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Frequent-wildfires with shortened time-since-fire affect soil microbial functional stability to drying and rewetting events

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ABSTRACT

This study analysed the resistance and resilience to 1 and 4 successive drying and rewetting (D/Rw) cycles of some processes driven by soil microbes, when soils have previously suffered from frequent wildfires with both short and longer time since fire. We hypothesised that frequent and recent wildfires destroying sensitive microbial species together with resource availability (C and N) might hamper the stability of microbial functions against droughts especially narrow processes. Our findings showed that microbial respiration was stable against frequent and recent wildfires (no additional change), but not against drying and rewetting events. Indeed, microbial respiration increased after 1 D/Rw cycle mainly attributed to a loss of 18% of microbial active biomass (not resistant) and decreased fourteen days after rewetting the dry soil (not resilient). Even more, 4 D/Rw cycles immediately brought back this activity at lower level (i.e. not resistant) concomitantly with a loss of metabolic quotient (qCO_2) especially with frequent and recent wildfires. Contrariwise, some specific activities such as cellulase activities and also catabolic level physiological profiles of cultivable bacteria (Biolog) were heavily impacted by the combination of frequent and recent wildfires and droughts. Alkaline phosphatases, which are synthesised by many bacterial and fungal species, increased at short term (i.e. not resistant) indicating an increase in microbial phosphorus demand for a long time (i.e. also not resilient). In this study, addition of unlimited availability of resources as cellulose and ammonium nitrate, suppressed the effect of wildfire regimes on functional stability of microbial communities. Hence, we concluded that resource availability poorly explained the stability against stresses of microbial processes, mainly driven by hydric stress, except for alkaline phosphatase activities which were depressed by an experimental fertilisation.

1. Introduction

The high biodiversity of Mediterranean regions is due to the diversity of geological and edaphic contexts, a strong heterogeneity of climatic conditions, the importance of agro-pastoral practices for centuries and wildfires. The combined contribution of these factors have created a strong spatial and temporal heterogeneity of landscapes and favoured various evolutionary strategies and adaptations (Blondel and Aronson, 1995). However, socio-economic changes from the early 19th century, especially rural exodus and industrialisation, have led to changes in historical wildfire regimes and frequency and intensity of climatic stresses (Pausas and Fernández-Muñoz, 2011). Indeed, the abandonment of agricultural lands following the rural depopulation, resulted in the closure of open areas which increased the size of fires (Schelhaas et al., 2003) and thus locally the fire frequency (Pausas, 2004) that doubled in Western Mediterranean Basin (Pausas and Fernández-Muñoz, 2011). Currently, the observation of an increase in drought-driven wildfire is being extended to other regions of the world (Dubinin et al., 2001). Moreover, global warming circulation models predict changes in spatial and temporal patterns of precipitation for the next decades, including shifts in the frequency and intensity of drought events and heat-waves (IPCC, 2007; Good et al., 2008), while recent studies already demonstrated its increase (e.g. Della-Marta et al., 2007). This is expected especially to be true within the current context of Mediterranean (Gibelin and Déqué, 2003), where surface soils undergo periods of prolonged drying,

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added to heat-wave events and interrupted with relatively rapid rewetting events. Shifts in historical wildfire regimes through a disruption of the existing equilibrium and an impoverishment of available resource (Guénon et al., 2011b), could lead to a decrease in ability of soil microbes to withstand climate stress (i.e. resistance) and recover from it (i.e. resilience), and thus could affect some ecosystems services (i.e. turn-over of SOM and dynamic of nutrient cycles).

Among all European regions, the Mediterranean appeared most vulnerable to climate changes (Schröter et al., 2005). This is predicted to be partly a consequence of a water shortage and an increase in fire frequency which i) alter both the plant community composition and richness (Schröter et al., 2005), ii) decrease the amount and quality of soil resources (nutrients and organic matter) affecting microbial biomass and diversity (Guénon et al., 2011a), and iii) decrease mineralising activities of soil microbial communities (Acea and Carballas, 1996; Sardans and Peñuellas, 2005; Sardans et al., 2008). Highly diversified and functionally redundant (Torsvik and Øvreås, 2002; Allison and Martiny, 2008), microbial communities are one of the major components of soil quality that ensure the sustainability of ecosystem services (Coleman and Whitman, 2005). Recently, Orwin et al. (2006) stressed the necessity to consider the functional stability of soil micro-organisms against disturbances because of their critical role in ecosystem processes such as turn-over of SOM and soil C-sequestration (Six et al., 2006), nutrient cycling, and also plant productivity (Wardle, 2002).

