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

Running head: Ecological drivers of biodiversity.

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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: Biodiversity; Terrestrial Ecosystems; Archaea; Bacteria; Eukaryotes; Australia; Antarctica.

Introduction

The inverse relationship between distance from the equator and the diversity of aboveground macro-organisms is a widely recognized global biogeographical pattern (MacArthur 1975; Pianka *et al.* 1966; Rohde *et al.* 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.

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.* 2016a). 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 *et al.* 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; Aislabie et al. 2006; Fell et al. 2006; Niederberger et al. 2006; Smith et al. 2006; Yergueau et al. 2006; 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 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 (Weider *et al.* 2013; Zhou *et al.* 2016), temperature, *i.e.*, physiological constraints (Menezes *et al.* 2015; Currie *et al.* 2004) 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 micro-invertebrates (Santruckova *et al.* 2003; Fierer *et al*. 2009; Delgado-Baquerizo *et al.* 2016a; Zhou *et al.* 2016; Newsham 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 *et al.* 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; Wang *et al.* 2016; Delgado-Baquerizo et al. 2016a). 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 14237 (16S rRNA gene), 3000 (archaeal 16S rRNA gene) and 4866 (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; 10km 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 6792 taxa including 5085 bacteria, 46 archaea and 1661 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 (Barberan *et al.* 2012). We considered a co-occurrence to be robust if the Spearman's correlation coefficient was > 0.50 and $P < 0.01$ (see Barberan *et al.* 2012 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 (AICc; Burnham and Anderson 2002). The lower the AICc index the better the model. Here, we consider a ΔAICc > 2 threshold to differentiate between two substantially different models and then select the best of those models (Delgado-Baquerizo *et al.* 2016b). When more than two models were similar (*i.e*., ΔAICc < 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.* (2016c), 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 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 and 2; Appendix S3: Table S2), while Modules#2 and #3 peaked at mid-latitudes (Figs. 1b and 2; Table S2). Two modules (Modules#4 and #5; Figs. 1b and 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: Figs. 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 and 2; Appendix S1: Fig. S4).

The biodiversity of Antarctic soil microbial communities was lower than that of those in continental Australia (Fig. 3). 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, 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 (Figs. S6 and 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 and S7), although the relative importance of these environmental factors was highly taxa and module dependent (Appendix S1: Figs. S6 and 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. 2017). 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 (Fig. 10). 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 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 (Figs. 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 *et al.* 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 northern hemisphere to Antarctica (Delgado-Baquerizo *et al.* 2016a) 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; Aislabie et al. 2006; Fell et al. 2006; Newsham et al. 2016; Niederberger et al. 2006; Smith et al. 2006; Yergeau et al. 2006; Pointing et al. 2009; Czechowski 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; Wang *et al.* 2016; Delgado-Baquerizo et al. 2016a).

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 *et al.* 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.* 2016a), 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.*, 10000 years 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.

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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.

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Data accessibility:

The primary data have been deposited in figshare: https://figshare.com/s/feb050570e177fcf78a8 (DOI: 10.6084/m9.figshare.5089990).

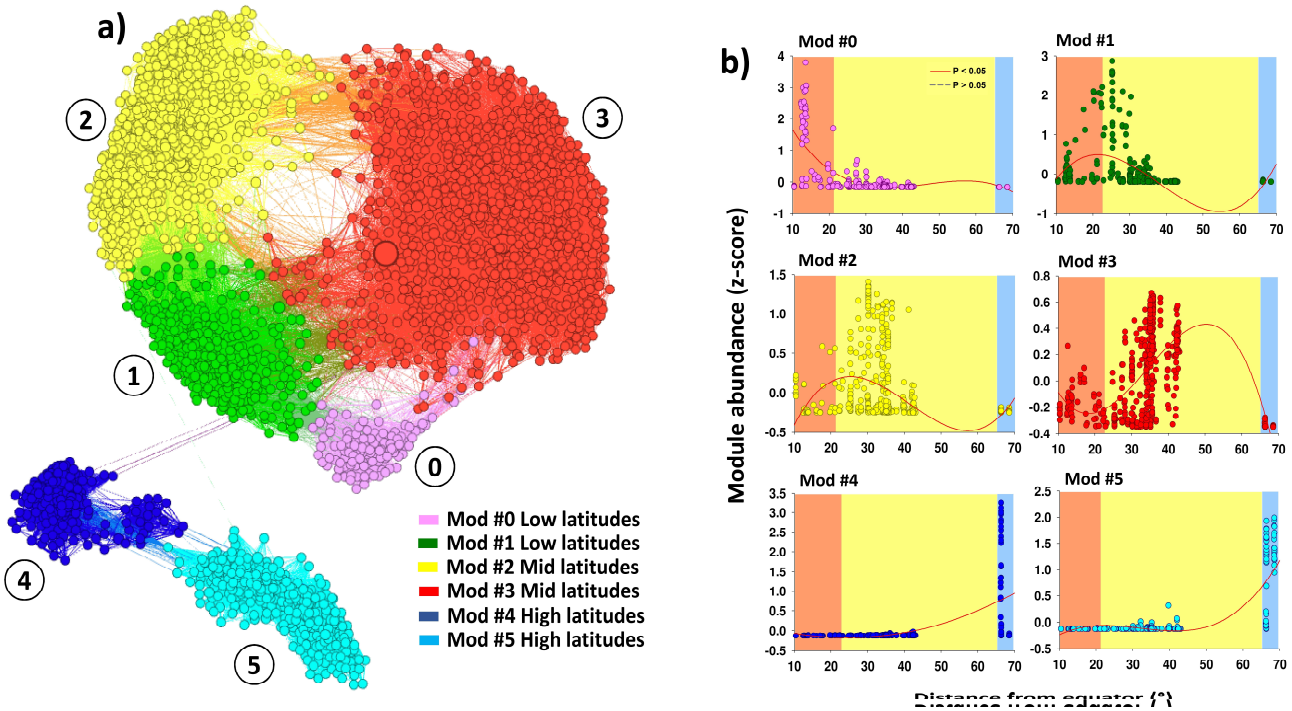

Figure 1. Soil correlation network. Panel (a) represents a network diagram with nodes (taxa of archaea, bacteria and eukaryotes) colored by each of the major six identified modules in the Southern Hemisphere (Australia and Antarctica). Panel (b) includes the relationships between latitude (absolute)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

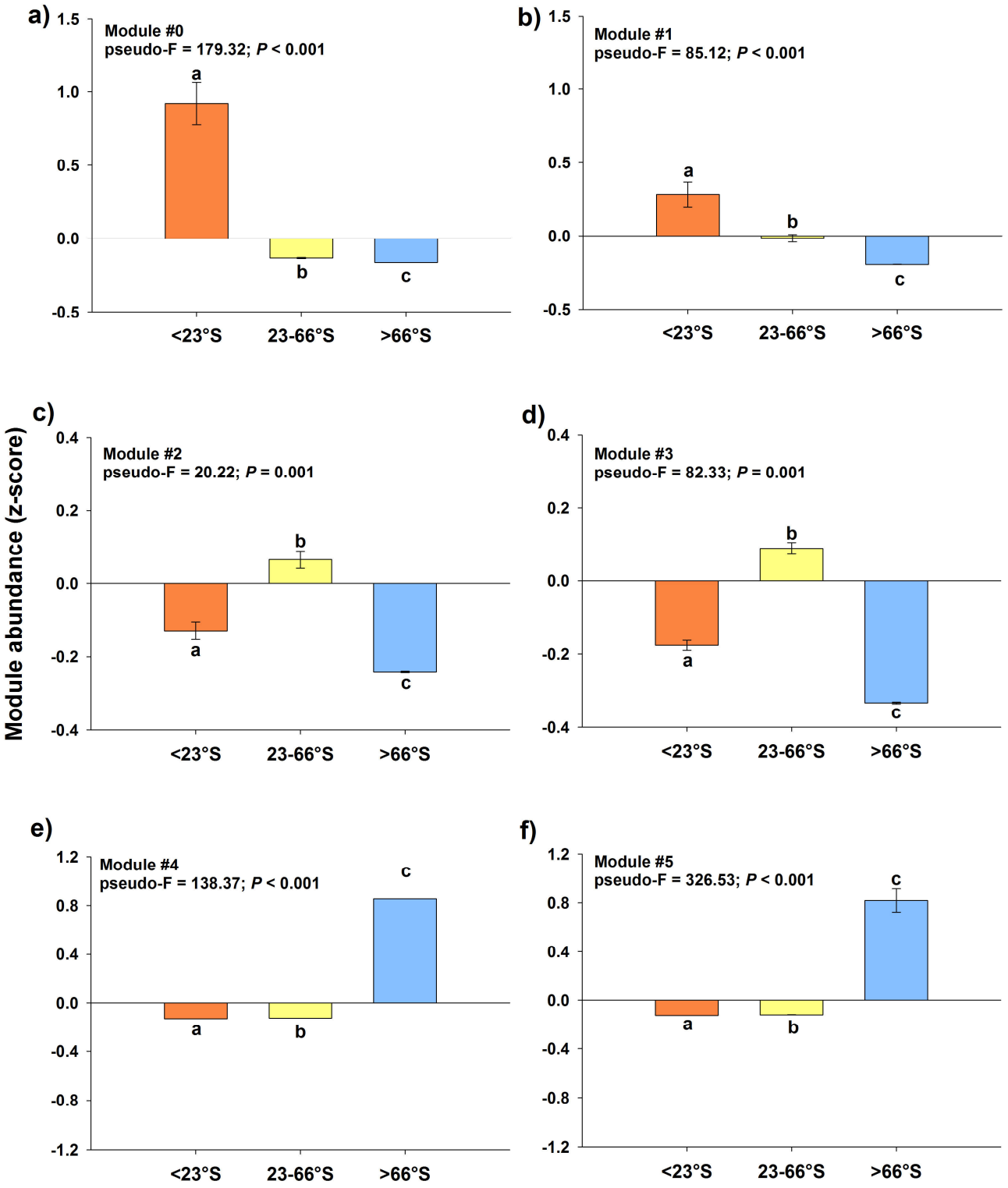

Figure 2. Mean values (±SE) for the relative abundance of modules #1-6 across three different geographical regions. Geographical regions as follows: low latitudes [23°N to 23°S], middle latitudes [23–66°S] and high latitudes [>66°S] (Marsh and Kaufman 2013). Different letters in this panel indicate significant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

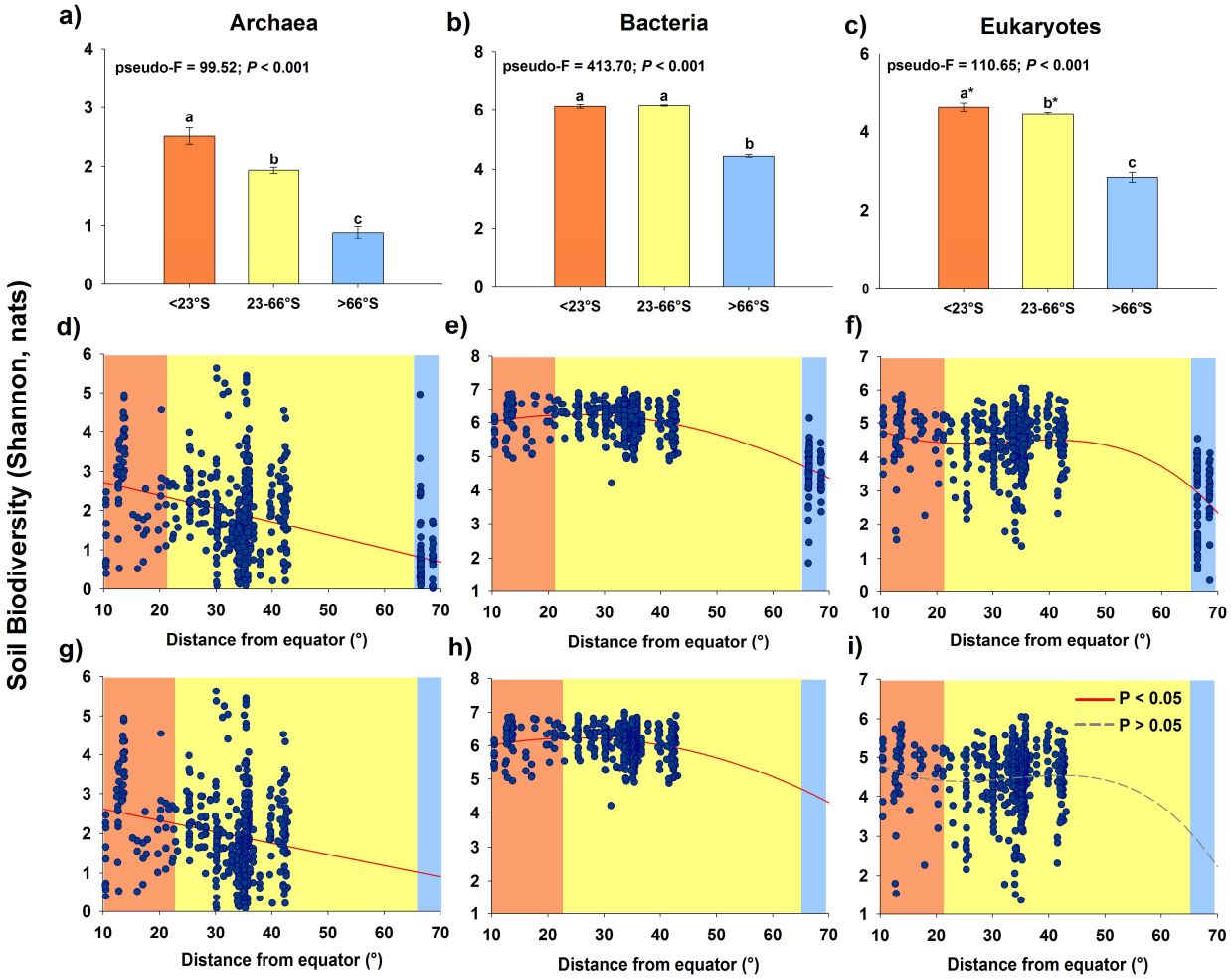

Figure 3. Shifts in soil biodiversity with distance from the equator in the Southern Hemisphere. Panels (a-c) show mean values (±SE) for the diversity of archaea, bacteria and eukaryotes across three different geographical regions. Geographical regions as follows: low latitudes [23°N to 23°S], middle 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 AICc index describing the relationship between latitude (absolute) and soil biodiversity (Shannon) are available in Appendix S3: Table S2.

