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Resilience to fire of phylogenetic diversity across biological domains

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Abstract

Fire alters the structure and composition of above- and belowground communities with concurrent shifts in phylogenetic diversity. The inspection of postfire trends in the diversity of ecological communities incorporating phylogenetic information allows to better understand the mechanisms driving fire resilience. While fire reduces plant phylogenetic diversity based on the recruitment of evolutionarily related species with postfire seed persistence, it increases that of soil microbes by limiting soil resources and changing the dominance of competing microbes. Thus, during postfire community reassembly, plant and soil microbes might experience opposing temporal trends in their phylogenetic diversity that are linked through changes in the soil conditions. We tested this hypothesis by investigating the postfire evolution of plant and soil microbial (fungi, bacteria and archaea) communities across three 20-year chronosequences. Plant phylogenetic diversity increased with time since fire as pioneer seeders facilitate the establishment of distantly related late-successional shrubs. The postfire increase in plant phylogenetic diversity fostered plant productivity, eventually recovering soil organic matter. These shifts over time in the soil conditions explained the postfire restoration of fungal and bacterial phylogenetic diversity, which decreased to prefire levels, suggesting that evolutionarily related taxa with high relative fitness recover their competitive superiority during community reassembly. The resilience to fire of phylogenetic diversity across biological domains helps preserve the evolutionary history stored in our ecosystems.

KEYWORDS
archaea, bacteria, chronosequence, community structure, fungi, plants

1 | INTRODUCTION

Ecological disturbance can disassemble biological communities by changing their structure and composition, a topic of prime relevance in the face of the current unprecedented rates of environmental change (Cairney & Bastias, 2007; Keeley, 1986; Mikita-Barbato, Kelly & Tate, 2015). Ecological communities can, however, experience no significant changes due to disturbance (resistance) or be capable of returning to their predisturbance structure and composition (resilience). The processes of community reassembly in resilient communities can be better studied using phylogenetic metrics of diversity, which inform on the evolutionary relationships among community members (Webb, Ackerly, McPeek & Donoghue, 2002). This is due to the fact that phylogenetically related organisms tend to respond similarly to disturbance (Amend et al., 2016; Verdú & Pausas, 2007), as functional resemblances among species can be predicted using their common ancestry (Blomberg, Garland & Ives, 2003; Goberna & Verdú, 2016). Furthermore, community resilience depends on the set of initial conditions, including the phylogenetic diversity of the species pool from which the community is reassembled (Tan, Pu, Ryberg & Jiang, 2012).

The phylogenetic diversity of plants and soil microbes is governed by sequentially operating assembly rules (Goberna, García & Verdú, 2014; Keddy, 1992). Abiotic filtering is a pervasive community structuring force across biological groups, and biological interactions further fine-tune the community structure (HilleRisLambers, Adler, Harpole, Levine & Mayfield, 2012; Goberna, Navarro-Cano, Valiente-Banuet, García & Verdú, 2014; but see Cadotte & Tucker, 2017). Both assembly mechanisms determine the phylogenetic structure of plant and soil microbes, which in turn show intricate linkages. Plant phylogenetic diversity, which increases biomass production through species complementarity (Cadotte, 2013; Cadotte, Cardinale & Oakley, 2008), has been observed to either have a positive or a negative reflection on soil microbial phylogenetic diversity (Barberán et al., 2015; Goberna, Navarro-Cano & Verdú, 2016). These divergent patterns can be theoretically explained by two alternative mechanisms of community assembly (Goberna et al., 2016; HilleRisLambers et al., 2012). First, diverse plant assemblages may supply a higher diversity of organic substances to the soil (Steinauer, Chatzinotas & Eisenhauer, 2016) leading to higher microbial phylogenetic diversity through niche differences. Second, diverse plant assemblages can supply more organic substances to the soil (Lange et al., 2015), thus increasing the competitive dominance of a few clades with high relative fitness that exclude entire lineages and lower microbial phylogenetic diversity. In addition to these top-down effects, evidence suggests that belowground diversity may affect plant diversity by changing herbivory, pathogenesis or soil nutrient availability, among others (Bardgett & van der Putten, 2014). The general view that abiotic and biotic filters act sequentially has been recently refined, as both filters seem to have no separable effects on species and their interactions (Cadotte & Tucker, 2017). Indeed, the study of the phylogenetic diversity of biological communities has allowed detecting abiotic filters and biotic interactions that simultaneously operate to reassemble communities after an ecological disturbance (Pérez-Valera et al., 2017; Verdú & Pausas, 2007).

