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Fungal communities are more sensitive indicators to non-extreme soil moisture variations than bacterial communities

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ABSTRACT

Many studies have focused on the impact of intense drought and rain events on soil functioning and diversity, but little attention has been paid to the response of microbial communities to non-extreme soil moisture variations. However, small fluctuations of soil water content represent a common situation that ought to be examined before understanding and deciphering the impact of extreme events. Here, we tested the impact of a decrease in average soil water content and small water content fluctuations in non-extreme conditions on microbial community composition and C mineralisation rate of a temperate meadow soil. Two soil microcosm sets were incubated at high and low constant moisture and a third set was subjected to 4 short dry–wet cycles between these two soil moistures. No robust change in bacterial community composition, molecular microbial biomass, and fungal:bacterial ratio were associated with soil water content change. On the contrary, the fungal community composition rapidly alternated between states corresponding to the high and low levels of soil moisture content. In addition, gross C mineralisation was correlated with soil moisture, with a noteworthy absence of a Birch effect (C over-mineralisation) during the wetting. This study suggests that some fungal populations could coexist by occupying different moisture niches, and high fungal community plasticity would classify them as more sensitive indicators of soil moisture than bacteria. Moreover, under non-stressed conditions, the community composition did not affect metabolic performance so a future decrease in average soil moisture content should not result in a supplemental loss in soil carbon stocks by a Birch effect.

1. Introduction

Microbial community structure could play a role in the ability of communities to realize different functions but also to resist environmental disturbance (Torsvik and Øvreås, 2002). In the context of global change, microbial community structure could be modified and therefore impact ecosystem functioning. Soil moisture is one of the major factors influencing microbial community structure (Brockett et al., 2012) and the shift of microbial community structure is suspected to contribute to important pulses in net mineralisation during the rewetting of dry soils (Borken and Matzner, 2009). But where some authors have suggested that periods of soil water restriction and wetting of dry soil affect microbial community structure through induced osmotic stress and resource competition occasioning selective pressure (Fierer et al., 2003; Castro et al., 2010), others reported no change in microbial community structure (Griffiths et al., 2003).

These contradictory findings in the literature may be due to the specificity of studied ecosystems but also to differences in experimental approaches (Borken and Matzner, 2009). On one hand, the assumed change of the microbial community structure is often made from circumstantial evidence (*e.g.* changes in biomass or activity). On the other hand, the effects of drying and wetting are frequently not distinguished, and "drying soil" and "drought" often merged. Climatic models forecast a decrease of average soil moisture and an intensification of extreme events (IPCC, 2007), but it is still uncertain to what extent the soil system can become unbalanced under these perturbations. While many studies have focused on intense water-stress, little attention has been paid to the response of microbial communities in non-extreme conditions to characterise their stability to natural variability (Meier et al., 2008). However, small fluctuations of soil water content in non-extreme conditions represent a common situation that needs to be

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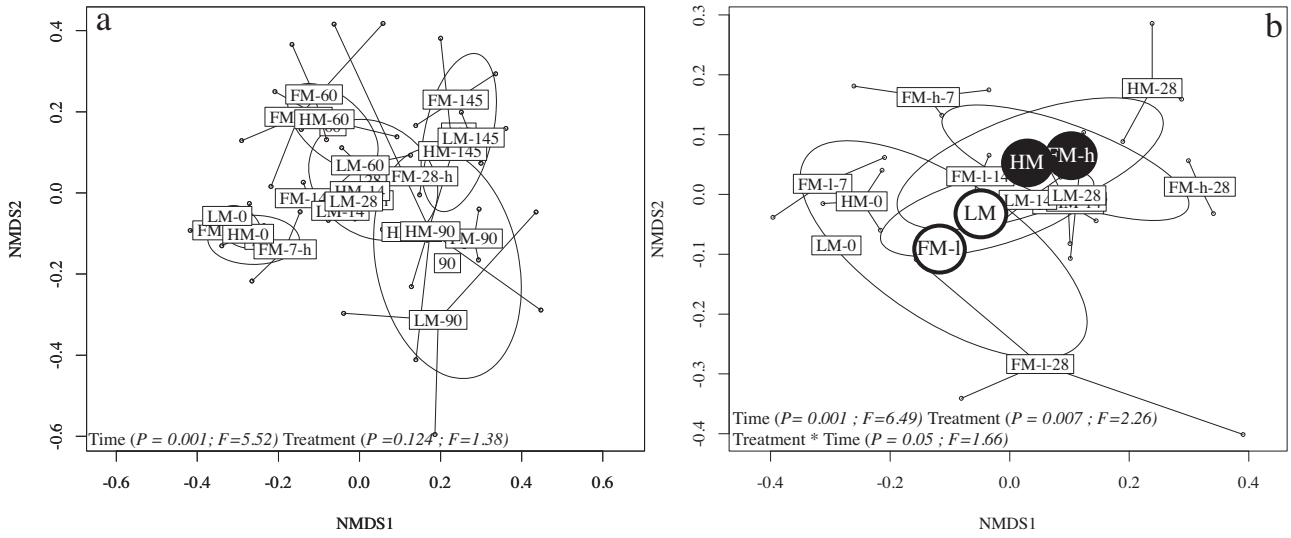

