for archaea, bacteria and eukaryotes across the Southern Hemispheres samples (Australia and Antarctica). The solid lines represent the fitted linear regressions.

together. Similar trends were found when limiting analyses to Australia only (Appendix S1: Fig. S11). Temperature had a positive total standardized effect on soil biodiversity (Fig. 7) in Australia and Antarctica together. Importantly, the effect of temperature on the diversities of bacteria and archaea was reversed when limiting analyses to Australia (Fig. 7 vs. Appendix S1: Fig. S11). When samples from Australia and Antarctica are analyzed together, distance from the equator was shown to indirectly drive soil biodiversity via strong reductions in mean annual temperatures. These in turn drove soil biodiversity directly (archaea) and indirectly for bacteria (via changes in vegetation types) in Australia and Antarctica together. Distance from equator effects on diversity of bacteria and archaea were mainly direct in Australia only (Appendix S1: Fig. S11). Regarding eukaryotes, distance from the equator was shown to drive the diversity of these organisms via soil-C in both Australia and Antarctica together and Australia only (Fig. 7; Appendix S1: Fig. S11). Aboveground biodiversity showed positive effects for bacteria (direct) and eukarya (indirect via soil-C), but was negatively related to the diversity of archaea (Fig. 7). Croplands and/or grasslands showed a positive direct effect on the diversity of bacteria and eukaryotes (vs. other ecosystem types; Fig. 7 and Appendix S1: Fig. S11). Soil pH had a positive direct effect on the diversity of bacteria. See Appendix S4 and Appendix S3: Table S4 for correlations between richness of multiple soil trophic levels and environmental drivers.

DISCUSSION

Our study provides the first cross-continental survey simultaneously identifying the major environmental predictors of soil biodiversity and the abundance of ecological clusters within a network of soil archaea, bacteria and eukaryotes in the Southern Hemisphere. We provide novel evidence for substantial changes in the relative abundances of modules within the correlation network of archaea, bacteria and eukarya across a wide gradient of latitudes and environmental conditions. Our findings further indicate that the diversities of soil archaea, bacteria and microeukarya largely co-vary across multiple locations in the Southern Hemisphere. These results suggest that the diversity of particular soil taxa can predict the diversity of other soil organisms and that sites that are more diverse in bacteria and archaea also support a more diverse community of micro-eukaryotes. Ultimately this suggests that there are key environmental drivers that influence the diversity and distribution microbes from all domains of life across large spatial areas. Finally, we detected a strong reduction in soil biodiversity in Antarctica vs. continental Australia. These results confirm that similar to the diversity of plants and animals for the Southern Hemisphere (MacArthur 1975, Rohde 1992, Gaston 2000), the biodiversity of soil microbial (bacteria, archaea and microeukarya) is strongly reduced in Antarctica. These results are supported by a recent meta-analysis showing a decrease in the diversity of soil bacteria from the

