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Fire modulates ecosystem functioning through the phylogenetic structure of soil bacterial communities

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ABSTRACT

The ecosystem functions performed by soil microbial communities can be indirectly altered by ecological disturbances that deeply modify abiotic factors. Fire, a widespread disturbance in nature, is well known to alter soil abiotic properties but we still ignore how these shifts are translated into changes in the structure of soil microbial communities and the ecosystem functions they deliver. The phylogenetic structure of soil bacterial communities has been shown to be a good predictor of ecosystem functioning, and therefore we used it as a measure linking the temporal variation of soil abiotic properties and ecosystem functions caused by an experimental fire in a Mediterranean shrubland. Fire immediately favoured a basal phylogenetic clade containing lineages that are able to thrive with high temperatures and to take advantage of the post-fire nutrient release. Later changes in the phylogenetic structure of the community were dominated by phyla from another basal clade that show competitive superiority coinciding with high levels of oxidizable carbon in soil. The phylogenetic structure of the bacterial community significantly explained not only microbial biomass, respiration and specific enzymatic activities related to C, N and P cycles but also the community-weighted mean number of 16S rRNA gene copies, an integrative proxy of several functions. While most of the ecosystem functions recovered one year after the fire, this was not the case of the structure of bacterial community, suggesting that functionally equivalent communities might be recovering the pre-disturbance levels of ecosystem performance.

1. Introduction

Microbial communities are an essential component of ecosystems, involved in many processes that impact the biogeochemical cycles and ecosystem productivity (Van der Heijden et al., 2008; Bardgett and van der Putten, 2014). Soil bacteria are an extraordinarily diverse group of organisms with enormous functional capabilities that are fundamental for ecosystem performance, including mineral weathering, primary production and organic matter decomposition (Van der Heijden et al., 2008; Schimel and Schaeffer, 2012; Bardgett and van der Putten, 2014). Soil abiotic factors are crucial to predict microbially-mediated ecosystem processes including nitrification, denitrification or N and C mineralization (Graham et al., 2014, 2016; López-Poma and Bautista, 2014), but these processes can be better predicted by incorporating measures of microbial community structure and diversity (Powell et al., 2015; Graham et al., 2016). An increasing body of evidence suggests that adding a phylogenetic component (i.e. taking into account the species evolutionary relationships) to measures of community composition and diversity improves the prediction of ecosystem functions (EF), since common evolutionary history defines shared functional abilities (Maherali and Klironomos, 2007; Cadotte et al., 2008; Srivastava et al., 2012). This statement holds true for soil bacterial communities (Gravel et al., 2012; Venail and Vives, 2013; Pérez-Valera et al., 2015), as bacterial traits that are relevant both to community assembly and EF such as optimum pH for growth or response to different organic sources are phylogenetically conserved (Goberna and Verdú, 2016; Morrissey et al., 2016). Most of these traits are genetically complex, a characteristic that has been linked to phylogenetic trait conservatism (Martiny et al., 2015).

Wildfires alter the functioning of forest ecosystems through changes in their biotic and abiotic components (Certini, 2005; Hart et al., 2005; Mataix-Solera et al., 2009; Keeley et al., 2012). Fire exposes soil microbial communities to extremely high temperatures and shifts their abiotic environment, thus altering their taxonomic and phylogenetic composition (Pérez-Valera et al., 2018). Fire tends to favour those lineages with heat-resistance capacities (e.g. spore-formers) and/or

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potential fast-growth strategies (Smith et al., 2008; Bárcenas-Moreno et al., 2011; Ferrenberg et al., 2013). Since microbial traits conferring capabilities to cope with fire such as spore formation exhibit a significant phylogenetic signal, i.e. closely related taxa tend to be more similar in their trait values (Goberna and Verdú, 2016), changes in the community may be phylogenetically structured (Pérez-Valera et al., 2017). That is to say, the probability of taxa to survive and thrive after fire are determined by their evolutionary history. From an ecological perspective, fire also alters the competitive relationships among bacterial community members by shifting the availability of soil resources, mainly organic matter, nutrients and water (Pérez-Valera et al., 2017). Such variations in the competitive interactions can shift the dominance of main lineages, ultimately conditioning the overall microbial productivity (Knelman and Nemergut, 2014; Pérez-Valera et al., 2015). Indeed, fire-induced shifts in the communities of soil microbes change microbial biomass, total activity and the rates at which organic compounds are decomposed and hydrolysed (Hernández et al., 1997; Choromanska and DeLuca, 2002; Fontúrbel et al., 2012; Goberna et al., 2012). Recent evidence suggests that changes in ecosystem functions rapidly occur in the earliest stages of the secondary succession, in line with changes in soil properties, emphasizing the need of studies focused on the post-fire dynamics on the scale of months to years (Knelman et al., 2017).

Incipient evidence exists that the phylogenetic composition of soil bacterial communities in Mediterranean shrublands is resilient to fire (Pérez-Valera et al., 2018), but the effects of post-fire community assembly on ecosystem performance have not been explored. By assembling bacterial communities through immigration experiments, Tan et al. (2012) showed that the initial phylogenetic relatedness among lineages determines the final composition of assembled communities. In these experimental communities, phylogenetic diversity was systematically related to ecosystem functioning, but the assembly history determined EF depending on the identity of community members (Tan et al., 2012). For instance, the assembly history of *Staphylococcus* communities determined both bacterial productivity and decomposition, while that of *Bacillus* communities influenced only productivity. These enticing experiments suggest that surveying the relationship between microbial diversity and EF should incorporate phylogenetically-informed metrics that take taxon identity into account. This is the case of the measures of phylogenetic community structure, such as that proposed by Pillar and Duarte (2010), which is able to identify the lineages and the phylogenetic nodes associated with environmental gradients (Duarte et al., 2016) and predict microbially-driven EF (Pérez-Valera et al., 2015). In addition, by showing the differential response of bacterial productivity and decomposition to community composition, the experiments by Tan et al. (2012) encourage using a battery of microbial indicators of ecosystem functioning. Community-level EF indicators that have been traditionally used include microbial biomass, activity, carbon use efficiency (i.e. organic carbon transformed into microbial biomass), as well as the rates of organic matter decomposition and enzymatic hydrolysis of carbon, phosphorous and nitrogen-containing organic compounds (Zak et al., 2003; Maestre et al., 2012; Goberna et al., 2012; Navarro-Cano et al., 2014). Recent studies have shown that the rRNA operon copy number in bacterial genomes might predict traits related to EF, since the copy number seems to be associated with potential microbial growth and sporulation efficiency and negatively related to carbon use efficiency and protein yield (Lauro et al., 2009; Yano et al., 2013; Nemergut et al., 2016; Roller et al., 2016). Indeed, Nemergut et al. (2016) found a generalizable pattern of successional changes in the average rRNA operon copy number calculated at the community level across a variety of systems, including post-fire ecosystems. In addition, they also suggested that the copy number trait might scale over multiple levels of biological organization (i.e. from cells to communities) (Nemergut et al., 2016). Therefore, it could be expected that the immediate burst of nutrients caused by fire (Certini, 2005) leads to the dominance of bacteria adapted to high resource availability showing high rRNA operon copy numbers, but low carbon use efficiency and reduced rates of enzymatic activity.