Fire induces the death of sensitive species to soil heating (Hart et al., 2005) which in turn, can promote the proliferation and activity of surviving species, reducing competition and facilitating their access to resources. This can lead to changes in diversity and create a new community structure particularly well adapted to stresses and having a significant functional stability (Schimel et al., 1999; Aarts and Nienhuis, 1999). Alternatively, the loss of sensitive species can lead to an impairment of soil functions mediated by micro-organisms (Schimel et al., 1999). The population strategy of micro-organisms, in other words the efficiency of resource use and the physiological strategy of energy allocation (Schimel et al., 2007), is also a potential factor that can control microbial stability. In soil microbial communities, as described for plants by Grime (2001), species with slower growth rate (K strategists) tend to be resistant but not resilient to stress, while fast growing species (r strategists) tend to be resilient but not resistant to stress (Gerson and Chet, 1981; Schimel et al., 2007).

Beside changes in community composition, fire is known to decrease C and N content and to increase the recalcitrant fractions of soil organic matter (Knicker, 2007). Some abiotic factors such as nutrient availability or the amount of carbon and its availability, can control microbial stability (Moore et al., 1993; Wardle, 1998). Prior to disturbance, soil resources are assumed to provide the energy needed to produce osmolytes and thus avoid dehydrating and dying (Harris, 1981), and to rebuilt the damage caused by a stress (Aarts and Nienhuis, 1999).

The aim of this study was to assess the effects of changes in wildfire regimes in Mediterranean region on the stability of microbial functions against an increase in the frequency of drying/rewetting events. Drying/rewetting cycles are usual stressor in Mediterranean soils (Schimel et al., 2007) and reported as major driving factor into the turn-over of soil microbial communities (Fierer and Schimel, 2002; Orwin et al., 2006). Our first hypothesis is that activities of microbial communities affected by frequent and recent fires (Guénon et al., 2011b) may be less resistant and/or resilient to an intensification of climate stresses. To test this first hypothesis, we assessed both resistance and resilience of microbial activities to experimental drying and rewetting events. We compared a low hydric stress history (i.e. 1 cycle) *versus* an intensive stress history (4 cycles), when microbial communities have previously suffered from frequent wildfires (1 fire by decade) in comparison to infrequent wildfire regime (1 fire by 2 decades) and also, after both short and longer time of recovery (4 and 17 years of time since the last fire). Some microbial activities defined as ‘broad’ processes resulting from the activity of a multitude of redundant species (i.e. basal and microbial biomass assessed by glucose induced respiration, FDA hydrolases and alkaline phosphomonoesterases) should be more stable against frequent wildfires and stresses (Malchair et al., 2010). Contrariwise, specialised or ‘narrow’ processes (sensu Schimel, 1995) such as C-substrate utilisation profiles and cellulase activities were used to measure active components of some specific microbial groups “(i.e. cultivable microbes, mainly bacteria for C-substrate utilization profiles, and fungi for cellulase activities)” and should be more vulnerable. Moreover, soil resource availability is expected to control microbial stability against drying/rewetting cycles (Schimel et al., 2007). Our second hypothesis to be tested in our study is that repeated fires, destroying the organic matter and volatilising nutrients, would limit resource availability and thus the energy required to protect or repair damages caused by stress. For this reason, we added C and N to soils in laboratory, simulating a non-limiting resource that is assumed to optimise the levels of resistance and resilience of microbial functions.

2. Material and methods

2.1. Study area, wildfire history and soil sampling

The study was conducted in Var, SE France, in the south-eastern part of the mountain range of Les Maures. The region is characterised by a Mediterranean climate with dry, hot summers combined with wet and temperate winters. The mean annual precipitation is 920 mm (1962–2003) with a high inter-annual variability (300–1800 mm). A persistent drought was recorded during the 2003–2007 period (640 mm per year) with a dramatic drop in 2007 (430 mm), the year of soil sampling. The average monthly temperature varies from 7 °C in January to 22 °C in July, with mean annual temperatures close to 14 °C.

Burned areas were mapped using a series of aerial pictures spanning a 57-years period from 1950 to 2007 and public fire databases. This mapping allowed us to reconstitute the history of the wildfire regimes over this period (Guénon et al., 2011b). Twelve independent plots (minimum to 200 m^2) were selected and four different burning histories or wildfire regimes were identified (Table 1).

Soils of these sites were developed on migmatitic gneiss (crystalline siliceous rock) as parent rock. Soils are classified as Dystric Leptosol (IUSS Working Group WRB, 2006) with only A- and CR-horizons present. Under a thick litter layer (1–3 cm), there was a 5-cm A horizon, relatively rich in organic matter as shown by its brown colour, and poor in coarse particles (>2 mm, 10–30%) in comparison to the C horizon (20–30 cm depth). The main chemical and microbiological characteristics of the soils are presented in Table 2 (Guénon et al., 2011a, 2011b). Moreover, these sites present similar exposition (SE–SW), slope (10–40 percent), altitude (60–360 a.s.l.) and corresponded to different plant successional states of the same vegetation chronosequence with Cork oak as the dominant plant species and hence, directly related to the time after the last fire and fire recurrence. Thus, in this work, we may consider that fire frequency was the major influencing factor. Vegetation structure and dominant species are given in Table 1.

For each plot, after removing the litter layer from the soil surface, 5 soil cores 20 × 20 cm, were randomly taken in February