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Local and regional influences over soil microbial metacommunities in the Transantarctic Mountains

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Abstract. The metacommunity concept provides a useful framework to assess the influence of local and regional controls over diversity patterns. Culture-independent studies of soil microbial communities in the McMurdo Dry Valleys of East Antarctica (77° S) have shown that bacterial diversity is related to soil geochemical gradients, while studies targeting edaphic cyanobacteria have linked local diversity patterns to dispersal-based processes. In this study, we increased the spatial extent of observed soil microbial communities to cover the Beardmore Glacier region in the central Transantarctic Mountains (84° S). We used community profiling techniques to characterize diversity patterns for bacteria and the cyanobacterial subcomponent of the microbial community. Diversity partitioning was used to calculate beta diversity and estimate among-site dissimilarity in the metacommunity. We then used variation partitioning to assess the relationship between beta diversity and environmental and spatial gradients. We found that dominant groups in the soil bacterial metacommunity were influenced by gradients in pH and soil moisture at the Transantarctic scale (800 km). Conversely, beta diversity for the cyanobacterial component of the edaphic microbial metacommunity was decoupled from these environmental gradients, and was more related to spatial filters, suggesting that wind-driven dispersal dynamics created cyanobacterial biogeography at a local scale (<3 km).

Key words: Antarctica; beta diversity; biogeography; diversity partitioning; McMurdo Dry Valleys; metacommunities; soil microbial ecology; Transantarctic Mountains; variation partitioning.

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INTRODUCTION

Ecological context can affect the balance of niche- and dispersal-based metacommunity dynamics, which influence biodiversity patterns and how they are structured by environmental gradients (Caruso et al. 2011). For example, community composition is more closely tied to habitat characteristics for good dispersers than dispersal-limited organisms (De Bie et al. 2012), random drift in community composition is more likely in assemblages in stable habitats with high productivity (Chase 2007, 2010), and assemblages in high stress habitats (e.g., frequent drought, low productivity) are more likely to converge upon similar community compositions of tolerant taxa (Chase 2007). Understanding how ecological context influences local and regional

controls over soil microbial diversity (Dumbrell et al. 2009, Caruso et al. 2011, Soininen 2012) is imperative for Antarctic soils because these relatively simple ecosystems (Hogg et al. 2006) may be particularly sensitive to climate change (Nielsen and Wall 2013). Antarctic soils are predicted to become warmer and wetter (Bracegirdle et al. 2008), and an increased frequency of pulse melt/flood events (IPCC 2007) will likely alter the temporal and spatial distribution of liquid water, which can significantly affect soil ecological processes (Barrett et al. 2008, Nielsen et al. 2012, Nielsen and Wall 2013). Therefore, it is essential to resolve the influences of local and regional controls over soil microbial community composition, which may allow us to predict how Antarctic terrestrial ecosystems will respond to climatic shifts.

A metacommunity is a group of biotic communities that are potentially connected by regional dispersal dynamics (i.e., immigration and emigration). Thus, the metacommunity concept (Leibold et al. 2004) provides a useful framework for evaluating the influence of local and regional controls over biodiversity. In niche-based metacommunity hypotheses (H1: niche-based species sorting), the compositions of assemblages in a metacommunity are determined by the local habitat, which acts to restrict the types of organisms that can occur there (Keddy 1992, Chase and Leibold 2003, Van der Gucht et al. 2007). H1 predicts that variation in community composition will track variation in habitat characteristics that act as environmental filters. In dispersal-based hypotheses (H2: dispersal-based biogeography) (Hubbell 2001, 2005), emigration and immigration rates in a metacommunity control the composition of local communities and regional diversity patterns; consequently, spatially autocorrelated diversity patterns (spatial structure) arise in a landscape because more propagules move between sites in close spatial proximity than sites that are far apart. Metacommunity theory further predicts that habitat heterogeneity and functional diversity determine the degree to which local (H1, species-sorting by environmental filters) and regional (H2, source-sink dispersal-based dynamics) processes interact to determine local assemblage composition and regional diversity patterns (Martiny et al. 2006, Dumbrell et al. 2009, Bru et al. 2010, Caruso et al. 2011, Logue et al. 2011, Heino et al. 2012).

Culture-independent techniques have demonstrated that microbial communities in arid soils in the Transantarctic Mountains of East Antarctica are more diverse than previously thought (Adams et al. 2006, Aislabie et al. 2006, 2008, Niederberger et al. 2008, 2012, Takacs-Vesbach et al. 2010, Lee et al. 2012), and that these soils harbor phylum-level diversity similar to that of other soil ecosystems worldwide (Barrett et al. 2006, Cary et al. 2010). Recent evidence has shown that soil communities in the McMurdo Dry Valleys can respond rapidly to shifts in the local habitat, indicating the potential for local environmental controls over microbial community composition (McKnight et al. 2007, Tiao et al. 2012) and providing support for H1. Inter-valley differences in soil microbial community profiles (Lee et al. 2012) suggest that regional processes also influence microbial community composition. However, it is unclear whether these regional-scale diversity patterns result from local species-sorting dynamics (H1) (e.g., Van der Gucht et al. 2007) scaled up to the landscape level, or spatial heterogeneity associated with dispersal-based metacommunity dynamics and historical factors (H2) (Fenchel 2003, Martiny et al. 2006, 2011, Takacs-Vesbach et al. 2008).

For this study, we conducted a geospatially referenced survey of soil microbial communities and geochemical variables in two areas spanning across 7° in latitude within the Transantarctic Mountains. We assessed diversity patterns for both the total and the cyanobacterial subcomponent of soil bacterial communities, because cyanobacterial community composition appears to be related to local dispersal dynamics (i.e., proximity of an aquatic habitat to serve as a source for cyanobacterial propagules) (Wood et al. 2008, Michaud et al. 2012, Niederberger et al. 2012), whereas total bacterial diversity patterns appear to be related to environmental gradients (Aislabie et al. 2008, Lee et al. 2012, Tiao et al. 2012). The nature of these relationships is linked to the ecological context—the characteristics of the organisms populating a metacommunity (i.e., dispersal ability [Fenchel and Finlay 2004, Shurin et al. 2009, Hájek et al. 2011, De Bie et al. 2012] and prevalence of dormancy [Jones and Lennon 2010, Lennon and Jones 2011]), which in turn

Table 1. Site description and coordinates of ice-free geographic features where samples were collected.

Region	Site	Latitude	Longitude	Elevation range (m)	No. observations
MDV	Alatna Valley	−76.90897	161.04310	970–1030	15
MDV	Miers Valley	−78.10618	163.98832	250–370	15
MDV	Taylor Valley	−77.62854	163.24954	70–95	15
BG	Cloudmaker	−84.26848	169.82540	885–990	15
BG	Kyffin	−83.81664	171.95883	555–585	10

Note: Three 100-m transects were located in each valley, except at Kyffin, where samples were only collected from two transects.

determine how the metacommunity can respond to environmental gradients in a given landscape.

We used diversity patterns derived from our survey to infer the scales at which different metacommunity dynamics organize community composition. We quantified local (alpha) and regional (gamma) diversity patterns to estimate multiplicative beta diversity (variation in community composition among assemblages) (Jost 2007, Chao et al. 2012), which can also be related to scale of metacommunity mixing (Barton et al. 2013). Using variation partitioning, we assessed the spatial scale of community composition heterogeneity in the metacommunity (spatial component of beta diversity) and the spatial scales at which community composition responds to environmental gradients (environmental component of beta diversity) (Borcard et al. 1992, Peres-Neto et al. 2006, Van der Gucht et al. 2007, Dumbrell et al. 2009, Bru et al. 2010, Logue and Lindström 2010, Caruso et al. 2011, Logue et al. 2011, De Bie et al. 2012).

Methods

Site description

Surface soils were collected from two of the largest ice-free regions in the Transantarctic Mountains (Hopkins et al. 2006, Bockheim 2008): a northern group of sites was located in the McMurdo Dry Valleys (MDV, 77° S) in southern Victoria Land, and a southern group of sites was located in the Beardmore Glacier (BG, 85° S) region in the Central Transantarctic Mountains (Table 1, Fig. 1). The MDV region has mean annual temperatures ranging between −15°C and −35°C (Doran et al. 2002), and receives 50 to 150 mm water equivalent yr^{-1} precipitation (Fountain et al. 2010). In general, MDV soils are extremely cold and liquid water-limited (Barrett et al. 2006), but there is considerable within-valley variation in microclimate conditions (Marchant and Denton 1996, Doran et al. 2002). Comparable soils were selected in the BG region, where mean annual temperatures range from −30°C to −35°C (Bockheim 2008). In this study, we included arid soils collected from Alatna, Taylor, and Miers Valleys in the MDV region and Kyffin and Cloudmaker in the BG region.

Sample collection

The sampling design of this study was spatially stratified so that the scale of environmental gradients and biodiversity patterns could be quantified (Fig. 1, Table 1, Appendix: Table A1). Each soil sample was a composite of five sub-samples collected from the top 10 cm of soil in a 1-m^2 plot (see Appendix for methods for sample collection and geochemical analysis). Five samples were collected along a 100-m transect with paired sampling plots (separated by 1 m) located at the ends of a transect, which generated local, within-transect, spatial lags of 1 m, 10 m, and 100 m. At each site, samples were collected along three replicate transects spaced 1 km apart ($n = 15$), except for one case where the area of exposed soil only allowed for two transects ($n = 10$, Kyffin). This sampling pattern resulted in inter-transect spatial lags of 1 to 3 km. Inter-site comparisons provided spatial lags of 50–200 km, and comparisons between the MDV and BG regions occurred over spatial lags of ~800 km. This design created a distribution of between-plot comparisons spanning nearly 6 orders of magnitude, with pairwise comparisons representing spatial lags of 1 m, 10 m, 100 m, 1–3 km, 50–200 km, and 800 km (Fig. 2).