We speculated that the post-fire succession of the phylogenetic composition of soil bacterial communities would drive the ecosystem functions related to microbial productivity, decomposition and nutrient cycling. To test this hypothesis, the phylogenetic structure of soil bacterial communities was analysed, and several microbial indicators of ecosystem functioning measured immediately before and during one year after an experimental fire in a Mediterranean ecosystem. In addition, it was tested whether i) soil abiotic properties that are altered by fire drive the recovery of the phylogenetic structure of soil bacterial communities, and ii) the phylogenetically structured shifts in the soil bacterial communities determine the post-fire recovery of indicators of microbial biomass, growth rate, carbon use efficiency, organic matter decomposition, as well as three enzymatic activities related to carbon, phosphorous and nitrogen cycling.

2. Material and methods

2.1. Experimental design

This study was carried out in a Mediterranean ecosystem that was exposed to an experimental fire in April 2009. Temperature during the fire was measured using thermocouples and reached on average 611 °C (with a range between 423 and 719 °C, n = 3) at 50 cm over the soil surface, 338 °C (17–670 °C, n = 9) on the soil surface and 106 °C (39–279 °C, n = 8) at 2 cm deep. The vegetation, a dense shrubland dominated by *Rosmarinus officinalis* L., was immediately burned out. Fire severity was low, as soil organic matter remained unaltered after 1 day (see below) (Keeley, 2009). Plant cover recovered to ca. 10% four months after the fire, a level that remained constant during the study period. Soils were Humic Leptosols (FAO–ISRIC–IUSS, 2006), mean annual rainfall 446 mm and temperature 13.7 °C. Further details about the site, experimental fire and sampling can be found in Goberna et al. (2012). Briefly, surface soil samples (0–2 cm) were collected from ten 1 × 1 m plots located from one to three m apart from each other within a 150 m^2 area. A single soil sample (ca. 300 g) was taken per plot and sampling point, thus making a total of seventy samples (10 plots × 7 time points) that were collected immediately prior to fire and 1 day, 1 week, 1 month, 4.5 months, 9 and 12 months after the fire. Pre-fire samples were considered as the unburned control to minimize the environmental and spatial heterogeneity that results from sampling an adjacent unburned area. Variations with time in the climatic conditions throughout the experiment were accounted for in the statistical analyses (see below). Samples were transported to the laboratory on ice, sieved (2 mm) and stored at 4 °C. Several physical and chemical variables were analysed using standard procedures, as in Goberna et al. (2012).

2.2. DNA extraction and sequencing

A thorough description of DNA extraction, purification and pyrosequencing procedures is given in Pérez-Valera et al. (2017). Briefly, DNA from soil samples was extracted within the first 24 h after sampling from ca. 0.25 g of soil with the PowerSoil DNA isolation kit (MO BIO Laboratories, Carlsbad, California). After quality check of DNA fragments by electrophoresis in 1% agarose gels run in 0.5 × Tris–acetate–EDTA buffer, 16S rRNA genes were PCR amplified using the universal bacterial primers 8F (5′-AGAGTTTGATCCTGGCTCAG-3′; Turner et al., 1999) and 534R (5′-ATTACCGCGGCTGCTGGC-3′; Muyzer et al., 1993). Each sample included a 454-sequencing adaptor (5′-CCA TCTCATCCCTGCGTGTCTCCGACTCAG-3′) and a barcode in its 5′-end selected from Hamady et al. (2008). Amplicons were purified and sequenced using the Roche 454 GS-FLX platform. Raw DNA sequences were processed in order to remove short (< 200 bp) and low-quality sequences, including those with ambiguous base calls or with