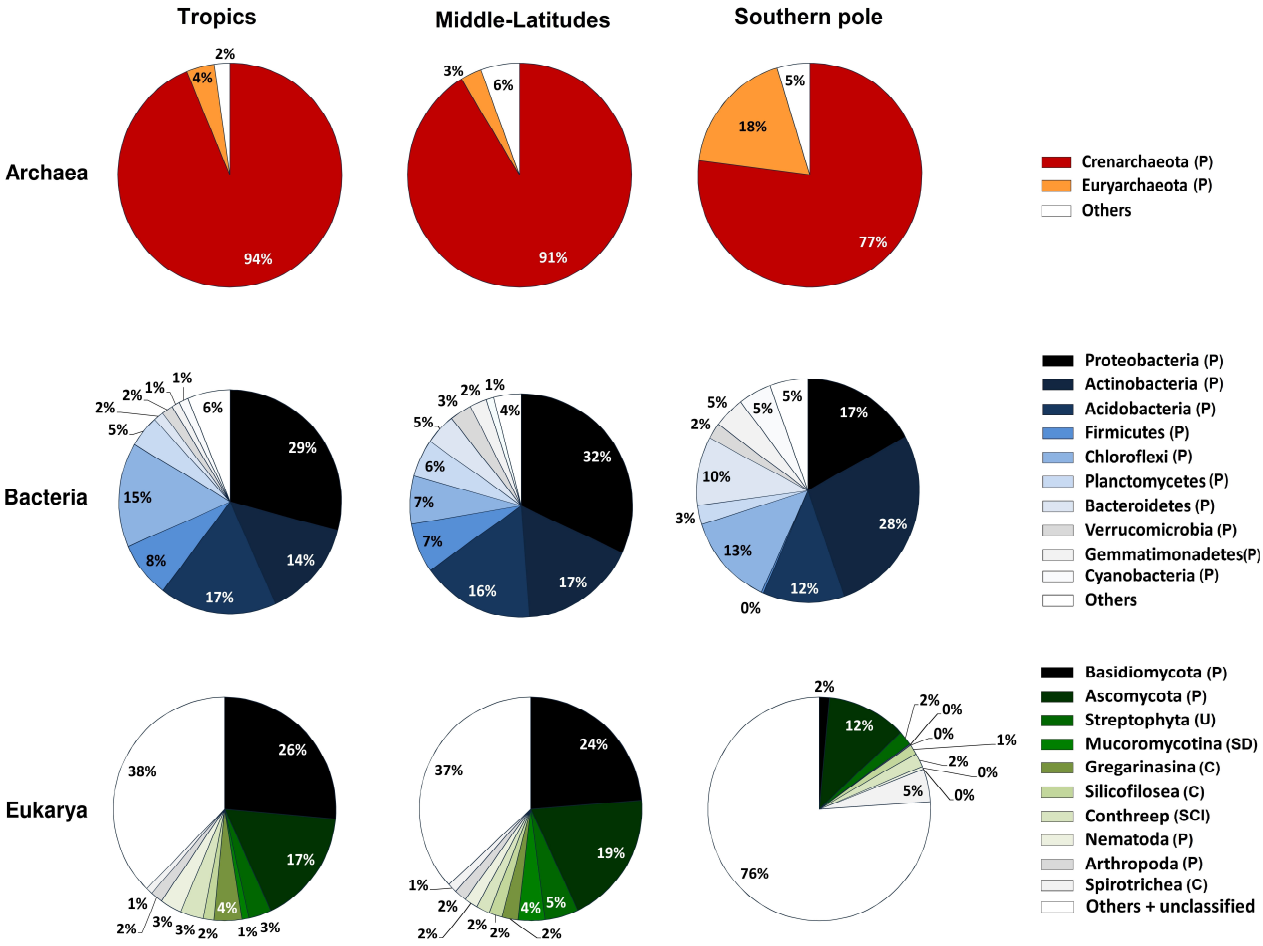

Figure 4. Relative abundance of main groups of archaea, bacteria and eukaryotes across different latitudinal regions from the Southern Hemisphere. P = Phylum; C = Class; SCl = Super clade; U = Uncladed; SD = Subdivision. Geographical regions as follows: low latitudes [23°N to 23°S], middle latitudes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

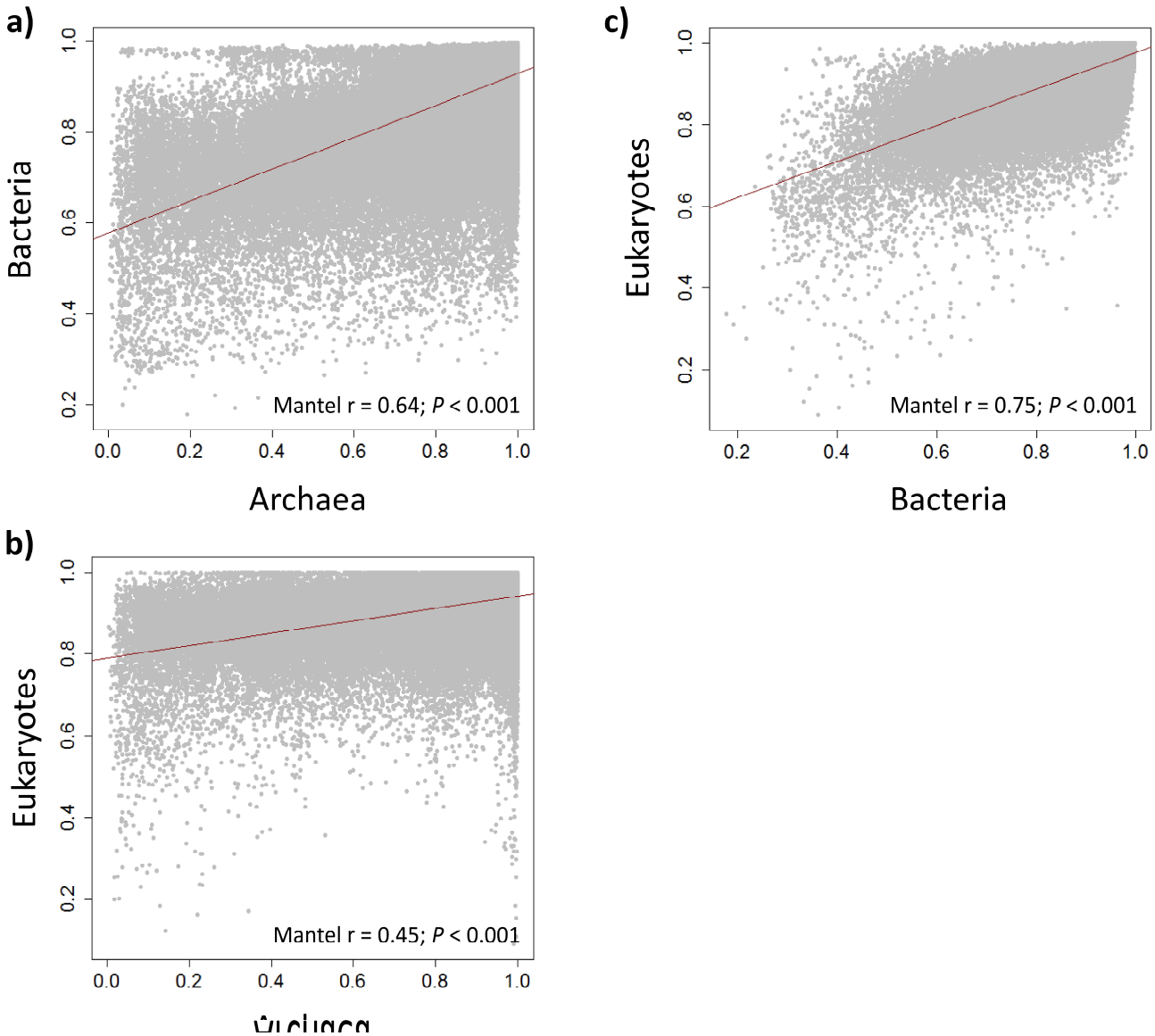

Figure 5. Relationship between β-diversity (community dissimilarity) based on Bray-Curtis distance for archaea, bacteria and eukaryotes across the Southern Hemispheres samples (Australia and Antarctica). The solid lines represent the fitted linear regressions.

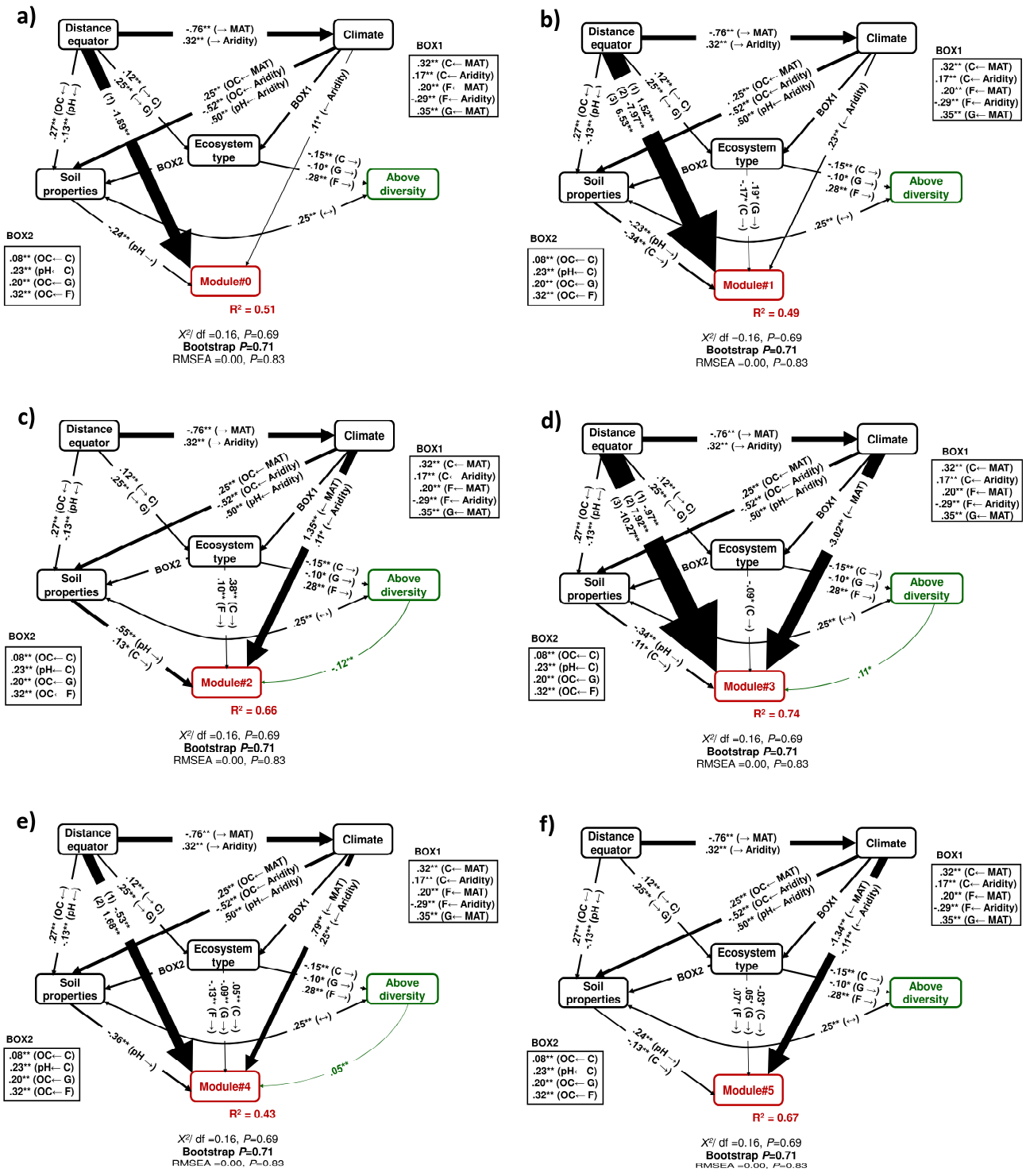

Figure 6. Structural equation model describing the effects of multiple drivers on the relative abundance of Modules#1-6 in the Southern Hemisphere (Australia and Antarctica; See Fig. S9 for Australia only). Numbers adjacent to arrows are indicative of the effect size of the relationship. R^2 denotes 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.