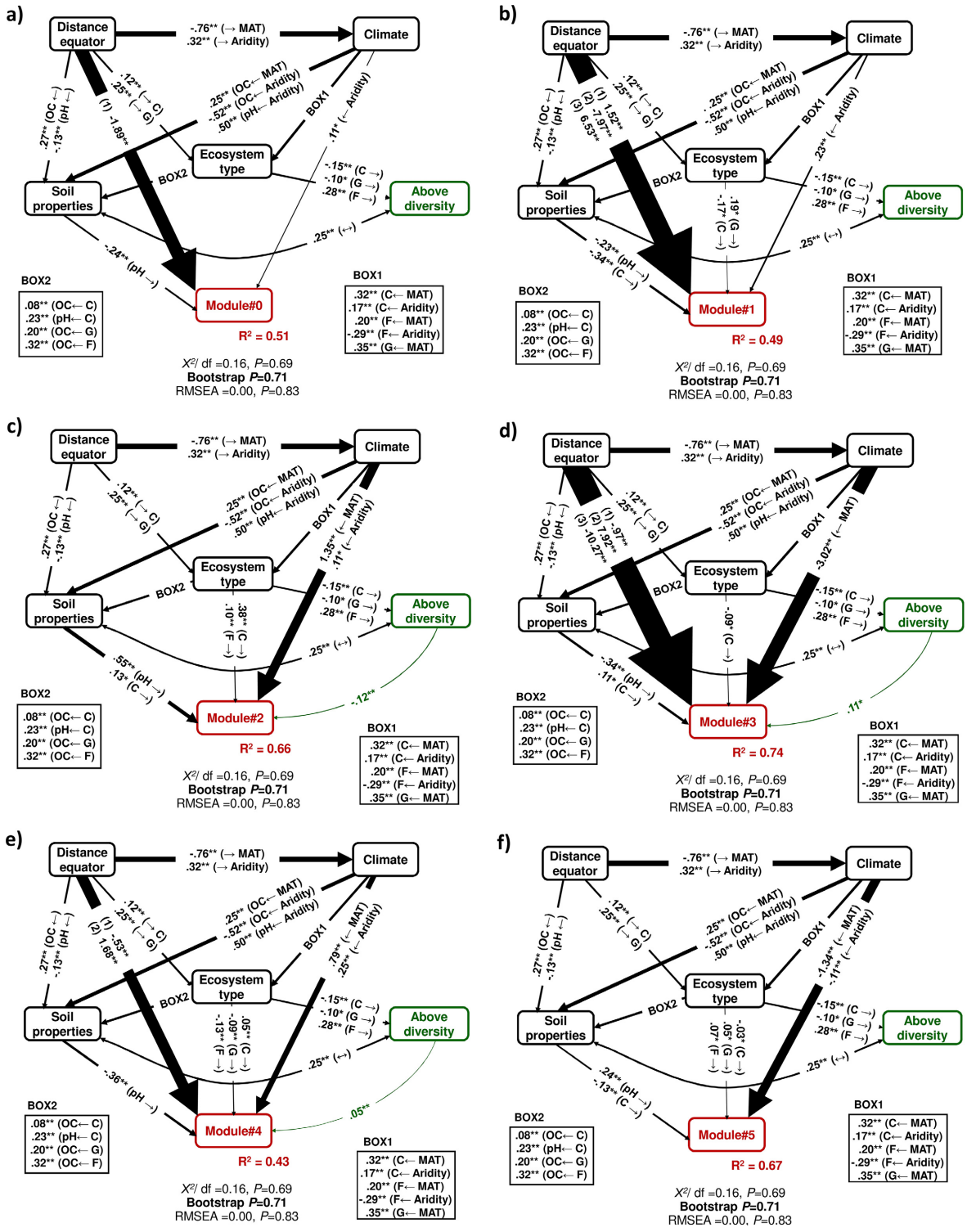

FIG. 6. Structural equation model describing the effects of multiple drivers on the relative abundance of Modules#1–6 in the Southern Hemisphere (Australia and Antarctica; See Appendix S1: Fig. S9 for Australia only). Numbers adjacent to arrows are indicative of the effect size of the relationship. R^2 denotes the proportion of variance explained. Significance levels of each predictor are $*P < 0.05$, $**P < 0.01$. C = Croplands; G = Grasslands. STE = Standardized total effects from SEM–this is the sum of direct and indirect effects from each environmental predictor on a particular response variables (diversity of archaea, bacteria and eukaryotes). The components within climate, soil properties and vegetation types are included as independent observable variables in the model, however we group them in the same box in the model for graphical simplicity. We did not include the relationship between mean annual temperature and pH in this model to release a degree of freedom which allow us to test the goodness of the model. All variables within the climate (aridity and MAT), soil properties (soil C and pH) and vegetation types (crops, forests and grasslands) boxes are allow to co-vary with each other.

