**Taxonomic and functional biogeographies of soil bacterial communities across the Tibet plateau are better explained by abiotic conditions than distance and plant community composition**

Qingqing Lianga,1, Heidi K. Modc, d,1, Shuaiwei Luob, Beibei Maa, Kena Yanga, Beibei Chena，Wei Qib, Zhigang Zhaob, Guozhen Dub, Antoine Guisand, e, Xiaojun Maa, 2,\* & Xavier Le Rouxf,2

*a School of Life Sciences,* *Lanzhou University, Lanzhou, China*

*b College of Ecology, Lanzhou University, Lanzhou, China*

*c Department of Geosciences and Geography, University of Helsinki, Finland*

*d Department of Ecology and Evolution, University of Lausanne, Switzerland*

*e Institute of Earth Surface Dynamics, University of Lausanne, Switzerland*

*f INRAE, CNRS, Université de Lyon, Université Lyon 1, vetAgroSup, UMR 1418 INRAE, UMR 5557 CNRS, Ecologie Microbienne LEM, Villeurbanne, France*

1 *Both authors contributed equally*

2 *Both authors led this work*

*\*Corresponding author:* Tianyan Building, School of Life Sciences, Lanzhou University, NO.222 Tianshui South Road, Lanzhou, 730000, Gansu Province, China. E-mail address: xjma@lzu.edu.cn

**Abstract**

The processes governing soil bacteria biogeography are still not fully understood. It remains unknown how the importance of environmental filtering and dispersal differs between bacterial taxonomic and functional biogeography, and whether their importance is scale-dependent. We sampled soils across the Tibet plateau, with distances among plots ranging from 20 m to 1 550 km. Taxonomic composition of bacterial community was characterized by 16S amplicon sequencing and functional community composition by qPCR targeting 9 functional groups involved in N dynamics. Factors representing climate, soil and plant community were measured to assess different facets of environmental dissimilarity. Both bacterial taxonomic and functional dissimilarities were more related to abiotic dissimilarity than biotic (vegetation) dissimilarity or distance. Taxonomic dissimilarity was mostly explained by differences in soil pH and mean annual temperature (MAT), while functional dissimilarity was linked to differences in soil N and P availabilities and N:P ratio. Soil pH and MAT remained the main determinants of taxonomic dissimilarity across spatial scales. In contrast, the explanatory variables of N-related functional dissimilarity varied across the scales, with soil moisture and organic matter having the highest role across short distances (<~330 km), and available P, N:P ratio and distance being important over long distances (>~660 km). Our results demonstrate how biodiversity dimension (taxonomic versus functional aspects) and spatial scale influence the factors driving soil bacterial biogeography.

**Introduction**

The composition of biological communities varies across space, expressed as gradually changing beta-diversity along geographical and environmental gradients, with a tendency to have distinct biological assemblages in different parts and habitats of a landscape (Aggemyr et al., 2018; Brown, 1995; Gaston & Blackburn, 2008). The knowledge of such patterns and their drivers regarding microorganisms, however, is scarce when compared to the knowledge available for macroscopic species (Clark et al., 2017; Fierer & Jackson, 2006; Griffiths et al., 2011; Hanson et al., 2012; Horner-Devine et al., 2004; Horner-Devine et al., 2007; Martiny et al., 2006; Nottingham et al., 2018). Baas Becking’s (1934) famous hypothesis ‘everything is everywhere, but environment selects’ suggests that the distribution of free-living microorganisms would be mainly governed by environmental selection (O'Malley, 2007). However, many recent studies have found that soil bacteria can show spatial patterns related to geographic isolation (Burns et al., 2015; Terrat et al., 2017; Whitaker et al., 2003; Zhou & Ning, 2017). Due to their dispersal modes (Choudoir & DeAngelis, 2022), soil bacteria might indeed be more dispersal-constrained than macroscopic and aquatic organisms (Astorga et al., 2012; Bell, 2010; Lenoir et al., 2012; Powell et al., 2015; Soininen et al., 2007a). Overall, an increased understanding of the drivers of the distribution of soil microorganisms and of their community composition is still needed. This need is further intensified in the context of ongoing global changes, such as climate warming, N deposition and acidification which affect soil biota distribution and assemblages (Guo et al., 2018; Zhang et al., 2013).

Hanson et al. (2012) and Nemergut et al. (2013), following the synthesis by Vellend (2010), distinguished four fundamental assembly processes defining the spatial patterns in diversity and composition of microbial communities. These processes are selection (through environmental filtering and biotic interactions), dispersal, drift and mutation/diversification, with the main processes identified being environmental filtering and dispersal (Chalmandrier et al., 2019; Landesman et al., 2014; Lenoir et al., 2012; Martiny et al., 2006; Noguez et al., 2005; Wang et al., 2013; Whitaker et al., 2003; Xiao et al., 2018; Yao et al., 2017; Yashiro et al., 2016). Environmental filtering represents a process where environmental conditions shape community composition by filtering taxa that have suitable strategies to establish in a site. For soil bacteria, this includes abiotic (mostly climate and physio-chemical soil conditions) and biotic variables, mostly the composition of plant communities since plant species can shape soil bacterial communities through exudation of specific organic compounds, modification of soil characteristics and selective recruitment of soil bacteria (Bulgarelli et al., 2013; El Moujahid et al., 2017; Yang et al., 2020). Dispersal affects community composition by influencing the establishment of organisms in new sites, with increasing geographic distance hindering the movement of micro-organisms depending on their dispersal ability and – when relevant – dispersal vectors (Choudoir & DeAngelis, 2022). Taken together, these processes lead to a distance decay effect where communities further away are less similar than the communities close-by, because of increasingly different environmental conditions and/or higher isolation with increasing distance (Clark et al., 2021; Nekola & White, 1999; Ranjard et al., 2013; Soininen et al., 2007b; Zeng et al., 2019). While dissimilarity of environmental conditions can correlate with geographical distance, environmentally similar conditions can be found from distant locations too, or reversely, sharp environmental transitions can occur across small distances (Stenger et al., 2002). Thus, sampling soil bacterial habitats over broad spatial and environmental transects including both fine- and broad-scale variations can allow tearing the effects of environmental filtering and dispersal apart based on the covariance between bacterial community dissimilarity and environmental dissimilarity and geographic distance (Karimi et al., 2020; Wang & Bradburd, 2014).