Soil bacterial and cyanobacterial community profiling

To characterize the edaphic bacteria and cyanobacterial assemblages for each sampling

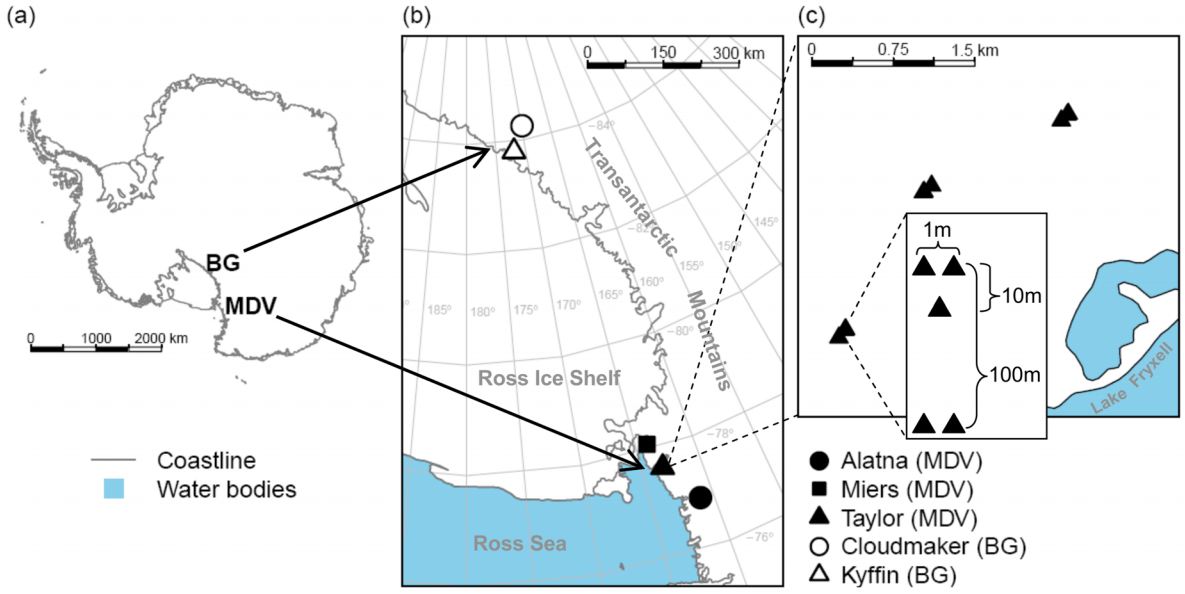

Fig. 1. Map of Beardmore Glacier (BG) and McMurdo Dry Valley (MDV) region locations in Antarctica (a), site locations in the Transantarctic Mountains (b), and sampling transect layout at a site (c, sampling plot locations in Taylor Valley in the MDV region).

plot, environmental DNA was extracted from soil samples at the University of Waikato, New Zealand using a modified cetyltrimethyl-ammonium bromide-polyvinylpyrrolidone-βmercaptoethanol (CTAB) extraction protocol described by Barrett et al. (2006, but also see Dempster et al. 1999, Coyne et al. 2001). The bacterial communities were characterized using terminal restriction fragment length polymorphism (tRFLP; see Appendix) (Tiao et al. 2012), and automated ribosomal intergenic spacer analysis (ARISA; see Appendix) (modified from Wood et al. 2008) was used to characterize the cyanobacterial subcomponent of the soil microbial community. Because we were only able to extract small amounts of environmental DNA from some of the samples, we used a relatively small amount of template (1 ng) in PCR amplifications of 16S rDNA prior to tRFLP profiling. We assumed the cyanobacteria-specific primers used in amplification prior to ARISA would target a much smaller subset of the total bacterial community, therefore we used an order magnitude more template in these PCRs (10 ng template DNA in each reaction).

To determine community composition and structure in each sample, electropherograms were processed using PeakScanner v1.0 (PE Applied Biosystems) with a peak-height cutoff of 5 relative fluorescence units. "Signal" peaks and "noise" peaks were separated using a heavily modified implementation of Abdo et al. (2006), where noise peaks were modeled using a log-normal distribution with alpha = 0.01 for delineation of noise. Relative abundance of each peak was calculated using peak areas and those comprising less than 0.1% of the total community in each sample were omitted. Peaks from all samples were then size-binned with one another using an agglomerative clustering algorithm with a width of 1 nucleotide to form a sample by fragment length (FL) relative abundance table.

Statistical analysis

All statistical analyses were performed using the R 2.13.1 statistical environment (R Development Core Team 2011) unless otherwise specified. Environmental variables were log $(x + c)$ transformed, where c is a constant representing the first percentile value, except for pH measurements. Using a constant set to the first percentile value, instead of the arbitrary $c = 1$, results in a similar rescaling across all transformed variables (Legendre and Legendre 1998, McCune and Grace 2002). Relative abundances of community

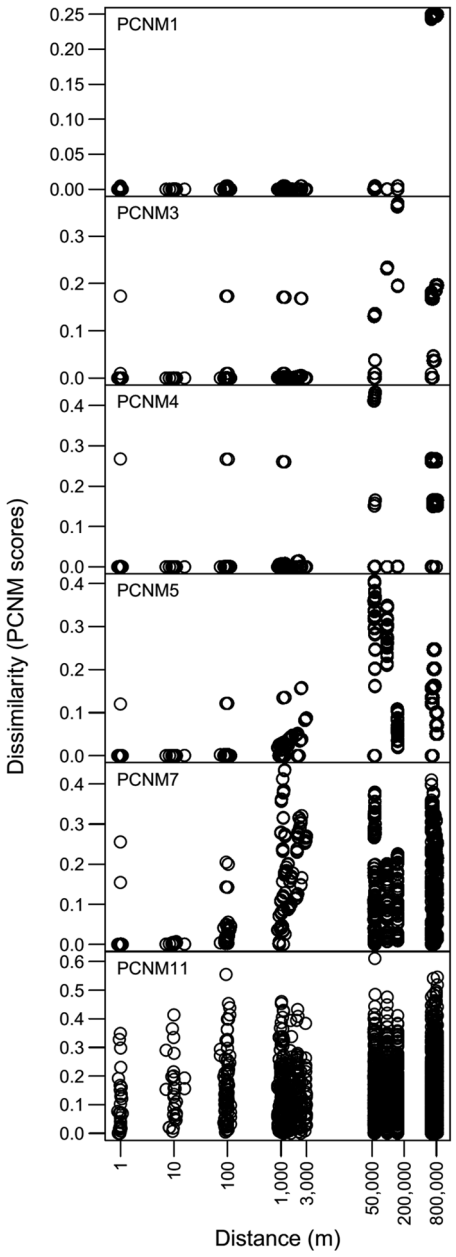

Fig. 2. Spatial scales represented by select spatial filters (PCNM eigenvectors). Pairwise differences in PCNM eigenvector scores plotted against spatial lag. Selected spatial filters for PCNM eigenvectors 1, 3, 4, 5, 7, and 11. PCNM scores calculated for 70 sites. Number of pairwise comparisons for each spatial lag group (in increasing order) are 28, 28, 84, 325, 825, and 1,125. Appendix: Table A2 shows which PCNM eigenvectors differentiate among regions and sites. See Appendix: Fig. A1 for georeferenced maps of PCNM 1 and PCNM 11 scores.

profiles were not transformed prior to analysis because the dissimilarity indices used in the community analyses have inherent rescaling properties that are difficult to interpret when data are transformed prior to analysis (see Jost 2007, Jost et al. 2011).

We used Principal Coordinates of Neighbor Matrices (PCNM, see Appendix and Supplement) (Borcard et al. 2004), which is a special case of distance-based Moran Eigenvector Map (MEM) analysis (Peres-Neto et al. 2006), to calculate spatial filters from sampling plot coordinates (Borcard and Legendre 2002, Borcard et al. 2004, De Bie et al. 2012, Legendre et al. 2012, Heino et al. 2012). PCNM eigenvectors with positive eigenvalues were used as variables to represent different scales of heterogeneity (i.e., spatial filters), with the first eigenvector (PCNM 1) representing the broadest spatial gradient, and each successive eigenvector representing finer scale spatial structure (Fig. 2).

We used Principal Component Analysis (PCA) to assess the variation in soil chemistry among sampling plots (Legendre and Legendre 1998, McCune and Grace 2002). All values were scaled to a zero mean and unit variance prior to analysis. We used forward stepwise selection (Blanchet et al. 2008) based on adjusted R^2 values (Peres-Neto et al. 2006) to build a redundancy analysis (RDA) model to describe variation in soil chemistry as a function of the spatial variables calculated using PCNM analysis. This analysis can be used to relate the overall environmental variation described in the PCA to spatial gradients. We used stepwise model selection based on AIC to build univariate spatial models for each environmental variable using the stepAIC function in the MASS package for R (Venables and Ripley 2002).

All diversity metrics in this analysis are based on Hill numbers (Jost 2006, 2007, Jost et al. 2011, Chao et al. 2012), which typically represent "species equivalents", but represent "FL equivalents" in this analysis. We estimated diversity for bacterial tRFLP and cyanobacterial ARISA community profiles using Hill numbers (${}^qD$) of order $q = 0$ and $q = 2$. Order $q = 0$ Hill numbers represent richness (i.e., alpha diversity = no. peaks observed in a tRFLP profile), and are more sensitive to variation in the presence/absence of less dominant FLs. Alternatively, Hill numbers of

order $q = 2$ are biased toward differences in the relative abundances of dominant FLs. Thus we refer to order $q = 0$ diversity measures as rare-biased and $q = 2$ diversity measures as dominant-biased.

We partitioned FL diversity into alpha, beta, and gamma components at the site, region, and whole-study levels of organization. Alpha diversity (${}^qD_\alpha$) represents the local diversity of a 1-m^2 sampling plot. Mean alpha diversity (${}^qD_{\bar{\alpha}}$) for a group of observations is calculated as exp(mean[${}^qH_\alpha$]), where ${}^qH = \log({}^qD)$ and represents the Renyi entropy of order q. Gamma diversity (${}^qD_\gamma$) is an estimate of the total FL richness when $q = 0$, or an estimate of the total number of dominant-biased FL equivalents when $q = 2$, for a group of sites. Using the multiplicative formula ${}^qD_\beta = {}^qD_\gamma/{}^qD_{\bar{\alpha}}$, we partitioned gamma diversity into alpha and beta components. We calculated ${}^qD_{\bar{\alpha}}$, ${}^qD_\beta$, and ${}^qD_\gamma$ for sites, regions, and all assemblages pooled. We used bootstrap resampling to calculate 95% confidence intervals for each diversity estimate (Hesterberg et al. 2007) for each level of organization (see Appendix and Supplement). This multiplicative measure of beta diversity is an estimate of "distinct" communities in a group of assemblages (Jost 2007, Jost et al. 2011, Chao et al. 2012), making it more robust to the problems associated with fingerprinting methods (i.e., multiple FLs associated with a single taxon, or multiple taxa associated with one or more FLs) (Crosby and Criddle 2003, Okubo and Sugiyama 2009) than comparisons based on FL richness (alpha or gamma diversity).

We used model selection to build a logistic regression model to predict the presence of amplifiable cyanobacterial DNA as a function of environment. We used the stepAIC function to conduct a forward model selection based on AIC values to select the environmental variables that best predicted the presence of peaks in the ARISA community profile. We used the glm function in the stats package with a binomial distribution and a logit linking function to create the logistic regression models (Venables and Ripley 2002). We calculated the coefficient of determination using log likelihood values of the best fit model and the null model (a model with an intercept but no predictor variables).

