Soil Biology & Biochemistry xxx (2015) 1–11

Contents lists available at ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Impact of forest management practices on soil bacterial diversity and consequences for soil processes

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ARTICLE INFO

Article history:
Received 6 May 2015
Received in revised form
13 November 2015
Accepted 28 November 2015
Available online xxx

Keywords:
Bacterial diversity
Ecosystem functioning
Forest management

ABSTRACT

Microbes are responsible for most soil processes but our knowledge of the relationship between belowground diversity and ecosystem functioning and how this is affected by land management is still incomplete. Here, we investigated the impact of forest management on bacterial communities and its consequences for soil functioning in a dryland forest ecosystem. We also evaluated the nature of the relationship between bacterial communities and soil functioning. We used high-throughput sequencing and quantitative PCR to determine the bacterial diversity and abundance and used a model-based approach to evaluate the contribution of microbial and edaphic factors to functions involved in carbon and nutrient cycling. Our results demonstrate that irrigation had stronger effects than fertiliser application on bacterial communities and soil processes, highlighting the significance of water availability for bacterial communities and their activity in dryland ecosystems. We then used structural equation modelling to identify direct and indirect impacts on management practices and provide evidence that the response of some of these key soil processes to management practices were mediated by changes in bacterial diversity and abundance. Overall, the functioning of forest soils was predicted by bacterial diversity and abundance and a positive linear relationship between these variables and soil processes was observed, suggesting that declining microbial diversity could have direct consequences for functioning of soil ecosystems.

1. Introduction

Microbial communities are essential components of biogeochemical cycles (Falkowski et al., 2008) and as such they represent a key factor influencing the functioning and the sustainability of soil ecosystems. Soil biological diversity represents one of the largest reservoirs of biodiversity on Earth (Wardle, 2002; Decaëns, 2010), but despite our growing understanding of how this diversity contributes to the functioning of belowground processes, the functional consequences of diversity loss in soil ecosystems remain largely unknown (Bardgett and van der Putten, 2014). The relevance of microbial diversity for soil functioning is challenged by the concept of functional redundancy, which predicts that, because different species can play the same role in a given ecosystem, an ecosystem-relevant loss of species (5–50%) might not influence the overall rate of processes catalysed (Loreau, 2000). It has been proposed that functional redundancy is greater for processes performed by a wide variety of soil microorganisms, such as community respiration or decomposition, than for processes carried out by a narrow group of specialised microorganisms (Schimel, 1995). While some studies supported this theory (Bardgett et al., 2008; Levine et al., 2011), contradictory results have been reported for both general and specific functions (Peter et al., 2011; Philippot et al., 2013). Land management practices can significantly alter soil physical, chemical, and biological properties, which in turn can have profound effects on many ecosystem functions, as observed in forest ecosystems (Waldrop et al., 2003; Purahong et al., 2014). In forest soils, the growth, activity and structure of the soil microbial community are affected by abiotic and biotic factors including quality and quantity of organic matter input, nutrient availability and physical disturbance (Leckie et al., 2004; Hannam et al., 2006; He et al., 2006). These factors may in turn be influenced by land-use

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http://dx.doi.org/10.1016/j.soilbio.2015.11.029
0038-0717/

change (*e. g.* natural forest vs. managed tree plantation) and management techniques (Zheng et al., 2005; He et al., 2006; Burton et al., 2010; Gao et al., 2014). Additionally, forestry plantation in Australia and in other dryland ecosystems routinely use fertilisers and irrigation in order to maximise wood production and to shorten rotation times. Despite the fact that some research has focussed on the impact of some silvicultural techniques on soil microbial communities (*e. g.* Burton et al., 2010; Hu et al., 2015; Martins et al., 2015), we still lack empirical evidence of how microbial diversity components (*e. g.* richness, evenness and taxonomic composition) are affected by different forest management practices. Even in agricultural soils, only few studies have investigated the impact of management practices on microbial diversity and findings remains inconclusive (Campbell et al., 2010; Fierer et al., 2012). Since 80–90% of the processes in soil are mediated by microbes (Nannipieri and Badalucco, 2003), it is essential to understand the degree of sensitivity of the microbial community to management practices in order to be able to predict the effects on the functioning of soil ecosystems.

The aims of this study were to examine the impact of land management in forest ecosystems on bacterial diversity and its consequences for soil functions, and to place these impacts in the context of the magnitude of impacts associated with land-use change. Soil samples were obtained from two sources: a forest management experiment, where a eucalypt plantation was subjected to different irrigation and fertiliser application treatments, and in the adjacent natural woodland. In addition to allowing us to compare the relative importance of these types of impacts, this also gave a wide range of environmental characteristics varying from management practices expected to influence diversity by changing edaphic properties, to changes in plant diversity, and thus a range of expected differences in soil microbial diversity, necessary to test the relationship between diversity and soil functioning. In fact, microbial communities may experience a reduction in diversity in response to nitrogen fertiliser (Kennedy et al., 2004, 2005), while irrigation is known to have positive effects on microbial biomass by increasing soil moisture (Litton et al., 2003; Samuelson et al., 2009). The link between bacterial communities and soil functioning was investigated by means of a model-based approach evaluating the contribution of microbial and edaphic factors to processes contributing to soil ecosystem functioning of naturally diverse communities. Soil processes involved in carbon and nutrient cycling were estimated by measuring community respiration, substrate-induced respiration and potential enzyme activities. Because positive relationships typically found between moisture and the availability of resources, we hypothesised that fertiliser application and irrigation would have opposite effects on bacterial diversity (negative and positive, respectively) and consequently on soil functions.