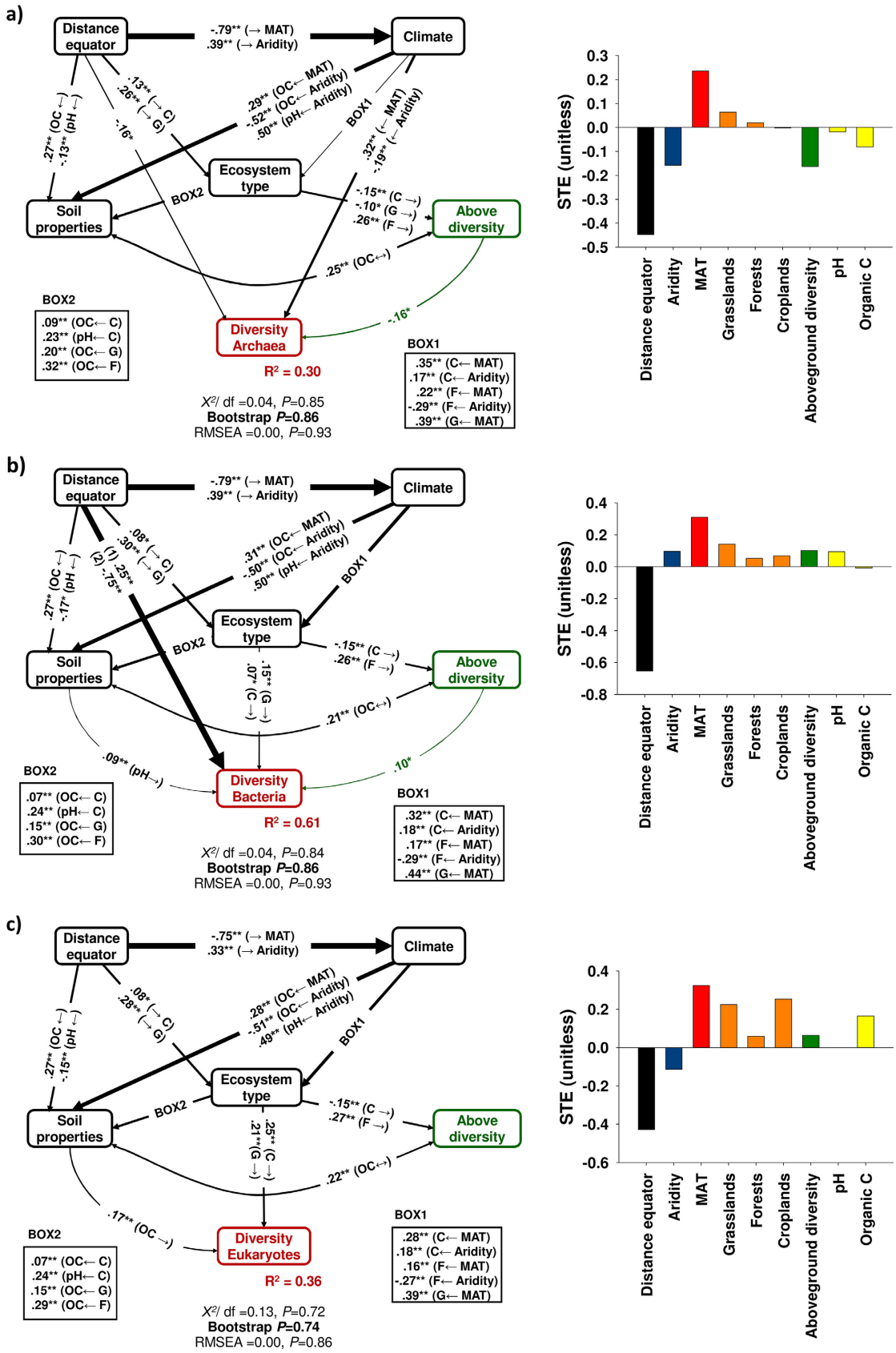

FIG. 7. Structural equation model describing the effects of multiple drivers on the diversity of soil archaea (a), bacteria (b) and eukaryotes (c) in the Southern Hemisphere (Australia and Antarctica; See Appendix S1: Fig. S11 for Australia only). Rest of the caption like in Fig. 6.

northern hemisphere to Antarctica (Delgado-Baquerizo et al. 2016*a*) and by two earlier studies reporting latitudinal diversity gradients in marine bacteria (Fuhrman et al. 2008, Ladau et al. 2013). It further supports the large body of the literature suggesting that the diversity of bacteria and eukaryotes is extremely limited in Antarctica (Adams et al. 2006, Fell et al. 2006, Smith et al. 2006, Yergeau et al. 2007, Aislabie et al. 2008, Niederberger et al. 2008, Pointing et al. 2009, Czechowski et al. 2016, Newsham et al. 2016). However, we relatively weak changes in the diversity of soil microbes across continental Australia, in agreement with those studies that did not find strong changes in soil microbial diversity across the Northern Hemisphere (Lawley et al. 2004, Lauber et al. 2009, Chu et al. 2010, Delgado-Baquerizo et al. 2016*a*, Wang et al. 2016).

