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Strong functional stability of soil microbial communities under semiarid Mediterranean conditions and subjected to long-term shifts in baseline precipitation

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ABSTRACT

We investigated the effect of soil microclimate on the structure and functioning of soil microbial communities in a Mediterranean Holm-oak forest subjected to 10 years of partial rain exclusion manipulations, simulating average drought conditions expected in Mediterranean areas for the following decades. We applied a high throughput DNA pyrosequencing technique coupled to parallel measurements of microbial respiration (R_H) and temperature sensitivity of microbial respiration (Q_{10}). Some consistent changes in the structure of bacterial communities suggest a slow process of community shifts parallel to the trend towards oligotrophy in response to long-term droughts. However, the structure of bacterial communities was mainly determined by short-term environmental fluctuations associated with sampling date (winter, spring and summer) rather than long-term (10 years) shifts in baseline precipitation. Moreover, long-term drought did not exert any chronic effect on the functioning of soil microbial communities (R_H and Q_{10}), emphasizing the functional stability of these communities to this long-term but mild shifts in water availability. We hypothesize that the particular conditions of the Mediterranean climate with strong seasonal shifts in both temperature and soil water availability but also characterized by very extreme environmental conditions during summer, was acting as a strong force in community assembling, selecting phenotypes adapted to the semiarid conditions characterizing Mediterranean ecosystems. Relations of climate with the phylogenetic structure and overall diversity of the communities as well as the distribution of the individual responses of different lineages (genera) to climate confirmed our hypotheses, evidencing communities dominated by thermotolerant and drought-tolerant phenotypes.

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1. Introduction

Microorganisms are responsible for at least half of CO_2 emitted by terrestrial ecosystems to the atmosphere (Bond-Lamberty et al., 2004), representing, therefore, a very big source of CO_2 to the atmosphere. Microorganisms are thus key players in maintaining atmospheric gas concentrations and temperatures within acceptable limits for life. They are also primarily responsible for the degradation and detoxification of many environmental pollutants (Lamar and Dietrich, 1990; Aelion and Bradley, 1991), and we are starting to elucidate the functional role of these communities on the dynamics of soil Carbon (C) (e.g. Aerts, 2006; Waldrop and Firestone, 2006; Balser and Wixon, 2009; Fierer et al., 2007; Curiel Yuste et al., 2010, 2011; Wieder et al., 2013). We further know that microbial diversity is strongly affected by environmental changes, e.g. site productivity (Waldrop et al., 2006), pH (Fierer and Jackson, 2006), plant health and composition (Peay et al., 2010; Curiel Yuste et al., 2012) or drought (Curiel Yuste et al., 2011; Lau and Lennon, 2012). However, the question of whether models should explicitly include microbial diversity to predict ecosystem processes still remains unanswered, given the alleged high functional redundancy of these hyper-diverse communities (Finlay and Fenchel, 2004; Allison and Martiny, 2008; Wieder et al., 2013).

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Because climate affects both soil microbial activity (e.g. Rey and Jarvis, 2006; Curiel Yuste et al., 2007) and soil microbial community structure (e.g. Zogg et al., 1997; Castro et al., 2010; Curiel Yuste et al., 2011) it is crucial to understand how the ongoing changes in climate may affect the structure and functioning of soil microbial communities. Mediterranean-type ecosystems, where water availability is the most important environmental constraint due to the combination of high summer temperatures and low rainfall (Specht and Moll, 1983; Larcher, 2000) are expected to be extremely vulnerable to the effects of climate change (Schroter et al., 2005). Global circulation and regional models predict an increase in temperatures in the Mediterranean Basin during the present century, while rainfall is predicted to decrease and become more irregular (Gibelin and Deque, 2003; IPCC et al., 2007) which makes Mediterranean ecosystems an exceptional playground to test how microbial communities would evolve under more arid conditions.

Since it is well known that drought strongly limits the physiological performance of microbes and the diffusion of nutrients in the soil pore space (e.g. Davidson and Janssens, 2006; Sardans and Penuelas, 2005, 2008), ultimately affecting soil metabolic activity and soil CO_2 emissions (Curiel Yuste et al., 2007; Asensio et al., 2007), it might be expected that the predicted climatic changes might chronically affect the structure and functioning of soil microbial communities. However, the strong functional stability shown by soil microbial communities (Allison and Martiny, 2008; Wieder et al., 2013) which includes the components of resistance (the degree to which a community is insensitive to a disturbance) and resilience (the rate at which a community returns to pre-disturbance conditions) (see Shade et al., 2012) might help counteracting possible climate-driven pressures. A growing body of studies are experimentally evidencing this functional and structural stability against long-term climatic changes (e.g. Williams and Rice, 2007; Zul et al., 2007; Cruz-Martínez et al., 2009; Landesman and Dighton, 2010; Curiel Yuste et al., 2010; Curiel Yuste et al., 2011). This high functional stability is mainly a cause of the high functional redundancy of these hyper-diverse communities (Schimel, 2001), their physiological plasticity to quickly respond to environmental changes (e.g. Placella et al., 2012) and their enormous potential to acquire new genes with respect to other kingdoms (Whitman et al., 1998; Achtman and Wagner, 2008) through recombination, mainly in the form of homologous recombination (Fraser et al., 2007) or horizontally transfer genes (HGT) (Doolittle and Papke, 2006). However, we still need to gather experimental evidences to properly test to what extent soil microbial communities are functionally stable under the adaptive pressures associated with climate-change.