Fig. 1. Nonmetric multidimensional scaling analysis generated from independent triplicates of bacterial ARISA profiles for the three treatments High Moisture (HM), Low Moisture (LM) and Fluctuating Moisture (FM) at the end of drying periods (FM-l) and two days after the wetting events (FM-h). Figure (a) shows that the genetic structure of bacterial community from day 0 to day 145 (number indicates the sampling day) is grouped by sampling date. Figure (b) focuses on the first month when the moisture fluctuated, for the first (7), second (14) and fourth (28) dry–wet cycles.

explored before understanding and deciphering the impact of extreme events.

A limited decrease in soil moisture may be a stressful process for some microorganisms, due to physical constraints that affect bacterial or fungal habitats (Or et al., 2007). At the scale of soil aggregates, the basic units of microbial habitats, drying is heterogeneous and can induce a localized drought that stresses microorganisms; particularly in larger pores (Ruamps et al., 2011). Besides, the decrease of pore connectivity could also modify the microbial community structure by decreasing bacterial mobility and the rate of substrate diffusion (Carson et al., 2010). Fungal communities, on the other hand, are thought to be better adapted to drying than bacteria thanks to hyphal networks which facilitate access to water and nutrients. The question therefore arises as to how fluctuating water content without total drought influences microbial community structure and if the sensitivity of bacterial and fungal community is the same. Beyond the fact that it is still unclear whether a microbial community is associated with a given soil water content, it could be unaltered or alternate between states reflecting the different levels of soil moisture, but also experience another state, reflecting a transient community associated with drying or wetting or both.

The objectives of this study were to examine in non-extreme moisture conditions: (i) whether the composition of bacterial and fungal communities is similar at two contrasting water contents; (ii) how the microbial community composition responds to water content fluctuation within a narrow range of soil moisture; and (iii) whether the microbial community composition can contribute to explain soil functioning. We performed a microcosm experiment consisting of two sets of microcosms kept steadily wet at 64% and 33% Water-Holding Capacity (WHC), respectively. A third set was subjected to 4 dry–wet cycles over a one-month period and subsequently kept steadily at 64% WHC for 4 additional months. At several incubation times, the soil bacterial and fungal communities were characterised by molecular tools (crude DNA quantity for molecular microbial biomass, A-RISA fingerprinting method for structure and qPCR for abundance), and C mineralisation rate was measured through CO_2 quantification.

2. Materials and methods

2.1. Site description and soil characteristics

Soil was sampled from uncultivated meadow bordering cultural field at Versailles, France (mean annual precipitation: 630 mm; mean annual temperature: 10.5 °C); which is an ecosystem with a high ecological importance in urban locations (Manninen et al., 2010). Vegetation (ruderal nitrophilous dominated by *Trifolium repens*) and soil properties of this site are representative of the northern region of France. Fourteen random samples of one kilogram were collected from the topsoil (0–6 cm depth) in August 2010 then combined and homogenized in order to obtain one unique microbial community representative of this ecosystem by lessening spatial heterogeneity. The soil was air-dried, sieved to 4 mm, and vegetation debris, rocks and any fauna visible to the naked-eye were removed before use. The soil is classified as a silty loam (Eutric Cambisol, WRB) with 148 g kg^{-1} of clay, 347 g kg^{-1} of silt and 496 g kg^{-1} of sand. Characterised according to standard methods (http://www.lille.inra.fr/las/methodes_d_analyse/sols), the pH_{H2O} was 6, and there was 20.6 g kg^{-1} of organic C, less than 1 g kg^{-1} of $CaCO_3$, 1.6 g kg^{-1} of total N hence a C/N of 12.6. Water-holding capacity (WHC) was of 0.41 g of water per g of dry soil.

2.2. Experimental design

Microcosms, consisting of 40 g dry soil equivalent in 126 mL glass bottles, were pre-incubated for 6 weeks at 18.5 °C in the dark at desired moisture in order to stabilize the soil microbial communities. Microcosms of high moisture treatment (HM) were maintained at 64% WHC (pF = 2.24), corresponding to the maximum expected microbial activity, and microcosms of low moisture treatment (LM) at 33% WHC (pF = 3.67) by sealing them with parafilm®. Fluctuating moisture treatment (FM) consisted of 4 cycles of air-drying for one week from 64% WHC until about 33% WHC then wetting to 64% WHC by addition of sterile Milli-Q water. As moisture levels were monitored gravimetrically throughout the incubation (Fig. 3a), the quantity of added water