Most importantly, the current study provides a reliable set of mechanisms to explain the major ecological drivers of soil biodiversity in the Southern Hemisphere as well as of the relative abundances of particular strongly co-occurring soil modules. Structural equation modeling indicates that the sharp decline in biodiversity in Antarctica vs. Australia is coupled directly and indirectly to a reduction in temperature with distance from the equator for all soil trophic levels. Temperature was the most universal driver of soil biodiversity in the southern hemisphere, always showing positive effects on the diversity of the main groups within archaea, bacteria and eukarya when data of Australia and Antarctica is analyzed together. These findings support the physiological tolerance hypothesis, which suggests that physiological constraints linked to cold temperature limits biodiversity and alters the correlation network of soil inhabitants far from the tropics (Currie et al. 2004). Temperatures below 0°C strongly limit the existence of vegetation in Antarctica vs. Arctic regions, negatively impacting soil diversity both directly via a lack of existence of plant-soil interactions and indirectly via reductions in litter inputs and resource availability, e.g., soil carbon (Appendix S1: Fig. S12), explaining the lowest soil biodiversity found in the high latitude zones. Interestingly, the positive effects of temperature on diversity of bacteria and archaea were reversed when analyzing data from Australia only, suggesting that within ranges of high temperatures—average of 25.6°C and 14.9°C for low and middle latitudes—increases in temperature might negatively impact on the diversity of these organisms. Similarly, temperature largely regulated the relative abundance of soil modules of co-occurring taxa both when analyses Australia and Antarctica together and Australia only. For example, temperature had the highest negative effect on the relative abundance of Module#3. This module included multiple bacterial taxa—listed in the results section—with low temperature preferences previously reported by Oliverio et al. (2016).

The large distance between Antarctica and Australia may also explain the strong reductions in soil biodiversity reported from the low and middle to high latitudinal regions. Reductions in aboveground biodiversity toward the Antarctic may also alter both the diversity and the correlation network of soil inhabitants. Interestingly, while the diversity of archaea and bacteria slightly decreased with latitude both within Australia and in Australia and Antarctica together, the diversity of eukaryotes was only lower in Antarctica vs. Australia. The most likely reason to support such a pattern is that key drivers of eukaryotic diversity such as the availability of resources, e.g., soil carbon, a common proxy of organic matter and litter inputs, are largely reduced in Antarctica, but are very similar for the middle and low-latitude regions within Australia (Appendix S1: Fig. S11). Thus, while aridity largely increased toward Antarctica, strongly decreasing the amount of soil C available for soil organisms (Fig. 7), distance from equator did not affect aridity within Australia (Appendix S1: Fig. S11). This lack of relationship between latitude and aridity within Australia might ultimately explain the lack of relationship between latitude and diversity of eukaryotes within this continent.

Although temperature was the major environmental driver of soil biodiversity and the relative abundance of ecological clusters across Australia and Antarctica, other factors such as aboveground diversity, aridity and soil properties may also help to explain the reported changes in the diversities and correlation networks of soil organisms across Australia and Antarctica, but especially within Australia. Aboveground biota directly affect the diversity of soil organisms by providing different types of carbon, altering micro-habitat conditions (e.g., shading, water regulation) and soil chemistry (e.g., root exudation). Similarly plant and animal diversity may alter the diversity and the correlation network of soil inhabitants via plant/animal-microbial interactions (e.g., mycorrhizae, rhizobia and plant/animal pathogens), and by controlling the quality and quantity of resource inputs via root exudates and litter (Hooper et al. 2000, Scherber et al. 2010). For example, the relative abundances of Modules#0, #2 and #3, which contain multiple mycorrhizal and animal pathogenic taxa, was strongly reduced toward the Antarctic, where vegetation influence is strongly limited. For bacteria, decreases in soil pH with distance from the equator may also help explain the reductions in bacterial diversity. Soil pH is a main driver of bacterial diversity (Fierer and Jackson 2006), thus a reduction in soil pH with distance from the equator may also influence the total diversity of these organisms. Moreover, the relative abundance of soil Module#1 was strongly positively related to aridity—a module which included the dryland bacteria *Geodermatophilus obscurus* and *Rubrobacter* sp. (Chen et al. 2004, Mohammadipanah and Wink 2016). Actinobacteria species may outcompete other dominant groups such as Acidobacteria under the most arid conditions in low organic soils, likely due to their high resistance to desiccation and starvation conditions (Battistuzzi and Hedges 2009, Lennon and Jones 2011). Similarly, Basidiomycota seem to be much more affected by increases in aridity, pH and reductions in soil carbon than Ascomycota.