The main objective in this study is to explain variation in soil microbial community profiles among sampling plots, which is a measure of beta diversity. We calculated dissimilarity matrices from the FL relative abundance tables produced from tRFLP profiles for bacteria and from ARISA profiles for cyanobacteria. For both profile types, we calculated incidence-based dissimilarity matrices using Jaccard distances and relative-abundance-based dissimilarity matrices using the Morisita-Horn index, which represent all two-sample, pairwise calculations of rare-biased (${}^0D_\beta$) and dominant-biased (${}^2D_\beta$) beta diversity, respectively (Chao et al. 2008, Jost et al. 2011). We used principal coordinate analysis (PCoA) to plot ordinations of bacterial and cyanobacterial community composition using both the incidence-based Jaccard dissimilarities and the relative-abundance-based Morisita-Horn dissimilarities. Vectors representing the influence of environmental gradients over variation in community composition were added to the PCoA plots using the envfit function in the vegan package (Oksanen et al. 2012).

We used variation partitioning to assess how environmental and spatial gradients influenced the structure of microbial metacommunities (see Supplement) (Borcard et al. 1992, Peres-Neto et al. 2006). First, we used distance-based redundancy analysis (dbRDA) to model variation in community profiles as a function of either environmental [E] or spatial [S] variables. We used forward stepwise model selection (Blanchet et al. 2008) based on adjusted R^2 (Beisner et al. 2006, Peres-Neto et al. 2006, Nabout et al. 2009, Legendre et al. 2012) to select environmental variables that best explained variation in community profiles. The same technique was used to select spatial variables (PCNM eigenvectors) that best explained among-site variation in community profiles. We then combined the environmental and spatial variables into a single dbRDA model to calculate the total variation in community profiles explained by environmental and spatial variables [E + S]. Using the adjusted R^2 values for the environmental, spatial, and environmental + spatial models, we classified among-site variation in community profiles as pure environmental [E|S], spatially structured by the environment [E ∩ S], pure spatial [S|E], or unexplained (Borcard et al. 1992, Peres-Neto et al. 2006).

Results

Spatial filters and spatial structure of soil geochemical properties

Spatial filters in this study were modeled using the scores for 36 positive PCNM eigenvectors. Pairwise differences in eigenvector scores were plotted against spatial lag to identify the scale of heterogeneity represented by each PCNM eigenvector (Fig. 2). The first eigenvector (PCNM 1) characterized broad scale (640–840 km) heterogeneity, differentiating the two regions, MDV and BG (Appendix: Fig. A1, Table A2). PCNM 3 and PCNM 4 represented inter-valley scale (50–200 km) heterogeneity in the MDV and BG regions, respectively. PCNM 5 and PCNM 7 represented intermediate scale spatial structure (1–3 km). Spatial variables PCNM 8 through PCNM 36 modeled within-site spatial heterogeneity at scales as fine as 1 m.

The spatial structure of edaphic gradients was predominantly organized over broad scales. PCA showed that different sampling locations within a site tended to have similar soil chemical characteristics (Fig. 3; see Appendix: Table A3 and Fig. A2 for environmental variable values); soils from Miers and Taylor (MDV region), and Alatna and Kyffin (MDV and BG regions, respectively) clustered together, indicating those pairs of sites had comparatively similar soil characteristics. The Cloudmaker site in the BG region appeared to be unique in terms of the soil characteristics measured in this study. The best-fit spatial model for all environmental variables described 65% of measured environmental variation, and only included spatial filters that described heterogeneity at the inter-site scale or larger (PCNM 4, 1, 3, 5, and 7; Table 2; the order in which spatial variables are listed reflects their importance in the model). PCNM 4, which primarily differentiated between sites in the BG region, was mainly associated with water content and major ion concentrations and described the largest amount of environmental variation observed in this study. The next most prevalent spatial variable in the overall model, PCNM 1, reflected inter-regional scale heterogeneity. Spanning 7° latitude and 800 km, PCNM 1 represented the broadest spatial gradient and it was strongly associated with soil water and organic matter content. PCNM 3 and PCNM 5 both differentiated between sites in the MDV region. PCNM 3 was most strongly correlated with gradients in pH, ammonium concentrations, and C:N ratio, and thus indicated more pronounced inter-site differences in the MDV region with respect to these environmental variables.

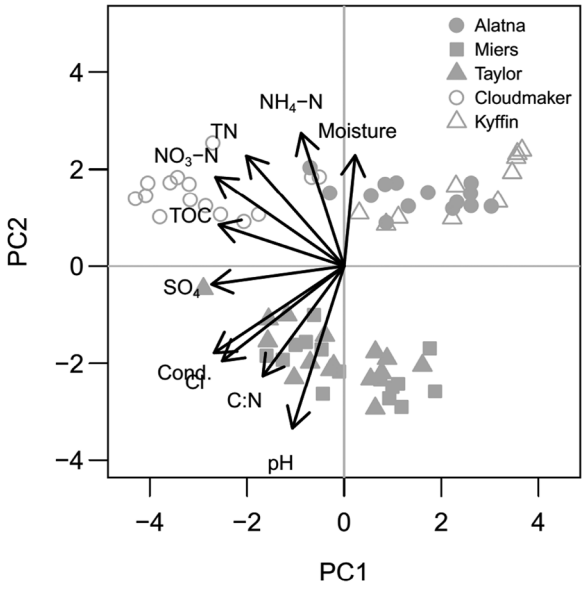

Fig. 3. Biplot of a PCA ordination of sites in geochemical space. First two axes explained 70% of among-site environmental variation (69 sites in the five valleys listed above). Each point represents a sampling plot, and shapes represent site. Filled symbols are from the MDV region, open symbols are from the BG region. Vectors represent loading of geochemical variables onto the first two principal components.

Extractable DNA

Environmental DNA was successfully extracted from soil from all sampling plots in the MDV region, with total DNA yields ranging between 41 and 4,800 ng·g^{-1} wet weight soil (Appendix: Table A3, Fig. A2). DNA extractions from soils from the BG region were less successful and resulted in lower yields than in the MDV region, presumably reflecting lower biomass in these soils ($F_{1,68} = 5.8$, $P = 0.02$; Appendix: Table A4). We were unable to extract DNA from two samples at the Cloudmaker site, and yields from the other 13 samples did not exceed 152 ng·g^{-1} wet weight soil. Extractions from the Kyffin site were more successful and yields ranged between

Table 2. Best-fit models describing spatial structure of environmental gradients.

Environmental variable	Adj. R^2	F	df	P	Spatial filters†
All‡	0.65	25.8	5, 63	0.005	4, 1, 3, 5, 7
pH	0.90	54.9	11, 57	<0.001	3, 1, 5, 4, 6, 7, 2, 26, 29, 19, 36
Conductivity	0.73	13.9	14, 54	<0.001	4, 3, 5, 6, 17, 10, 12, 1, 13, 30, 29, 9, 2, 15
Soil moisture	0.66	20.2	7, 61	<0.001	1, 7, 6, 8, 3, 27, 4
NH_4-N	0.64	14.7	9, 59	<0.001	3, 4, 1, 7, 21, 5, 30, 19, 6
NO_3-N	0.70	12.6	14, 54	<0.001	4, 1, 2, 6, 26, 10, 13, 12, 17, 33, 3, 5, 9, 18
Cl	0.72	12.0	16, 52	<0.001	4, 3, 5, 1, 12, 13, 2, 29, 33, 8, 6, 16, 26, 10, 17, 21
SO_4	0.60	8.4	14, 54	<0.001	4, 5, 6, 19, 34, 2, 17, 11, 31, 13, 10, 12, 25, 1
TOC	0.89	32.6	17, 51	<0.001	1, 4, 3, 7, 5, 10, 21, 14, 6, 17, 20, 26, 18, 8, 2, 22, 15
TN	0.91	49.3	15, 53	<0.001	1, 4, 6, 5, 10, 2, 17, 7, 8, 13, 20, 21, 26, 33, 15
C:N	0.74	20.8	10, 58	<0.001	3, 4, 7, 6, 14, 36, 21, 10, 22, 18

Notes: The spatial organization of all environmental variables was assessed using dbRDA. Multiple linear models were fit to individual environmental variables. Models were selected using stepwise model fitting. Predictor variables are scores from positive eigenvectors representing spatial filters calculated using PCNM analysis on spatial coordinates. TOC, total organic carbon; TN, total nitrogen.

† PCNM eigenvectors, listed in order of influence.

‡ The response variable for dbRDA model selection was a Euclidean distance matrix of scaled, transformed environmental variables and represents overall environmental variability.

9 and 1,804 $ng \cdot g^{-1}$ wet weight soil.

Total bacterial diversity

Bacterial community tRFLP profiles were determined for 60 assemblages from sites in both the BG and MDV regions. Diversity partitioning (Table 3) indicated that estimates of alpha-, beta-, and gamma diversity were influenced by the scale at which assemblages were pooled. In general, dominant-biased estimates of diversity were lower because there were fewer "species equivalents" (or "FL equivalents" in this case) when rare FLs were discounted in the diversity measurement. Miers Valley was anomalous with higher estimates for both rare- ($^0D_{\bar{\alpha}}$) and dominant-biased ($^2D_{\bar{\alpha}}$) alpha diversity.

Beta diversity represents the number of "distinct" communities in a group of pooled samples. Estimates of rare-biased beta diversity ($^0D_\beta$) were between 2.9 and 5.5 at the site level and 7.6 (4.9, 8.5, 95% CL) for the entire study. For dominant-biased beta diversity ($^2D_\beta$), values were between 1.4 and 2.1 at the site level and 2.2 (1.9, 2.5, 95% CL) for the entire study. Beta diversity increased with sampling effort (scale at which observations were pooled, Fig. 4), but the slope was only significantly different from 0 for dominant-biased beta diversity (Fig. 4c).

Cyanobacterial diversity

Cyanobacterial community ARISA profiles were detected in 28 assemblages (see Table 3). In particular, no peaks were detected at the Cloudmaker site in the BG region. Diversity partitioning (Table 3) showed that Miers Valley supported the highest local diversity estimates for cyanobacteria. More distinct communities (beta diversity) were detected in the cyanobacterial community profiles than in the bacterial tRFLP profiles. Estimates of $^0D_\beta$ were between 5.2 and 10 distinct communities at the site level and 22.7 across all assemblages. Estimates of $^2D_\beta$ were between 1.5 and 4.4, and a total of 6.5 distinct communities were observed across all assemblages. Dominant-biased beta-diversities were positively correlated with sampling effort (Fig. 4d), meaning more distinct communities were observed when more assemblages from a larger geographic area were pooled together. A comparison of slopes (Fig. 4c, d) indicated distinct communities accumulated more rapidly with sampling effort in cyanobacterial ARISA profiles than bacterial tRFLP profiles.