Here we present the results of a study designed to explore how soil bacterial communities respond to both short-term (three bioclimatically contrasting times of the year) and long-term (10 years of treatment under partial precipitation exclusion) climatic variations. Taxonomic composition and structure of soil bacterial community was studied at a Mediterranean site where experimental precipitation exclusion has reduced soil moisture by up to 25% (10 years average reduction of 13%) with respect to controls during 10 years (Ogaya and Penuelas, 2007; Ogaya et al., 2011). We used large-scale pyrosequencing of partial 16S rRNA genes to study the structure (taxonomic composition and the relative presence of different taxons within the community) of soil bacterial communities. This technique has recently emerged as a powerful tool that has discovered a vast microbial diversity in soils and a large heterogeneity of microbial communities across biomes (Roesch et al., 2007; Jones et al., 2009; Lauber et al., 2009), land uses (Acosta-Martinez et al., 2008; Will et al., 2010; Nacke et al., 2011), soil horizons (Will et al., 2010) or forest successional stages (Curiel Yuste et al., 2012). This diversity far exceeded the values obtained using the commonly used fingerprinting techniques, such as terminal restriction fragment length polymorphisms (TRFLP; see. Curiel Yuste et al., 2011). These results were compared with parallel measurements of SOM decomposition and its response to temperature in order to assess the functional performance of the microbial community. The general objectives of this study were to understand how soil microbial communities respond to changes in climate. More in detail our objectives were to assess the degree of structural and functional stability (resistance and/or resilience) of soil microbial communities to environmental changes associated with climatic fluctuations at synoptic time scales (winter, spring and summer) and to long-term shifts in baseline precipitation.

2. Materials and methods

2.1. Experimental site

Soil samples were collected from the natural Holm-Oak (*Quercus ilex* L.) forest of the Prades Mountains, located in Southern Catalonia (North-Eastern Iberian Peninsula) (41° 21′N, 1° 2′E, 950 m altitude), on a south-facing slope (25%). The soil is a Dystric Cambisol over Paleozoic schist. Its depth ranges between 35 and 100 cm, and Horizon A occupies the 25–30 cm upper layer. The average annual temperature is 12.8 °C and the average annual rainfall is 658 mm. Summer drought is pronounced and usually lasts for 3 months. The vegetation is a dense forest dominated by *Q. ilex* as a dominant tree with abundant presence of *Phillyrea latifolia* L. and *Arbutus unedo* L. and other evergreen species well adapted to drought conditions (*Erica arborea* L., *Juniperus oxycedrus* L., *Cistus albidus* L.), and occasional individuals of deciduous species (*Sorbus torminalis* (L.) Crantz and *Acer monspessulanum* L.). Eight 15 × 10 m plots were established at the same altitude (930 m above sea level) along the slope in 1999. Four of the plots received the drought treatment and the other four were used as control. The drought treatment consisted of partial throughfall exclusion by suspending PVC strips with wood sticks at a height of 0.5–0.8 m above the soil surface. Strips covered approximately 30% of the total plot surface. Two plastic strips of 14 m long and 1 m wide were placed along the drought treatment plots from the top until the bottom part. A 0.8–1 m deep ditch was excavated along the entire top edge of the upper part of the treatment plots to also intercept runoff water supply. The water intercepted by strips and ditches was conducted outside the plots, below their bottom edge. This drought treatment reduced soil moisture of drought plots by up to 25% (10 years average reduction of 13%) with respect to controls during 10 years, being the reduction larger during wet seasons and lower during dry seasons (Ogaya et al., 2011). For more information about the experimental site, equipment and drought treatment see Ogaya and Penuelas (2007) and Curiel Yuste et al. (2011).

2.2. Soil organic matter decomposition and temperature sensitivity

Soil cores, 4.5 cm diameter and 10 cm depth, were collected using a stainless steel core soil sampler. Samples were collected during three different periods of the year, winter (cold and moist with limited vegetation photosynthetic activity), spring (warm and wet with maximum vegetation photosynthetic activity) and summer (very warm and very dry, with minimum vegetation photosynthetic activity). Three samples were randomly collected within each plot for each date-treatment (winter, spring and summer in control and drought plots). In total 72 soil samples were collected throughout the year, 24 samples per period (three periods), 12 for control and 12 for drought treatment. Each individual soil sample was sieved (2 mm) and analyzed for humidity (gravimetrically), soil organic carbon and microbial biomass (Curiel Yuste et al., 2011).

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