Fires are worldwide disturbances that disrupt the composition and phylogenetic structure of biological communities (Pérez-Valera et al., 2017; Verdú & Pausas, 2007; Xiang et al., 2014). Different lineages have evolved a wealth of ecological strategies to cope with heat-induced mortality or cell damage resulting in contrasting disassembly processes. Plant species may persist in a population after fire by recruiting from a fire-resistant seed bank (i.e., seeders) or by the vegetative regrowth of adults (i.e., resprouters; Keeley, 1986). High fire intensity, especially in arid ecosystems, acts as an abiotic filter favouring the seeder over the resprouter strategy (Pausas & Keeley, 2014). Because seeding is a phylogenetically conserved trait, the high abundance of seeders after fire often results in the overrepresentation of closely related species (Verdú & Pausas, 2007). Thus, the phylogenetic fingerprint of plant community disassembly produced by fire, although it depends on the prefire proportion of seeders and resprouters, is generally the loss of phylogenetic diversity (Verdú, Rey, Alcántara, Siles & Valiente-Banuet, 2009).

Soil microbes also have functional traits related to heat resistance. Archaea are the most tolerant to high temperatures given their characteristic cell wall and membrane lipid structure, based on ether bonds instead of the ester linkages found in most bacteria and eukaryotes (Rothschild & Mancinelli, 2001; Stetter, 1999). Bacterial living cells are generally not as heat-resistant, except for some groups of thermophiles, but many bacteria are able to produce resistant structures (e.g., spores, cysts, akinetes) that can withstand high temperatures, desiccation, radiation and other extreme abiotic conditions (Dworkin, 2006). Fungal cells are sensitive to heating (Rothschild & Mancinelli, 2001). However, fungi may produce thick-walled spores in hypogeous fruiting bodies or highly compacted mycelia that provide them with fire resistance (Horton, Cázares & Bruns, 1998; Tedersoo, Hansen, Perry & Kjøller, 2006). As evidence suggests that microbial functional traits tend to be phylogenetically conserved (Goberna & Verdú, 2016; Kia et al., 2017; Martiny, Treseder & Pusch, 2013), it could be expected that, similar to plants, the overrepresentation of heat-resistant microbes would reduce soil microbial phylogenetic diversity immediately after fire. However, existing evidence for bacteria and fungi points the opposite way, as fire increases the phylogenetic diversity of soil microbial communities (Pérez-Valera et al., 2017; Rincón, Santamaría-Pérez, Ocaña & Verdú, 2014). This increase in phylogenetic diversity could be attributed to (a) a stronger competitive exclusion between closely related fire-resistant species with similar niches and/or (b) a reduced competitiveness of the dominant fire-sensitive taxa from entire clades with high relative fitness (Dix & Webster, 1995; Goberna, Navarro-Cano et al., 2014; Pérez-Valera et al., 2017; Rincón et al., 2014). Specifically, fire can increase competition by limiting the availability of soil moisture and organic substances (Certini, 2005; Hart, DeLuca, Newman, MacKenzie & Boyle, 2005; Mataix-Solera, Guerrero, García-Orenes, Bárcenas & Pilar Torres, 2009; Neary, Klopatek, DeBano & Ffolliott, 1999).

The high resilience of Mediterranean plant communities to fire has been attributed to the fact that fire alters species abundance rather than composition and therefore recovery only involves the return to prefire abundances (Lavorel, 1999). Postfire recovery of soil bacterial and fungal communities, which are broadly fire-sensitive and predominantly heterotrophic microbes, requires the amelioration of soil conditions (Cairney & Bastias, 2007; Treseder, Mack & Cross, 2004; Xiang et al., 2014). Soil archaea, generally heat-tolerant and including many chemolithotrophic organisms, seem to be more resilient to fire although scarce and contrasting results have been described (Goberna, García, Insam, Hernández & Verdú, 2012; Mikita-Barbato et al., 2015). Incorporating phylogenetic information to postfire diversity trends would allow a better understanding of the assembly mechanisms driving the resilience of ecological communities across biological groups. We hypothesize that the resilience to fire of plant communities in Mediterranean ecosystems might induce changes in the soil conditions that, in turn, trigger the reassembly of soil microbial communities. Specifically, we test whether the postfire reassembly of plant communities enhances plant phylogenetic diversity up to prefire levels, fostering plant biomass (Cadotte, 2013; Cadotte et al., 2008) and in turn soil fertility (Goberna et al., 2016), thus ultimately recovering (i.e., decreasing) the phylogenetic diversity