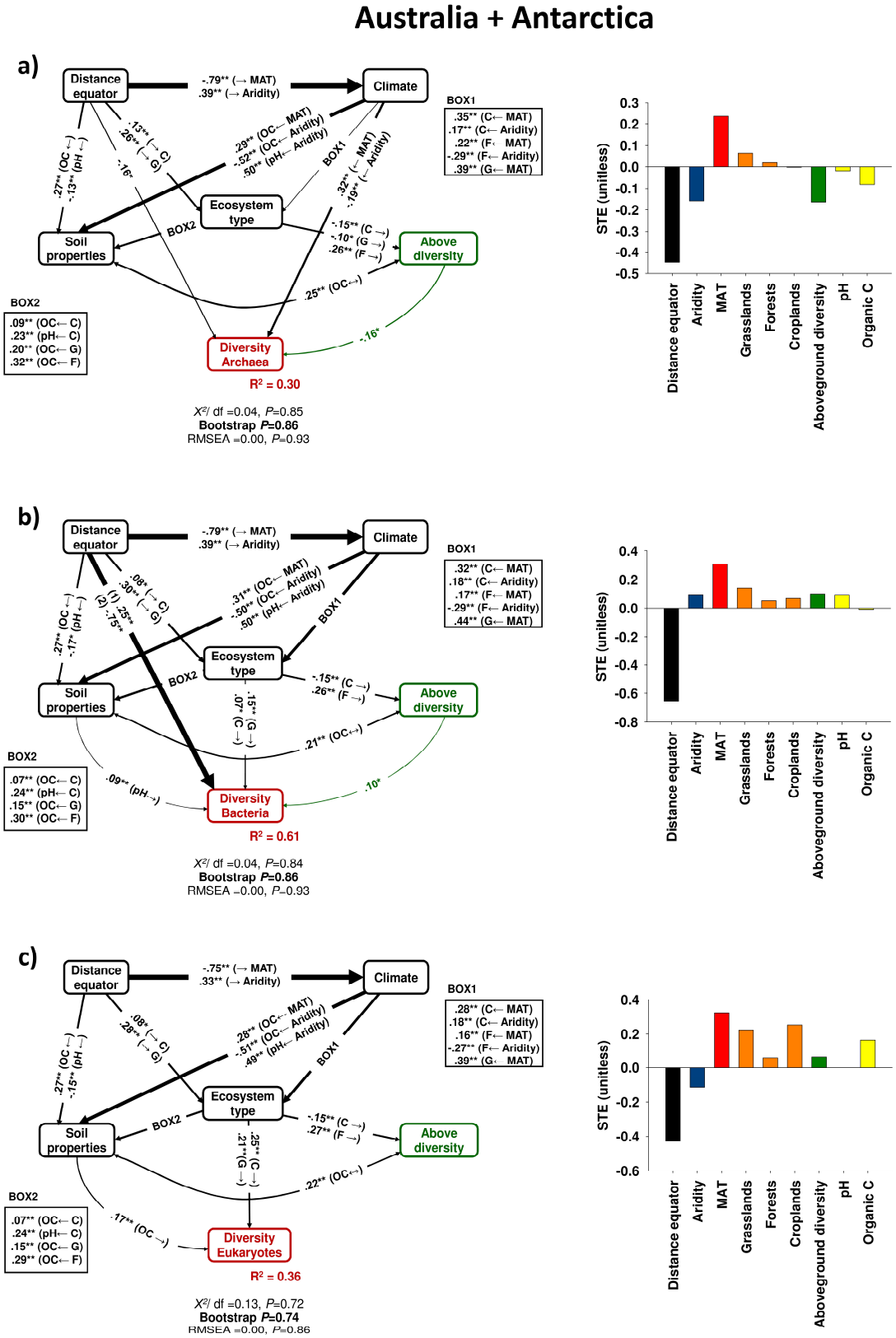

Figure 7. Structural equation model describing the effects of multiple drivers on the diversity of soil archaea (a), bacteria (b) and eukaryotes (c) in the Southern Hemisphere (Australia and Antarctica; See Fig. S11 for Australia only). Rest of the caption like in Fig. 6.

Supporting information

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

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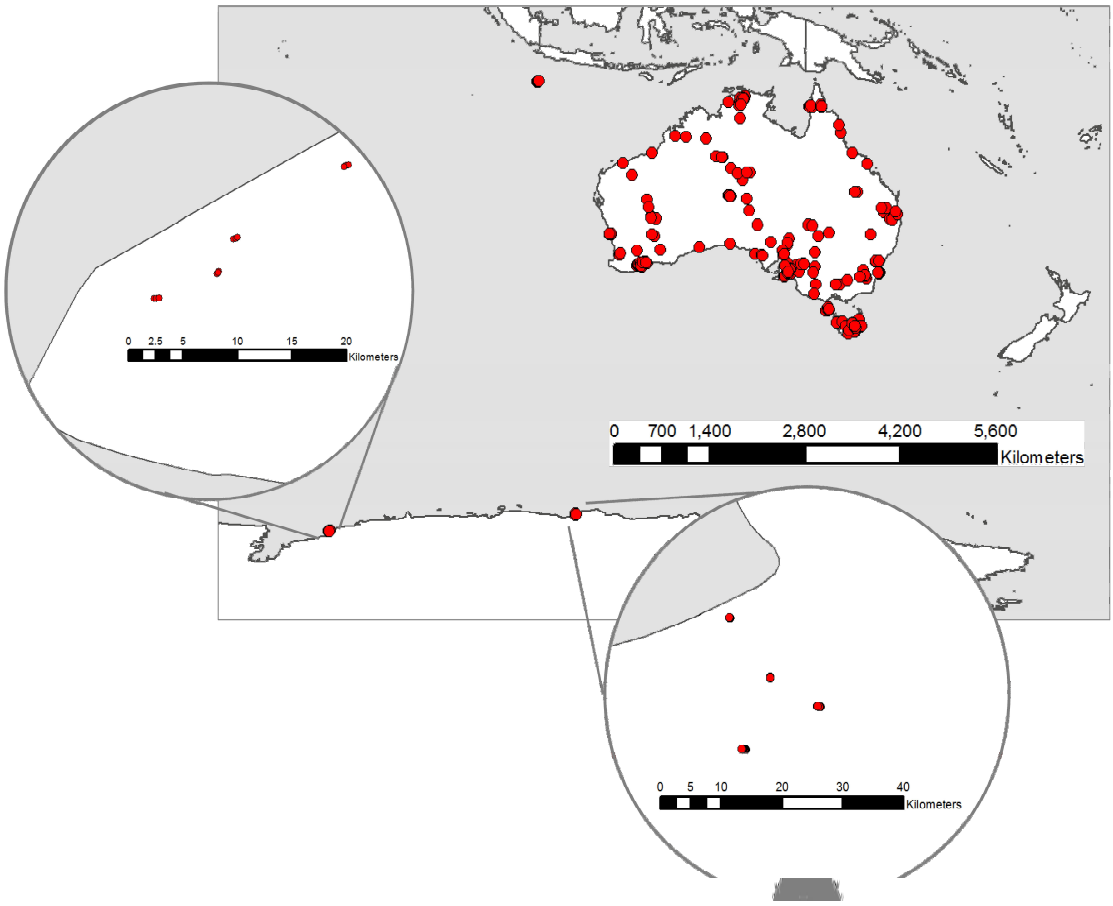
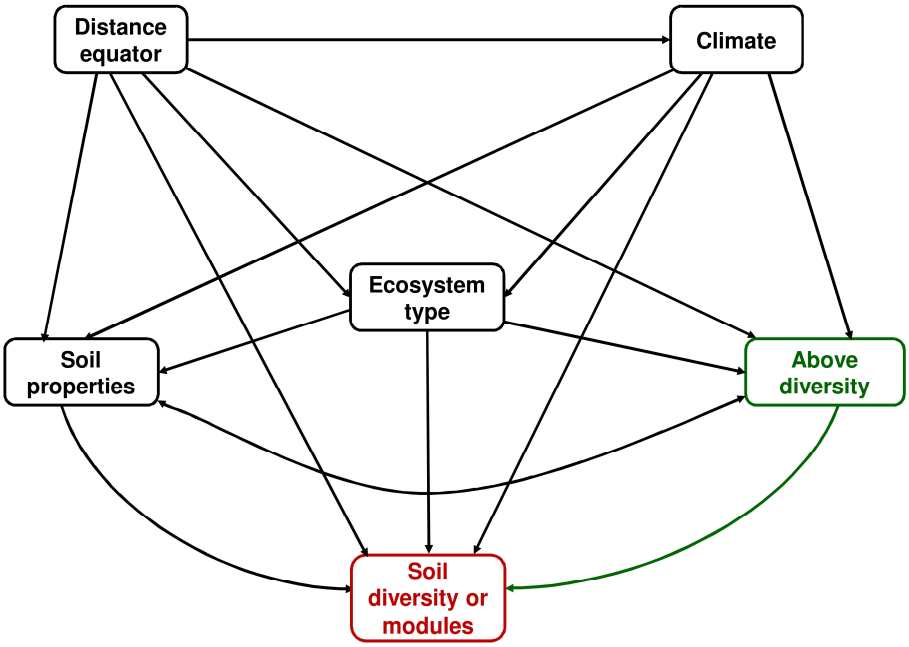
This PDF file includes:

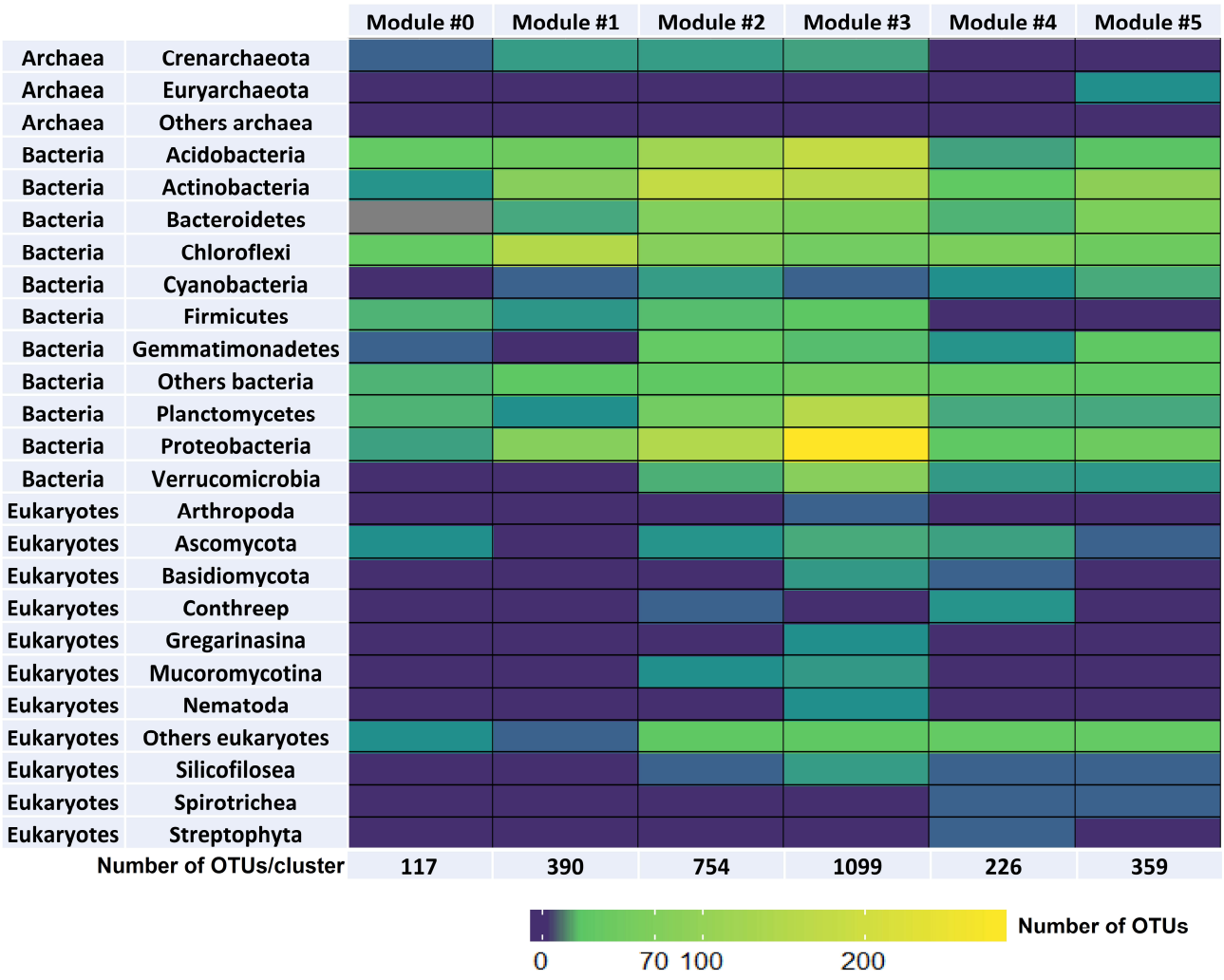
Appendix S1: Figure S1. Locations of the Australian and Antarctic sites included in this study.



