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Mapping and validating predictions of soil bacterial biodiversity using European and national scale datasets

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ABSTRACT

Recent research has highlighted strong correlations between soil edaphic parameters and bacterial biodiversity. Here we seek to explore these relationships across the European Union member states with respect to mapping bacterial biodiversity at the continental scale. As part of the EU FP7 EcoFINDERs project, bacterial communities from 76 soil samples taken across Europe were assessed from eleven countries encompassing Arctic to Southern Mediterranean climes, representing a diverse range of soil types and land uses (grassland, forest and arable land). We found predictable relationships between community biodiversity (ordination site scores) and land use factors as well as soil properties such as pH. Based on the modelled relationship between soil pH and bacterial biodiversity found for the surveyed soils, we were able to predict biodiversity in ~1000 soils for which soil pH data had been collected as part of national scale monitoring. We then performed interpolative mapping utilising existing EU wide soil pH data to present the first map of bacterial biodiversity across the EU member states. The predictive accuracy of the map was assessed again using the national scale data, but this time contrasting the EU wide spatial predictions with point data on bacterial communities. Generally the maps were useful at predicting broad extremes of biodiversity reflective of low or high pH soils, though predictive accuracy was limited for Britain particularly for organic/acidic soil communities. Spatial accuracy could however be increased by utilising published maps of soil pH calculated using geostatistical approaches at both global and national scales. These findings will contribute to wider efforts to predict and understand the spatial distribution of soil biodiversity at global scales. Further work should focus on enhancing the predictive power of such maps, by harmonising global datasets on soil conditioning parameters, soil properties and biodiversity; and the continued efforts to advance the geostatistical modelling of specific components of soil biodiversity at local to global scales.

1. Introduction

Soil bacteria contribute the largest proportion of the soil genetic resource (Urich et al., 2008; Fierer et al., 2012), reflecting their ubiquity and high abundance across all soil systems. Given bacterial importance in the regulation of soil ecosystem services (Comerford et al., 2013), increased understanding of the environmental controls of bacterial biodiversity is required from both scientific and policy perspectives in order to predict biodiversity change, and determine functional consequences of change due to future climatic or land use pressures. Attempts to characterise the bacterial communities in soils and understand ecological drivers have previously been hampered by methodological difficulties in assessing taxonomic diversity due to the limited culturability of many bacterial taxa coupled with vast taxonomic diversity (e.g. Janssen et al., 2002). These problems have to some extent been overcome through the development of molecular technologies to assess the diversity of taxonomic marker genes (particularly the 16S rRNA gene) PCR amplified from extracted soil DNA (Hirsch et al., 2010).

The application of molecular methods to wide ranging globally dispersed soil samples has revealed that soil bacterial communities are broadly structured along gradients of soil properties, with strong correlations between measures of bacterial biodiversity and

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key soil variables such as soil pH and organic matter, which are co-related with broader environmental parameters such as land use, climate, and parent material (Fierer and Jackson, 2006; Lauber et al., 2009; Griffiths et al., 2011). Therefore, whilst the causal mechanisms underlying these relationships are complex it is apparent that the same pedogenic factors which determine the nature of soils (e.g. Jenny, 1941) also determine the taxonomic characteristics and structure of the soil bacterial community. This new knowledge permits spatial forecasting of bacterial biodiversity at a range of scales and under change scenarios; which together with parallel developments in understanding microbial biodiversity-function relationships, may allow for enhanced prediction of soil processes under future environmental change.

Molecular surveys permit the production of range maps of soil bacterial distributions at various spatial scales. Spatial distribution maps provide a visual representation of the forces shaping populations or communities and therefore provide the foundation for macro ecological understanding (Elton, 1927). Maps can also guide policy decisions with respect to land management, and can be useful visual resources guiding scientific experimentation and enquiry. Importantly, more recently rasterised maps provide georeferenced data which can feed wider ecological, climatic or biogeochemical models. Already there has been several attempts to map soil microbial properties at national and regional scales, using molecular methodologies applied to nationwide soil monitoring schemes (Bru et al., 2011; Griffiths et al., 2011; Dequiedt et al., 2009, 2011). These studies mapped point sampled microbial data using interpolative methods (e.g. inverse distance weighting, kriging; see Bivand et al., 2008) to fit surfaces predicting the microbial properties at unsampled locations by weighted averages of surrounding measured values. These methods are useful to show large differences in microbial properties over large areas but local accuracy is limited by the spatial scale of sampling.