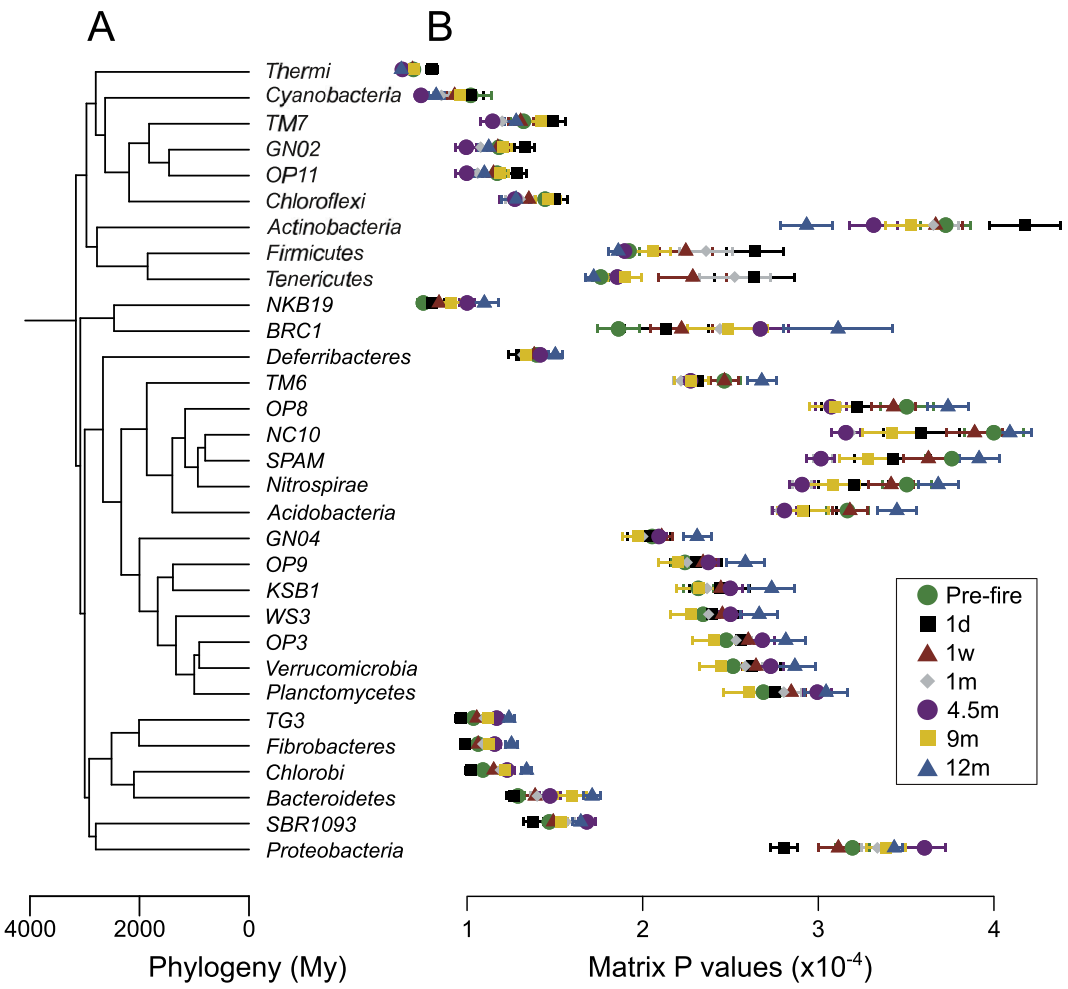

Fig. 1. A) Phylogenetic relationships and B) scores per sampling time of main bacterial phyla in matrix P. Matrix P scores are obtained after averaging OTU values per phylum and sample and indicate the contribution of each taxa to the phylogenetic composition of the community. Taxa with elevated scores in matrix P are those coexisting in the community with closely-related and high-abundance OTUs. Bars indicate SE.

homopolymers (> 6 bp). Chimeric and singleton sequences were excluded from the analysis. A total of 3474 operational taxonomic units (OTUs) were obtained after grouping sequences at the 97% sequence similarity level. The relative abundance of OTUs was then calculated as the ratio between absolute reads per OTU and the total number of sequences per sample. As 16S rRNA gene copies range from 1 to 15 in different bacterial OTUs, it is necessary to control for such variation to accurately estimate the relative abundance of different OTUs (Kembel et al., 2012). The number of 16S rRNA gene copies for each OTU was estimated using ancestral state reconstruction methods following Kembel et al. (2012) and used it to correct the relative abundance of each OTU in the subsequent analyses. This correction was not used to calculate community-weighted means of rRNA operon copy numbers to avoid circularity (see details below).

2.3. Phylogeny reconstruction and phylogenetic community structure

Sequences representative of each OTU were PyNAST-aligned, manually checked, and the hypervariable regions removed (Pérez-Valera et al., 2017). To deal with the uncertainty produced by reconstructing phylogenies from short DNA sequences, i) the topology of the basal nodes was constrained according to the OTU taxonomy and the SILVA database (Release 108, (Quast et al., 2013)) and ii) three phylogenetic trees were constructed using the maximum likelihood algorithm in RAxML 7.3 (Stamatakis, 2006). All trees were calibrated so as branch lengths represent chronological time (in million years) by using the function *chronos* in APE 4.0 (Paradis et al., 2004) for R (R Core Team, 2017). Such a function uses a penalized likelihood approach to estimate the divergence times through a "correlated" model, which allocates similar diversification rates to closely-related tips. Phylogenetic trees were calibrated by using eight dated nodes at the phylum-level (Table S1) according to Sheridan et al. (2003) and Marin et al. (2017).

The phylogenetic structure of soil bacterial communities was estimated through the phylogenetic fuzzy-weighted method originally described by Pillar and Duarte (2010). Unlike other phylogenetic community structure metrics (i.e., Unifrac, Net Relatedness Index), fuzzy weighting is not blind to the identity of each taxon and then it can discern communities with similar levels of phylogenetic clustering but composed by different lineages (Pillar and Duarte, 2010). This procedure calculates an OTU × plot matrix (matrix P) that describes the phylogenetic composition of the community by taking into account the abundance and the pairwise phylogenetic relatedness of each OTU with every other OTU in the community. The less diverse the phylogenetic neighbourhood of an OTU in a sample, the higher its score in matrix P. Therefore, taxa with the highest scores in matrix P will be those coexisting with closely-related and high relative abundant neighbours. Second, the method reduces the dimensionality of matrix P through principal coordinate analysis (PCoA) using Bray Curtis dissimilarity matrices and extracts the loadings of each taxon (i.e. OTU) to the principal coordinates of phylogenetic structure (PCPS). We separately calculated the contribution of each lineage to the first (PCPS1) and

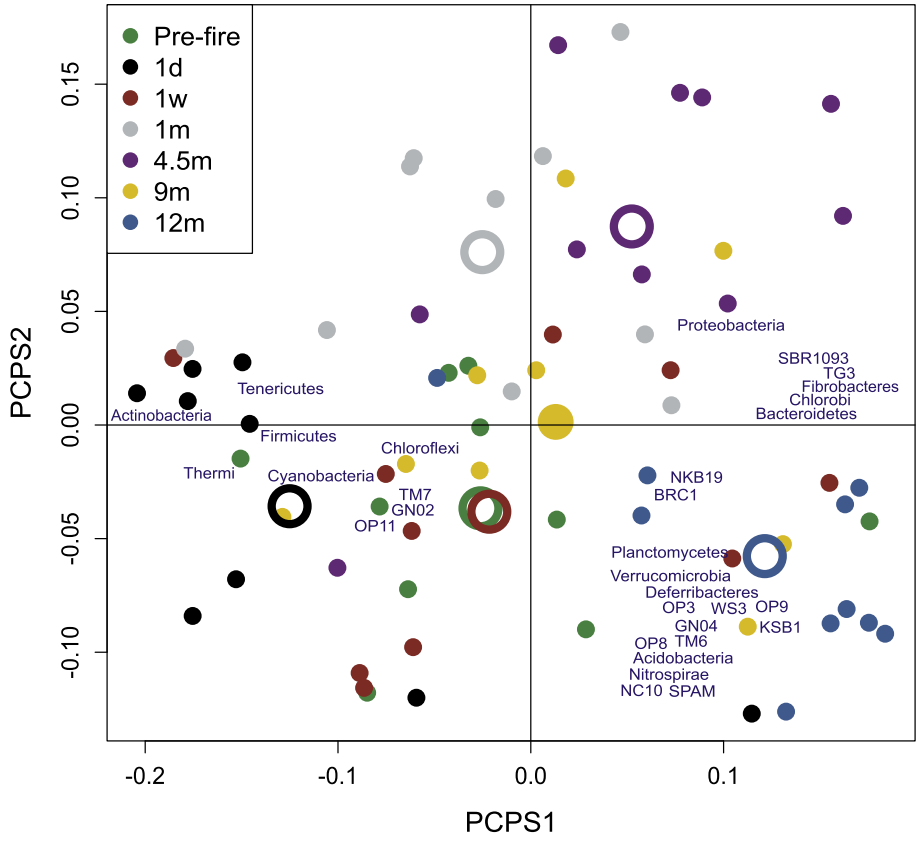

Fig. 2. Ordination biplot of the two first principal coordinates of phylogenetic structure (PCPS) of bacterial communities before and after an experimental fire. Taxon names indicate loading factors of bacterial phyla on PCPSs. Open circles represent average PCPS scores per time point.

second (PCPS2) axes of the PCoA by averaging the OTU loadings in each axis *per* phylum. While PCPS1 accounts for differences at the basal nodes of the phylogeny, PCPS2 and all subsequent axes tend to catch shallower phylogenetic levels in the tree (Duarte et al., 2012, 2016). Then, by using only two PCPS axes we are capturing phylogenetic composition at a broad taxonomic scale, which is the relevant scale for evolutionarily conserved functions (Martiny et al., 2015; Goberna and Verdú, 2018). Both matrix P and PCoA calculations were run with the PCPS package for R (Debastiani and Duarte, 2014).