For soil bacteria, most studies on the relative roles of environmental filtering and dispersal have focused on community dissimilarity based on the taxonomic compositions of communities (using e.g. phyla or operational taxonomic units = OTUs; Burns et al., 2015; Karimi et al., 2020; King et al., 2010; Yashiro et al., 2016). However, bacterial communities can be assessed using other entities too, such as functional attributes, that do not necessarily correlate with taxonomy (Cardoso et al., 2014; Fierer et al., 2012; Louca et al., 2018; Nelson et al., 2016) because functional redundancy, i.e. the capacity of multiple species representing a variety of taxonomic groups to ensure similar functions in ecosystems (Hubbell, 2005), can be particularly high within bacterial communities (Wertz et al., 2006). For example, communities in two distant but environmentally similar places might considerably differ taxonomically due to the dispersal barrier, whereas their functional composition might be relatively more similar due to prevailing environmental conditions favouring or requiring certain functions or functional attributes (Louca et al., 2018). Thus, the importance of environmental filtering and dispersal as drivers of soil bacteria biogeography might vary depending on the type of the community measure used (Graco-Roza et al., 2022; Meynard et al., 2011; Rocha et al., 2019; Shi et al., 2015). More particularly, geographic distance would better explain taxonomic dissimilarity among soil bacterial communities if dispersal plays an important role, whereas some previous reports suggested that community functional dissimilarity, which is affected by local gradients in resource availability, might be less related to distance and more to environmental dissimilarity (Zhang et al., 2016) (Fig. 1). Incorporating both taxonomic and functional compositions of communities might better reveal the major drivers of soil bacterial biogeography (Haggerty & Dinsdale, 2017; Louca et al., 2016; Nelson et al., 2016). Since soil bacteria communities are connected to ecosystem functioning such as nutrient and carbon cycles (Bardgett & van der Putten, 2014; Cavicchioli et al., 2019; Van Der Heijden et al., 2008), understanding bacterial biogeography from both the taxonomic and functional points of view is crucial to forecasting future impacts of global changes on ecosystems.

In this study we thus aim to advance the understanding of soil bacteria biogeography by incorporating both taxonomic and functional dissimilarities of bacterial communities and linking these to a large range of abiotic conditions, plant community compositions, and geographic distances, in order to compare the relative roles of environmental dissimilarity (a surrogate for environmental filtering by abiotic and biotic variables) and geographic distance (seen here as a surrogate for dispersal) in explaining the taxonomic and functional biogeography of soil bacteria. For this purpose, we sampled soils along a 1 550 km transect across the Tibet plateau (Fig. 1). Taxonomic community composition was defined based on the relative abundances of OTUs determined by *16S* amplicon sequencing, while one aspect of functional community composition was defined based on the abundances of nine nitrogen (N) cycle-related functional groups determined by quantitative PCR. For each plot, environmental conditions were derived based on factors representing climate, soil and plant communities. The relationships between taxonomic or functional dissimilarity of soil bacterial communities, and environmental abiotic and biotic dissimilarities as well as geographic distances among sampling locations were then assessed (Fig. 1). We assumed that the taxonomic and functional community compositions would not be akin, and that environmental dissimilarity and geographic distance would not correlate strongly. We also assumed that functional dissimilarity would better correlate with environmental dissimilarity than with geographic distance (Fig. 1), and that distinct variables would explain bacterial taxonomic and functional biogeography. Given that plants can directly influence soil bacteria on top of reflecting the local abiotic conditions, we hypothesised that the dissimilarity of soil bacteria communities would better correlate with the dissimilarity of biotic environment than dissimilarity of abiotic environment. Finally, we also evaluated the possible influence of spatial scale on the conclusions derived.

**Materials and methods**

*Study area and soil sampling*

The study area covers a large part of the Tibetan Plateau and stretches 800 km along latitude and 1 250 km along longitude (Fig. 1). The climate is high altitude plateau climate with precipitation mainly falling during the short, cool summer in July and August (Ma et al., 2016). The mean annual temperature ranges from -15 to 5 °C (You et al., 2013) and mean annual precipitation from 170 to 600 mm (Karger et al., 2017). Soil sampling was performed randomly along a ca. 1 500 km SW-NE transect in the Qinghai Province and Tibetan Autonomous Region, China (Fig. 1), during the peak-growing season in July–August 2015, targeting non-forested vegetation types, mostly alpine meadows and steppes dominated by sedges and grasses (Tang et al., 2015). We collected soil samples from 39 sites. At each site, soil was sampled from five plots of ca. 1 m2 located at least 20 m from another (Fig. S1). From each plot, 5 soil cores (0–10 cm; 4 cm diameter) were collected and homogenized to form one composite sample per plot (i.e. 975 individual cores leading to 195 composite samples). The location and altitude of each site was measured using a Trimble JUNO SC GPS. The altitudes of the sites ranged from 2 988 m to 4 787 m above sea level.

Composite soil samples were sealed in plastic bags, stored a few days at 4 °C and brought back to the laboratory. Fresh sub-samples were used for measuring soil environmental variables. Other sub-samples were stored at -20°C for a few weeks before molecular biology assays. Extracted DNA was stored at -80℃ before sequencing and quantitative PCR assays (see below).