Assessing the influence of spatial and environmental filters

Among the 70 sampling locations considered in this study, bacterial rDNA was amplifiable in more samples (60) than cyanobacterial rDNA (28). We used model selection on logistic regression to determine the environmental variable(s) that best predicted sites with detectable cyanobacterial FLs. Total soil nitrogen (TN) was the only variable included in the best fit logistic model predicting the presence of amplifiable cyanobacterial 16S rDNA ($R^2 = 0.143$, $P < 0.005$; Table 4).

Table 3. Alpha, beta, and gamma components of total bacterial tRFLP and cyanobacterial ARISA community profiles.

Site	n	Rare-biased diversity			Dominant-biased diversity		
		${}^0D_{\bar{\alpha}}$	${}^0D_{\beta}$	${}^0D_{\gamma}$	${}^2D_{\bar{\alpha}}$	${}^2D_{\beta}$	${}^2D_{\gamma}$
Bacteria (tRFLP)							
ALL	**60**	**38**	**7.6**	**289**	**12.5**	**2.2**	**28.1**
		(40.6, 54.3)	**(4.9, 8.5)**	**(237, 387)**	**(10.7, 14.6)**	**(1.9, 2.5)**	**(22.7, 31.5)**
BG region	**19**	**35.8**	**6.5**	**231**	**11.4**	**2.1**	**24.3**
		(37.8, 65.7)	**(3.3, 6.8)**	**(174.7, 326.7)**	**(7.6, 16)**	**(1.6, 2.3)**	**(15.1, 30.1)**
Cloudmaker	11	36.8	4.5	167	12.7	2.1	26.1
		(31.2, 58.3)	(2.5, 7.2)	(106.6, 300.9)	(9.3, 16.6)	(1.5, 2.1)	(16.8, 29.8)
Kyffin	8	34.4	5.5	190	9.8	1.7	16.7
		(32.3, 89.1)	(1.9, 7)	(114.5, 332)	(4.8, 20.3)	(1, 1.8)	(7.2, 28)
MDV region	**41**	**39**	**5.6**	**218**	**13.1**	**2.1**	**27**
		(38.5, 52.3)	**(3.9, 6.8)**	**(176.5, 302.4)**	**(10.9, 15.2)**	**(1.8, 2.3)**	**(21.9, 30.3)**
Alatna Valley	13	34.6	4.6	158	9.8	1.4	13.6
		(28.6, 55.5)	(2.6, 8.8)	(91.8, 324)	(6.8, 13.6)	(1.1, 1.7)	(8.7, 19.9)
Miers Valley	14	50.1	2.9	146	16.6	1.4	23.3
		(43.7, 63.4)	(2.2, 3.8)	(118, 189.4)	(14.2, 19.4)	(1.2, 1.5)	(18.3, 27.3)
Taylor Valley	14	34	4	136	13.5	1.9	26.3
		(30.7, 53.3)	(2.4, 5.2)	(103.5, 194.6)	(10.2, 17.5)	(1.5, 2.1)	(18.8, 28.8)
Cyanobacteria (ARISA)							
ALL	**28**	**4.8**	**22.7**	**108**	**2.7**	**6.5**	**17.5**
		(5, 12.1)	**(8.1, 24.5)**	**(74, 162.5)**	**(2.1, 3.6)**	**(3.3, 7.7)**	**(8, 23.9)**
BG region	**4**	**3.7**	**5.2**	**19**	**2.2**	**2.2**	**4.8**
		(1.5, 12)	**(1.2, 27.8)**	**(4, 147)**	**(1.3, 2.9)**	**(1, 2.4)**	**(1.7, 6.6)**
Kyffin	4	3.7	5.2	19	2.2	2.2	4.8
		(1.8, 12.3)	(1.3, 27.8)	(4, 147)	(1.3, 2.9)	(1, 2.4)	(1.7, 6.6)
MDV region	**24**	**5**	**20.5**	**102**	**2.8**	**5.1**	**14.2**
		(5.4, 13.5)	**(7.1, 24)**	**(69, 171.7)**	**(2.1, 3.8)**	**(2.6, 6.4)**	**(6.4, 21)**
Alatna Valley	8	3.7	10	37	1.8	1.5	2.8
		(2.8, 12.1)	(2.4, 32.6)	(12.1, 172.5)	(1.2, 2.8)	(1, 2.1)	(1.5, 4.8)
Miers Valley	8	8.4	7.2	60	4.5	4.4	19.8
		(6, 24)	(2.1, 25.4)	(30, 215.6)	(2.8, 7)	(1.9, 4.2)	(7.1, 20.3)
Taylor Valley	8	4	10	40	2.7	4.2	11.3
		(2.8, 10.8)	(2.9, 44.3)	(13, 224.1)	(1.7, 4.3)	(1.9, 4.3)	(3.8, 15.4)

Note: Diversities are calculated from Hill numbers of order $q = 0$ and $q = 2$. Alpha, beta, and gamma components were calculated for the entire study, observations grouped by region, and observations grouped by site. 95% CLs for mean alpha and beta were calculated using bootstrap resampling.

We found that both environmental and spatial gradients influenced bacterial and cyanobacterial community composition (Table 4). According to best-fit dbRDA models, environmental gradients [E] were better predictors of variation in community composition for total bacterial community profiles than cyanobacterial community profiles. This was true for rare-biased diversity estimates (bacteria vs. cyanobacteria = 11.5% vs. 6.2%) as well as dominant-biased diversity estimates (bacteria vs. cyanobacteria = 30.4% vs. 15.1%). In rare-biased bacterial community profiles, the best-fit dbRDA model indicated pH, moisture, TN, and conductivity to be the most important variables explaining plot-to-plot variation (Fig. 5a), whereas pH, moisture, C:N ratio, conductivity, and NH_4-N were most important when dominant-biased dissimilarities were used (Fig. 5b). In rare-biased cyanobacterial community profiles, the best fit dbRDA model indicated soil C:N, NO_3-N, and conductivity to be the most important variables explaining plot-to-plot variation (Fig. 5c), whereas soil C:N, TN, and NO_3-N were most important when dominant-biased dissimilarities were used (Fig. 5d).

For both bacterial and cyanobacterial community profiles, spatial filters [S] explained dominant-biased diversity better than rare-biased diversity. For bacterial tRFLP community profiles, rare-biased diversity was organized at a broader spatial scale (PCNM 1 and 3, adj. $R^2 = 0.084$) than dominant-biased diversity (PCNM eigenvectors 3, 5, 1, 11, and 28; adj. $R^2 = 0.316$). For cyanobacterial ARISA community profiles, rare-biased diversity correlated with both broad and local scale spatial filters (PCNM 3, 1, and 10, adj. $R^2 = 0.094$). Dominant-biased diversity was organized at a similar scale (PCNM 3, 1, 5, and

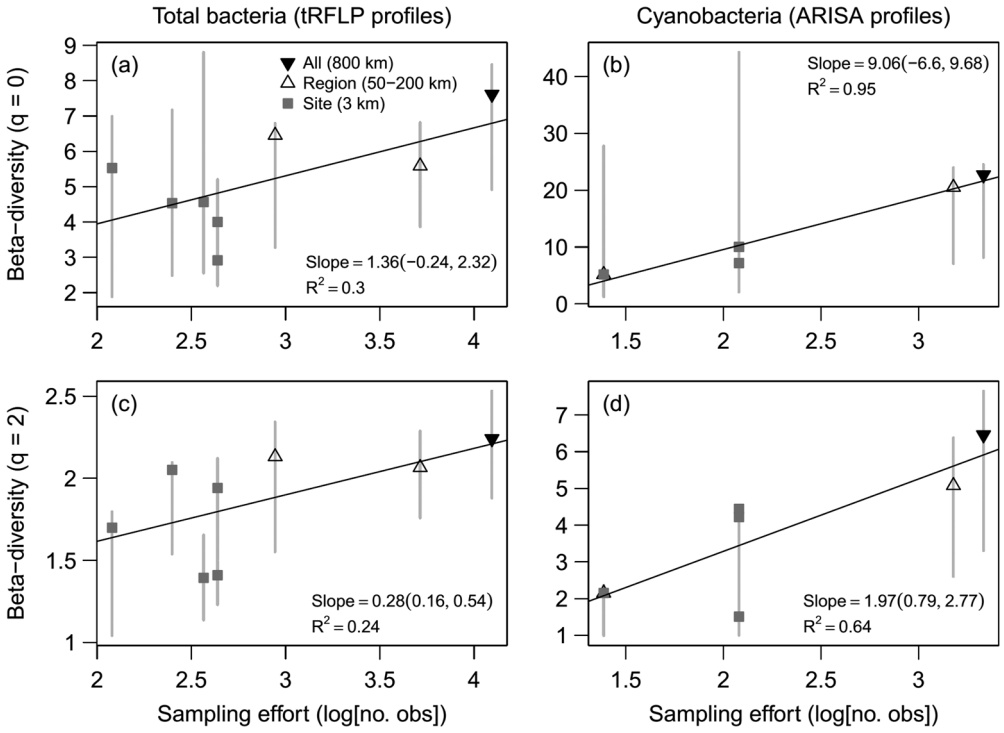

Fig. 4. Beta diversity estimates for samples pooled by site, by region, and for the entire study, plotted against sampling effort (see Table 3). Panels represent rare-biased beta diversity for total bacterial (a) and cyanobacterial (b) community profiles and dominant-biased beta diversity for total bacterial (c) and cyanobacterial (d) community profiles. Sampling effort represents the number of assemblages pooled at a given scale. Error bars reflect estimates of 95% CIs using 1,000 bootstrapped iterations (resampling with replacement). 95% CLs of the slope of the best fit lines were calculated using 10,000 bootstrapped iterations.

10; adj. $R^2 = 0.189$). A fraction of the spatial structure of both the bacterial and cyanobacterial community profiles was explained by spatially structured environmental gradients [E ∩ S]; however, all profiles had significant spatial structure that was independent of measured environmental gradients [S|E]. Only the dominant-biased cyanobacterial community profile had a significant local [S|E] component.