2.4. Microbial indicators of ecosystem functioning

Five soil biochemical or physiological variables acting as indicators of ecosystem functions (*sensu* Hooper et al., 2005), were measured as in Goberna et al. (2012). Microbial biomass C (MBC) was quantified by the fumigation-extraction procedure as a surrogate of total soil microbial biomass. Basal respiration was measured during a 28 d aerobic incubation experiment at 28 °C in darkness as an indicator of the activity of decomposers in mineralizing organic C into CO_2. Enzymatic activities related to C (β-glucosidase), P (alkaline phosphatase) and N (urease) cycling were determined colorimetrically and used as indicators of specific microbial activities. Two indices, the microbial quotient (microbial biomass C per unit organic C) and the metabolic quotient (qCO_2, respired C per unit microbial biomass) were respectively calculated as indicators of C use efficiency and C conservation efficiency (Anderson and Domsch, 1990; Wardle and Ghani, 1995). Finally, we estimated the community-weighted mean of the rRNA operon copy numbers as an integrative proxy of several ecosystem functions (potential microbial growth, sporulation efficiency and carbon use efficiency; Lauro et al., 2009; Yano et al., 2013; Fierer et al., 2014; Nemergut et al., 2016; Roller et al., 2016). The community-weighted mean 16S rRNA copy number was calculated following the formula by Garnier et al. (2004) as follows:

$$Community - weighted\ mean = \sum_{i=1}^{S} Pi \times trait_i$$

where S is taxon richness, Pi is the relative abundance of each taxon i, and trait i is the trait value of species i. In our case, the trait value is the number of 16S rRNA copies per bacterial OTU reconstructed based on phylogenetic methods (Kembel et al., 2012).

The full dataset used here corresponds to soil physical, chemical, biochemical and pyrosequencing data from 10 plots before and during one year after the fire. Some data have been already published as follows. Goberna et al. (2012) used soil abiotic variables to explain the short-term (1 week) shifts in the genetic profiles of fungi, bacteria and archaea. Pérez-Valera et al. (2015) used all data corresponding to the pre-fire plots to analyse the power of several metrics of diversity as predictors of ecosystem functions. Finally, Pérez-Valera et al. (2017) used network analysis to interpret the mechanisms of community assembly in the post-fire scenario. Here, all the variables are explored together throughout the study period seeking for the immediate changes and recovery trends of ecosystem functions mediated by the phylogenetic structure of the soil bacterial communities.

2.5. Statistical analyses

The OTU composition and geographic distance matrices across plots in the pre-fire samples were correlated through Mantel tests in the ADE4 package for R (Mantel, 1967; Dray and Dufour, 2007), finding no spatial autocorrelation in the bacterial community composition (see Pérez-Valera et al. (2015) for further details).

The post-fire succession of the soil bacterial phylogenetic community structure was evaluated by testing the effect of time since fire on the two principal coordinates of phylogenetic structure (PCPS) using

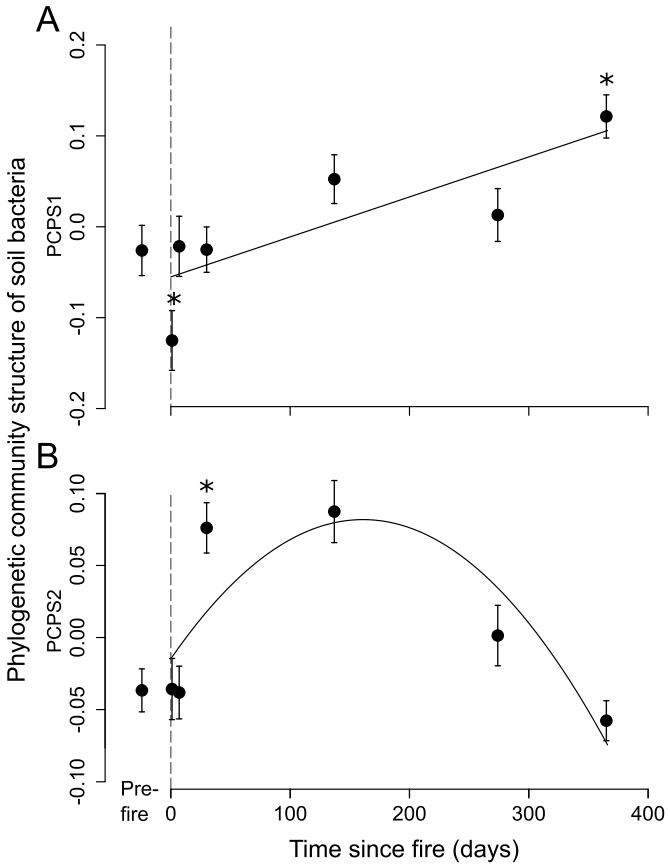

Fig. 3. Succession of the phylogenetic structure of soil bacterial communities before and after an experimental fire considering A) PCPS1 and B) PCPS2. Experimental fire was performed at Time 0. Solid lines indicate linear (PCPS1) and quadratic (PCPS2) regressions as a function of time since fire. Bars indicate SE for n = 10. Asterisks indicate significant differences between each time point and the pre-fire level after accounting for the variations with time in climatic conditions.

Bayesian generalized linear models (GLMs). Plot was included as a random factor in all GLMs to take into account the potential temporal autocorrelation resulting from the repeated sampling of plots after fire. Since the sampling covered time points varied in the climatic conditions, the effect of the air temperature and precipitation on PCPS1 and PCPS2 was tested in two separate Bayesian GLMs (data on the climatic conditions are given in Pérez-Valera et al. (2017)). The residuals of the initial 'climatic' model were then used as the dependent variable in a second Bayesian GLM in which time since fire was used as a continuous independent variable. In this second model, the effect of time since fire (taken as a continuous variable) was tested independently on the residuals of PCPS1 and PCPS2. The square of time since fire in the model was also used to test for quadratic relationships. In all Bayesian GLMs, the uncertainty of phylogenetic reconstructions was accounted for by running three GLMs, each one using a PCPS calculated from an independent tree, and integrated over the posterior samples by drawing 1000 random samples across models in the MCMCglmm package in R (Hadfield, 2010). Default priors were used, with 130,000 MCMC iterations, a burnin period of 30,000 iterations and a thinning of 100.

