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Ecological network analysis reveals the inter-connection between soil biodiversity and ecosystem function as affected by land use across Europe

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ABSTRACT

Soil organisms are considered drivers of soil ecosystem services (primary productivity, nutrient cycling, carbon cycling, water regulation) associated with sustainable agricultural production. Soil biodiversity was highlighted in the soil thematic strategy as a key component of soil quality. The lack of quantitative standardised data at a large scale has resulted in poor understanding of how soil biodiversity could be incorporated into legislation for the protection of soil quality. In 2011, the EcoFINDERS (FP7) project sampled 76 sites across 11 European countries, covering five biogeographical zones (Alpine, Atlantic, Boreal, Continental and Mediterranean) and three land-uses (arable, grass, forestry). Samples collected from across these sites ranged in soil properties; soil organic carbon (SOC), pH and texture. To assess the range in biodiversity and ecosystem function across the sites, fourteen biological methods were applied as proxy indicators for these functions. These methods measured the following: microbial diversity: DNA yields (molecular biomass), archaea, bacteria, total fungi and arbuscular mycorrhizal fungi; micro fauna diversity: nematode trophic groups; meso fauna diversity: enchytraeids and Collembola species; microbial function: nitrification, extracellular enzymes, multiple substrate induced respiration, community level physiological profiling and ammonia oxidiser/nitrification functional genes. Network analysis was used to identify the key connections between organisms under the different land use scenarios. Highest network density was found in forest soils and lowest density occurred in arable soils. Key taxonomic units (TUs) were identified in each land-use type and in relation to SOC and pH categorisations. Top-connected taxonomic units (i.e. displaying the most co-occurrence to other TUs) were identified for each land use type. In arable sites this was dominated by bacteria and fungi, while in

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grassland sites bacteria and fungi were most connected. In forest soils archaeal, enchytraeid and fungal TUs displayed the largest number of neighbours, reflecting the greatest connectivity. Multiple regression models were applied to assess the potential contribution of soil organisms to carbon cycling and storage and nutrient cycling of specifically nitrogen and phosphorus. Key drivers of carbon cycling were microbial biomass, basal respiration and fungal richness; these three measures have often been associated with carbon cycling in soils. Regression models of nutrient cycling were dependent on the model applied, showing variation in biological indicators.

1. Introduction

Soil organisms are considered as drivers of ecosystem services, in particular those soil ecosystem services associated with sustainable agricultural production. These include primary production of food, fibre and fuel, nutrient cycling, carbon cycling and storage, and water infiltration and purification (Hooper et al., 2005). As such, soil biodiversity is therefore highlighted in the Soil Thematic Strategy (EU (European Union), 2002) as a key component of soil quality. Soil quality is defined as the capacity of soil to function, within natural or managed ecosystem boundaries, to sustain plant and animal production, maintain or enhance water and air quality, and support human health and habitation (Karlen et al., 1997). Many of these functions depend on the diversity and activities of soil organism communities. Increasingly we require a multi-faceted approach to land management, with an increasing need for greater food production, while simultaneously delivering other ecosystem services or soil functions, such as carbon (Tardy et al., 2015) and nutrient cycling (Fierer et al., 2012). Land management can lead to the degradation of carbon stocks in soils, and therefore understanding the role of soil biota in carbon cycling and storage is vital. The soil carbon pool is 3.3 and 4.5 times the size of the atmospheric (760 Gt) and the biotic pool (560 Gt), respectively (Lal, 2004). It is essential from a climate change perspective that we protect carbon storage potential in our soils, furthermore, active cycling of carbon, combined with large amounts of organic carbon temporarily stored in soils, increases primary productivity, stabilises soil structure, increases nutrient retention and water filtration (Turbé et al., 2010 De Vries et al., 2013). Land management also has a significant impact on the capacity of the system to cycle nutrients, providing a constant supply to crops as needed to ensure optimum productivity. This has traditionally been a high input system, with the addition of synthetic fertilisers to promote availability of essential nutrient for plant growth (especially nitrogen (N) and phosphorus (P)), however it is becoming increasingly apparent that soil organisms have a strong role to play in the cycling of nutrients due to their involvement in the geochemical cycles (Lemanceau et al., 2015).