Discussion

Lee et al. (2012) reported significant intervalley variation in soil bacterial community composition in the MDV region and also demonstrated that variation in community composition was correlated with gradients in soil geochemistry associated with microclimate and the influence of liquid water (also see Aislabie et al. 2008). The cyanobacterial component of the soil microbial community appears to be associated with different environmental gradients at finer spatial scales (Wood et al. 2008, Michaud et al. 2012, Niederberger et al. 2012). In this study, our sampling design allowed us to identify the spatial filters and environmental gradients associated with variation in soil microbial community composition, and thus provide insight to the scales at which niche-based species sorting (H1) and dispersal-based biogeography (H2) influence diversity patterns. Increasing the extent of our survey beyond the MDV region (~200 km) to include sites that were geochemically similar (e.g., Kyffin soils were similar to Alatna; Fig. 3), but up to 800 km away from the MDV region, provided an opportunity to test predictions of H1 and H2 over a broad spatial scale. H1 predicts that the relationship between community composition and environmental gradients will be maintained as spatial lags are increased, whereas

Table 4. Best-fit environmental and spatial models for bacterial and cyanobacterial community composition in Antarctic soils.

Response variable (model type)	Environmental variables	Spatial filters	Fraction of variation as partial adj. R^2					
			[E]	[S] (local [S])	[E|S]	[E ∩ S]	[S|E] (local [S|E])	[E + S]
Bacteria (tRFLP)								
Rare-biased community composition (multivariate, dbRDA)	pH, Moisture, TN, Cond.	1, 3	0.115*	0.084* (NA)	0.049*	0.066	0.019* (NA)	0.133*
Dominant biased community composition (multivariate, dbRDA)	pH, Moisture, C:N, Cond., NH_4-N	3, 5, 1, 11, 28	0.304*	0.316* (0.103*)	0.093*	0.210	0.106* (NA)	0.410*
Cyanobacteria (ARISA)								
Detectable PCR product (univariate, logistic)	(−) TN		0.143*					
Rare-biased community composition (multivariate, dbRDA)	C:N, NO_3-N, Cond.	3, 1, 10	0.062*	0.080* (0.023*)	0.041*	0.021	0.059* (NA)	0.121*
Dominant biased community composition (multivariate, dbRDA)	C:N, TN, NO_3-N	3, 1, 5, 10	0.151*	0.218* (0.042*)	0.006^{ns}	0.145	0.073* (0.033*)	0.224*

Notes: Both environmental and spatial (eigenvectors from PCNM analysis) variables were used to explain variation in community composition. Variation in community composition was partitioned using dbRDA for presence/absence data using Jaccard distances (rare-biased, emphasizes the influence of rare taxa) and for relative-abundance data using Morisita-Horn distances (dominant-biased, emphasizes the influence of abundant taxa). Environmental and spatial explanatory variables were identified with a forward, stepwise selection. Adjusted R^2 is the proportion of variation in community composition explained by environmental [E] or spatial [S] variables, where [E|S] is the environmental influence independent of spatial variables, [E ∩ S]—intersection between [E] and [S]—represents spatially structured environmental variables, [S|E] represents spatial structure independent of environmental influence, and [E + S] is the total variation explained by environmental and spatial variables. An asterisk indicates a significant adjusted R^2 (P value < 0.05) based on a permutation test, "ns" indicates a P value > 0.05. Adjusted R^2 values in parentheses describe local (e.g., within a site or valley, <3 km) spatial heterogeneity. Logistic regression was used to predict cyanobacteria presence/absence using environmental variables.

H2 predicts that community composition will be decoupled from environmental variation.

Total soil bacterial diversity corresponds with broad environmental gradients

Total bacterial diversity assessed with tRFLP profiling showed the most common taxonomic groups (associated with most abundant FLs) of the metacommunity were relatively well mixed throughout the Transantarctic Mountains and responded to broad scale environmental gradients spanning 7° of latitude, reaching as far south as 84.3° S (evidence for H1). However, this data set represents a relatively coarse taxonomic resolution (Crosby and Criddle 2003, Danovaro et al. 2006, Novis et al. 2007, Gao and Tao 2012), and dispersal-based metacommunity dynamics (H2) may create biogeography at a finer taxonomic resolution (i.e., species or strain).

In the MDV region of the Transantarctic Mountains, regional scale gradients in soil physiochemical properties that correspond with elevation, lithology, and climate have been shown to organize microbial community composition (Aislabie et al. 2006, 2008, Barrett et al. 2006, Pointing et al. 2009, Cary et al. 2010, Zeglin et al. 2011, Lee et al. 2012). Total bacterial diversity patterns presented here provide evidence in support of the possibility that MDV and BG regions share a source pool, and local assemblages are derived from similar species-sorting processes (H1). Specifically, soil pH and moisture, which are globally ubiquitous abiotic drivers of bacterial community composition (Fierer and Jackson 2006, Angel et al. 2010), appeared to be organizing niche-based sorting at the taxonomic resolution that could be distinguished with tRFLP in soils in the Transantarctic Mountains (Table 4, Fig. 5a, b).

Multiplicative beta diversity values, reported as Hill numbers, represent the number of "distinct" communities in a data set (Jost 2007, Chao et al. 2012). Beta diversity is expected to increase with scale (i.e., pooling samples from an increasingly large area) as new communities are encountered with an expanded sampling effort across the landscape. This can occur at local scales as new niches are encountered along

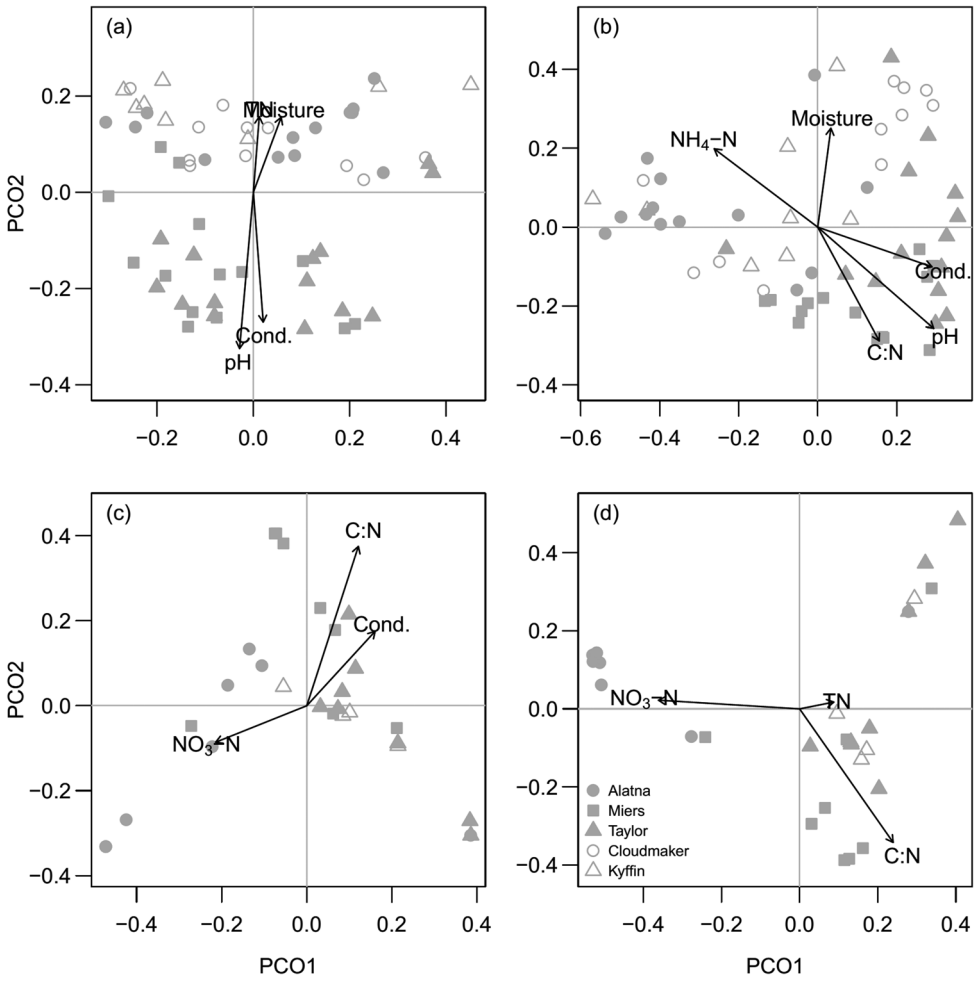

Fig. 5. Principal coordinate analysis of sites based on community composition profiles, with environmental vector overlays. Ordinations calculated for total bacterial profiles (tRFLP) using Jaccard distances (a) and Morisita-Horn distances (b), and for cyanobacterial profiles (ARISA) using Jaccard distances (c), and Morisita-Horn distances (d).

environmental gradients, or over broad spatial scales as new biogeographic regions are encountered (Barton et al. 2013). However, beta diversity is expected to be scale invariant at intermediate ("regional") scales when a metacommunity is sufficiently mixed, and no new habitats with novel communities are encountered with increased sampling effort (Barton et al. 2013). Observed beta diversity was relatively scale invariant for total soil bacterial tRFLP profiles (Fig. 4), indicating the same taxonomic groups, as identified using tRFLP, were dominant in the same niches across the Transantarctic Mountains.

Edaphic cyanobacteria exhibit biogeography

The presence of cyanobacterial FLs was negatively correlated with total soil nitrogen (Table 4, univariate logistic model). This empirical relationship may exist because both edaphic cyanobacterial profiles (Moorhead et al. 1999, 2003) and major ion concentrations (including nitrate) (Bockheim 2008) are influenced by the historical availability of liquid water. Dry Valleys without prominent aquatic features (e.g., lakes, ponds or streams, which source cyanobacterial communities in neighboring soils) tend to be depauperate in soil cyanobacteria (Moorhead et al. 1999, 2003, Wood et al. 2008, Pointing et al. 2009). Excep-

tionally old surfaces that are not exposed to liquid water during the austral summer (Marchant and Denton 1996) accumulate high concentrations of soluble nitrate from atmospheric deposition (Michalski et al. 2005, Bockheim 2008), which may explain why soil TN levels negatively covaried with cyanobacterial presence in edaphic habitats.

Among plots with detectable cyanobacterial FLs, diversity patterns in ARISA community profiles exhibited heterogeneity in community composition over localized spatial gradients represented by transects $\leq$3 km (i.e., within a valley, Table 4, local [S] and local [S|E] components of beta diversity). Previous studies in the MDV region have shown wind-driven dispersal redistributes propagules from aquatic and intermittently saturated habitats to neighboring, more water limited soils (Wood et al. 2008, Michaud et al. 2012, Niederberger et al. 2012). These dynamics could have created the local (i.e., within a valley) spatial heterogeneity in cyanobacterial diversity that we detected in this study. Community composition was also correlated with soil C:N, suggesting the cyanobacterial influence over soil stoichiometry that has been documented in the Dry Valleys (Barrett et al. 2007) may be general to soils throughout the Transantarctic Mountains.