Our network analyses provided evidence of strong co-occurring patterns of parasite-hosts and predator-prey relationships across the studied latitudinal gradient in the Southern Hemisphere, which are both interactions of paramount importance in soil systems (Geisen et al. 2015, Mahé et al. 2017). For example, Module#3, whose abundance peaked at middle latitudes and was negatively related to temperature (Fig. 2). It contained the parasite group Gregarinasina and multiple invertebrate organisms. *Gregarina* spp. are often found to be a parasite of soil invertebrates including arthropoda, and annelids (Omoto and Cartwright 2003). Interestingly, Module#3 also included arachnid species, a group of invertebrates that have recently been reported to be

parasitized by *Gregarina* species (Dias et al. 2017). Furthermore, Module#4, abundant in high latitudes included several phylotypes from phylum *Ciliophora* (Protozoa), a group of organisms that is well-known to feed on bacteria, an interaction that might allow phylum *Ciliophora* to colonize the thrive under the extreme conditions found in Antarctica. Our results suggest that co-occurrence network analyses can be potentially used to identify new parasite-hosts and predator-prey interactions (Stopnisek et al. 2015). Moreover, our results suggest that the relative abundance of particular modules is predictable using common environmental factors. Therefore, this approach can be used to provide new ideas for future experimental work and can further help us to identify potential locations where particular interactions (e.g., parasite-hosts or predator-prey) are expected to be dominant.

Overall, we provide empirical evidence that the soil biodiversity and the relative abundance of modules within the correlation network of multiple soil trophic levels show large differences between continental Australia and Antarctica. We acknowledge that we had lower number of samples in Antarctica vs. continental Australia, which is a consequence of the considerable logistical constraints in accessing locations in Antarctica. Previous studies have also reported very low levels of microbial diversity in Antarctica (Fuhrman et al. 2008, Delgado-Baquerizo et al. 2016*a*), suggesting our results are robust to this unequal sampling coverage. Moreover, we would like to clarify that information on Tasmania (41° S) is included in the Middle-latitude region. Thus, any specific effect coming from the island should be reduced. Also, although Tasmania is currently an island, it was part of the Australian continent until relatively recently, i.e., 10,000 yr ago, in geological as well as evolutionary terms. Moreover, it might be argued that Tasmania might well have evolved a different community of microorganisms—as a consequence of the largely expected rapid evolutionary rates for soil microbial communities. However, the approach used here—identifying OTUs by clustering 16S/18S ribosomal RNA at 97% similarity—is relatively insensitive to rapid genetic change driven by isolation and adaptation to new environments. Ribosomal RNA genes are highly conserved and exhibit much slower rates of mutation/change than other parts of an organism's genome (Woese and Fox 1977). We, therefore, did not expect any particular confounding effects derived from island biogeography theory in our conclusions.

In conclusion, this study provides solid evidence that the diversities of soil archaea, bacteria and eukaryotes are strongly limited in Antarctica vs. continental Australia. Similar to what has been reported in the Northern Hemisphere, we only detected small variations in the diversity of soil microbes across continental Australia. Moreover, we provide novel evidence for substantial latitudinal changes in the relative abundance of ecological clusters (modules) within the correlation network of soil bacteria, archaea and eukaryotes. Reductions in soil biodiversity and changes in the relative abundance of soil modules of strongly co-occurring taxa were linked to strong latitudinal declines in temperature, changes in aridity, vegetation type and reductions in aboveground biodiversity, soil carbon and pH. In addition, our work provides new insights on the mechanisms driving soil biodiversity in the Southern Hemisphere, a region largely unexplored by previous studied.