*DNA extraction from soil and 16S rRNA* *sequencing*

Total genomic DNA was extracted from composite soil samples using 0.25 g of soil, according to the MoBio Power Soil DNA isolation protocol (MO BIO laboratories, Carlsbad, CA, USA). The taxonomic compositions of bacterial communities were determined by amplifying the V4 hypervariable regions of bacterial 16S ribosomal RNA. This was done for 99 samples only, first by randomly selecting three plots from the five available at each of the 39 sites (i.e. leading to 117 plots) and then removing 18 of these 117 plot. These 18 plots were randomly chosen among the vegetation types the mostly represented in our dataset. DNA was amplified using the 338F/806R primers (Table S1). Amplification problem was encountered for one site, finally leading to amplicons for 96 samples. Amplicons were extracted from 2 % agarose gels and purified using the AxyPrep DNA Gel Extraction Kit (Axygen Biosciences, Union City, CA, USA). The purified products were pooled in equimolar and paired-end sequenced on an Illumina MiSeq platform (Shanghai Majorbio Bio-pharm Technology Co., Ltd., Shanghai, China).

The quality of the sequencing reads was checked using the high-throughput sequence data quality checking program Fastp (version 0.19.6; https://github.com/OpenGene/fastp). Following adapter trimming, sequences were checked in particular for correcting each mismatched base pair with an imbalanced quality score (the sequencer indeed assigns each nucleotide base a Phred quality score, which corresponds to the probability that the base has been erroneously called), which was followed by the use of a sliding window method to drop the low-quality bases of each read’s head and tail according to (Chen et al., 2018; a 50 bp sliding window was used). We also used fastp for the filtering of reads using a low-quality base percentage, N base number and read length. The filtered reads 1 and reads 2 were overlap by FLASH v 1.2.11 by paired-end mode, considering a minimum 10 bp overlap length and a maximum error ratio of overlap of 0.2. All paired-end reads were de-duplicated into unique reads and then sorted by abundance by UPARSE (v11). The reads with at least two sequences across the whole data set (i.e., across all samples) were kept.

The rarefaction curves corresponding to the sequences retrieved after checking the sequence quality are presented in Fig. S2. Sequences were rarefied to obtain 14 619 sequence reads for each of the 96 plots using the software mothur (Schloss, 2020; Schloss et al., 2009). These reads were then clustered into operational taxonomic units (OTUs) with UPARSE (v11; Edgar et al., 2011), using a 3% dissimilarity cutoff. A total of 6 380 different OTUs were observed across the 96 plots, and the OTU richness varied from 1 357 to 2 177 OTUs per plot.

As an alternative to the clustering into OTUs, we also tested the results obtained by clustering the sequences into Amplicon Sequence Variants (ASVs). To do so, DADA2 within QIIME 2 was used for the last steps of sequence data treatment to denoise the reads and cluster them into ASVs (<https://john-quensen.com/tutorials/processing-16s-sequences-with-qiime2-and-dada2/>). We found a positive correlation between taxonomic dissimilarities based on OTUs and ASVs. However, the use of ASVs resulted in higher values of taxonomic dissimilarities among the plots, because the computation of Bray–Curtis dissimilarity assumes that all the sequences are equally dissimilar despite the number of differences in nucleotides. OTU clustering, on the other hand, better takes into account the differences in nucleotides by clustering together similar sequences, and taxonomic dissimilarity was hence computed based on the OTU table in this study.

*Quantitative PCR assays*

Nine different functional groups involved in soil N cycling were targeted (Fig. S3). For all the 195 samples, the abundances of free N2-fixers, ammonia oxidizing bacteria (AOB), two groups of nitrite oxidizing bacteria (*Nitrobacter* and *Nitrospira*), nitrate-reducers, two groups of nitrite-reducers, and two groups of N2O-reducers were quantified by quantitative PCR targeting sequences of the following genes (Ma et al., 2016): *nifH* (coding for the nitrogenase); bacterial *amoA* (coding for the bacterial ammonia monooxygenase); *nxrA* (coding for nitrite oxido-reductase specific of the bacterial genus *Nitrobacter*); *16S* specific of the bacterial genus *Nitrospira*; *narG* (coding nitrate reductase); *nirK* and *nirS* (both coding for a nitrite reductase); and *nosZ*1 and *nosZ2* (coding for N2O reductase). The abundances of *Nitrobacter* and *nosZ2*-N2O reducers were quantified on a lightcycler 480 (Roche Dignostic, Meylan, France) using 20 ul reaction volume with 40 ng, and 25 ul with 20 ng of DNA templates, and 0.5 uM and 1 uM of each primer, respectively. The abundances of the seven other groups were quantified on an iCycler iQ5 thermocycler (Bio-Rad, USA), using 20 ml reaction volume with 2 μl of DNA templates, and 1.6 ml (0.8 mM) of each primer and 10 ml SYBR Premix ExTaq™Ⅱ(Takara, Japan). Plasmids carrying sequences of the targeted genes were constructed by cloning the targeted gene fragments into plasmid pGEM-T Easy Vector (Promega, Madison, USA). Details for the qPCR methodologies and standards used are presented in Table S1. Ten-fold serial dilutions of the linearized plasmid DNA were used to establish a standard curve for each gene, and the data were then transformed into gene copy numbers per gram of dry soil. Inhibition tests were performed on 64 samples (randomly chosen) for the *nifH* gene by diluting 5 and 10 times DNA extracts before qPCR, and this showed no inhibition.

The largest variations in abundances were observed for the free N2 fixers (*nifH*) and the *nosZ1*-N2O reducers, with abundances ranging from 3.9×104 to 1.3×1010 and from 1.4×105 to 4.2×109 gene copies g-1 soil, respectively (Fig. S4). In comparison, *Nitrospira* abundance varied over three orders of magnitude. The less abundant groups were AOB and the nitrite-oxidizing *Nitrobacter*, with median abundances being 3.5 105 and 1.2 104 gene copies g-1 soil, respectively.