Beta diversity was highly and positively correlated with sampling effort (Fig. 4d), indicating new "distinct" cyanobacterial communities were detected with increased sampling coverage and extent. Localized spatial structure and lack of correlation with environmental gradients (other than C:N) support the hypothesis (H2) that spatially limited dispersal creates spatial heterogeneity in the cyanobacterial metacommunity over relatively small (<3 km) distances (Wood et al. 2008, Michaud et al. 2012, Niederberger et al. 2012).

Local and regional influences over Antarctic microbial metacommunities in arid soils

We did not detect spatial heterogeneity in community composition that was not explained by gradients in soil geochemistry in total soil bacterial tRFLP community profiles. The lack of detectable biogeography in total soil bacteria may be due to phylogenetic niche conservatism (Losos 2008), reflecting a phylum level response to broad environmental gradients detected in this data set because of the coarse taxonomic resolution of tRFLP profiling techniques (Crosby and Criddle 2003, Gao and Tao 2012). The possibility exists that dispersal-based metacommunity dynamics may influence the biogeography of species or strains within a phylum or functional group (e.g., Dumbrell et al. 2009, Caruso et al. 2011).

Such is the case for the cyanobacterial subset of the total bacterial community. We detected biogeographic patterns using a profiling technique with higher taxonomic resolution (ARISA). However, edaphic cyanobacterial diversity patterns are not representative of total bacterial diversity in arid soils, and this finding is consistent across community profiling methodologies, including tRFLP, ARISA, and amplicon pyrosequencing (Lee et al. 2012, Tiao et al. 2012). Similar to this study, but using ARISA for both total bacterial and cyanobacterial community profiles, Lee et al. (2012) showed more distinct cyanobacterial assemblages than total bacterial assemblages in Dry Valley soils. The consistency of these diversity patterns across community profiling techniques suggests the lack of detectable biogeography in the total bacterial metacommunity reported in this study cannot be explained solely by the phylogenetic resolution of the fingerprinting technique. An alternative, though not mutually exclusive, hypothesis is that the taxonomic groups that dominate the total soil bacterial pool represent a cosmopolitan metacommunity that is well mixed throughout the Transantarctic Mountains. The cyanobacterial subcomponent represents a minor fraction of the total bacterial metacommunity in arid soils (e.g., Lee et al. 2012), and thus may have a negligible influence on total soil bacterial diversity patterns.

Aeolian redistribution by saltation provides a localized dispersal mechanism (i.e., within valley) that has been demonstrated to create spatially autocorrelated distribution patterns in the Dry Valleys for soil micro- and meiofauna (Nkem et al. 2006, Adams et al. 2007), including cyanobacteria (Wood et al. 2008, Michaud et al. 2012, Niederberger et al. 2012), and drives local scale (i.e., within valley) heterogeneity in community composition. Aeolian redistribution of cyanobacterial cells (Wood et al. 2008) combined

with the legacy of the historical influence of liquid water in the landscape (Moorhead et al. 1999, 2003) appear to interact to create a heterogeneous patchwork of cyanobacterial assemblages over spatial gradients <3 km. As such, it appears that the distribution of aquatic features in the landscape act as an environmental filter (H1) that determines the presence of cyanobacteria (logistic model, Table 4), and dispersal-based metacommunity dynamics (H2) create biogeographic patterns within the cyanobacterial component of the soil microbial community (dbRDA models, Table 4).

Diversity patterns in the total bacterial community appear to be organized by different metacommunity dynamics than the cyanobacterial subcomponent. Taxa that dominate the total bacterial community may represent groups that become entrained in the atmosphere (Morris et al. 2008, Bowers et al. 2011) and redistributed over broad scales. While the near-ground aeolian redistribution of cyanobacteria has been documented in the Dry Valleys (Wood et al. 2008, Michaud et al. 2012), cyanobacteria appear to be a minor component in more broadly dispersed bioaerosols (Bottos et al. 2013). Past studies have shown beta diversity will have a larger environmental [E|S] component in a well-mixed metacommunity, and a larger [S|E] component when dispersal is limited (De Bie et al. 2012). In this study, we found diversity of the cyanobacterial subcomponent of the soil microbial community to be significantly correlated with local [S|E], and total bacterial diversity was more strongly correlated with [E|S] (Table 4). This result is consistent with the hypothesis that metacommunity mixing occurs over different spatial scales for different subgroups of the soil microbial community.

The dynamic rank-abundance curve hypothesis (Lennon and Jones 2011) suggests that the rare biosphere (Sogin et al. 2006) provides a dormant seed bank of propagules that can be recruited to the active component of the community when local environmental conditions are appropriate (Jones and Lennon 2010, Lennon and Jones 2011). For soil microbial communities worldwide, >80% of the cells and ~50% of species are dormant (Lennon and Jones 2011), and nutrient poor habitats tend to have larger proportions of dormant cells (Jones and Lennon 2010). The presence of such a cryptobiotic seed bank has been demonstrated for MDV soils (McKnight et al. 2007, Antibus et al. 2012, Tiao et al. 2012). Diversity patterns observed in this study for total bacteria (i.e., [S|E] only significant over broad spatial scales in Table 4, shallower slope than cyanobacteria in Fig. 4) suggest a substantial proportion of FLs present in the tRFLP profiles not only represent a relatively well mixed metacommunity, but also demonstrate that the seed bank can respond consistently to broad environmental gradients at the Transantarctic scale.

However, because abundance and distribution tend to be correlated (Nemergut et al. 2011), rare-biased diversity likely also represents the more dispersal limited, endemic members of the microbial metacommunity, including the cyanobacterial subcomponent. Edaphic cyanobacteria are sourced from nearby aquatic habitats (Wood et al. 2008) that tend to be relative hotspots for primary productivity (Zeglin et al. 2009). Such habitats are more likely to be influenced by ecological drift (i.e., priority effects, endemism) and produce diversity patterns with local scale spatial heterogeneity (Chase 2007, 2010). Thus, edaphic cyanobacterial community composition is more closely linked to the proximity of aquatic source pools rather than immediate measures of soil moisture (Wood et al. 2008, Niederberger et al. 2012), and dispersal dynamics strongly influence cyanobacterial diversity at local spatial scales.

Antarctic soil microbial communities can rapidly respond to shifts in the local habitat (McKnight et al. 2007, Tiao et al. 2012), but an effective conceptual model of metacommunity dynamics must account for both regional and local influences over the active and dormant pools to scale this response to a landscape (Leibold et al. 2004, Martiny et al. 2006, 2011, Logue et al. 2011, Nemergut et al. 2011, Soininen 2012). The survey data and analyses presented here are a first step to identifying the scales at which niche- and dispersal-based dynamics are likely driving patterns in soil microbial diversity. Moreover, the balance of local and regional drivers of community composition appears to depend on the life history characteristics (e.g., dispersal ability, dormancy) of the community of interest. How functional traits of individuals

scale up to determine metacommunity level responses to regional environmental gradients will depend on how well a metacommunity is mixed, the level of endemism, and the extent and functional diversity of the dormant seed bank. Understanding the scales at which these dynamics interact will be essential for creating models to predict how Antarctic soils will respond in a changing environment.

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Supplemental Material

Appendix

Detailed methods

Sample collection.—Aseptic sampling techniques were used to collect a 500-g composite soil sample from the upper 10 cm in a plot, excluding pebbles >2 mm in diameter. Each composite sample was homogenized in a polyethylene Whirl-Pak (Nasco International, Fort Atkinson, WI, USA), and split into subsamples for geochemical analysis, soil moisture analysis, and DNA extraction. The DNA extraction split (1 g soil) was preserved in ~600 µl CTAB extraction buffer (Dempster et al. 1999, Coyne et al. 2001) in a 2-ml CryoVial, stored on ice in the field, and stepped down to −80°C as soon as possible.

Geochemical analysis.—Standard methods for Antarctic soils (Barrett et al. 2002, 2009) were used to measure physicochemical soil properties (gravimetric soil moisture, conductivity, and pH) and to extract soluble ions in deionized water and inorganic nitrogen in 2M KCl at the Crary Laboratory at McMurdo Station. Soil samples and analytes were shipped to Virginia Tech for chemical analysis. Ion concentrations in DI extracts were measured on a DIONEX DX500 ion chromatograph (DIONEX, Sunnydale, CA) and inorganic N concentrations in KCl extracts were measured on a LACHAT QuicChem 8500 FIA System (Hach, Loveland, CO). Soil from each sample was air dried and ground in a ball mill; organic C and total C and N (TN) were determined on acidified and unacidified samples on an Elantech EA 1112 elemental analyzer (Elantech, Lakewood, NJ, USA) (Barrett et al. 2004).

Soil bacterial and cyanobacterial community profiling.—The bacterial communities were characterized using terminal restriction fragment length polymorphism (tRFLP) as follows (Lee et al. 2012): PCR of the 16S ribosomal RNA gene was carried out in 25-µl reactions containing 300 nM of FAM-labeled forward primer 27F (5′ - /56 - FAM/AGA GTT TGA TCC TGG CTCAG - 3′) (Lane 1991), 300 nM of reverse primer 1492R (5′ - GGT TAC CTT GTT ACG ACTT - 3′) (Lane 1991), 3 mM MgCl2, 1× Platinum Taq PCR buffer, 1.25 U of Platinum Taq DNA polymerase (Invitrogen Ltd., Carlsbad, CA), 2.5 µg bovine serum albumin, 200 µM of each dNTP (Roche Diagnostics, New Zealand), 1 ng of extracted template DNA, and UltraPure distilled water (Invitrogen Ltd.). Amplification was performed using an initial denaturation step at 94°C for 3 min followed by 30 cycles of 94°C, 30 sec; 55°C, 30 sec; 72°C, 90 sec; and a final extension step of 72°C for 5 min. Duplicate PCR reactions were pooled together, and 30 µL of pooled product was purified (QuickClean 5M PCR purification kit, GenScript). Purified amplicons (10 µL of purified product) were digested at 37°C for 3 h in 20 µl reactions containing 40 U of MspI, 1× Buffer 4 (NE Biolabs) and DNAse-free water (MoBio), followed by heat inactivation at 80°C for 20 min. All reactions were stored at −20°C until being sent to the University of Waikato DNA Sequencing Facility (University of Waikato, New Zealand) for standard desalting and fragment size