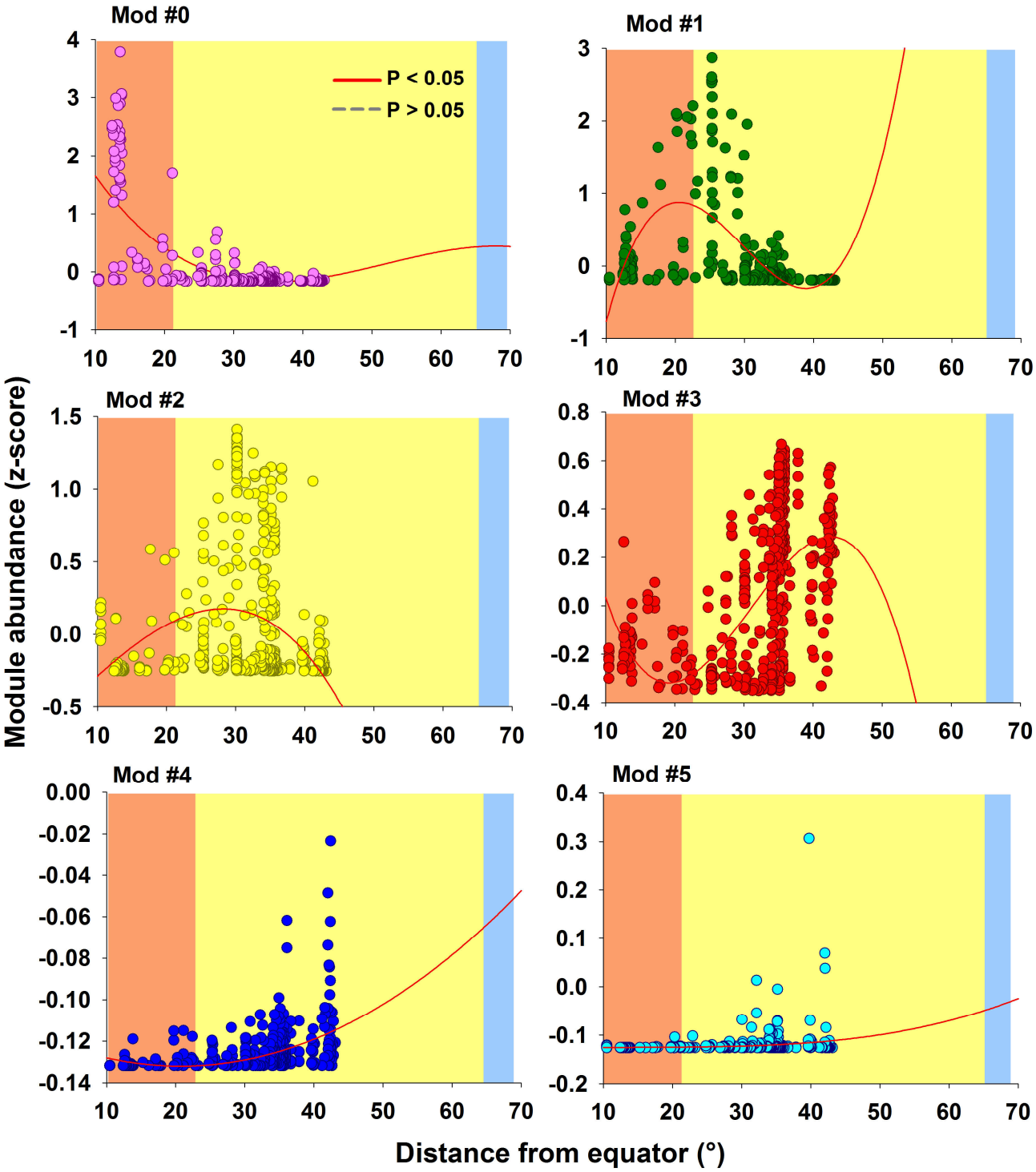
Appendix S1: Figure S2. *A priori* structural equation model including the direct and indirect effects of distance from equator (absolute latitude), climate (mean annual temperature and aridity), soil properties (carbon and pH), ecosystem types (forests, grasslands and croplands) and aboveground diversity on the relative abundance of diversity of soil archaea, bacteria or eukaryotes and the relative abundance of soil modules formed by taxa strongly co-occurring with each other. 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 was not included 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.



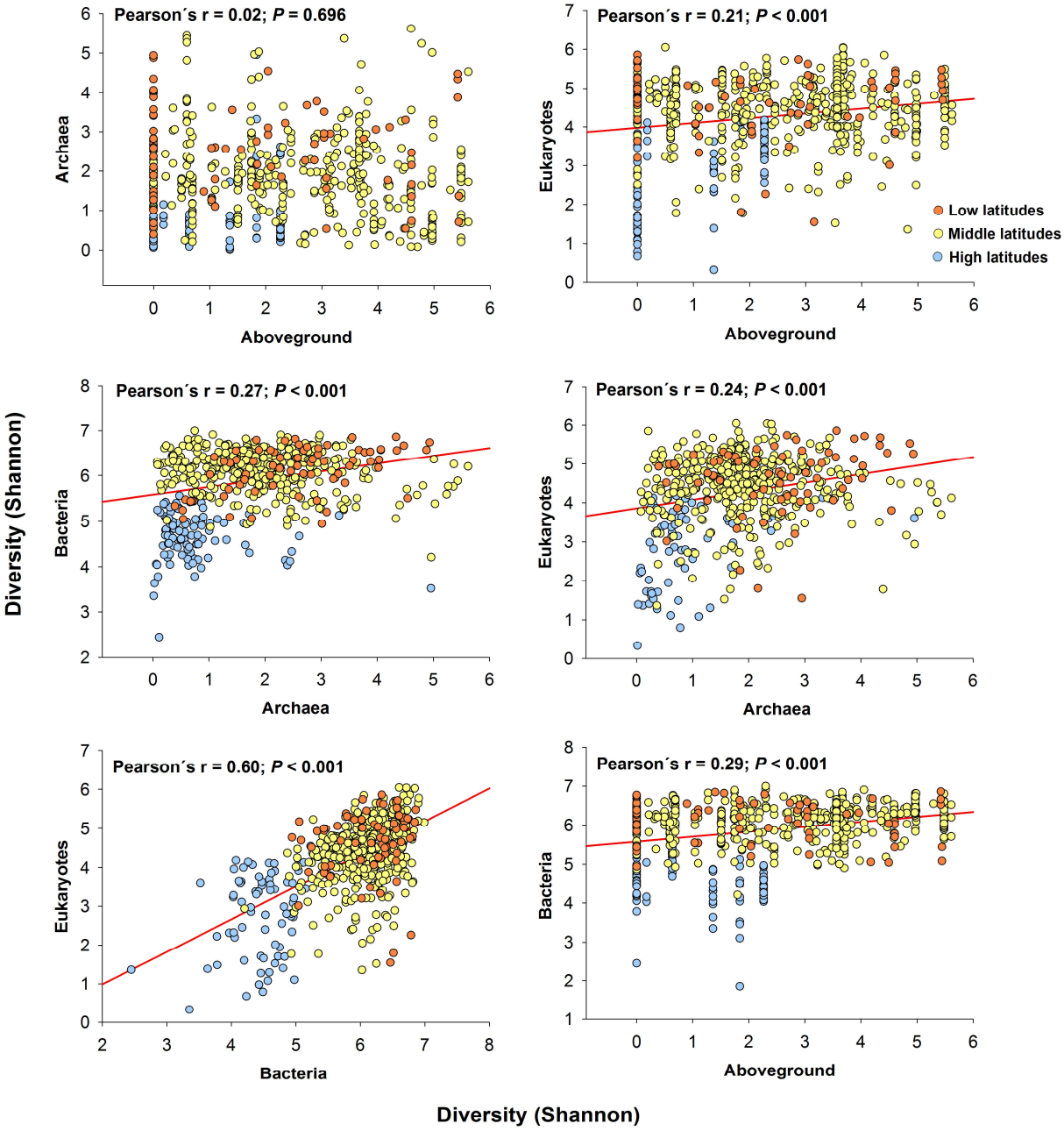
Appendix S1: Figure S3. Percentage of phylotypes (OTUs) from different taxanomic groups included in each module.



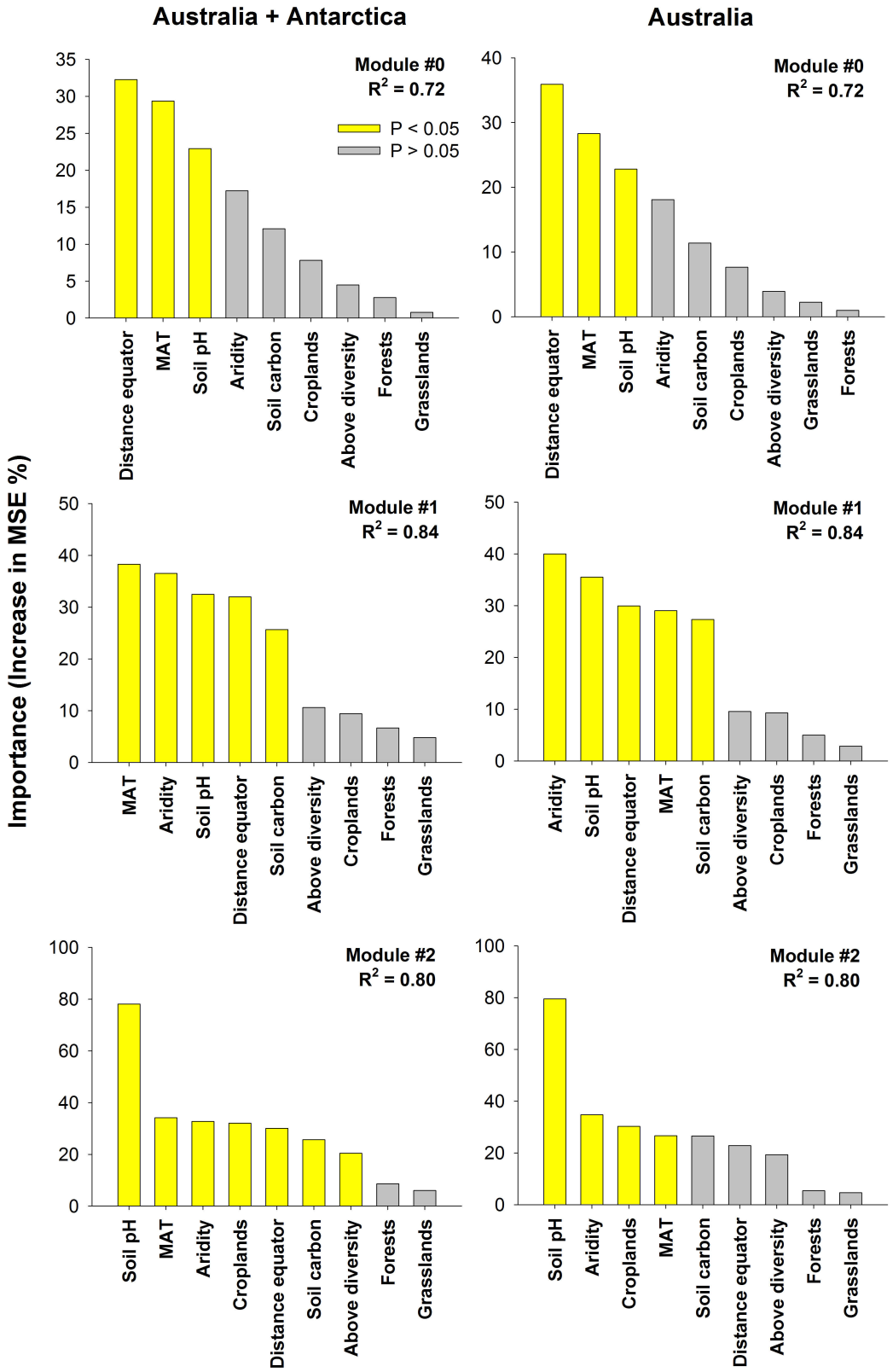
Appendix S1: Figure S4. Relationships between latitude (absolute) and the relative abundance of each soil module in Australia only. Model fit statistics and AICc index describing the relationship between latitude (absolute) and the relative abundance of modules #1-6 are available in Data S1.