*Deriving environmental data*

Environmental factors represent soil, climate and vegetation, and the density distributions of their values are presented in Fig. S5. Edaphic variables were quantified for the collected soil samples and included soil organic matter concentration (OM; determined by the potassium dichromate method; Bao, 2000), total nitrogen (TN) and total phosphorus (TP) concentrations (both determined with a SAN++ system flow injection analyzer (SAN++, Brampton, Canada) after digesting; Bao, 2000), ammonium (NH4+) and nitrate (NO3-) concentrations (both measured using a SAN++ system flow injection analyzer after extraction with KCL; Smolders et al., 2001), available phosphorus (AP; extracted according to Mehlich, 1984), soil moisture (gravimetric content) and pH (quantified using a PHS-3C pH meter (Shanghai, China) with 1:2.5 vol soil:H2O solutions; Yang et al., 2012). Soil carbon (C) concentration was obtained by dividing OM by the van Bemmelen factor (1.72), and TN, TP and C were used to compute three stoichiometric ratios: C:N, N:P and C:P.

Climatic variables were obtained from CHELSA climatologies over 1981-2010 (2.1; Karger et al., 2017, 2021). As there was strong multicollinearity among most variables, only three not-highly correlated (<|0.7|) variables were included. To represent temperature conditions, we included mean annual air temperature (MAT), and to represent precipitation, we included mean annual precipitation sum (MAP). Mean diurnal air temperature range (DRT) was also included as it was not highly correlated to the two other climate variables and was found as the most important factor in explaining microbial diversity at the global scale in the study by Delgado-Baquerizo et al. (2016).

Information on biotic environment (here plant communities) was based on living aboveground biomass of vascular plant species collected from 179 of the 195 plots used for soil sampling (Qi et al., 2021a; Qi et al., 2021b). Collected biomasses per species on the 1 m2 plot were dried at 75 °C for 48 h and then weighted. Plant community composition corresponded to the matrix of species biomass data (g m-2), while we also derived further variables, namely total aboveground plant biomass (BM; g m-2), plant species richness (SR; number of species per plot), Shannon-Weiner diversity index of the plant community (SW), and the biomass fraction per plot of sedges, graminoids, forbs, shrubs, legumes and cushion plants.

*Statistical analyses*

All in all, the bacterial, climate, soil and vegetation data listed above were available for 88 plots which were used in all the core analyses presented here. Additionally, some analyses concerning bacterial functional dissimilarity were repeated for 177 plots for which data on N-related functions and abiotic and biotic environment were available, and these analyses are provided in appendices. These additional analyses were done to assess the robustness of our conclusions, i.e., to test if the amount of data affected the ecological interpretations drawn at least for bacterial functional dissimilarity.

The dissimilarities among bacterial communities were calculated as Bray-Curtis dissimilarities for each pair of plots based on the double square root-transformed relative abundances of OTUs (for taxonomic dissimilarity) and double square root-transformed abundances of the nine N-related functional groups (for functional dissimilarity). By transforming the data prior to calculating dissimilarities, more weight is given to OTUs and functional groups with low abundance which would be overlooked otherwise. Double square root transformation was chosen based on preliminary analyses (e.g., having the highest model performance, see below) and favoured over logarithmic transformation because it avoids the troubles of transforming zeros and resulting negative numbers. Nevertheless, the dissimilarity values do not drastically change depending on the transformation (Fig. S6-7).

Abiotic and biotic dissimilarities among plots were calculated using Bray-Curtis dissimilarity. For abiotic dissimilarity, the eleven soil variables and three climate variables were used. The variables representing resources (water, C and nutrients) were log-transformed prior to deriving the dissimilarity. Biotic dissimilarity was calculated in two ways: (i) dissimilarity of plant species compositions, and (ii) dissimilarity of plant growth form compositions. For the first, we used double square root transformed biomasses per species per plot, and for the latter, double square root transformed proportional biomasses of sedges, graminoids, forbs, shrubs, legumes and cushion plants per plot. In addition, distances among plots were derived using the geographic coordinates of the sites (each consisting of 5 plots located 20 m from the centre of the site). To obtain unique coordinates for all plots and reflect the non-zero distances among the plots of a same site, we randomly added or subtracted 20 meters from y- and/or x-coordinates of the sites so that minimum distance among sites remained in 20 m. General relationships among taxonomic, functional and environmental dissimilarities and geographic distances among the plots were then assessed by Mantel tests.

To assess in detail the influence of individual environmental variables and distance on taxonomic and functional dissimilarities of bacterial communities, we implemented generalized dissimilarity modelling (GDM; Ferrier et al., 2007; Manion et al., 2018). GDM is suited to analyse spatial patterns of pairwise dissimilarities in community data as a function of environmental conditions and/or geographic distance (see e.g. in Bell et al., 2013). Non-linear responses are possible by applying link and variance functions, and I-splines (see Ferrier et al., 2007). The included environmental variables in this analysis were both abiotic (eleven soil and three climate variables) and biotic (plant BM, SR and SW, and biomass fractions of sedges, graminoids, forbs, shrubs, legumes and cushion plants). No transformations were applied to environmental variables or distance for GDM analyses, as GDM can model non-linear responses. Using GDM, we addressed four questions:

*(1) To what extent each environmental variable or geographic distance alone explains taxonomic and functional dissimilarities.* We modelled taxonomic and functional dissimilarity using each environmental variable or distance as a single explanatory variable (univariate models) and recorded the models’ explanatory power.