We tested whether taxa abundance, PCPS and microbial EF indicators in post-fire communities differed significantly from pre-fire values by fitting GLMs with taxa abundances, PCPS or EF indicators as dependent variables and time since fire as a categorical independent factor. In this case, the variations with time in the climatic conditions were also taken into account as above.

We then tested whether changes in soil abiotic properties determine the phylogenetic structure of bacterial communities using PCPS1 or PCPS2 as the dependent variable and the soil abiotic factors as independent variables in a single GLM. Finally, the effect of the phylogenetic community structure (PCPS1 and PCPS2) on each EF microbial indicator was evaluated. Time since fire was included as a random factor in all models and variation with time in climatic variables was accounted for as above.

3. Results

We have previously described how fire altered the soil abiotic factors and the relative abundance of main phyla (Pérez-Valera et al., 2015, 2017). Briefly, fire triggered an immediate (1 day) pulse in inorganic forms of N (i.e. NO_3^--N and NH_4^+−N) and electrical conductivity (EC) (Fig. S1). In addition, fire significantly decreased soil humidity after 1 week, while 1 month was needed to detect increased total organic C (TOC) and decreased pH values (Fig. S1). Changes in NO_3^--N and NH_4^+−N reverted to pre-fire levels after several months while TOC, humidity, pH or EC did not recover during the study period (Fig. S1). Changes in main bacterial phyla included the immediate increase in the relative abundance of *Firmicutes* after fire, mainly due to the genus *Bacillus* (Fig. S2), recovering their pre-fire levels after 4.5 months. On the contrary, *Proteobacteria* was initially reduced, due to the decline in *Alphaproteobacteria*, but surpassed its pre-fire values after 1 month caused by a peak of a root-colonizing genus (i.e. *Massilia*) belonging to the *Betaproteobacteria* (Fig. S2). A delayed response was detected in the relative abundance of *Bacteroidetes* and *Actinobacteria*, which respectively showed increased and reduced levels one month and one year after fire compared with pre-disturbance levels.

In this study, the phylogenetic composition of the bacterial communities was described through matrix P, in which each OTU has a value per sample that depends on the dominance and distance of the phylogenetic neighbourhood. An average matrix P value per phyla is shown before and after the experimental fire, together with the phylogenetic relationships among phyla in Fig. 1A and B. Under pre-fire conditions, OTUs belonging to *Actinobacteria*, *Proteobacteria* and the phylogenetic clade containing *Nitrospirae* and *Acidobacteria* showed high matrix P values on average, indicating that OTUs within each clade tend to coexist with close relatives (Fig. 1B). Conversely, *Thermi* and *Cyanobacteria* exhibited low matrix P values, suggesting that OTUs within these lineages share their neighbourhood with more distantly related bacteria. Fire altered matrix P values distinctly depending on the lineage (Fig. 1B). The clade including *Proteobacteria* and *Bacteroidetes* had lower matrix P values 1 day after fire and progressively higher values towards the end of the study period, whereas the opposite tendency was detected for the clade containing *Actinobacteria*, *Firmicutes*, *Thermi* and *Cyanobacteria*.

Variations in matrix P values with fire translated into shifts in the two principal coordinates of phylogenetic structure (PCPS). According to the taxon loadings on PCPS1, this axis segregated two clades at the deepest phylogenetic level (Fig. 2). One of these basal clades, including *Actinobacteria*, *Firmicutes*, *Thermi* and *Cyanobacteria* (Fig. 1A), contributed to the negative pole of PCPS1 (Fig. 2). The second clade, including *Proteobacteria*, *Bacteroidetes*, *Planctomycetes* and *Deferribacteres* (Fig. 1A), had positive loadings on PCPS1 (Fig. 2). PCPS1, which explained 26% of the total variance, was linearly correlated with time since fire (post-mean estimate [95% credible interval] = 4×10^{-4} [3×10^{-4}, 6×10^{-4}]) after accounting for climatic oscillations (Fig. 3A). PCPS1 scores 1 day after fire were significantly lower than pre-fire scores and reached significantly higher values 1 year later. PCPS2 (14% of total variance) was also significantly correlated with time since fire, once the climatic variations were considered, following a quadratic model (post-mean estimate of time = 4×10^{-4} [-1×10^{-4}, 9×10^{-4}]; time^2 = -1×10^{-6} [-3×10^{-6}, -9×10^{-8}]) (Fig. 3B). This quadratic relationship indicates that microbial communities related to PCPS2 recovered after fire as follows:

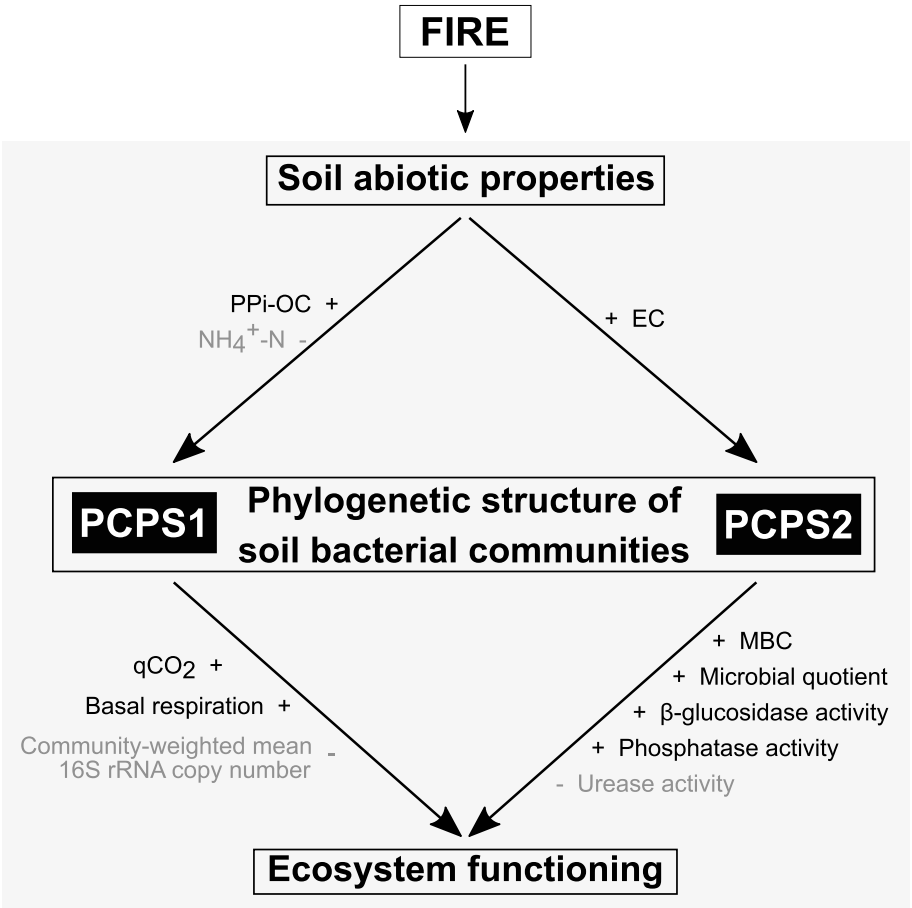

Fig. 4. Schematic depiction of the fire-induced shifts on ecosystem functions driven by changes in the soil abiotic environment that ultimately modify the phylogenetic structure of soil bacterial communities. Positive and negative significant relationships are respectively shown in black and grey. Post-mean estimates and credible intervals (95%) are given in Tables 1 and 2.

Table 1
Bayesian post-mean estimates and their expected 95% credible intervals for the effect of soil abiotic properties on the phylogenetic structure of bacterial communities. Significant values are shown in bold type.

	PCPS1	PCPS2
Total organic C (g kg^{-1})	3.1×10^{-3} [-9.2×10^{-3}, 1.4×10^{-2}]	2.9×10^{-3} [-5.0×10^{-3}, 1.1×10^{-2}]
Total N (%)	-2.4×10^{-2} [-3.4×10^{-1}, 3.0×10^{-1}]	1.2×10^{-1} [-7.8×10^{-2}, 3.2×10^{-1}]
pH	4.2×10^{-2} [-1.4×10^{-1}, 2.5×10^{-1}]	4.6×10^{-2} [-7.6×10^{-2}, 1.8×10^{-1}]
Gravimetric humidity (%)	-4.0×10^{-3} [-1.5×10^{-2}, 7.7×10^{-3}]	3.1×10^{-3} [-2.2×10^{-3}, 7.8×10^{-3}]
NO_3^--N (mg kg^{-1})	-7.6×10^{-4} [-1.5×10^{-3}, 2.9×10^{-5}]	-2.1×10^{-4} [-7.8×10^{-4}, 3.7×10^{-4}]
NH_4^+–N (mg kg^{-1})	**-8.4×10^{-3} [-1.5×10^{-2}, -2.3×10^{-3}]**	-8.2×10^{-4} [-4.7×10^{-3}, 3.7×10^{-3}]
Pyrophosphate oxidizable C (g kg^{-1})	**1.0×10^{-5} [1.2×10^{-6}, 1.9×10^{-5}]**	-4.1×10^{-6} [-1.1×10^{-5}, 9.2×10^{-7}]
Electrical conductivity (μS cm^{-1})	-1.8×10^{-4} [-8.1×10^{-4}, 1.6×10^{-4}]	**6.5×10^{-4} [3.0×10^{-4}, 9.8×10^{-4}]**

Table 2
Bayesian post-mean estimates and their expected 95% credible intervals for the effect of bacterial phylogenetic structure (PCPS1 and PCPS2) on ecosystem function indicators. Significant values are given in bold type.

	PCPS1	PCPS2
Microbial biomass C (mg C kg^{-1})	109 [-263, 464]	**894 [290, 1488]**
Microbial quotient (%)	−0.1 [-0.8, 0.5]	**1.1 [0.1, 2.1]**
16S rRNA copy number (weighted mean)	**−0.9 [-1.7, -0.1]**	1.3 [-0.1, 2.4]
qCO_2 (μg C–CO_2 mg^{-1} MBC h^{-1})	**3.2 [1.0, 6.1]**	−0.5 [-3.9, 3.3]
Basal respiration (mg C–CO_2 kg^{-1} d^{-1})	**24.5 [3.8, 45.0]**	34.3 [-1.3, 64.0]
β-glucosidase activity (μmol PNP g^{-1} h^{-1})	1.3 [-1.0, 3.5]	**7.4 [4.1, 10.9]**
Phosphatase activity (μmol PNP g^{-1} h^{-1})	9.2 [-4.1, 19.5]	**36.1 [18.5, 55.6]**
Urease activity (mg N–NH_4^+ g^{-1} h^{-1})	0.1 [-0.4, 0.7]	**−0.8 [-1.8, -0.01]**

PCPS2 scores were significantly higher than pre-fire scores 1 month after fire, and then recovered pre-fire levels (Fig. 3B). *Proteobacteria* had the highest loadings on PCPS2 (Fig. 2).

Fire-induced shifts in the phylogenetic structure of soil bacterial communities were determined by changes in main soil abiotic properties (Fig. 4). Specifically, the levels of NH_4^+–N and pyrophosphate extractable C (i.e. a measure of the total amount of oxidizable C) were the main predictors of PCPS1, whereas EC significantly explained PCPS2 (Fig. 4, Table 1). In turn, the phylogenetic community structure of soil bacteria determined microbial EF indicators. PCPS1 correlated