Acknowledgments

M.D-B. conceived this study. M.D-B. developed the conceptual basis for this manuscript in consultation with A.B., F.R., B.K.S. and P.G.D. All the authors except M.D-B., B.K.S., J.R.P. conducted field surveys and collected the soils used in this study under the coordination of A.B. M.D-B. conducted statistical analyses. A.B. conducted bioinformatics analyses. The first draft of this paper was written by M.D-B., and all co-authors (especially P.G.D., F.R., B.K.S. and A.B.) significantly contributed to improve it. We thank the anonymous reviewers for their careful reading of our manuscript and for their intellectual contributions to our work. We would like to acknowledge the contribution of the Biomes of Australian Soil Environments (BASE) consortium (https://data.bioplatforms.com/organization/pages/bpa-base/acknowledgements) in the generation of data used in this publication. The BASE project is supported by funding from Bioplatforms Australia through the Australian Government National Collaborative Research Infrastructure Strategy (NCRIS) https://doi.org/10.1186/s13742-016-0126-5, We thank the BASE project and its contributors (https://downloads.bioplatforms.com/base/acknowledgements) for sequence and edaphic data used in this work. The data used in this study is available from the BASE dataportal (https://downloads.bioplatforms.com/base/). M.D-B. also acknowledge support from the Marie Sklodowska-Curie Actions of the Horizon 2020 Framework Program H2020-MSCA-IF-2016 under REA grant agreement no. 702057. M.D-B. and B.K.S. also acknowledge support from the Australian Research Council (project DP13010484).

Literature Cited

Adams, B. J., et al. 2006. Diversity and distribution of Victoria Land biota. Soil Biology & Biochemistry 38:3003–3018.

Aislabie, J. M., K. Chhour, D. J. Saul, S. Miyauchi, J. Ayton, R. F. Paetzold, and M. R. Balks. 2008. Dominant bacteria in soils of Marble Point and Wright Valley, Victoria Land, Antarctica. Geoderma 144:9–20.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Barberán, A., E. O. Casamayor, and N. Fierer. 2014. The microbial contribution to macroecology. Frontiers in Microbiology 5:203.

Bardgett, R. D., and W. H. van der Putten. 2014. Belowground biodiversity and ecosystem functioning. Nature 515:505–511.

Barrett, J. E., R. A. Virginia, D. H. Wall, A. N. Parsons, L. E. Powers, and M. B. Burkins. 2004. Variation in biogeochemistry and soil biodiversity across spatial scales in a polar desert ecosystem. Ecology 85:3105–3118.

Bastian, M., S., Heymann, and M., Jacomy (2009). Gephi: an open source software for exploring and manipulating networks. International AAAI Conference on Weblogs and Social Media.

Battistuzzi, F. U., and S. B. Hedges. 2009. Major clade of prokaryotes with ancient adaptations to life on land. Molecular Biology and Evolution 26:335–343.

Bissett, A., et al. 2016. Introducing BASE: the Biomes of Australian Soil Environments soil microbial diversity database. GigaScience 5:21.

Breiman, L. 2001. Random forests. Machine Learning 45:5–32.

Burnham, K. P., and D. R. Anderson. 2002. Model selection multimodel inference a practical information-theoretic approach, Second edition. Springer, New York, New York, USA.

Chen, M. Y., S. H. Wu, G. H. Lin, C. P. Lu, Y. T. Lin, W. C. Chang, and S. S. Tsay. 2004. *Rubrobacter taiwanensis* sp. nov., a novel thermophilic, radiation-resistant species isolated from hot springs. International Journal of Systematic and Evolutionary Microbiology 54:1849–1855.

Chu, H., N. Fierer, C. L. Lauber, J. Caporaso, R. Knight, and P. Grogan. 2010. Soil bacterial diversity in the Arctic is not fundamentally different from that found in other biomes. Environmental Microbiology 12:2998–3006.

Currie, D. J., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. Nature 329:326–327.

Currie, D. J., et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecology Letters 7:1121–1134.

Czechowski, P., L. J. Clarke, A. Cooper, and M. I. Stevens. 2016. Antarctic eukaryotic soil diversity of the Prince Charles Mountains revealed by high-throughput sequencing. Soil Biology & Biochemistry 95:112–121.

Delgado-Baquerizo, M., F. T. Maestre, P. B. Reich, P. Trivedi, Y. Osanai, Y.-R. Liu, K. Hamonts, T. C. Jeffries, and B. K. Singh. 2016*a*. Carbon content and climate variability drive global soil bacterial diversity patterns. Ecological Monographs 86:373–380.

Delgado-Baquerizo, M., L. Giaramida, P. B. Reich, A. N. Khachane, K. Hamonts, C. Edwards, L. A. Lawton, and B. K. Singh. 2016*b*. Lack of functional redundancy in the relationship between microbial diversity and ecosystem functioning. Journal of Ecology 104:936–946.

Delgado-Baquerizo, M., F. T. Maestre, P. B. Reich, T. C. Jeffries, J. J. Gaitan, D. Encinar, M. Berdugo, C. D. Campbell, and B. K. Singh. 2016*c*. Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications 7:10541.