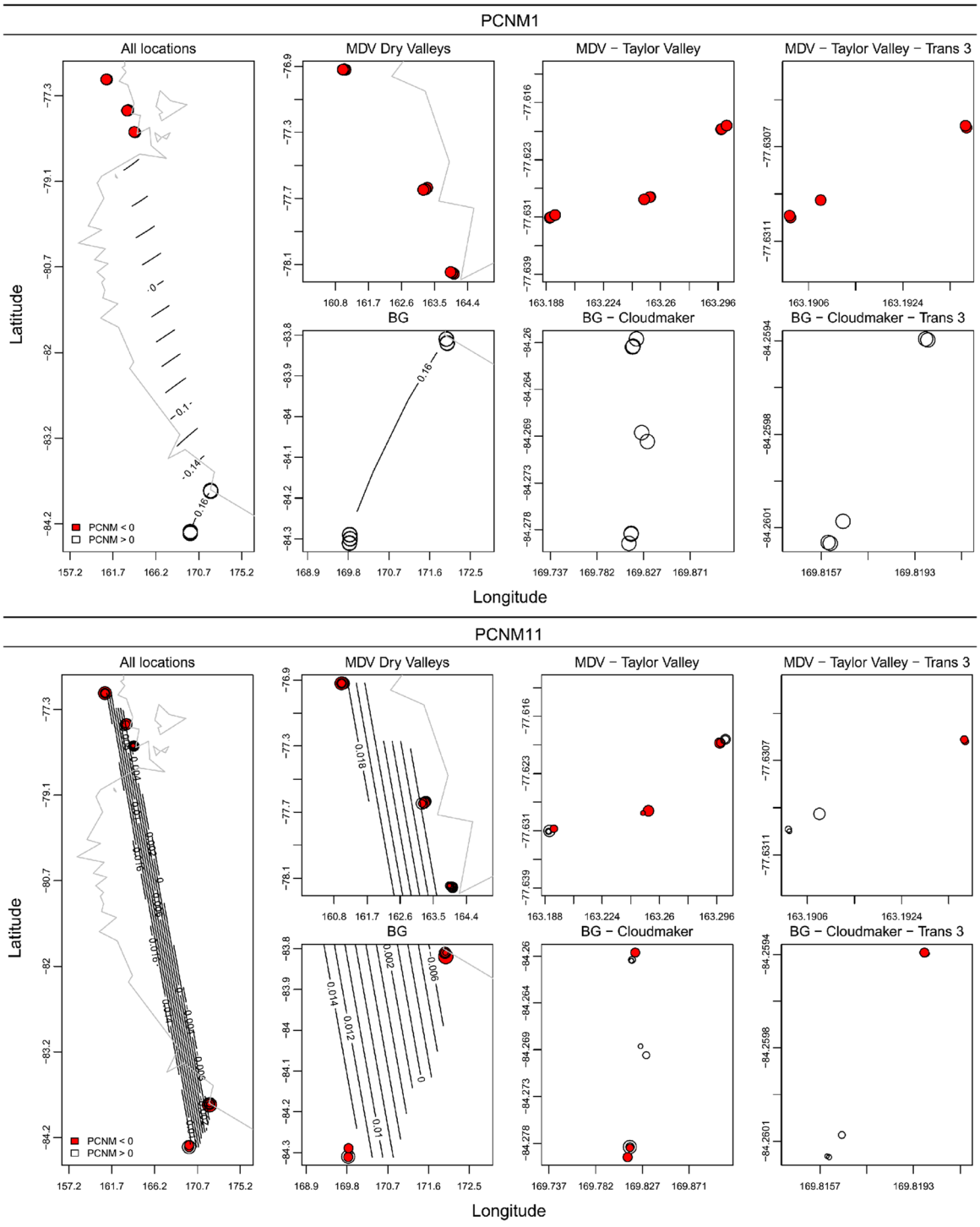

Fig. A1. Map of sampling locations and scores representing the broadest spatial filter (PCNM 1) and a fine scale spatial filter (PCNM 11). Contours represent the spatial gradient interpolated from the PCNM scores for each sample location. Size of symbols are correlated with the absolute value of the PCNM score at a location, filled symbols represent a negative score. Note that PCNM 1 distinguishes between the MDV and CTAM regions, and PCNM 11 represents heterogeneity at a local scale (~1 m).

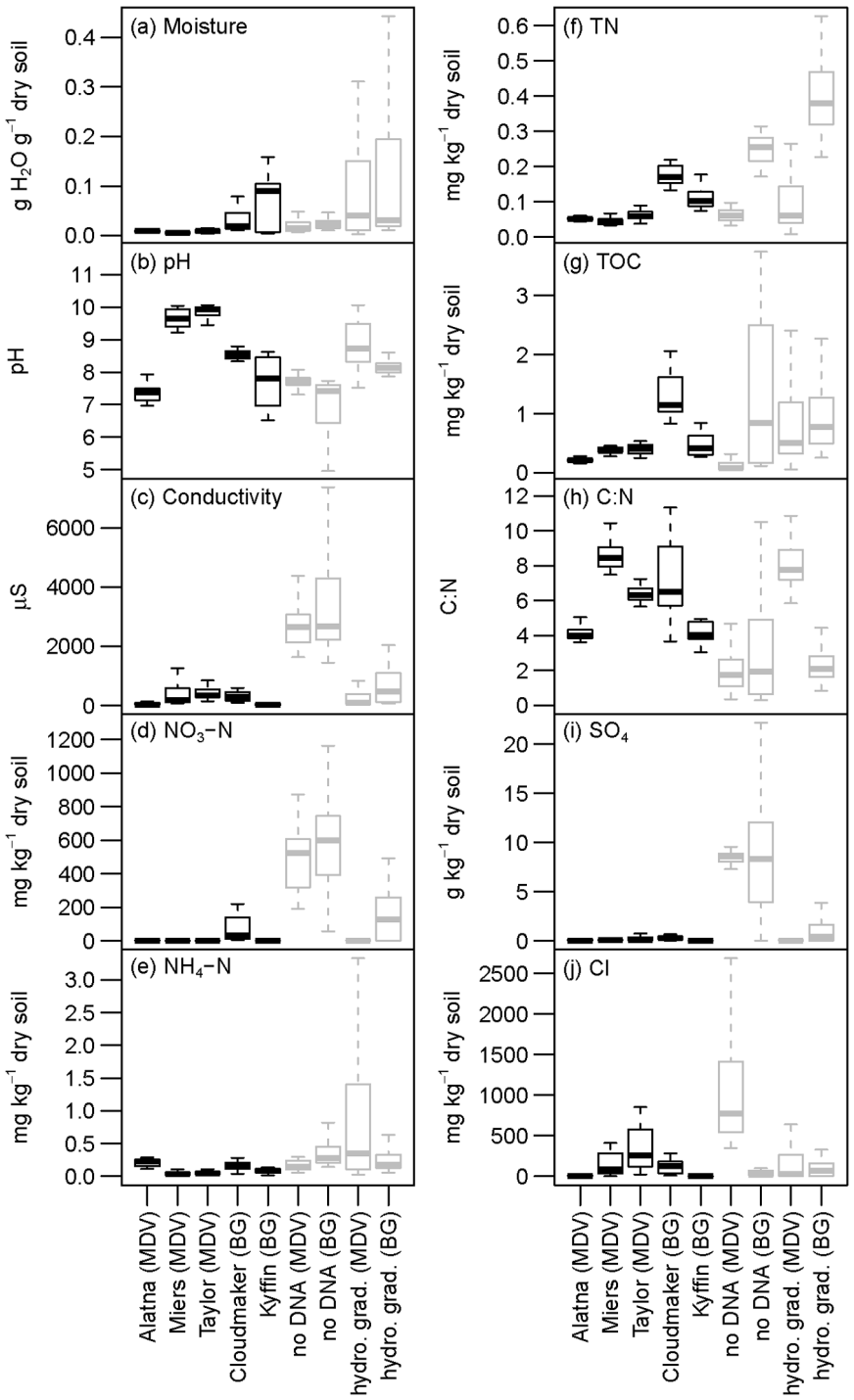

Fig. A2. Geochemical properties of soils collected from valleys in the MDV and BG regions (in black). For reference (in gray), geochemical values from locations from each region with low/no DNA yields (not reported in the study), and from localized (~100 m) hydrologic gradients from each region (Taylor Valley in MDV, Meyer Desert in BG, not reported in the study). See Table A3 for means and range of observed values for the sites used in this study.

Table A1. Sampling locations and dates.