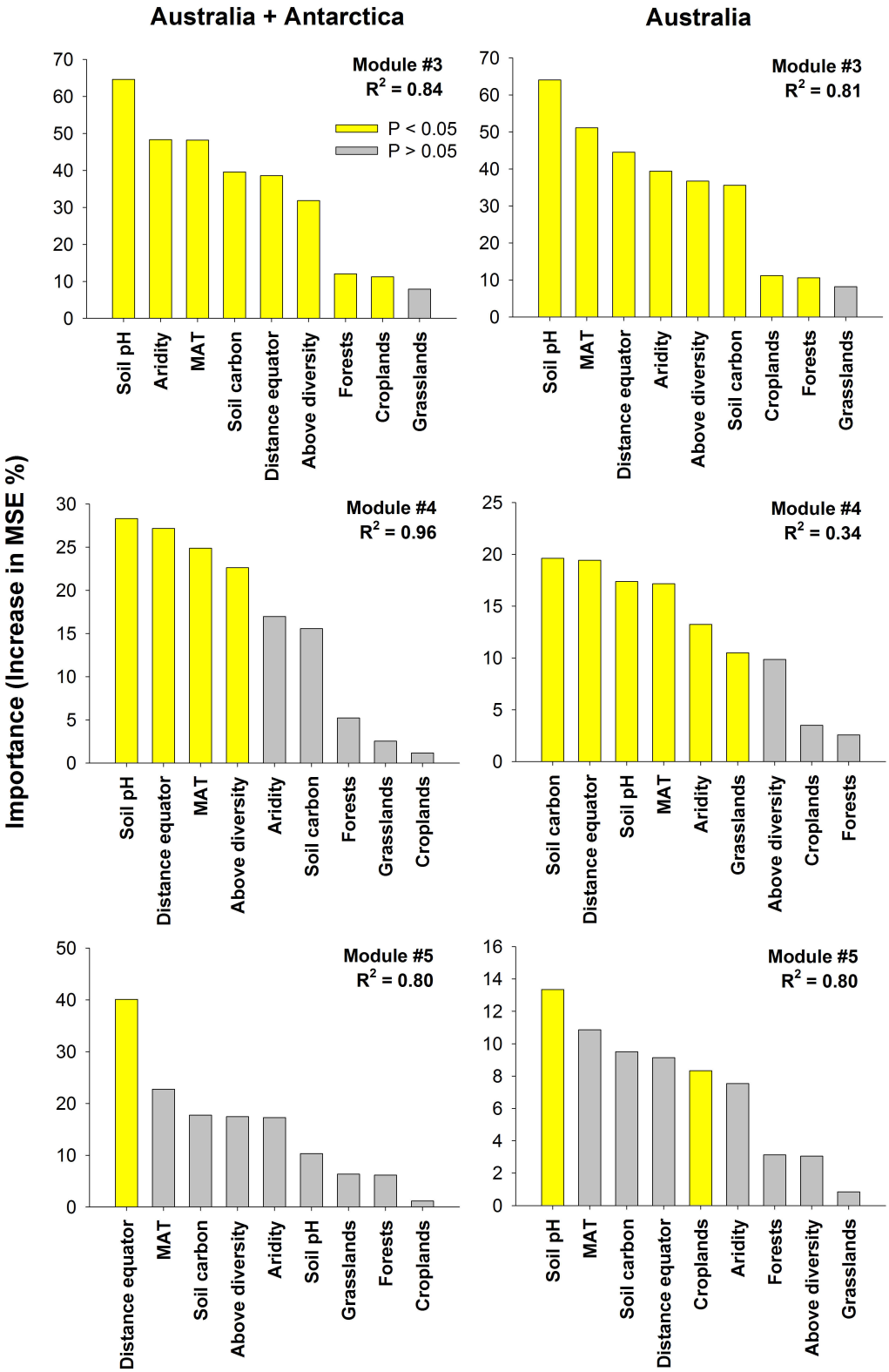
Appendix S1: Figure S5. Relationships between the diversity of archaea, bacteria, eukaryotes and aboveground diversity in the Southern Hemisphere (Australia and Antarctica).



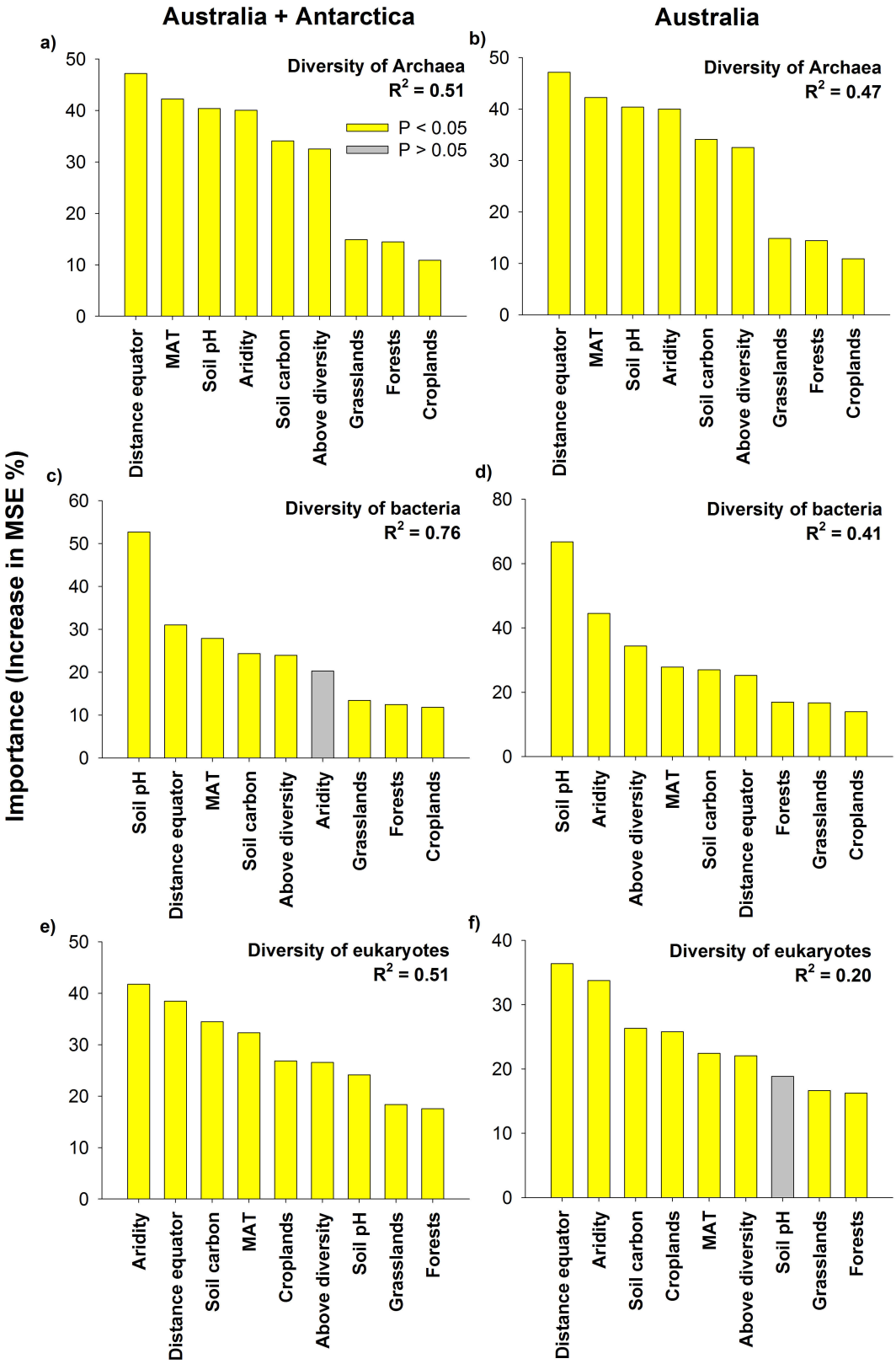
Appendix S1: Figure S6a. Results from a Random Forest aiming to identify the main significant ($P < 0.05$) environmental predictors of the relative abundance of modules #0-2 in Australia and Antarctica and Australia only.



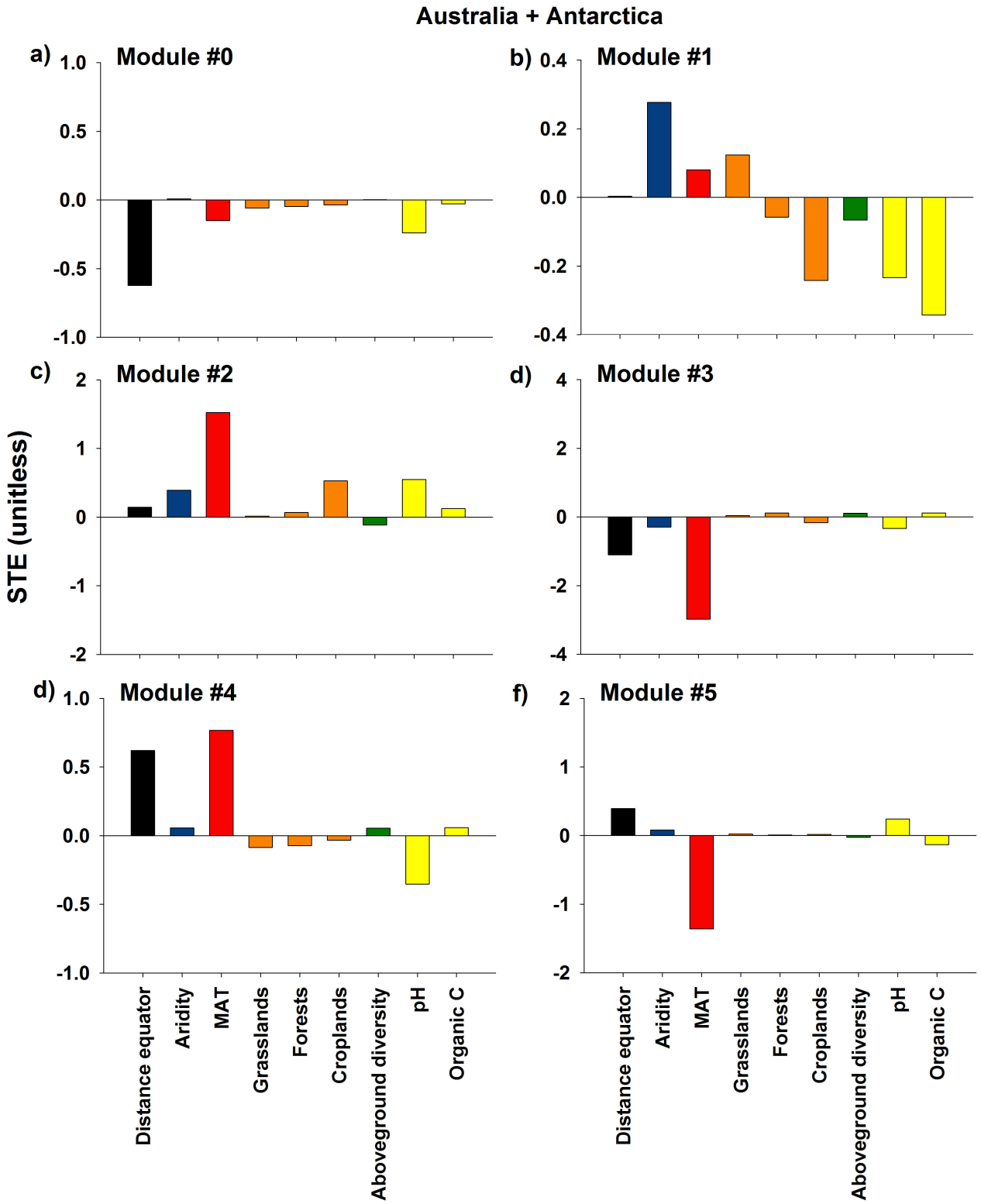
Appendix S1: Figure S6b. Results from a Random Forest aiming to identify the main significant ($P < 0.05$) environmental predictors of the relative abundance of modules #3-5 in Australia and Antarctica and Australia only.