Dias, G., R. Dallai, A. Carapelli, J. P. P. Almeida, L. A. O. Campos, L. R. A. Faroni, and J. Lino-Neto. 2017. First record of gregarines (Apicomplexa) in seminal vesicle of insect. Scientific Reports 7:175.

Fell, J. W., G. Scorzetti, L. Connell, and S. Craig. 2006. Biodiversity of micro-eukaryotes in Antarctic Dry Valley soils with <5% soil moisture. Soil Biology & Biochemistry 38:3107–3119.

Fierer, N., and R. B. Jackson. 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences USA 103:626–631.

Fierer, N., M. S. Strickland, D. Liptzin, M. A. Bradford, and C. C. Cleveland. 2009. Global patterns in belowground communities. Ecology Letters 12:1238–1249.

Fuhrman, J. A., J. A. Steele, I. Hewson, M. S. Schwalbach, M. V. Brown, J. L. Green, and J. H. Brown. 2008. A latitudinal diversity gradient in planktonic marine bacteria. Proceedings of the National Academy of Sciences USA 105:7774–7778.

Gaston, K. J. 2000. Global patterns in biodiversity. Nature 405: 220–227.

Geisen, S., I. Laros, A. Vizcaíno, M. Bonkowski, and G. A. de Groot. 2015. Not all are free-living: high-throughput DNA metabarcoding reveals a diverse community of protists parasitizing soil metazoa. Molecular Ecology 24:4556–4569.

Grace, J. B. 2006. Structural equation modeling natural systems. Cambridge University Press, Cambridge, UK.

Hooper, D. U., et al. 2000. Interactions between aboveground and belowground biodiversity in terrestrial ecosystems: patterns, mechanisms, and feedbacks. BioScience 50:1049–1061.

Ladau, J., T. J. Sharpton, M. M. Finucane, G. Jospin, S. W. Kembel, J. O'Dwyer, A. F. Koeppel, J. L. Green, and K. S. Pollard. 2013. Global marine bacterial diversity peaks at high latitudes in winter. ISME Journal 7:1669–1677.

Lane, D. J. 1991. Nucleic acid techniques in bacterial systematics. John Wiley and Sons, New York, New York, USA.

Lane, D. J., B. Pace, G. J. Olsen, D. A. Stahl, M. L. Sogin, and N. R. Pace. 1985. Rapid determination of 16S ribosomal RNA sequences for phylogenetic analyses. Proceedings of the National Academy of Sciences USA 82:6955–6959.

Lauber, C. L., M. Hamady, R. Knight, and N. Fierer. 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Applied and Environment Microbiology 75:5111–5120.

Lawley, B., S. Ripley, P. Bridge, and P. Convey. 2004. Molecular analysis of geographic patterns of eukaryotic diversity in Antarctic soils. Applied and Environment Microbiology 70:5963–5972.

Lennon, J. T., and S. E. Jones. 2011. Microbial seed banks the ecological and evolutionary implications of dormancy. Nature Reviews Microbiology 9:119–130.

MacArthur, J. W. 1975. Environmental fluctuations and species diversity. Pages 74–80 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap, Cambridge, Massachusetts, USA.

Mahé, F., et al. 2017. Parasites dominate hyperdiverse soil protist communities in Neotropical rainforests. Nature Ecology & Evolution 1:91.

Marsh, W. M., and M. M. Kaufman. 2013. Physical geography: great systems and global environments. Cambridge University Press, Cambridge, UK.

Menezes, A. B., M. T. Prendergast-Miller, A. E. Richardson, P. Toscas, M. Farrell, L. M. Macdonald, G. Baker, T. Wark, and P. H. Thrall. 2015. Network analysis reveals that bacteria and fungi form modules that correlate independently with soil parameters. Environmental Microbiology 17:2677–2689.

Mohammadipanah, F., and J. Wink. 2016. Actinobacteria from arid and desert habitats: diversity and biological activity. Frontiers in Microbiology 6:1541.

Newsham, K. K., D. W. Hopkins, L. C. Carvalhais, P. T. Fretwell, S. P. Rushton, A. G. O'Donnell, and P. G. Dennis. 2016. Relationship between soil fungal diversity and temperature in the maritime Antarctic. Nature Climate Change 6:182–186.