More advanced geostatistical approaches can be used to predict a variable of interest at unsampled locations based on known relationships between the dependent variable and other predictor variables (e.g. climate, soil type, land cover). Such approaches are commonly used in wider ecology (sometimes termed environmental-, ecological-, or species-distribution modelling: Elith et al., 2006), and can be used to predict either species or communities at unsampled locations (Chapman and Purse, 2011). These environmental correlational approaches have so far been used to predict historical change in soil bacterial biodiversity due to land use at regional scales (Fierer et al., 2013); and also to improve on the interpolated maps of bacterial biodiversity across Great Britain (Griffiths et al., 2011) by modelling the observed relationships between bacterial communities and environmental variables, and then forecasting communities in unsampled locations using remote sensed land cover information and parent material maps (Henrys et al., 2015). This paper aside there are few studies which have examined in detail the predictive performance of such maps compared to simple interpolation. More widely, large scale spatial predictions of soil parameters are increasingly being disseminated through downloadable map resources (e.g. soilgrids.org, ukso.org), and there is now a need to identify specific predictive limitations in order to further improve accuracy (Hengl et al., 2014).

Here as part of this special issue reporting results from the EU FP7 EcoFINDERs project coordinated soil sampling campaign, we seek to assess the bacterial communities in 76 soils sampled across Europe in order to produce a soil bacterial map at the European scale, which can be validated against national scale datasets. We predict that soil pH will be the strongest correlate with measures of community biodiversity, which will then allow us to predict and spatially interpolate communities based on publicly available European scale point data on soil pH (from the LUCAS survey: Tóth et al., 2013). The predictive accuracy of this map will be assessed by comparing predictions with observed point data on bacterial communities collected with similar methods from over 1000 soils across Great Britain (Griffiths et al., 2011). We will also explore whether the predictions from this simple interpolated map can be improved upon, by spatially predicting communities based on existing soil pH maps produced using more advanced environmental correlation approaches (from soilgrids.org and ukso.org).

2. Materials and methods

2.1. Sampling

Bacterial communities were examined in soils sampled across the EU member states as part of the EcoFINDERs project "transect" sampling campaign, full details of which are provided elsewhere in this issue (Stone et al., 2015). Briefly, a range of sites spanning a gradient of soil properties (principally pH, organic matter and texture), climatic zones, and land uses (grassland, arable, forest) were targeted for sampling following examination of EU wide datasets (see Supplementary material for site locations, S1). Samples were collected at the end of summer 2012 according to standardised protocols to 5 cm depth, and sent to a central processing lab for homogenisation and distributing to various partner labs for further analyses. In total eighty-two soils from 11 countries encompassing Arctic to Southern Mediterranean climes of which 76 are assessed in this study. Soil chemical determinations were also conducted by a single laboratory to provide measures of volumetric moisture content, pH (in water), texture, and total/organic carbon (C) and nitrogen (N) contents.

2.2. DNA extraction and community analyses

Total genomic DNA was extracted from all soil samples using a previously described DNA extraction procedure (Plassart et al., 2012). Briefly, 1 g of soil was mixed at 70 °C with a extraction buffer containing 100 mM Tris–HCl (pH 8), 100 mM EDTA (pH8), 100 mM NaCl, 2% (w/v) polyvinylpyrrolidone (40 g mol^{-1}) and 2% (w/v) sodium dodecyl sulphate. Proteins were precipitated from the supernatant with 1/10 volume of 3 M sodium acetate, before nucleic acid precipitation with isopropanol. DNA was further purified through polyvinylpolypyrrolidone (PVPP) Microbiospin minicolumns (BIORAD, Marnes-la-Coquette, France) and finally using the Geneclean Turbo kit (MP-Biomedicals, NY, USA).

Bacterial communities were examined using TRFLP as described by Griffiths et al. (2011) using the forward primer 63F (5′-CAGGCCTAACACATGCAAGTC-3′) labelled at the 5′ end with D4 blue fluorescent dye and reverse primer 530R (5′-GTA TTA CCGCGG CTG CTG-3′). Amplifications were performed in 50 μl reactions under the following conditions: 94 °C for 90 s, followed by 35 cycles of 94 °C for 45 s, 55 °C for 1 min and 72 °C for 3 min, followed by a final extension of 72 °C for 10 min. Amplicons were then purified using the ZR-96 DNA clean-up kit (Zymo research, Freiburg, Germany), prior to enzymatic digestion. Purified bacterial DNA was digested with MspI restriction enzyme (New England Biolabs Inc., Ipswich, MA, USA) at 37 °C for 3 h. Fragment analysis was performed with a Beckman Coulter CEQ 2000XL capillary sequencer (Beckman Coulter Corporation, California, USA). Peak height data were analysed using GeneMarker software (Softgenetics, LLC, PA, USA). Relative abundances were calculated as the ratio between the fluorescence of each terminal restriction fragment (T-RF) and the total integrated fluorescence of all T-RFs.

2.3. Statistical analyses

A site by taxon (TRF) relative abundance table derived from the TRFLP analyses was used to explore community relationships with