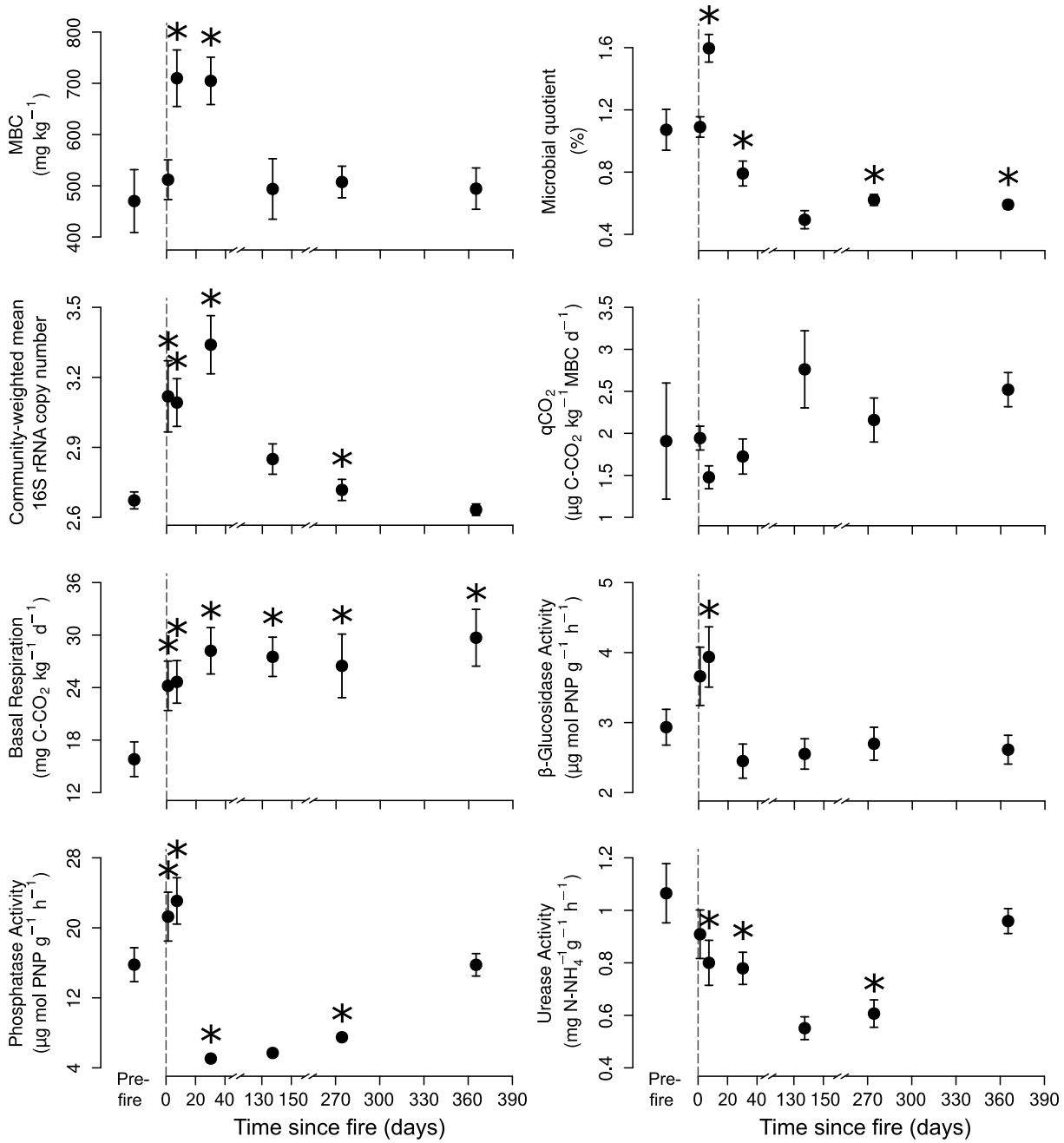

Fig. 5. Post-fire succession of microbial parameters indicative of biomass, potential growth rate, organic matter decomposition, carbon use efficiency, and C, N and P cycling. Asterisks indicate significant differences between each time point and the pre-fire level after accounting for the variations with time in climatic conditions.

negatively with the community-weighted mean 16S rRNA copy number and positively with respiration and qCO_2 (Fig. 4, Table 2). PCPS2 significantly explained MBC, the microbial quotient and enzymatic activities related to C, P and N cycling (Fig. 4, Table 2).

Fire produced both immediate and mid-term effects on microbial EF indicators once changes explained by climatic variations were accounted for (Fig. 5). Fire increased the levels of basal respiration, community-weighted mean 16S rRNA copy numbers or phosphatase activity after 1 day and that of microbial biomass C (MBC), microbial quotient and β-glucosidase after 1 week, whereas it did not alter the metabolic quotient (qCO_2) and decreased urease activity. Most of the initial peaks were reverted 1 month after fire, some variables such as the microbial quotient and phosphatase activity significantly decreasing even below pre-fire levels. While fire-driven changes in MBC, community-weighted mean 16S rRNA copy number and enzymatic activities recovered pre-fire values within the first year, the shifts in basal respiration and microbial quotient were long-lasting (Fig. 5).

4. Discussion

Our results show that fire, by modifying soil abiotic properties, shifted the phylogenetic structure of bacterial communities and modified ecosystem functions related to microbial productivity, decomposition and nutrient cycling. Fire distinctly affected the two principal components (PCPS) that describe the phylogeny-weighted bacterial OTU composition. While PCPS1 scores increased in a linear fashion during post-fire succession, those of PCPS2 followed a hump-shaped curve and recovered pre-fire levels. Scores of either PCPS responded to different soil abiotic parameters and eventually determined specific ecosystem functions. Although the bacterial phylogenetic community

structure did not completely recover within the first year, most ecosystem functions returned to pre-disturbance levels.

4.1. Fire and the phylogenetic structure of soil bacterial communities

Fire instantly altered the phylogenetic structure of soil bacterial communities. As soon as one day after fire, significantly lower PCPS1 scores were detected, a pattern that was driven by the response of organisms within the same basal clade in the bacterial phylogenetic tree. Many bacteria in these lineages are able to cope with high temperatures, either by producing resistance structures such as endospores (*Firmicutes*), spores (*Actinobacteria*) and akinetes (*Cyanobacteria*) or because of their thick cell walls (*Thermi*) (Dworkin, 2006). Indeed, several studies have found increases in these groups after fire, particularly in *Firmicutes* and *Actinobacteria,* as consequence of their resistance to heat (e.g. Ferrenberg et al., 2013; Prendergast-Miller et al., 2017), but maybe also because of the ability of *Actinobacteria* to colonize the post-fire environment (Isobe et al., 2009). Our results suggest that the immediate response to fire of organisms belonging to this basal clade was most likely promoted by high temperatures, which stimulate spore germination (Dworkin, 2006) and the ephemeral pulse in ammonium nitrogen, a direct product of combustion (Certini, 2005). Indeed, we found that ammonium nitrogen correlated with PCPS1, suggesting that heat-resistant microbes thriving immediately after fire might have taken advantage of the burst in mineral nitrogen (Smith et al., 2008; Bárcenas-Moreno et al., 2011). Those bacterial lineages that could harbour heat-resistant organisms showed not only different dominance in the community (ranging from < 1% to 25% of the total abundance for *Thermi* and *Actinobacteria*, respectively) but also a different response in terms of abundance after fire (Pérez-Valera et al., 2017). However, the response of their phylogenetic neighbourhood to fire was similar, that is, they tended to coexist with closer relatives immediately after fire. This observation suggests that fire acts as an environmental filter that promotes the heat-resistance traits shared by these evolutionarily related organisms. For example, closely related OTUs belonging to *Bacillus* and *Paenibacillus* (*Firmicutes*) followed a similar abundance pattern after fire ($r = 0.5$, $P < 0.001$), probably because of a shared phylogenetically conserved sporulation trait (Goberna and Verdú, 2016). The fact that such heat-resistance syndrome was captured by PCPS1, a metric that accounts for differences at the most basal phylogenetic nodes, is consistent with those traits being deeply conserved in the phylogeny (Goberna and Verdú, 2016).