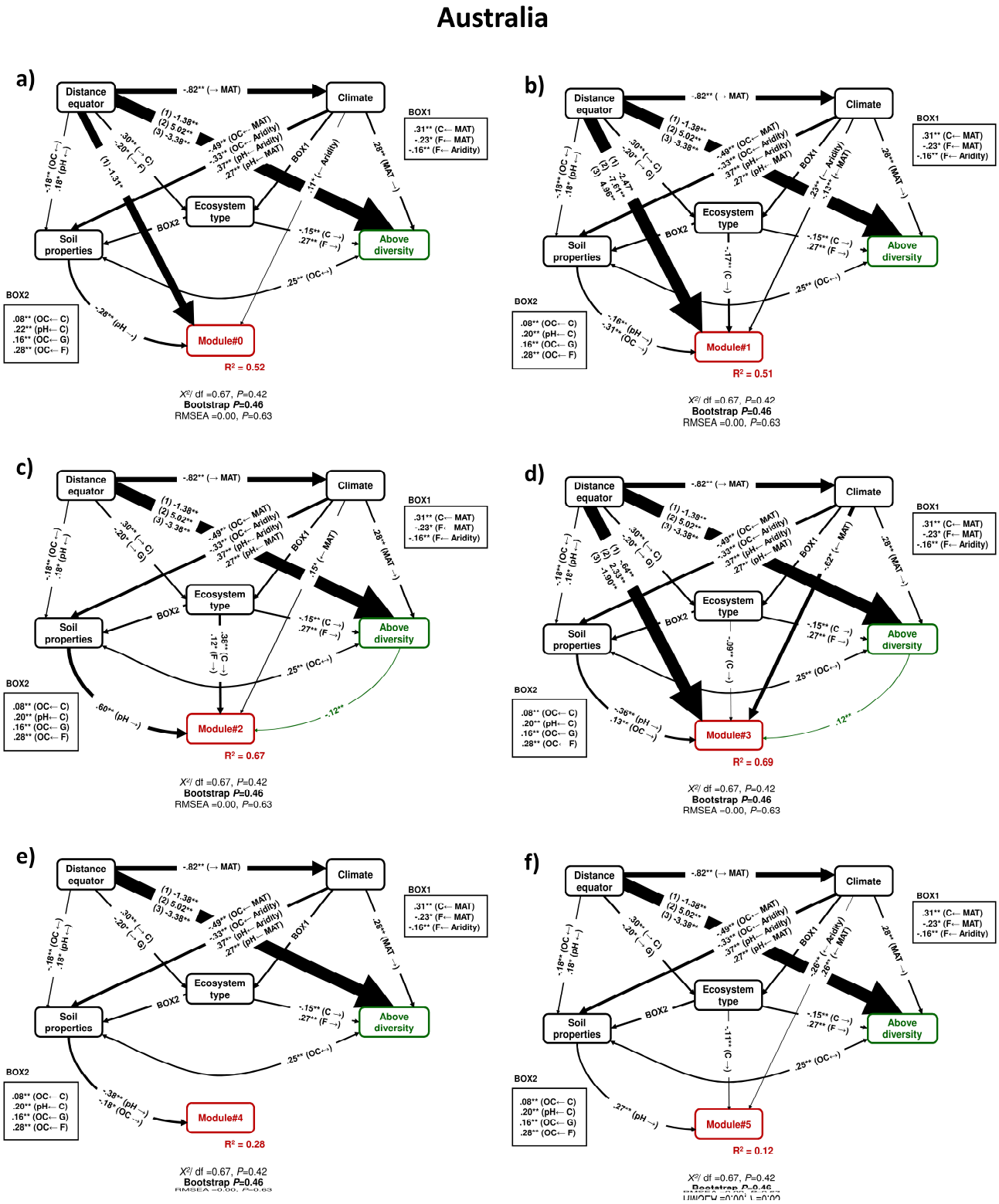
Appendix S1: Figure S7. Results from a Random Forest aiming to identify the main significant ($P < 0.05$) environmental predictors of the diversity of relative abundance of archaea, bacteria and eukaryotes in Australia and Antarctica together and Australia only.



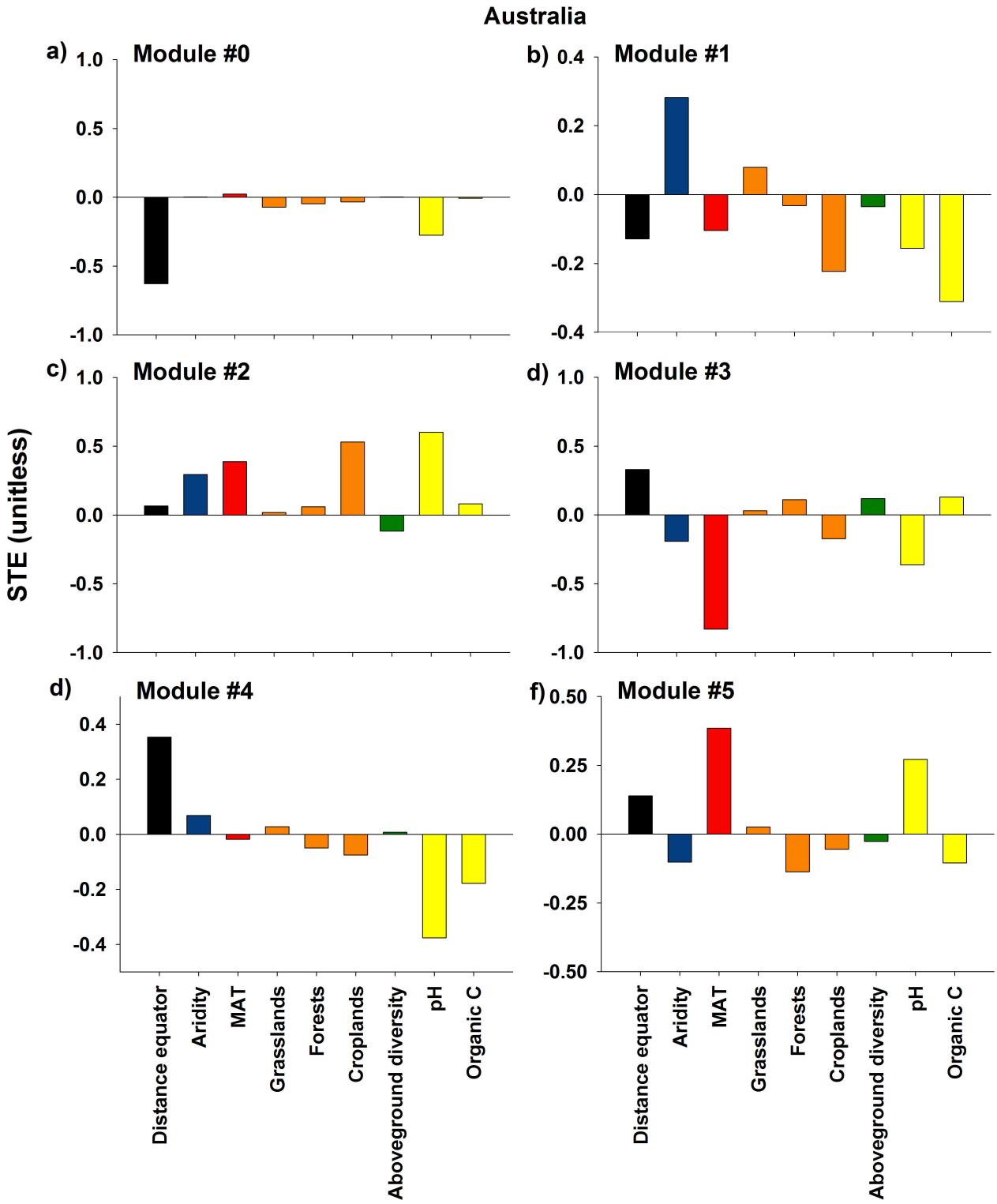
Appendix S1: Figure S8. Standardized total effects (STE) from SEM. Sum of the direct and indirect effects of multiple environmental predictors on the relative abundance of modules #1-6 in Australia and Antarctica.



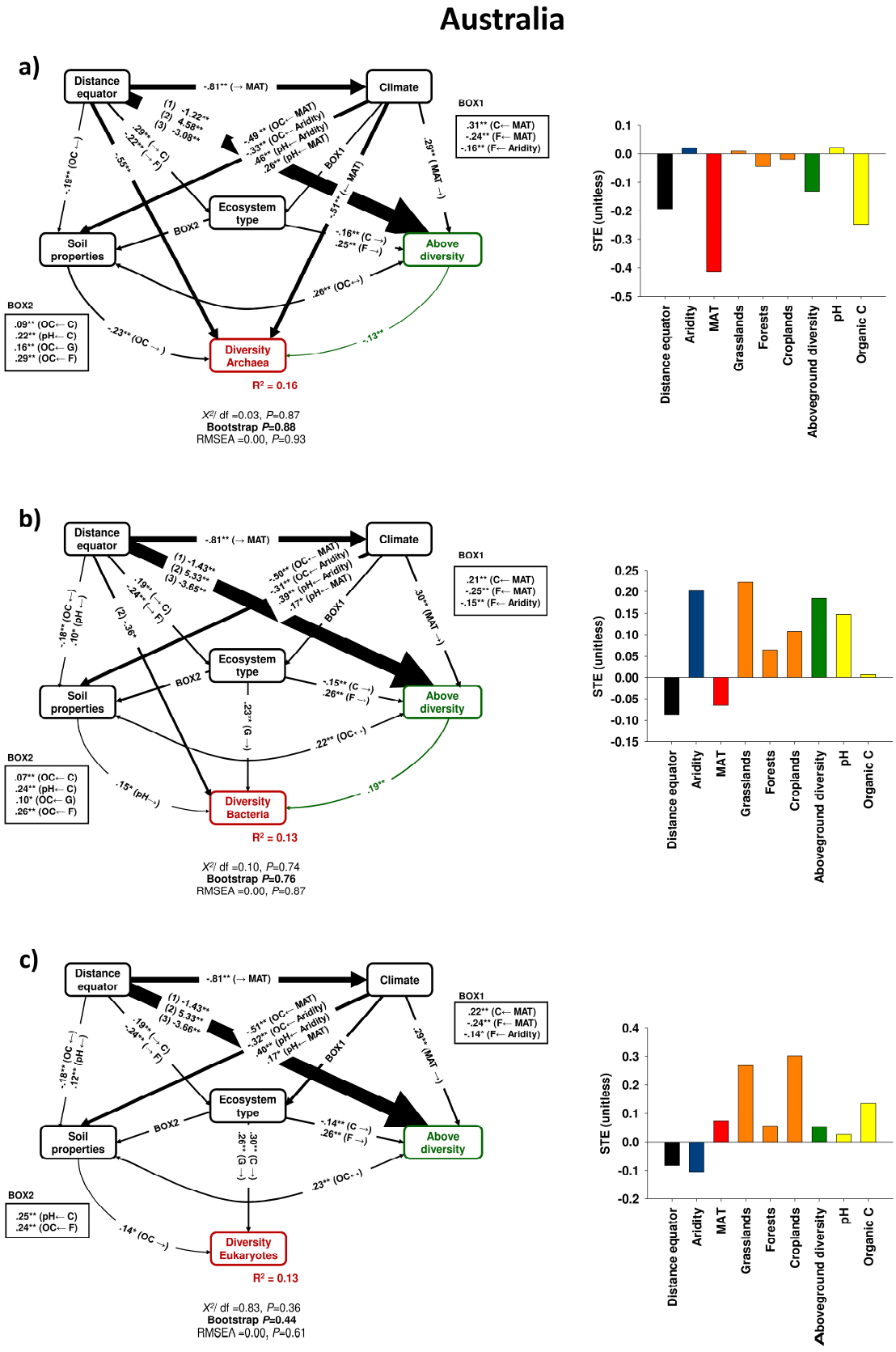
Appendix S1: Figure S9. Structural equation model describing the effects of multiple drivers on the relative abundance of modules #1-6 in Australia only. Rest of the caption like in Fig. 6.