Region	Valley	Transect	Location	Latitude	Longitude	Sampling date†
MDV	Alatna Valley	1	10	−76.9111	161.080742	20101119
MDV	Alatna Valley	1	0A	−76.911	161.080385	20101119
MDV	Alatna Valley	1	0B	−76.9111	161.080367	20101119
MDV	Alatna Valley	1	100A	−76.9114	161.084079	20101119
MDV	Alatna Valley	1	100B	−76.9114	161.08406	20101119
MDV	Alatna Valley	2	10	−76.9089	161.046669	20101119
MDV	Alatna Valley	2	0A	−76.909	161.047066	20101119
MDV	Alatna Valley	2	0B	−76.9089	161.047067	20101119
MDV	Alatna Valley	2	100A	−76.909	161.043102	20101119
MDV	Alatna Valley	2	100B	−76.909	161.043099	20101119
MDV	Alatna Valley	3	10	−76.9103	161.003367	20101119
MDV	Alatna Valley	3	0A	−76.9103	161.00301	20101119
MDV	Alatna Valley	3	0B	−76.9103	161.002992	20101119
MDV	Alatna Valley	3	100A	−76.91	161.006648	20101119
MDV	Alatna Valley	3	100B	−76.91	161.006632	20101119
BG	Cloudmaker	1	10	−84.2685	169.8254	20101208
BG	Cloudmaker	1	0A	−84.2684	169.824889	20101208
BG	Cloudmaker	1	0B	−84.2684	169.824814	20101208
BG	Cloudmaker	1	100A	−84.2693	169.830301	20101208
BG	Cloudmaker	1	100B	−84.2693	169.830224	20101208
BG	Cloudmaker	2	10	−84.2782	169.814667	20101208
BG	Cloudmaker	2	0A	−84.2781	169.814729	20101208
BG	Cloudmaker	2	0B	−84.2781	169.814642	20101208
BG	Cloudmaker	2	100A	−84.279	169.812479	20101208
BG	Cloudmaker	2	100B	−84.279	169.812391	20101208
BG	Cloudmaker	3	10	−84.2601	169.816567	20101208
BG	Cloudmaker	3	0A	−84.2602	169.816076	20101208
BG	Cloudmaker	3	0B	−84.2602	169.815993	20101208
BG	Cloudmaker	3	100A	−84.2594	169.819826	20101208
BG	Cloudmaker	3	100B	−84.2594	169.819742	20101208
BG	Kyffin	1	10	−83.8215	171.968083	20101209
BG	Kyffin	1	0A	−83.8216	171.968522	20101209
BG	Kyffin	1	0B	−83.8216	171.968447	20101209
BG	Kyffin	1	100A	−83.8208	171.964582	20101209
BG	Kyffin	1	100B	−83.8208	171.964511	20101209
BG	Kyffin	2	10	−83.8118	171.947033	20101209
BG	Kyffin	2	0A	−83.8119	171.946829	20101209
BG	Kyffin	2	0B	−83.8118	171.946772	20101209
BG	Kyffin	2	100A	−83.8112	171.952799	20101209
BG	Kyffin	2	100B	−83.8112	171.952737	20101209
MDV	Miers Valley	1	10	−78.1112	164.025	20101122
MDV	Miers Valley	1	0A	−78.1111	164.024745	20101122
MDV	Miers Valley	1	0B	−78.1111	164.024722	20101122
MDV	Miers Valley	1	100A	−78.1116	164.028561	20101122
MDV	Miers Valley	1	100B	−78.1116	164.028541	20101122
MDV	Miers Valley	2	10	−78.1062	163.988317	20101122
MDV	Miers Valley	2	0A	−78.1062	163.988763	20101122
MDV	Miers Valley	2	0B	−78.1062	163.988736	20101122
MDV	Miers Valley	2	100A	−78.1056	163.985414	20101122
MDV	Miers Valley	2	100B	−78.1056	163.985387	20101122
MDV	Miers Valley	3	10	−78.1015	163.93835	20101122
MDV	Miers Valley	3	0A	−78.1015	163.938704	20101122
MDV	Miers Valley	3	0B	−78.1015	163.938695	20101122
MDV	Miers Valley	3	100A	−78.1013	163.934438	20101122
MDV	Miers Valley	3	100B	−78.1014	163.934428	20101122
MDV	Taylor Valley	1	10	−77.6191	163.2982	20101118
MDV	Taylor Valley	1	0A	−77.6191	163.297861	20101118
MDV	Taylor Valley	1	0B	−77.6191	163.297837	20101118
MDV	Taylor Valley	1	100A	−77.6186	163.301295	20101118
MDV	Taylor Valley	1	100B	−77.6186	163.301272	20101118
MDV	Taylor Valley	2	10	−77.6282	163.253033	20101118
MDV	Taylor Valley	2	0A	−77.6282	163.253424	20101118
MDV	Taylor Valley	2	0B	−77.6282	163.253409	20101118
MDV	Taylor Valley	2	100A	−77.6285	163.249542	20101118
MDV	Taylor Valley	2	100B	−77.6285	163.249525	20101118
MDV	Taylor Valley	3	10	−77.6309	163.190883	20101118
MDV	Taylor Valley	3	0A	−77.631	163.19031	20101118

Table A1. Continued.

Region	Valley	Transect	Location	Latitude	Longitude	Sampling date†
MDV	Taylor Valley	3	0B	−77.631	163.19029	20101118
MDV	Taylor Valley	3	100A	−77.6306	163.193659	20101118
MDV	Taylor Valley	3	100B	−77.6306	163.19364	20101118

† Sampling dates are in the form: yyyymmdd.

determination using an ABI 3130 xl sequencer (PE Applied Biosystems, Foster City, USA).

For profiling of cyanobacterial community profiles using automated ribosomal intergenic spacer analysis (ARISA), PCR of the intergenic spacer of the rRNA operon was carried out in 25-μl reactions containing 300 nM of forward FAM labeled primer CY-ARISA-F (5′ - TET/TG GYC AYR CCC GAA GTC RTT A - 3′) (modified from Wood et al. 2008); 300 nM of reverse primer 23S30R (5′ - CHT CGC CTC TGT GTG CCW AGG T - 3′) (modified from Taton et al. 2003, Wood et al. 2008) 1.5 mM MgCl2, 1× Platinum Taq PCR buffer, 1.25 U of Platinum Taq DNA polymerase (Invitrogen Ltd., New Zealand), 0.5 μg bovine serum albumin, 200 μM of each dNTP (Roche Diagnostics, New Zealand), 10 ng of extracted template DNA and UltraPure distilled water (Invitrogen Ltd.). The master mix, containing all reagents except the fluorescently labeled forward primer was treated with 0.1 μg/μl ethidium monoazide bromide (Biotium Inc., Hayward, CA) by incubation in the dark for 1 min followed by exposure to high wattage light for 1 min (Rueckert and Morgan 2007). Amplification was performed using an initial denaturation step at 94°C for 2 min followed by 35 cycles of 94°C, 20 sec; 55°C, 15 sec; 72°C, 90 sec and a final extension step of 72°C for 7 min. Duplicate PCR reactions were pooled together and diluted 1:20 and stored at −20°C until being sent to the University of Waikato DNA sequencing facility (University of Waikato, New Zealand) for fragment size determination using an ABI 3130 xl sequencer (PE Applied Biosystems, Foster City, USA).

Calculating spatial filters (PCNM eigenvectors) from sampling plot coordinates.—Sampling plot coordinates were recorded as latitude and longitude and locations were visually confirmed using Google Earth. We used the distm function in the geosphere package for R (Hijmans and Williams 2011) to calculate a geographic distance matrix of great circle distances, in meters, using the Vicenty ellipsoid method and the WGS84 ellipsoid. We used the pcnm function in the vegan package (Oksanen et al. 2012) to calculate Principal Coordinates of Neighbor Matrices (PCNM) (Borcard et al. 2004), which is a special case of distance based MEM analysis (Peres-Neto et al. 2006). PCNM provides a method to calculate eigenvectors from a truncated distance matrix, and we used a truncation threshold of the minimum distance that kept sites connected in a spanning tree (Borcard et al. 2004). The maximum distance in the truncated matrix was 4 times the threshold distance (Borcard et al. 2004). Eigenvectors with positive eigenvalues were used as variables to represent different scales heterogeneity (i.e., spatial filters), with the first eigenvector (PCNM 1) representing the broadest spatial gradient, and each successive eigenvector representing finer scale spatial structure.

Calculating 95% confidence intervals for alpha, beta, and gamma components of diversity.—We used bootstrap resampling to calculate 95% CLs for each diversity estimate (Hesterberg et al. 2007) for each level of organization (see Supplement). Diversity was partitioned for each bootstrapped sample, and the 2.5% and 97.5% percentiles are reported as CLs. Rare-biased gamma diversity (${}^0D_\gamma$) was calculated for bootstrapped assemblages using the incidence based Chao estimate of richness for each bootstrapped sample (Chao 1987), which estimates the number of unobserved taxa (FLs in this case) based on the frequency observed rare groups. Because dominant-biased gamma diversity (${}^2D_\gamma$) emphasizes regional diversity of dominant groups, we did not include a correction for unobserved rare FLs when calculating 95% CLs.

Table A2. ANOVAs comparing within and between site spatial variable (PCNM) scores.

				Results from Tukey's HSD test				
				MDV region			BG region	
Spatial variable	*F*	df	*P*	Taylor	Miers	Alatna	Kyffin	Cloudmaker
PCNM1	639959.5	4, 65	0	a	a	a	b	b
PCNM2	0.964	4, 65	0.433					
PCNM3	578.523	4, 65	0	a	b	c	d	d
PCNM4	241.429	4, 65	0	a	a	a	b	c
PCNM5	344.386	4, 65	0	a	b	c	d	d
PCNM6	0.008	4, 65	1					
PCNM7	0.004	4, 65	1					
PCNM 8–36			NS					

Note: Among-site variation in PCNM scores was greater than within-site variation for PCNM variables 1, 3, 4 and 5, indicating these variables represent broad scale (among-site) spatial heterogeneity.

Table A3. Summary of geochemistry and DNA yields (see Fig. A2).

	MDV			CTAM	
Variable	Alatna	Miers	Taylor	Cloudmaker	Kyffin
pH	7.40 (6.97, 8.3)	9.64 (9.21, 10.04)	9.74 (8.40, 10.06)	8.52 (8.33, 8.79)	7.72 (6.52, 8.62)
Conductivity (μS)	62.8 (15, 229)	373 (72.0, 1264)	483 (147, 1786)	373 (97, 1059)	36.1 (8, 71)
Soil moisture (g H_2O/g dry soil)	0.010 (0.007, 0.022)	0.007 (0.004, 0.021)	0.009 (0.004, 0.015)	0.032 (0.01, 0.079)	0.071 (0.005, 0.158)
NH_4-N (mg/kg)	0.22 (0.11, 0.5)	0.04 (0, 0.11)	0.06 (0.01, 0.11)	0.18 (0.04, 0.41)	0.09 (0.02, 0.14)
NO_3-N (mg/kg)	4.03 (0.03, 20.51)	2.32 (0.03, 15.75)	0.64 (0.04, 3.11)	93.07 (4.5, 542)	0.34 (0.07, 1.32)
Cl (mg/kg)	14.2 (1.3, 99.2)	244.9 (1.2, 1165.5)	346.8 (23.2, 853)	178.2 (7.9, 861)	2.7 (0.9, 9.3)
SO_4 (mg/kg)	129 (4.1, 628)	76.8 (4.4, 268)	774 (24.2, 8753)	342 (36.8, 1098)	4.8 (0.5, 17)
TOC (mg/kg)	0.22 (0.16, 0.28)	0.39 (0.28, 0.57)	0.41 (0.25, 0.69)	1.37 (0.83, 2.88)	0.46 (0.27, 0.84)
TN (mg/kg)	0.05 (0.04, 0.06)	0.05 (0.03, 0.07)	0.06 (0.04, 0.12)	0.18 (0.13, 0.29)	0.11 (0.07, 0.18)
C:N	4.16 (3.6, 5.24)	8.77 (7.48, 10.94)	6.36 (5.65, 7.24)	7.68 (3.66, 14.58)	4.13 (3.04, 4.93)
DNA (ng/g)	1491 (41, 4160)	328 (55, 708)	810 (114, 4800)	53 (0, 152)	613 (9, 1804)

Note: Means (min, max) reported for each site.

Table A4. ANOVA comparing MDV and BG total soil DNA yields.

Source of variance	df	Sum Sq	Mean Sq	*F*	*P*
Region	1	1445900	1445900	5.805	0.0187
Residuals	68	16937116	249075		

SUPPLEMENT

R script and data files used for diversity partitioning and to bootstrap confidence intervals for diversity metrics described in the main text (*Ecological Archives* C004-014-S1).