*(2) What are the best combinations of variables to explain taxonomic and functional dissimilarities.* We used backward selection of explanatory variables to identify the best combination of variables to model taxonomic and functional dissimilarity. For this, we compiled and run a model with all non-correlating explanatory variables (using threshold of ±0.7 and removing the variable of correlating pair that had a lower explanatory power in the univariate model; see Table S2). Then, at each model iteration, we removed the explanatory variable with the highest p-value in the model. The best model was determined as the model with the highest explanatory capacity and where all variables were significant (p-value < 0.01). Significance and contribution of explanatory variables in the models were tested using permutation tests randomizing variables and testing the significance and amount of decrease in deviance explained compared to the unshuffled model (see function gdm.varImp; Manion et al., 2018; Mokany et al., 2022).

*(3) How the explanatory variables of the best models influence taxonomic and functional dissimilarities (i.e., shape of the relationship between the explanatory variable and bacterial taxonomic or functional dissimilarity).* To examine the relationships between taxonomic and functional dissimilarities and explanatory variables, we plotted the I-splines (i.e., response curves) fitted to the variables retained for the best models. The height and slope of the curve indicate the amount and rate of change of community dissimilarity, respectively, along the explanatory variable. All models were fitted with three I-splines for all variables with default knots (see Manion et al., 2018).

*(4) How the importances of environmental variables and distance vary across spatial scales.* To assess the scale dependency of these relationships and of the importance of environmental dissimilarity and distance on bacterial taxonomic and functional dissimilarities, we divided all pairs of 88 plots into three equal sized groups based on the geographic distances among the plots (i.e. three groups corresponding to short, medium and long distances between plots, namely 20 m to 333 km, 333 to 662 km and 662 to 1 545 km, respectively). For each group, correlation tests and the GDM modelling of taxonomic and functional dissimilarity was repeated.

**Results**

*Relationships among taxonomic, functional and environmental dissimilarities and distance*

Mantel tests performed on the core set of 88 plots showed a positive correlation (r=0.38, p<0.001) between bacterial taxonomic and functional dissimilarities (Fig. 2). Among the environmental dissimilarities and distance, the strongest correlation occurred between abiotic (soil+climate) dissimilarity and dissimilarity of plant species composition (r=0.59, p<0.001) and the weakest between dissimilarity of plant growth form composition and distance (r=0.22, p<0.001; Fig. 2).

Both bacterial taxonomic and functional dissimilarities were most positively and strongly correlated to abiotic dissimilarity (r=0.66 and r=0.45 respectively, both p<0.001). The lowest correlations were observed between taxonomic dissimilarity and distance (0.23, p<0.001) and functional dissimilarity and dissimilarity of plant growth form composition (r=0.25, p<0.001; Fig. 2). Similar patterns were observed when using data from all 177 plots, where functional dissimilarity most strongly correlated with environmental dissimilarity (r=0.45, p<0.001) and least strongly with dissimilarity of plant growth form composition (r=0.2, p<0.001; Fig. S8).

*Best explanatory variables of bacterial taxonomic and functional dissimilarities*

The environmental variables reaching the highest explanatory power for bacterial taxonomic dissimilarity, when considered individually in GDMs, were soil pH (~50% of the variance explained) and to a lesser extent MAT and OM (37% and 33% of the deviance explained, respectively; Fig. 3). For the bacterial functional dissimilarity related to N cycling, AP, N:P, TN and OM had the highest explanatory powers (nearly 30% of the deviance explained for each) followed by soil moisture and C:P (20-25% of the deviance explained; Fig. 3). Distance explained 10 % and 15% of deviance of taxonomic and functional dissimilarity, respectively. Similar results were obtained when the analysis was performed using 177 plots (Fig. S9).

The best GDM for taxonomic dissimilarity explained 75% of the variance and included five explanatory variables (ranked according to their relative contribution in the model): pH > MAT > moisture > OM > distance (Fig. 4a). The best model for functional dissimilarity, based on the same 88 plots, explained 52% of the variance and included also five variables: AP > N:P > distance > BM > sedge (Fig. 4a). A model based on 177 plots indicated similar results for functional dissimilarity (Fig. S10).

*Shapes of relationships between explanatory variables and bacterial taxonomic and functional dissimilarities*

The I-splines (response curves) fitted to the explanatory variables retained in the best models showed that taxonomic dissimilarity was in a continuous manner and strongly related to change in soil pH (Fig. 4). Differences in MAT and moisture among the plots increased taxonomic dissimilarity the most strongly at lower ends of the gradients (i.e., in cold and dry environments, respectively), whereas differences in OM increased taxonomic dissimilarity the most strongly over the OM range 10–20%. Taxonomic dissimilarity increased with distance only when the plots were 20 m – 330 km apart.

The bacterial functional dissimilarity related to N cycling was linked to differences in N:P, plant biomass and percentage of sedges of total biomass among the plots in rather continuous manners along the corresponding gradients (Fig. 4). Functional dissimilarity was related to the difference in AP mostly at the lower end of the AP gradient. In contrast to the results obtained for taxonomic dissimilarity, the functional dissimilarity was mostly related to increase in distance for distances above 660 km.

*Scale dependency of the main drivers of bacterial biogeography*

Correlations among taxonomic, functional, abiotic and biotic dissimilarities and distance generally decreased from short to mid and long scales (see Table S3). The decreases were particularly strong, for example, between taxonomic dissimilarity and distance where the correlation was 0.42 (p<0.001) for short scale but -0.14 (p<0.001) at long scale. Similar decreases occurred also between abiotic dissimilarity and distance and between both measures of biotic dissimilarity and distance. The two exceptions to this decreasing trend were the correlation between functional and abiotic dissimilarities (0.21 at short scale, 0.43 at mid scale and 0.46 at long scale; all p <0.001) and the correlation between functional dissimilarity and distance (0.018 at short scale (p<0.001), 0.26 at mid scale (not significant) and 0.31 at long scale (p<0.001).