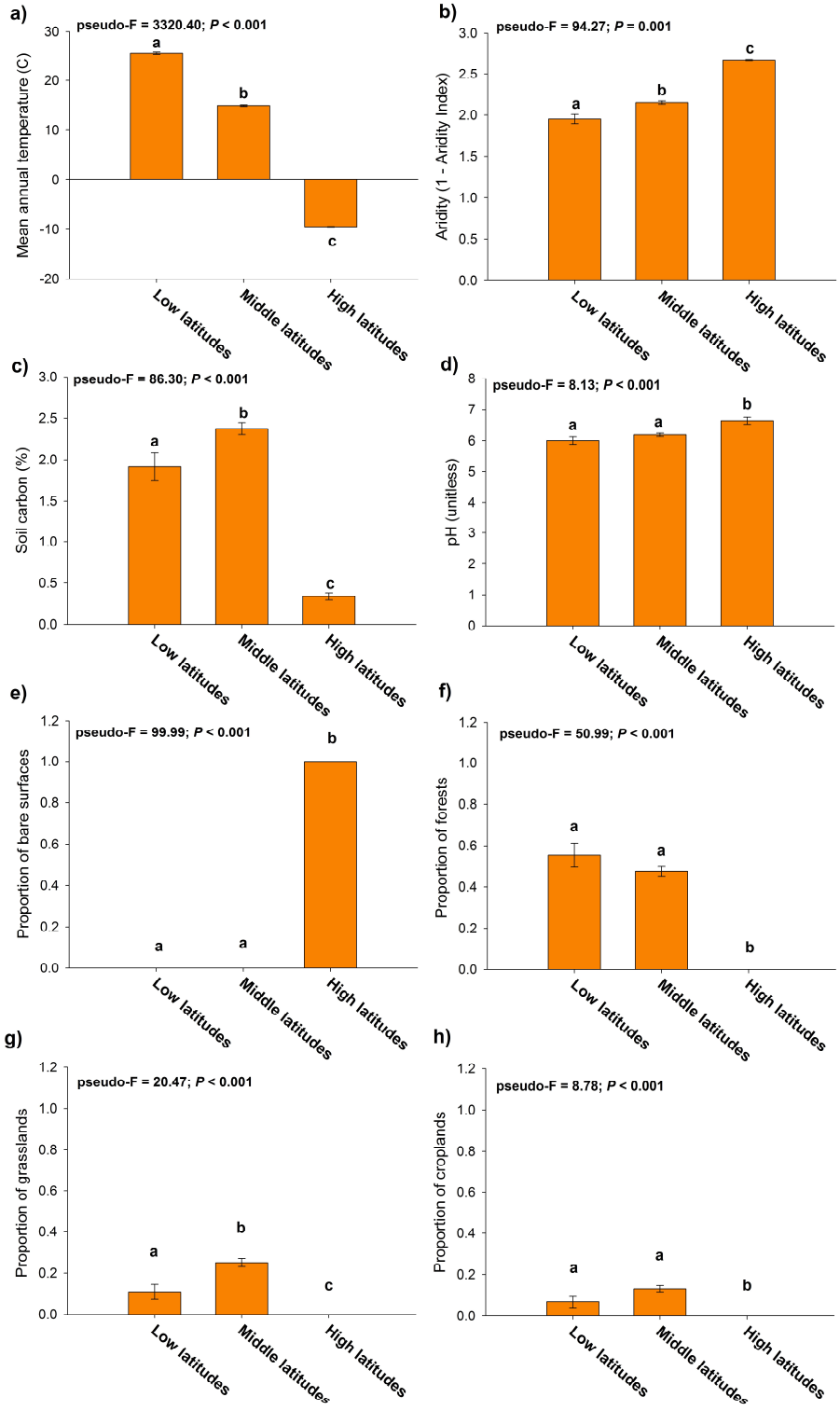
Appendix S1: Figure S10. Standardized total effects (STE) from SEM. Sum of the direct and indirect effects of multiple environmental predictors on the relative abundance of modules #1-6 in Australia.



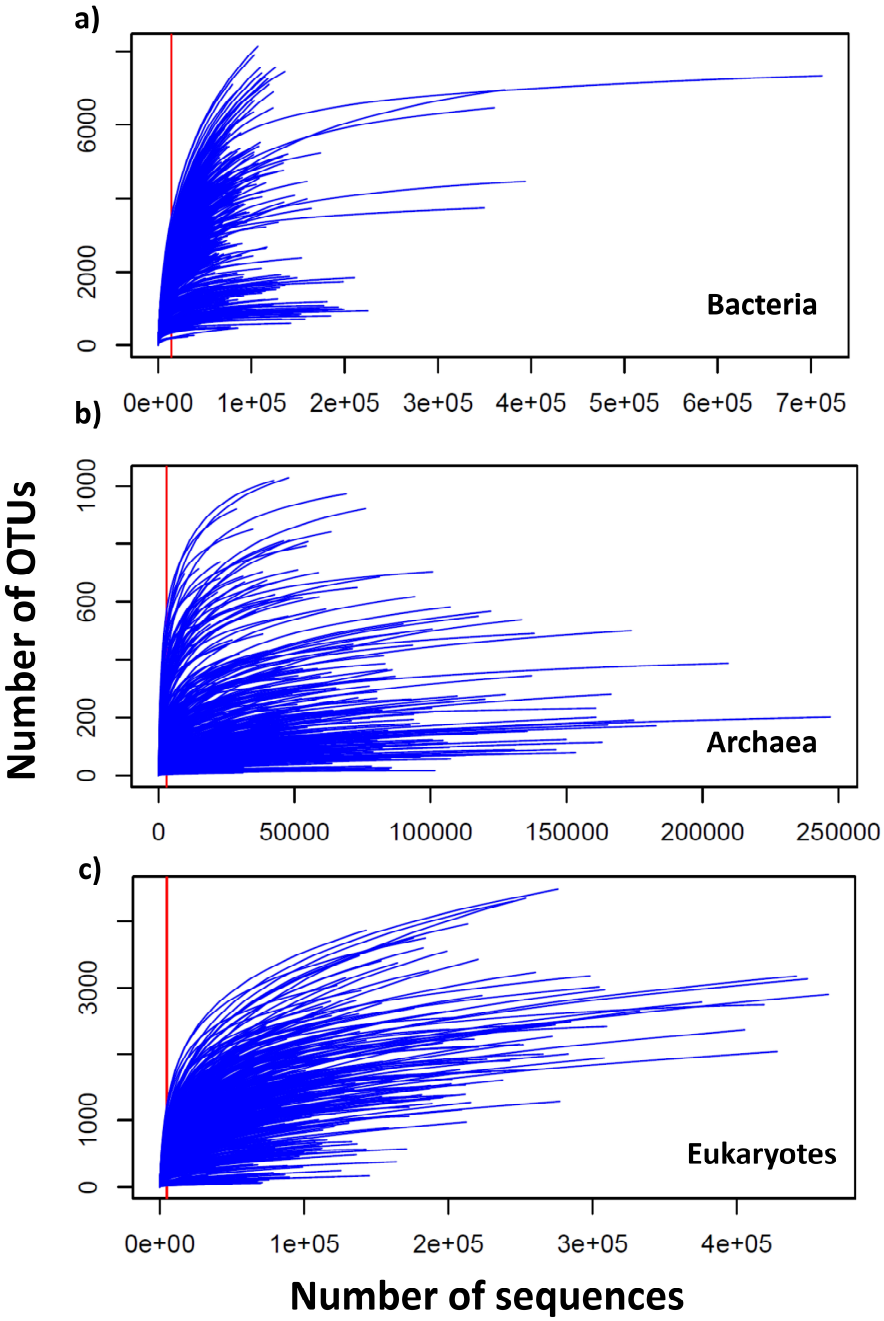
Appendix S1: Figure S11. Structural equation model describing the effects of multiple drivers on the diversity of soil archaea (a), bacteria (b) and eukaryotes (c) in Australia only. Rest of the caption like in Fig. 6.



Appendix S1: Figure S12. Climate, soil properties and proportion of ecosystem types across different geographical regions. Different letters in this panel indicate significant differences among latitudinal ranges ($P < 0.05$, post-hoc test after PERMANOVA). 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).



Appendix S1: Figure S13. Rarefaction curves for diversity of bacteria (a), archaea (b) and eukaryotes (c), respectively. Lines represent different soil samples.



Appendix S2. Extended methods

Environmental and physicochemical analyses.

Soil-pHs were determined in soil: water solution mix (1:5) using a pH electrode. Total organic carbon (TOC) was determined using the Walkley-Black method (Walkley & Black 1934). Mean annual temperature (MAT) and Aridity Index (AI; mean annual precipitation/potential evapotranspiration) were obtained from the Worldclim database (http://www.worldclim.org; Hijmans *et al.* 2005; Zomer *et al.* 2008). Climate gaps in the dataset were completed using local and regional databases. For clarity, we used aridity [maximum AI value in the dataset–AI] instead of the aridity index (see Delgado-Baquerizo *et al.* 2013 for a similar approach). Aridity is strongly negatively related to mean annual precipitation (Spearman $\rho = 0.95$; $P < 0.001$).

Molecular analyses.

All soil DNA was extracted in triplicate, according to the methods employed by the Earth Microbiome Project (Bissett *et al.* (2016). 16S rRNA gene amplicons were sequenced using 300 bp, paired end sequencing, while 18S amplicon reads were generated using 150 bp paired end sequencing. Bioinformatic analyses were conducted as explained in Bissett *et al.* (2016). We were able to successfully amplified 602 samples for 18S rRNA, 570 samples for archaea and 637 samples for 16S rRNA. OTU abundance tables were rarefied to ensure equal sampling effort across samples (Appendix S1: Fig. S13). The Shannon diversity index was calculated on these rarefied each OTU tables using Ecopy (https://github.com/Auerilas/ecopy/blob/master/docs/source/index.rst). We selected this metric for our main analyses because it provides a robust and informative estimation of taxonomic diversity for microbial communities (Haegeman *et al.* 2013).

Random Forest

Random Forest is especially recommended for datasets including categorical variables or variables with non-parametric distributions. Random Forest is a novel machine-learning algorithm that extends standard classification and regression tree (CART) methods by creating a collection of classification trees with binary divisions. Unlike traditional CART analyses, the fit of each tree is assessed using randomly selected cases (1/3 of the data), which are withheld during its construction (out-of-bag or OOB cases). The importance of each predictor variable is determined by evaluating the decrease in prediction accuracy, *i.e.*, increase in the mean square error between observations and OOB predictions, when the data for that predictor is randomly permuted. All analyses were conducted using the rfPermute package (Archer *et al.* 2016) of the R statistical software (http://cran.r-project.org/).

Structural Equation Modeling

Some data manipulation was required prior to modeling to improve the normality and linearity of our data. Distance from the equator, mean annual temperature, soil pH, soil carbon and archaeal diversity were log-transformed to improve normality. Similarly, bacterial and eukaryotic diversity were x^2-transformed. We included the main ecosystem types from the BASE database (forest, grasslands and croplands) in our model. In all cases the different ecosystem types were categorical variables with two levels: 1 (a particular ecosystem type) and 0 (remaining considered ecosystem types + others). To introduce polynomial relationships between latitude and aboveground and belowground diversity or relative abundance of soil modules into our model (based on analyses in Appendix S3: Table S2), we calculated latitude^2 and latitude^3 and introduced it into our model, in a similar manner to Laliberte *et al.* (2014).

When these data manipulations were completed, we parameterized our model using our dataset and tested its overall goodness of fit. There is no single universally accepted test of overall goodness of fit for SEM, applicable in all situations regardless of sample size or data distribution (Schermelleh-Engel *et al.* 2003). We used the Chi-square test (χ^2; the model has a good fit when $0 \leq \chi^2/\text{d.o.f} \leq 2$ and $0.05 < P \leq 1.00$) and the root mean square error of approximation (RMSEA; the model has a good fit when $RMSEA\ 0 \leq RMSEA \leq 0.05$ and $0.10 < P \leq 1.00$; Schermelleh-Engel *et al.* 2003). Additionally, and because some variables were not normal, we confirmed the fit of the model using the Bollen-Stine bootstrap test (the model has a good fit when 0.10 <bootstrap $P \leq$ 1.00). Our *a priori* model attained an acceptable fit by all criteria, and thus no post hoc alterations were made. With a good model fit, we were free to interpret the path coefficients of the model and their associated bootstrap-*P* values.

Literature Citations (not listed in the main text):

Archer, E. (2016) rfPermute: Estimate Permutation p-Values for Random Forest Importance Metrics. R package version 1.5.2.

Haegeman B, Hamelin J, Moriarty J, Neal P, Dushoff J, Weitz JS (2013) Robust estimation of microbial diversity in theory and in practice Robust estimation of microbial diversity in theory and in practice *The ISME J* 7: 1092–1101

Laliberté E, Zemunik G, Turner BL (2014) Environmental filtering explains variation in plant diversity along resource gradients Science 345: 1602

Schermelleh-Engel K, Moosbrugger H, Müller H (2003) Evaluating the fit of structural equation models, tests of significance descriptive goodness-of-fit measures *Methods of Psychological Research Online* 8: 23-74

Walkley, A, Black IA (1934) An Examination of Degtjareff Method for Determining Soil Organic Matter and a Proposed Modification of the Chromic Acid Titration Method Soil Sci 37: 29-37

Appendix S3: Table S1. Correlations (Spearman) between distance from equator and the diversity of multiple soil organisms and relative abundance of modules within our network of interactions using data from Australia and Antarctica combined, and from Australia only.