The first component of the phylogenetic structure of soil bacterial communities changed permanently during the study period. Our results suggest that such a shift was driven by organisms that belong to the second basal clade in the bacterial phylogeny, such as *Proteobacteria* and *Bacteroidetes*. These lineages include organisms that respond to the availability of organic carbon in soils (Fierer et al., 2007). In addition, members of *Betaproteobacteria* such as *Burkholderiales, Alphaproteobacteria* such as *Sphingomonadales* and *Gammaproteobacteria* such as *Alteromonadales* have been shown to exhibit a delayed response to abrupt environmental changes and competitively displace rapid responding (stress-tolerant) bacteria in laboratory experiments (Placella et al., 2012; Jurburg et al., 2017). The dominance of *Proteobacteria* and *Bacteroidetes* in response to fire were not alike. However, their neighbourhood shifted similarly during post-fire recovery, as they all bore higher phylogenetic resemblance to neighbouring OTUs towards the end of the study period. This pattern underlay the significant increase in PCPS1 scores one year after fire and is therefore responsible for the fact that PCPS1 did not recover pre-fire levels. This trend was linked to the total levels of oxidizable carbon in soil, which were positively correlated with PCPS1. This observation agrees with the notion that numerous taxa within *Proteobacteria,* mainly those belonging to *Burkholderiales* and *Rhodocyclales* (*Betaproteobacteria*), and *Enterobacteriales* and *Pseudomonadales* (*Gammaproteobacteria*), respond to organic carbon producing changes in the community that are phylogenetically structured (Goldfarb et al., 2011; Goberna et al., 2014; Morrissey et al., 2016). *Proteobacteria* were also key determinants of the second component of phylogenetic structure (PCPS2), to which this taxon contributed with the highest loadings. The post-fire succession of PCPS2 scores, peaking from 1 to 4.5 months after fire and then returning to pre-disturbance values specifically resembles that of the root-colonizing *Massilia,* a dominant genus within *Betaproteobacteria* in our study (Pérez-Valera et al., 2017). The promotion of these organisms was likely supported by the temporary increase in the availability of inorganic ions in the soil solution, which is common after fire (Certini, 2005), as PCPS2 scores were significantly explained by the electrical conductivity. The shifts detected in the phylogenetic structure of soil bacterial communities were the outcome of changes in the dominance of OTUs at basal and shallower clades. These changes in OTU abundance at different clade depths have been shown to impact ecosystem function (Goberna and Verdú, 2018).

4.2. Fire and microbial ecosystem functions

Fire initially increased soil microbial biomass, C use efficiency and mineralization rates, as well as some enzymatic activities related to C and P cycling. However, in the short term fire hampered the hydrolysis of organic N compounds, most likely due to product (ammonium N) inhibition of urease activity (Hoare and Laidler, 1950). Contrarily to wildfires that significantly reduce microbial biomass and activity (Hernández et al., 1997; Jiménez-Esquilín et al., 2008), prescribed or experimental fires, with their lower severity and shorter duration, have been shown to induce light shifts (even increases) in microbial activity, biomass and nutrient cycling activities (González-Pérez et al., 2004; Fontúrbel et al., 2012; Fultz et al., 2016; Muñoz-Rojas et al., 2016). Indeed, the increase one day after fire in the phosphatase activity is consistent with previous studies that suggest that increased N, such as those occurring after fire, stimulates phosphatase activity (Margalef et al., 2017). In addition, the post-fire increase in nitrate along with organic C could also favour microbial biomass (Andersson et al., 2004), as we detected after fire. Altogether, the short duration of the experimental fire along with the buffered temperatures with soil depth and resource availability support the higher activity and biomass we detected after the fire in the short-term.

An immediate increase in the community-weighted mean rRNA copy numbers was also detected, indicating that fire favoured microbial lineages with an elevated number of copies of the 16S rRNA gene. Our results therefore support the observation that bacterial communities during the first stages of succession feature high rRNA operon copy numbers, as has been previously detected both in experimental and natural, including post-fire, communities (Shrestha et al., 2007; Nemergut et al., 2016). Multiple rRNA operons have been suggested to be a discriminative genomic feature of the copiotrophic strategy (Lauro et al., 2009) that determines cell growth and sporulation efficiency (Yano et al., 2013). Thus, in the first stages of succession, bearing an elevated 16S rRNA copy number is thought to provide a selective advantage by increasing the ability to rapidly respond to nutrient inputs and/or to form spores (Nemergut et al., 2016). We could specifically attribute the increase in the number of rRNA operons to the initial rise of *Firmicutes* (Fig. S3), basically within the class *Bacilli* (Pérez-Valera et al., 2017). This peak lasted for the first month after fire, when the community weighted mean rRNA copy number was still abnormally high, but C use efficiency, and the rates of C, P and N cycling had significantly dropped to (or below) pre-disturbance levels. These patterns fit well with the idea that organisms with high numbers of the rRNA operon can exhibit high reproductive rates but low levels of C use efficiency and protein yield (Roller et al., 2016).

Most microbial EF indicators returned to pre-fire levels during the study period, specifically those related to microbial biomass, community-weighted mean rRNA operon copy number, and the rates of C, N and P cycling. Therefore, the recovery of most microbially-driven

ecosystem functions was faster than that of the phylogenetic community structure. This opens the possibility that bacterial communities were not fully recovered but replaced to a certain extent by another functionally equivalent community. Although functional redundancy has been suggested to operate in experimental bacterial communities (Bell et al., 2005), this is currently difficult to test in natural communities based on our still low knowledge on the contribution of specific microbial groups to ecosystem processes (Allison and Martiny, 2008). Alternatively, taxa in the post-fire scenario could be taxonomically and functionally different to those prior to disturbance but result in the same process rates measured at the community level (Allison and Martiny, 2008). In addition, a certain degree of functional dissimilarity between pre- and post-fire communities was detected, as not all microbial EF indicators recovered original levels throughout the study period. Microbial respiration and carbon use efficiency pointed to faster rates of organic carbon mineralization into carbon dioxide and a reduced conversion into microbial biomass one year after fire. Higher respiration rates correlate well with the delayed promotion of *Betaproteobacteria* and *Bacteroidetes*, whose relative abundance significantly explains C mineralization rates in soils (Fierer et al., 2007).

In conclusion, fire altered main ecosystem functions related to microbial productivity, decomposition and nutrient cycling through changes in the phylogenetic composition of soil bacterial communities. Microbial EF indicators showed dissimilar post-fire trajectories depending on the relative abundance of particular phylogenetic lineages. This observation emphasizes the importance of incorporating evolutionary information to understand how ecological disturbances may alter the relationship between biodiversity and ecosystem functioning.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2018.11.007.

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