2. Materials and methods

2.1. Site description and soil sampling

Soil samples were collected from two sites: the Hawkesbury Forest Experiment (HFE) site (33°36′40″ S, 150°44′26.5″ E), and the adjacent Cumberland Plain woodland (Richmond, NSW, Australia). The soil is a sandy loam with low organic matter content (0.7%), low fertility (available P, 8 mg kg^{-1}; exchangeable cations K 0.19 mEq 100 g^{-1}; Ca 1.0 mEq 100 g^{-1}; Mg 0.28 mEq 100 g^{-1}) and low water holding capacity (Barton et al., 2010). Complete description of soil characteristics and climate are provided by Barton et al. (2010). The HFE is a forest plantation experiment that consists of four treatments: control (C), irrigation (I), fertiliser application (F) and irrigation and fertiliser application (IF), replicated in four plots planted with *Eucalyptus saligna* in a randomized complete block design. Full description of the HFE experiment can be found in Hu et al. (2015). We chose this field site because it has been comprehensively characterised as a part of multiple projects including shifts in function and functional microbial communities. Previous studies from this experimental site provided strong evidence that functioning and functional microbial community response to treatments was consistent and easily distinguishable from minor spatial and temporal variability (Hu et al., 2015; Martins et al., 2015). This has provided high quality background data to present our diversity and functional data in an appropriate context.

In addition to the HFE plots, eight sites were sampled in the adjacent natural woodland along a spatial transect *circa* 1.72 km, following a vegetation gradient, to allow estimation of the relative importance of specific management practices compared to the shift from native woodland vegetation to this plantation system. In addition, we hypothesised that different vegetation assemblages and local environmental conditions would be associated with different levels of soil microbial diversity, providing a gradient to further investigate the relationship of diversity with soil functioning. Location and dominant vegetation characteristics of these sites (NW) are listed in Supplementary Table S1.

Soil samples were collected from the 16 plots of the HFE experiment and from the eight sites in the adjacent forest in March 2014. Eight soil cores (2 cm in diameter and 10 cm deep) were collected within ten meters from the edge of each of the four replicate HFE plots, between trees in multiple rows, and from the eight natural sites one meter around trees and peculiar vegetation. The cores were then pooled and homogenized into a composite sample for each plot or site, sieved through a 2 mm mesh, and stored in plastic bags at 4 °C in the dark until analyses.

2.2. Soil properties analyses

Total carbon and nitrogen were measured on a LECO macro-CN analyzer (LECO, St Joseph, MI, USA). Soil pH was measured with a Delta pH-meter (Mettler-Toledo Instruments, Columbus, OH, USA) after mixing 2 g of fresh soil in 10 ml of deionised water. Soil moisture content was measured by oven-drying the soil samples at 105 °C for 24 h. Soil nitrate was extracted from fresh soils (5 g) with 50 ml of 2 M KCl solution (Keeney and Nelson, 1982) by shaking at 150 r.p.m. for 60 min, and the filtered solution was analysed with a SEAL AQ2 Analyzer (SEAL Analytical, Maquon, WI, USA). The extractable phosphate was extracted with Bray's reagent (0.03 M NH_4F and 0.025 M HCl) from air-dried soils (40 °C for 48 h) following the Bray method (Bray and Kurtz, 1945). The filtered solution was analysed with a SEAL AQ2 Analyzer (SEAL Analytical, Maquon, WI, USA), after shaking for 1 min at 170 r.p.m.

2.3. Determination of relative bacterial diversity and taxonomic richness

Total genomic DNA was isolated from 0.25 g of soil using PowerSoil® DNA Isolation kit (MoBio Laboratories, CA, USA) according to manufacturer's instructions, with modifications that a FastPrep bead beating system (Bio-101, Vista, CA, USA) at a speed of 5.5 m s^{-1} for 30 s was used.

The bacterial community was examined using 16S amplicon sequencing. The 16S *rRNA* gene region V3–V4 was sequenced on an Illumina MiSeq sequencer (Illumina Inc. San Diego, CA, USA) by the Next Generation Sequencing Service at University of Western Sydney (Richmond, NSW, Australia). Paired-ends reads of 312 bp were obtained using the primers 341F and 805R (Herlemann et al., 2011). Data analysis was performed using the 'Quantitative Insights Into Microbial Ecology' (QIIME v 1.8.0) software package (Caporaso

Please cite this article in press as: Colombo, F., et al., Impact of forest management practices on soil bacterial diversity and consequences for soil processes, Soil Biology & Biochemistry (2015), http://dx.doi.org/10.1016/j.soilbio.2015.11.029