	Australia and Antarctica ρ	Australia ρ
Diversity archaea	-0.375 (<0.001)	-0.109 (0.018)
Diversity bacteria	-0.455 (<0.001)	-0.098 (0.024)
Diversity eukaryotes	-0.279 (<0.001)	-0.017 (0.698)
Module #0	-0.505 (<0.001)	-0.369 (<0.001)
Module #1	-0.727 (<0.001)	-0.650 (<0.001)
Module #2	-0.340 (<0.001)	-0.173 (<0.001)
Module #3	0.078 (0.072)	0.552 (<0.001)
Module #4	0.491 (<0.001)	0.466 (<0.001)
Module #5	0.454 (<0.001)	0.200 (<0.001)

Appendix S3: Table S2. Model fit statistics and AICc index describing the relationship between latitude (absolute) and soil biodiversity (Shannon), aboveground diversity (Shannon) and the relative abundance of soil modules of taxa strongly co-occurring with each other.

		Australia + Antarctica						Australia	
Microbial attribute	**Model**	**R^2**	***P***	**AICc**	**DeltaAICc**	**Selected Model(s)**	**Selection approach**	**R^2**	***P***
Diversity archaea (Shannon)	**Linear**	0.205	< 0.001	1628.141	0	✓	Parsimony	0.045	<0.001
	Quadratic	0.205	< 0.001	1629.983	-1.842				
	Cubic	0.208	< 0.001	1629.697	-1.556				
	Logarithmic	0.183	< 0.001	1643.59	-15.449				
Diversity bacteria (Shannon)	**Linear**	0.478	< 0.001	1011.963	-162.868				
	Quadratic	0.597	< 0.001	849.095	0	✓	ΔAICc > 2; Parsimony	0.031	<0.001
	Cubic	0.597	< 0.001	850.9808	-1.8858				
	Logarithmic	0.309	< 0.001	1190.616	-341.521				
Diversity eukaryotes (Shannon)	**Linear**	0.226	< 0.001	1551.662	-60.653				
	Quadratic	0.292	< 0.001	1500.36	-9.351				
	Cubic	0.305	< 0.001	1491.009	0	✓	ΔAICc > 2	0.007	0.274
	Logarithmic	0.145	< 0.001	1611.688	-120.679				
Module#0	**Linear**	0.173	< 0.001	791.932	-249.6462				
	Quadratic	0.445	< 0.001	582.8572	-40.5713				
	Cubic	0.488	< 0.001	542.2859	0	✓	ΔAICc > 2	0.483	<0.001
	Logarithmic	0.318	< 0.001	690.2589	-147.973				
Module#1	**Linear**	0.089	< 0.001	769.8057	-97.9092				
	Quadratic	0.108	< 0.001	761.0578	-89.1613				
	Cubic	0.249	< 0.001	671.8965	0	✓	ΔAICc > 2	0.360	<0.001

	Logarithmic	0.088	< 0.001	770.3993	-98.5028				
Module#2	**Linear**	0.036	< 0.001	576.0281	-50.6744				
	Quadratic	0.069	< 0.001	559.2836	-33.9299				
	Cubic	0.131	< 0.001	525.3537	0	✓	ΔAICc > 2	0.457	<0.001
	Logarithmic	0.012	0.011	588.6291	-63.2754				
Module#3	**Linear**	0.012	0.011	289.3192	-250.84061				
	Quadratic	0.282	< 0.001	122.5339	-84.05531				
	Cubic	0.390	< 0.001	38.47859	0	✓	ΔAICc > 2	0.297	<0.001
	Logarithmic	0.001	0.469	295.1789	-256.70031				
Module#4	**Linear**	0.240	< 0.001	744.7042	-51.1748				
	Quadratic	0.313	< 0.001	693.5294	0		ΔAICc > 2; Parsimony	0.185	<0.001
	Cubic	0.315	< 0.001	694.2221	-0.6927				
	Logarithmic	0.149	< 0.001	805.0171	-111.4877				
Module#5	**Linear**	0.415	< 0.001	313.2229	-202.343				
	Quadratic	0.574	< 0.001	146.8864	-36.0065				
	Cubic	0.604	< 0.001	110.8799	0	✓	ΔAICc > 2	0.018	0.037
	Logarithmic	0.250	< 0.001	444.2477	-333.3678				
Plant diversity (Shannon)	**Linear**	0.057	< 0.001	2469.85	-71.719				
	Quadratic	0.137	< 0.001	2414.679	-16.548				
	Cubic	0.1613	< 0.001	2398.131	0	✓	ΔAICc > 2	0.075	<0.001
	Logarithmic	0.024	< 0.001	2492.220	-94.089				

Appendix S3: Table S3. Pearson correlations between distance from the equator, climate, soil properties and vegetation types (i.e. relative effect of a particular vegetation types vs. others) with the richness (i.e. number of OTUs) of main groups of archaea, bacteria and eukaryotes, respectively. Significance levels of each predictor are *P < 0.05, **P < 0.01.

	Distance equator	MAT	Aridity	Soil C	pH	Croplands	Forests	Grasslands	Above diversity
Crenarchaeota	-0.57**	0.42**	-0.33**	0.12**	-0.24**	0.01	0.19**	0.05	0.00
Euryarchaeota	-0.12**	0.10*	0.02	-0.05	0.05	-0.11**	0.02	0.04	-0.03
Archaea	-0.20**	0.16**	-0.14**	0.06	-0.17**	-0.13**	0.16**	0.01	0.01
Acidobacteria	-0.55**	0.70**	-0.47**	0.46**	-0.12**	0.16**	0.36**	0.11**	0.33**
Actinobacteria	-0.35**	0.53**	0.10*	0.02	0.31**	0.14**	0.17**	0.10*	0.17**
Bacteroidetes	0.14**	0.16**	-0.09*	0.28**	0.24**	0.27**	-0.02	0.20**	0.16**
Cyanobacteria	-0.03	0.12**	-0.01	-0.150**	-0.12**	-0.15**	0.00	0.07	0.02
Chloroflexi	-0.51**	0.44**	0.16**	-0.12**	0.15**	0.13**	-0.01	0.15**	-0.05
Firmicutes	-0.44**	0.56**	-0.36**	0.30**	-0.14**	0.11**	0.12**	0.32**	0.24**
Gemmatimonadetes	-0.07	0.30**	0.12**	0.09*	0.47**	0.48**	0.00	0.06	0.14**
Planctomycetes	-0.30**	0.52**	-0.55**	0.58**	-0.22**	-0.02	0.43**	0.11**	0.48**
Proteobacteria	-0.41**	0.68**	-0.56**	0.51**	-0.18**	0.120**	0.32**	0.17**	0.36**
Verrucomicrobia	-0.06	0.36**	-0.54**	0.60**	-0.33**	-0.05	0.34**	0.17**	0.39**
Bateria	-0.46**	0.70**	-0.36**	0.40**	-0.03	0.15**	0.29**	0.21**	0.34**
Basidiomycota	-0.26**	0.38**	-0.54**	0.46**	-0.45**	-0.19**	0.51**	-0.11**	0.23**
Ascomycota	-0.29**	0.46**	-0.27**	0.27**	-0.27**	-0.05	0.25**	0.01	0.24**
Streptophyta	-0.23**	0.29**	-0.26**	0.28**	-0.05	-0.03	-0.10*	0.25**	0.07
Mucoromycotina	-0.07	0.39**	-0.47**	0.46**	-0.25**	0.12**	0.27**	0.06	0.23**
Gregarinasina	-0.19**	0.24**	-0.57**	0.51**	-0.39**	-0.13**	0.37**	-0.05	0.19**
Silicofilosea	-0.21**	0.41**	-0.46**	0.45**	-0.43**	-0.01	0.29**	0.05	0.39**
Conthreep	-0.38**	0.49**	-0.10*	0.16**	0.14**	0.21**	0.02	0.16**	0.13**

Nematoda	-0.27**	0.41**	-0.64**	0.47**	-0.31**	-0.03	0.20**	0.15**	0.21**
Arthropoda	-0.17**	0.27**	-0.61**	0.51**	-0.36**	-0.06	0.19**	0.12**	0.05
Spirotrichea	-0.10*	0.31**	-0.197**	0.31**	-0.01	0.13**	-0.09*	0.28**	0.14**
Eukaryotes	-0.28**	0.52**	-0.52**	0.55**	-0.29**	0.07	0.21**	0.20**	0.30**

Appendix S3: Table S4. Correlations (Pearson) between the richness of main taxa of archaea, bacteria and eukaryotes.

	Crenarchaeota	Euryarchaeota	Basidiomycota	Ascomycota	Streptophyta	Mucoromycotina	Gregarinasina	Silicofilosea	Conthreep	Nematoda	Arthropoda	Spirotrichea	Acidobacteria	Actinobacteria	Bacteroidetes	Cyanobacteria	Chloroflexi	Firmicutes	Gemmatimonadetes	Planctomycetes	Proteobacteria
Euryarchaeota	0.055																				
Basidiomycota	0.188**	0.024																			
Ascomycota	0.192**	-0.108*	0.509**																		
Streptophyta	0.177**	-0.027	0.057	0.248**																	
Mucoromycotina	0.044	-0.111*	0.526**	0.503**	0.200**																
Gregarinasina	0.242**	-0.008	0.567**	0.242**	0.140**	0.425**															
Silicofilosea	0.263**	-0.099*	0.500**	0.454**	0.167**	0.528**	0.454**														
Conthreep	0.203**	-0.091*	0.088*	0.448**	0.287**	0.274**	0.122**	0.388**													
Nematoda	0.289**	-0.023	0.525**	0.386**	0.337**	0.473**	0.557**	0.612**	0.393**												
Arthropoda	0.262**	-0.01	0.476**	0.208**	0.317**	0.404**	0.584**	0.432**	0.164**	0.618**											
Spirotrichea	0.133**	-0.069	0.116**	0.324**	0.350**	0.324**	0.181**	0.461**	0.637**	0.487**	0.362**										
Acidobacteria	0.434**	-0.062	0.528**	0.491**	0.291**	0.502**	0.358**	0.582**	0.539**	0.585**	0.359**	0.434**									
Actinobacteria	0.092*	-0.152**	0.062	0.426**	0.128**	0.142**	-0.139**	0.106**	0.510**	0.071	-0.143**	0.295**	0.548**								
Bacteroidetes	-0.143**	-0.075	0.031	0.091*	0.137**	0.319**	0.04	0.267**	0.417**	0.290**	0.145**	0.495**	0.421**	0.402**							
Cyanobacteria	0.128**	0.072	0.119**	0.216**	0.127**	0.016	-0.013	0.197**	0.254**	0.232**	0.051	0.188**	0.118**	0.172**	0.054						
Chloroflexi	0.373**	0.02	-0.066	0.217**	0.117**	-0.073	-0.208**	-0.012	0.410**	-0.034	-0.163**	0.122**	0.446**	0.543**	0.043	0.181**					
Firmicutes	0.405**	0.008	0.114**	0.235**	0.242**	0.298**	0.139**	0.502**	0.448**	0.431**	0.171**	0.455**	0.572**	0.368**	0.301**	0.102**	0.239**				
Gemmatimonadetes	-0.095*	-0.065	-0.101*	0.138**	0.120**	0.235**	-0.133**	0.100*	0.497**	0.061	-0.078	0.349**	0.471**	0.600**	0.719**	-0.018	0.352**	0.245**			
Planctomycetes	0.229**	-0.006	0.575**	0.410**	0.227**	0.554**	0.428**	0.714**	0.377**	0.668**	0.393**	0.380**	0.808**	0.339**	0.510**	0.158**	0.123**	0.499**	0.353**		
Proteobacteria	0.315**	-0.004	0.517**	0.475**	0.311**	0.528**	0.398**	0.656**	0.528**	0.711**	0.468**	0.565**	0.861**	0.500**	0.568**	0.239**	0.228**	0.620**	0.423**	0.844**	
Verrucomicrobia	0.055	-0.017	0.588**	0.295**	0.197**	0.573**	0.445**	0.638**	0.215**	0.636**	0.472**	0.385**	0.654**	0.133**	0.577**	0.082*	-0.098*	0.367**	0.269**	0.859**	0.751**

Appendix S4. Extended results

Correlations between the richness of multiple soil trophic levels and environmental drivers

Higher mean annual temperature had a universally positive effect on the richness of the main groups within archaea (Crenarchaeota and Euryarchaeota), bacteria (Acidobacteria, Actinobacteria, Chloroflexi, Firmicutes, Planctomycetes and Proteobacteria) and eukaryotes (Basidiomycota, Ascomycota, Streptophyta, Gregarinasina, Silicofilosea, Conthreep, Nematoda, Arthropoda and Spirotrichea; Appendix S3: Table S3). In contrast, increases in aridity generally correlated negatively to the richness of the main groups within archaeal, bacterial and eukaryotic (Appendix S3: Table S3). The richness of bacteria, archaea and eukaryotes responded in the same manner to increasing temperature and aridity, but was taxa-dependent for soil pH, soil carbon and vegetation types (Appendix S3: Table S3). Only bare surfaces showed an overall negative impact on the richness of the main bacterial, archaeal and eukaryotic taxa (Appendix S3: Table S3).