The GDMs also showed that the importances of individual environmental variables for taxonomic dissimilarity were largely stable across the three scales (Fig. 5a). In contrast, for functional dissimilarity, the explanatory power of environmental variables, especially of moisture, sedge fraction, AP and NH4.N, varied across the scales (Fig. 5b). In the best models, irrespective of the scale, soil pH, MAT and moisture and/or OM were always included for taxonomic dissimilarity, with pH always having by far the largest relative contribution (Fig. 6a). At mid scale, climatic variables MAP and DRT and plant species richness also played a role, and at long scale, fractions of sedges and grasses also appeared in the best models of taxonomic dissimilarity. In contrast, the explanatory variables in the best models for functional dissimilarity varied strongly across scales (Fig. 6b). The variables included soil moisture and OM at short scale, soil moisture and plant biomass at mid scale and AP, N:P and distance at long scale.

For the pairs of plots 20 m – 333 km apart, distance alone explained 27 % of deviance in taxonomic dissimilarity vs. 12 % in functional dissimilarity, whereas for the pairs of plots 662 – 1 545 km apart, these values were 0 % and 12 %, respectively. Distance was included as an explanatory variable only in the best model of functional dissimilarity at the long scale.

**Discussion**

A good understanding of soil bacteria biogeography and its determinants is needed to better understand ecosystems’ structure and functioning, and to anticipate their possible changes with global change (Chu et al., 2020; Le Roux et al., 2016; Zhang et al., 2013). Here, we studied if and how the taxonomic and N-related functional compositions of soil bacteria communities relate to environmental dissimilarity (i.e. climate, soil and vegetation) and geographic distance, hypothesising that, due to functional redundancy, environmental dissimilarity (proxy for environmental filtering) would more strongly drive functional than taxonomic composition whereas distance (proxy for dispersal) would be relatively more important for taxonomic than functional composition. We also hypothesised that dissimilarity of biotic environmental conditions (i.e., plant community composition) would better explain dissimilarity of soil bacteria communities than abiotic conditions (climate and soil), because plant species provide specific resources to the soil microbiota (El Moujahid et al., 2017), selectively favours or inhibits bacterial taxa and functional groups (Lata et al., 2022; Yang et al., 2020) and influences soil characteristics (Bezemer et al., 2006) on top of reflecting the local abiotic conditions. We based these different hypotheses on the underlying expectations that the taxonomic and functional compositions of bacterial communities would not be akin, and that abiotic and biotic dissimilarities and geographic distances among sites would not strongly correlate, thus allowing to unravel the effects of environmental filtering and dispersal.

Some hypotheses were supported by our analyses. In particular, bacterial taxonomic and functional community compositions were only weakly correlated, and we found support for the presence of functional redundancy (i.e. taxonomic dissimilarity was in general higher than functional dissimilarity as observed also, e.g., for fish assemblages; Cilleros et al., 2016). However, in contradiction with our hypotheses, abiotic environmental dissimilarity played a major role in comparison to biotic environmental dissimilarity and distance for both taxonomic and functional compositions. Finally, we observed a strong scale-dependency in the drivers of bacteria biogeography, including in that of the role of distance, which varied between taxonomic and functional biogeography. Below we elaborate on these findings in more detail.

*The taxonomic biogeography of soil bacteria is mostly driven by pH, while their N-related functional biogeography is determined by soil N and P availability*

The strong and positive correlation between taxonomic and abiotic dissimilarities was mainly related to soil pH. The strong influence of pH on soil bacterial communities has been reported for different parts of the world, including Great Britain (Griffiths et al., 2011), USA (Fierer & Jackson, 2006; Lauber et al., 2009), the Western Swiss Alps (Yashiro et al., 2016) and China (Shi et al., 2018; Tan et al., 2020). The only exception is the report by Plassart et al. (2019) indicating that soil bacterial composition varied greatly across a pan-European transect but that less than 5% of this variation was explained by soil pH. The overall conception is, thus, that pH is the major driver of soil bacterial communities by acting as a selective force for many bacterial taxa (Nicol et al., 2008). This could be due to direct effects of pH on soil bacteria (Rousk et al., 2010) but also to non-direct effects because pH often correlates with a number of other biotic and abiotic variables such as soil carbon and nitrogen substrate availabilities (Lyngstad, 1992), plant community diversity (Olsson et al., 2009) and composition (Yashiro et al., 2018), and bioavailability of some pollutants (Aciego Pietri & Brookes, 2008). However, since we included plant community composition explicitly in our analysis, our results show that the importance of soil pH was not due to an indirect effect through plant community. We acknowledge that the possible role of soil texture, which can be significant for bacterial taxonomic biogeography (Constancias et al., 2015), was not explored here since it was not characterized. However, soil texture is generally correlated to other soil characteristics that we studied, such as soil carbon content (Nichols, 1984).

Interestingly, we did not find pH as an important driver of functional community dissimilarity, here assessed based on functional genes related to N dynamics. This was not expected because some bacterial groups studied, e.g., AOB and *Nitrobacter,* are sensitive to pH (Nicol et al., 2008). However, this finding might be due to the fact that the effect of soil pH on some N-related groups is mostly indirect, acting for instance through altered N availability and changed plant diversity (Yang et al., 2020). Indeed, soil N was among the variables that explained functional dissimilarity the most. In addition, a weaker sensitivity to pH – in terms of abundance – of other groups like denitrifiers (Bru et al., 2011; Čuhel et al., 2010) could explain the minor role of pH when explaining the overall N cycle-related functional dissimilarity.