In 2012, the European Commission acknowledged the importance of soil biodiversity in the role of ecosystem functioning, stating that "these functions are worthy of protection because of their socio-economic as well as environmental importance" (Jones et al., 2012). However, the lack of quantitative standardised data on soil biodiversity at the European scale has resulted in poor understanding of both the role that soil organisms play in soil ecosystem services and the need to protect soil biodiversity to ensure the future provision of such functions. This was also highlighted in the EU's 6th Framework programme financed project: environmental assessment of soil for monitoring (ENVASSO) established in 2005, that recommended pan-European indicators to assess the potential loss of soil biodiversity (Bispo et al., 2009). This work has been followed up by the Ecological Function and Biodiversity Indicators in European Soils (EcoFINDERS) project, financed under the EU's 7th Framework programme and established in 2009, to support the European Union soil policy making by providing the necessary tools to design and implement strategies for sustainable use of soils, with a specific focus on soil biodiversity and associated ecosystem functioning.

There have been many studies which have quantified the impact of land management and land use on the diversity and functioning of soil biota (a few examples include; Trasar-Cepeda et al., 2008; Lohaus et al., 2013; Mills and Adl, 2011; Bartz et al., 2014). Tsiafouli et al. (2015) highlights the lack of integrative approach, with many of these studies focussing on one aspect of soil biodiversity (e.g. species richness, abundance, food webs, community structure), promoting the need for more multi-factorial approaches. Tsiafouli et al. (2015) analysed the effect of agricultural intensification across Europe on the structure, diversity, food web assembly and community dynamics of soil biota, summarising that agriculture intensification reduces soil biodiversity, resulting in fewer functional groups and reduce diversity.

Traditional methods such as diversity estimates and multivariate statistical techniques describe beta-diversity and can reveal the role of biotic and abiotic factors in shaping the communities. However, they do not take into account the interactions among organisms, a very important factor shaping any natural community (Bohan et al., 2013; Mulder et al., 2011). Much of the focus in nature conservation has been on protection of individual species while biotic interactions are increasingly at risk from local and global extinction as a consequence of (anthropogenic) environmental disturbances (Pocock et al., 2012). Using a network based approach, the relationship between organisms within and across taxonomic units/trophic levels can be analysed even from very large datasets. In ecology, networks have been long used for macro-organisms (Bascompte et al., 2003) but recently the approach of analysing large datasets using summarizing network analysis based on ecological theories has become popular in the field of soil microbial ecology (see for example Barberán et al., 2012).

The aim of this study was to investigate the biological diversity (soil microbial and faunal communities) associated with major land use management types found across Europe and to examine how these various ecological networks relate to two key ecosystem services in soil; (1) carbon cycling and storage potential and (2) nutrient cycling, specifically nitrogen (N) and phosphorus (P). To achieve this, a pan-European "transect" was sampled in 2011 at 81 sites, across 11 European countries, covering five biogeographical zones (Alpine, Atlantic, Boreal, Continental and Mediterranean) and three land use types (arable, grass, forestry) (Stone et al., 2016). These sites represent a wide range of soil properties, specifically chosen to provide a wide spectrum of measurements for SOC, pH and texture (sand, silt and clay content). Fourteen soil biological properties were measured: (i) microbial diversity; DNA yields (molecular biomass), archaea, bacteria, fungi, arbuscular mycorrhizal fungi (AMF), (ii) micro fauna diversity; nematodes trophic groups, (iii) meso fauna diversity; enchytraeid, and Collembola species, (iv) functional indicators; nitrification, extracellular enzyme assays (EEA), multiple substrate induced respiration (MSIR) and community level physiological profiling (CLPP), and