Nguyen, N. H., Z. Song, S. T. Bates, S. Branco, L. Tedersoo, J. Menke, J. S. Schilling, and P. G. Kennedy. 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecology 20:241–248.

Niederberger, T. D., I. R. McDonald, A. L. Hacker, R. M. Soo, J. E. Barrett, D. H. Wall, and S. C. Cary. 2008. Microbial community composition in soils of Northern Victoria Land, Antarctica. Environmental Microbiology 10:1713–1724.

Oliverio, A., M. A. Bradford, and N. Fierer. 2016. Identifying the microbial taxa that consistently respond to soil warming across time and space. Global Change Biology 23:2117–2129.

Omoto, C. K., and D. C. Cartwright. 2003. Investigating the diversity of parasitic protozoa using gregarine parasites of invertebrates. Tested Studies for Laboratory Teaching 24:77–85.

Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. American Naturalist 100:33–46.

Pointing, S. B., Y. Chan, D. C. Lacap, M. C. Lau, J. A. Jurgens, and R. L. Farrell. 2009. Highly specialized microbial diversity in hyper-arid polar desert. Proceedings of the National Academy of Sciences USA 106:19964–19969.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. Oikos 65:514–527.

Sabburg, R., F. Obanor, E. Aitken, and S. Chakraborty. 2015. Changing fitness of a necrotrophic plant pathogen under increasing temperature. Global Change Biology 21:3126–3137.

Santruckova, H., et al. 2003. Microbial characteristics of soils on a latitudinal transect in Siberia. Global Change Biology 9:1106–1117.

Scherber, C., et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 25:553–556.

Shi, S., E. E. Nuccio, Z. J. Shi, Z. He, J. Zhou, and M. K. Firestone. 2016. The interconnected rhizosphere: high network complexity dominates rhizosphere assemblages. Ecology Letters 6:926–936.

Siciliano, S. D., et al. 2014. Soil fertility is associated with fungal and bacterial richness, whereas pH is associated with community composition in polar soil microbial communities. Soil Biology & Biochemistry 78:10–20.

Smith, J. J., L. A. Tow, W. Stafford, C. Cary, and D. A. Cowan. 2006. Bacterial diversity in three different Antarctic cold desert mineral soils. Microbial Ecology 51:413–421.

Stopnisek, N., D. Zuhlke, A. Carlier, A. Barberan, N. Fierer, D. Becher, K. Riedel, L. Eberl, and L. Weisskopf. 2015. Molecular mechanisms underlying the close association between soil Burkholderia and fungi. ISME Journal 10:253–264.

Szoboszlay, M., A. B. Dohrmann, C. Poeplau, A. Don, and C. C. Tebbe. 2017. Impact of land use change and soil organic carbon quality on microbial diversity in soils across Europe. FEMS Microbiology Ecology 93:1–11. (in press)

Terrat, S., et al. 2017. Mapping and predictive variations of soil bacterial richness across France. PLoS One 12:e0186766.

Turner, M. G. 1987. Spatial simulation of landscape changes in Georgia: a comparison of 3 transition models. Landscape Ecology 1:29–36.

van der Heijden, M. G., R. D. Bardgett, and N. M. van Straalen. 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11:296–310.

Wang, J. T., Y. M. Zheng, H. W. Hu, J. Li, L. M. Zhang, B. D. Chen, W. P. Chen, and J. Z. He. 2016. Coupling of soil prokaryotic diversity and plant diversity across latitudinal forest ecosystems. Scientific Reports 6:19561.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629.

Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. Annual Review of Ecology, Evolution, and Systematics 34:273–309.

Woese, C. R., and G. E. Fox. 1977. Phylogenetic structure of the prokaryotic domain: the primary kingdoms. Proceedings of the National Academy of Sciences USA 74:5088–5090.

Yergeau, E., S. Bokhorst, A. H. Huiskes, H. T. Boschker, R. Aerts, and G. A. Kowalchuk. 2007. Size and structure of bacterial, fungal and nematode communities along an Antarctic environmental gradient. FEMS Microbiology Ecology 59:436–451.

Zhou, J., et al. 2016. Temperature mediates continental-scale diversity of microbes in forest soils. Nature Communications 7:12083. https://doi.org/10.1038/ncomms12083

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.2137/suppinfo

Data Availability

The primary data associated with this study have been deposited in figshare: https://figshare.com/s/feb050570e177fcf78a8.