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Short Communication

Climate shapes the protein abundance of dominant soil bacteria

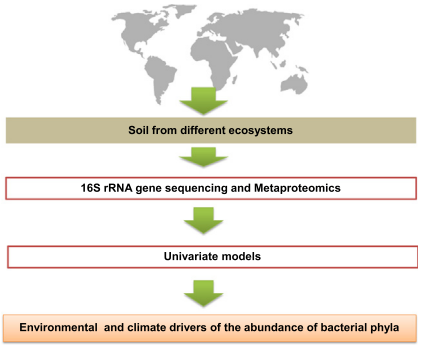
Felipe Bastida [a,*], Tom W. Crowther [b], Iván Prieto [a], Devin Routh [b], Carlos García [a], Nico Jehmlich [c]

[a] CEBAS-CSIC, Department of Soil and Water Conservation, Campus Universitario de Espinardo, 30100 Murcia, Spain
[b] Institute of Integrative Biology, ETH Zürich, Univeritätstrasse 16, 8006 Zürich, Switzerland
[c] Helmholtz-Centre for Environmental Research — UFZ, Department of Molecular Systems Biology, Permoserstr. 15, 04318 Leipzig, Germany

HIGHLIGHTS

- Soil microorganisms play a pivotal role in biogeochemical cycles.
- Soil proteins from boreal, temperate and semiarid ecosystems were extracted.
- Abiotic variables that explained protein abundance were evaluated.
- Soil protein content of some bacteria phyla was linked to climate indicators.

GRAPHICAL ABSTRACT



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ABSTRACT

Sensitive models of climate change impacts would require a better integration of multi-omics approaches that connect the abundance and activity of microbial populations. Here, we show that climate is a fundamental driver of the protein abundance of Actinobacteria, Planctomycetes and Proteobacteria, supporting the hypothesis that metabolic activity of some dominant phyla may be closely linked to climate. These results may improve our capacity to construct microbial models that better predict the impact of climate change in ecosystem processes.

1. Introduction

Soil microorganisms mineralize the soil organic matter thus playing a pivotal role in nutrient biogeochemical cycles. Because they also produce gaseous metabolites with potential greenhouse effects, they are also able to modify both the local and global climate (Bradford et al., 2016). In recent years, considerable efforts have been made to understand the factors governing soil microbial community composition through DNA sequencing approaches (Bastida et al., 2016; Delgado-Baquerizo et al., 2018a,b). However, soil microbes are often not active and a large percentage of soil DNA can belong to non-living cells (Carini et al., 2017). Consequently, conventional sequencing approaches (i.e. 16S rRNA gene amplicons) can be limited in their capacity to predict the connections between microbial populations and ecosystem functioning. While genomic information provides a wealth of important information about the potential molecular machinery that

* Corresponding author at: CEBAS-CSIC, Campus Universitario de Espinardo, PO Box 164, CP 30100 Murcia, Spain.
E-mail address: fbastida@cebas.csic.es (F. Bastida).

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might be employed for life processes, proteins are the direct catalyzers of cellular and environmental processes (Hettich et al., 2013).

As a result, soil metaproteomics (the direct identification of proteins in soil) has been proposed as a promising new approach for the evaluation of the active component of the soil microbiome at local scales (Hultman et al., 2015; Bastida et al., 2016, 2017). However, until now, metaproteomics have yet to be used to examine how the activity of soil microbes varies across broad spatial scales. Here, we use a comprehensive cross site investigation of soil metaproteomes in order to examine the abiotic factors that determine the global variability in the protein abundance of dominant bacterial phyla. Given that climate regulates the metabolic activity of soil bacteria and climate events can cause changes in the composition of soil microbial communities (Bell et al., 2014; Evans and Wallenstein, 2014), we hypothesize that climate factors will shape more the protein abundance of bacterial phyla than their abundance evaluated by phylogenetic gene markers.

2. Materials and methods

In order to span a large environmental gradient with strong climatic differences, soils from boreal, temperate and semiarid ecosystems were collected within a five-year period from 2010 to 2015 (Table S1, Supplementary Information). Soils were sampled from Long-term Ecological Research Stations in North-America and South-Europe. These soils are included in the studies of Crowther et al. (2014) and Bastida et al. (2016, 2017). Soils were collected using a sampling design extender to maximize variation in climatic conditions and biome types. Sites included: Bonanza Creek, Alaska 64.85°N, −147.84°E (BNZ); Coweeta LTER, North Carolina 35°N, −83.5°E (CWT); Hubbard Brook Experimental Forest, New Hampshire 43.94°N, −71.75°E (HBR); Konza Prairie Biological Station, Kansas 39.09°N, −96.57°E (KNZf); pre-desertic semiarid grassland, Murcia 37° 54′ N, 1° 24′ W (GEB); pre-desertic semiarid forest Murcia 37° 54′ N, 1° 24′ W (GEP); Mediterranean forest Albacete 38° 22′ N, 2° 20′ W (ALB); and Mediterranean forest, Granada 38° 0′ N, 2° 2′ W (MOJ). Three soil samples were collected in each of the sites. Each sample was a replicate. Soil samples were sieved (2 mm) and immediately preserved at −20 °C. The following parameters were determined for each site: content of clay, silt, salt, organic C, and total N, C-to-N ratio, pH, soil moisture, mean-annual temperature (MAT) and mean-annual precipitation (MAP) (Supplementary Information). The ratio between MAT and MAP was utilized as an aridity indicator: the higher the ratio, the higher the aridity. Soil organic C ranged between 0.5 and 15.5%; total N between 0.05 and 0.84%; pH between 4.2 and 8.6 (Table S1) and C/N ratio between 9 and 20. MAT ranged between −2.94 °C and 18 °C. MAP varied between 260 mm and 1400 mm. The bacterial community composition (16S rRNA gene amplicon sequencing) of studied samples was obtained from the abovementioned studies and compared to metaproteome data obtained here. Proteins were extracted and processed as described elsewhere (Chourey et al., 2010; Supplementary Information). Genomics and metaproteomics were analyzed in each replicate and utilized as individual replicate in the statistical analyses. The mass spectrometry data have been deposited in the PRIDE partner repository with the dataset PXD003572, PXD005447 and PXD009773.