Instead of pH, bacterial functional dissimilarity related to N cycling was mainly explained by the availabilities of N and P and the N:P stoichiometric ratio, and to a lesser extent soil organic matter and moisture. These drivers are largely consistent with the ecology of the 9 N-related functional groups studied and partly also identified in the study by Nelson et al. (2016). In addition, in grassland soils from the Tibetan plateau fertilised with N, P or NP, AOB, *Nitrobacter* and *Nitrospira* were sensitive to N availability and organic matter concentration, N2-fixers to the N:P ratio, *nirS*-nitrite reducers to soil N and organic matter, and *nirK*-nitrite reducers to organic matter and the N:P ratio (Ma et al., 2016). Similarly, soil moisture influences functional groups like nitrifiers and denitrifiers (Di et al., 2014). The nature of the environmental drivers of bacterial functional dissimilarity obviously depends on the functional groups considered, and other environmental drivers would likely be important with a focus on other specific groups like degraders of specific molecules or other functions related to aspects of other geochemical cycles. The nine functional groups selected here represent a comprehensive set of groups involved in major aspects of soil N dynamics and were chosen because N cycling is an important aspect of the functioning of ecosystems. However, we acknowledge that in the future, the functional biogeography of soil bacteria should also be assessed considering functions related to other biogeochemical cycles.

Our finding that environmental filtering does not happen through the same set of environmental variables for both taxonomic and functional dimensions is consistent with recent studies on Tibetan meadow soils reporting that the abundances of many bacterial functional groups involved in soil N dynamics depended on soil N availability, organic matter concentration and N:P ratio (Ma et al., 2016), but that the majority of bacterial taxa in the same soils were limited by other resources than N and P (Ma et al., 2019). A similar finding was reported by Nelson et al. (2016). Altogether, this has important implications to predict ecosystem functioning and anticipate the effect of global change (Purschke et al., 2013). Especially, while soil acidification or alkalinisation would strongly change the taxonomic composition of bacterial communities, their functional compositions might respond mostly to cascading effects on N:P availability and to soil moisture.

Finally, variables representing abiotic environmental conditions were found more important for soil bacterial biogeography than the variables representing biotic environmental conditions. Biotic conditions were represented by a range of descriptors of plant communities, including plant community diversity indices, plant species composition, and plant growth form composition, but none of these was identified as important for soil bacterial biogeography. In particular, the percentage of legumes in plant communities was not a good explanatory variable of the N cycle-related functional biogeography of soil bacteria, although legumes strongly influence microbial N functions (Le Roux et al., 2013). This is likely due to the fact that soil N and the N:P balance were more straightforward explanatory variables of bacterial functional biogeography than legume fraction.

*Scale dependency of the environmental drivers of taxonomic and functional bacterial biogeography*

Incorporating spatial scale to the analyses modulated some conclusions regarding the environmental explanatory variables important for bacterial biogeography. The dominant role of pH, and to some extent of MAT, moisture and OM, in explaining taxonomic dissimilarity did not vary much across the scales. This is consistent with the findings of soil pH being the main driver of soil bacterial taxonomic composition and richness e.g., at landscape scale (Constancias et al., 2015), national scale (Terrat et al., 2017), continental scale (Fierer & Jackson, 2006), and globally (Delgado-Baquerizo et al., 2016). However, no studies of drivers of functional community composition across scales exists. One possible explanation for having different influential drivers across scales could be the level of variation of explanatory variables (i.e., heterogeneity; as measured by variances or ranges of values; Viana & Chase, 2019). More specifically, a variable that has less heterogeneity for a given spatial scale might not be identified as having an important role and vice versa. Indeed, there was some link between the variability of the environmental variables (Fig. S11) and their importance for bacterial biogeography across the scales. For example, the variability of pH among the plots was high and relatively stable across the scales and so was its importance in explaining taxonomic dissimilarity, whereas the variability and importance in explaining functional dissimilarity of NH4.N and AP increased between short and long scales. Thus, when comparing the results of different studies covering different environmental heterogeneity, it is important to bear in mind that the importance of an environmental driver is not only linked to its capacity to influence bacterial community composition but also its variability across each study area. Nevertheless, we did not observe any correlation across scales between the variance and importance of environmental variables for e.g., OM, moisture, N:P, MAT and most biotic variables, which suggests that the relative importance of drivers across scales could also be linked to modified environmental filtering processes. In particular, while moisture was the main factor controlling the N cycle-related functional dissimilarity of soil bacterial communities over short distances, the influence of moisture progressively decreased with increasing scales, being entirely replaced by other drivers (mostly N/P availability) over long distances. Assessing the drivers of functional biogeography across scales should thus be a research focus in the future.

*The importance of geographic distance for taxonomic and functional community composition is weak and varies with scale*

Here, we used geographic distance as a proxy to assess the role of dispersal, yet it is important to note that organism’s dispersal is dependent of other factors too, such as possible biotic dispersal vectors. When considering all 88 plots, distance was a weak explanatory variable of functional and even more so of taxonomic community composition. However, when performing our analyses at different spatial scales (i.e., distinguishing short, medium and long geographic distances among the pairs of plots), the role of distance varied between taxonomic and functional dissimilarity depending on the scale. In particular, the role of distance in explaining taxonomic dissimilarity was detected only at short scale (until a limit of ca. 330 km) after which further distance had no further effect on taxonomic composition. This scale-dependency of the influence of distance is consistent with the results reported by Lindström and Östman (2011) where dispersal affected taxonomic community composition only when large amount of bacterial biomass was dispersed, which is more likely to occur at shorter distances. Also consistent with our results, the study of Shi et al. (2018) reported that stochastic processes (including dispersal) dominated over environmental filtering for the taxonomic composition of soil bacterial communities when distances among study sites were short, whereas environmental filtering dominated over stochasticity for larger distances. A comparison of this scale-dependency against the results obtained for plant species (and other organisms with varying dispersal abilities; Lenoir et al., 2012) would be important, since for them the effect of dispersal is commonly thought to act at coarser scale than environmental filtering (Lortie et al., 2004; Meynard et al., 2013).