Pearson correlation coefficients between the abundance of each phylum given by metaproteomics and that retrieved by 16S rRNA sequencing were obtained (Table S2, Supporting Information). These results revealed significant correlation coefficients in the case of Acidobacteria, Actinobacteria and Cyanobacteria, but not in the case of Bacteroidetes, Firmicutes, Planctomycetes and Proteobacteria.

Since not all variables were linearly related to soil abiotic variables, we first selected the best fitting approach (linear, quadratic, exponential or inverse fit) for each abiotic variable based on an Akaike information criterion (AIC) approach (Burnham and Anderson, 2002). AIC is an estimator of the relative quality of statistical models for a given dataset and provides a statistical method to select the best model among different ones. To do this, for each bacterial phyla or cellular functionality separately and each abiotic variable as the non-dependent variable we constructed all four possible models (linear, quadratic, exponential or inverse fit) and selected the best fitting approach using the AIC (Burnham and Anderson, 2002). The best fitting approach for each individual abiotic variable was selected on the basis of the lowest AIC for each set of four models containing this variable. Once the best fitting approach for each abiotic variable was selected, we tested which abiotic variable best explained the abundance of phyla through 16S rRNA sequencing or metaproteomics, as well as the abundance of proteins involved in cellular functionalities. To do this, we constructed all possible models with each abiotic variable as the non-dependent variable (12 models in total for the abundance of each bacterial phylum studied by sequencing and metaproteomics, and for the abundance of proteins involved in cellular functionality). The abiotic variable that best explained the abundance of bacterial phyla through 16S rRNA gene sequencing or metaproteomics, and the abundance of proteins involved in different cellular functionalities was selected on the basis of the model with the lowest AIC. We then calculated the adjusted R^2 and P values and extracted the regression equation coefficients for each best univariate model. Statistical analyses were done using the R software (version 3.3.2).

3. Results and discussion

Metaproteomics revealed that the abundance of the dominant bacterial phyla was best explained by pH and MAT/MAP (Table 1). In contrast, climatic factors were not selected in the univariate models that explained the abundance of bacterial phyla, studied by 16S rRNA gene sequencing. Previous studies based on 16S rRNA gene sequencing have highlighted the paramount role of pH on shaping the composition and diversity of soil microbial community (Fierer and Jackson, 2006), as we also observed here (Fig. 1). The protein abundance of Acidobacteria and that of Actinobacteria and Cyanobacteria were contrarily shaped by pH.

There is a need for accurately forecasting the ecological consequences of global change in soil microbial communities (Delgado-Baquerizo et al., 2018a). The protein abundance of Actinobacteria, Planctomycetes and Proteobacteria, as well as the abundance of proteins involved in the production and conversion of energy, were best explained by MAT/MAP (Table 1). Proteobacterial protein content was negatively related to MAT/MAP and was higher in temperate and boreal sites (lower MAT/MAP) than in semiarid sites (higher MAT/MAP), while actinobacterial protein abundance was favored in arid environments (Fig. 1). This phylum has been suggested to be adapted to harsh conditions such soil drying through their peptidoglycan layer (Battistuzzi and Hedges, 2009). Indeed, a sequencing study revealed that Actinobacteria can outcompete other dominant groups such Acidobacteria under arid conditions (Delgado-Baquerizo et al., 2018b). Considering the proposed univariate models, the increase in MAT/MAP, as predicted by climate change models in many areas of boreal, temperate and semiarid ecosystems (IPCC, 2013), will likely enhance the protein abundance of Actinobacteria and Planctomycetes, and decrease that of Proteobacteria. Moreover, the abundance of proteins related to cellular energetic processes (among them the F-type H^+-transporting ATPase was dominant) increased linearly with MAT/MAP (Table 1). These findings suggest an acceleration of energetic metabolic processes in soil (i.e. greater soil organic matter mineralization) induced by global warming (Bond-Lamberty and Thomson, 2010) and which is in line with the patterns of carbon losses occurring at a global scale (Crowther et al., 2016).

In despite the limitations of metaproteomics due to the absence of genome databases (Starke et al., 2017), the complicated protein extraction due to their interaction with humic substances and soil particles (Giagnoni et al., 2011), and the reduced number of analyzed samples, climatic conditions and biome types, our study provides the first tentative distribution of soil microbial proteins at broad spatial scales. As