At coarser scales, i.e., when the plots are >660 km apart, distance became relatively more important in explaining functional dissimilarity. A strong role of distance on bacterial communities was also observed at global scale in marine environments (Haggerty & Dinsdale, 2017), where the authors hypothesised that the effect of distance on the functional composition of marine bacterial communities was due to historical evolutionary constraints that select certain bacterial functions. This might also explain our finding, although the reasoning of Haggerty and Dinsdale (2017) concern free-living communities.

**Conclusions**

Our results demonstrate that i) in general, the importance of environmental dissimilarity exceeds that of geographic distance in explaining both taxonomic and functional dissimilarity of soil bacteria; ii) regarding environmental filtering, the role of abiotic (soil and climate) factors was more important than the role of biotic (plant community) factors; iii) taxonomic and functional biogeographic patterns are driven by different environmental variables, pH being the most important for taxonomic composition, while N/P availability as well as moisture and organic matter drive the N cycle-related functional composition; and iv) the importance of geographic distance is scale-dependent, with taxonomic dissimilarity being related to distance at short distances (< 330 km) only, and functional dissimilarity being related to distance only when distances are > 660 km. Overall, these findings indicate that (1) taxonomic and functional components of soil bacterial communities are not constrained similarly by environmental filtering and dispersal, and (2) interpretation of underlying mechanisms of bacterial biogeography are scale-dependent.

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**Conflict of interest**

The authors of this manuscript declare that there is no conflict of interest.

**Data Accessibility Statement**

The raw sequence data were submitted to NCBI Short Read Archive under project number PRJNA626532. The accession numbers are listed in Table S4. All other data (climate, soil and plant data, and geographic coordinates) will be added to Dryad upon acceptance of the manuscript.

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**Figure legends**

**Fig. 1.** Framework used to study the drivers of taxonomic and functional biogeography of soil bacteria, and working hypotheses. Soil was sampled from 195 plots (39 sites indicated with red dots; 5 plots per site) along a 1 550 km transect in the Tibet plateau (Top). Taxonomic and functional dissimilarities of soil bacterial communities (based on 16S sequencing and on abundances of functional genes related to N cycling, respectively), dissimilarity of abiotic environmental conditions (based on 11 edaphic and 3 climatic variables), dissimilarities of plant communities in terms of species (biomasses of 348 plant species) or growth forms, and geographic distances among plots were then computed (Middle) and compared. Effects of abiotic and biotic environmental variables and distance were assessed using generalized dissimilarity modelling. We hypothesised that geographic distance would better explain taxonomic dissimilarity of bacterial communities due to increasing isolation with distance, whereas bacterial functional dissimilarity would be more driven by environmental dissimilarity due to functional redundancy (Bottom). We further assumed that plant community dissimilarity would be the best explanatory variable for bacterial community dissimilarity because, in addition to reflecting abiotic conditions, plant community composition might influence soil bacteria by providing specific resources, altering soil physical and chemical conditions, and recruiting particular taxa or groups.

**Fig. 2.** Relationships among dissimilarity of soil bacteria communities based on their taxonomic compositions, N-cycling related functional dissimilarity of soil bacterial communities, dissimilarity of abiotic conditions, dissimilarity of plant communities based on species biomasses, dissimilarity of plant communities based on growth form fractions, and geographic distance. Correlations and significances are based on Mantel tests using the 88 plots for which all data are available. For results based on all the plots, see Fig S8.

**Fig. 3.** Percentage of deviance of bacterial taxonomic (green) and N cycling-related functional (yellow) dissimilarity explained by individual variables, i.e., dissimilarity of each of the environmental variables or distance. Analysis is based on 88 plots for which all data are available. For results for functional dissimilarity based on all the plots, see Fig S9. Contributions of individual explanatory variables are considered independently here (hence the sum can be >100 %). **pH** = soil pH, **MAT** = mean annual air temperature, **OM** = soil organic matter content, **C:P** = carbon to phosphorus content ratio in soil, **MAP** = mean annual precipitation sum, **TN** = soil total nitrogen content, **plant SR** = plant species richness, **moisture** = soil moisture, **sedge%** = percentage of sedges, **NH4.N** = soil ammonium content, **AP** = soil available phosphorus, **N:P** = nitrogen to phosphorus content ratio of soil, **plant SW** = Shannon-Wiener index of plant community, **TP** = soil total phosphorus content, **forb%** = percentage of forbs, **grass%** = percentage of grasses, **legume%** = percentage of legumes, **C:N** = carbon to nitrogen content ratio of soil, **plant BM** = total plant biomass, **NO3.N** = soil nitrate content, **DTR** = mean diurnal temperature range, **shrub%** = percentage of shrubs, **cushion%** = percentage of cushion plants, and **distance** = geographic distance among plots.

**Fig 4.** The models with highest deviance explained (with all their explanatory variables significant). a) Total deviance in bacterial taxonomic or functional dissimilarity explained by the model (bar height) and the relative importances of the selected explanatory variables (coloured bands). b) Predicted changes in taxonomic (in green) and functional dissimilarity (in yellow) according to changes in each explanatory variable along the range of variable values. The maximum height and slope of the curve indicate the amount and rate of change of bacterial community dissimilarity, respectively. Analyses were made based on the 88 plots for which all data were available (for 177 plots for functional dissimilarity, see the figure S10). Acronyms are as for Figure 3.

**Fig. 5.** Percentage of deviance of bacterial a) taxonomic (in green) and b) functional dissimilarity (in yellow) explained by individual variables across the three classes of distances between the plots: 20 m to 333 km, 333 to 662 km, and 662 to 1 546 km (in dark, intermediate and light shade, respectively). Analyses were made based on the 88 plots for which all data were available. Acronyms are as for Figure 3.

**Fig 6.** The models with highest deviance explained (with all explanatory variables significant), and the relative importances of the variables across the three classes of distances between the plots. Analyses were made based on the 88 plots for which all data were available. Acronyms are as for Figure 3.