of soil microbes (Goberna, García et al., 2014). These opposing phylogenetic temporal trends during the postfire recovery of plants and soil microbes would be coherent with the recovery of competitive microbial clades with high relative fitness. To test these hypotheses, we analysed the postfire evolution of the phylogenetic diversity of plant, and soil fungal, bacterial and archaeal communities across three 20-year fire chronosequences.

2 | MATERIAL AND METHODS

2.1 | Study area and experimental design

This study was carried out in three fire chronosequences that were located in the north, centre and south of Valencia (E Spain; Supporting Information Figure S1). Each chronosequence included eight to nine sites, making a total of 25 sites that had experienced a single wildfire event during the last 20 years (between 1994 and 2014). In the study area, the fire regime has changed in the last 130 years, fire recurrence dropping from 397 to 49 years around the early 1970s (Pausas & Fernández-Muñoz, 2012). For the selection of the sites, we identified numerous burned areas using a database provided by the Valencian Government that included the dates and burned perimeter of all fires. According to this database, only 1.7% of the total surface burned between 1994 and 2014 in the Valencian Community (c. 5,300 of 320,000 hectares) has experienced two or more fires. In order to reduce the environmental heterogeneity across sampling sites, we restricted the potential sites based on their similarities in lithology, slope orientation and plant cover with the help of lithological maps (Gabaldón, 1994), topographical maps (CNIG 2014a) and orthophotographs (CNIG 2014b) using QUANTUMGIS 2.2 (QGIS Development Team, 2016). Sampling sites were finally established after an extensive field inspection. All sites had calcareous lithology, and we selected S-SW oriented slopes with <36° where typical Mediterranean scrublands develop (see details below). The main features of all sites are given in Supporting Information Table S1.

To further control for the environmental variability, we established a paired experimental design, each site having a burned and an unburned plot. We considered as long unburned plots (hereafter referred to as "unburned plots") those that had similar environmental conditions and land-use history than its paired burned plot, but had no observable signs of fire during the field inspection either in the vegetation or throughout the soil profile (e.g., no layer of ashes or burned material) nor historical fire register (Supporting Information Table S1). Burned and unburned plots were located on average at (mean ± *SE*) 435 ± 49 m away, ensuring the avoidance of fire edge effects. All fires were most likely of high intensity according to the ignition dates (mainly in the hot and dry season) and the availability of fuel load (plant cover and biomass) in the control transects (see details below). Plant and soil sampling was carried out in spring 2014 along three linear 25-m transects *per* plot, thus making a total of 150 transects (i.e., 25 sites × 2 plots × 3 transects). Transects were drawn in the direction of the slope, located c. 10 m apart and systematically from west to east. Burned and control transects were paired for statistical purposes according to their position in the field (e.g., westernmost burned and control transects were considered as paired).

2.2 | Plant sampling and phylogeny reconstruction

Plant cover of each species was estimated through the line-intercept sampling method in the three 25-m transects in each plot (Butler & McDonald, 1983; Canfield, 1941). In each transect, we measured the horizontal distance of the interception of each plant individual. Plant cover was estimated by adding the intercept distances per species and expressing it over the total transect distance (25 m). Plant height was measured for each individual intercepting each transect, and its biomass estimated as plant height × horizontal interception. This quantifies the plant area that intercepts the transect, which we used as an estimate of the aboveground biomass supplying organic inputs to the soils that were sampled along the transect (details below).

To reconstruct plant phylogeny, we grafted our study species in the angiosperm tree derived from the Angiosperm Phylogeny Group III (https://github.com/camwebb/tree-of-trees/blob/master/megatrees/R20120829.new) using the PHYLOMATIC package in PHYLOCOM 4.2 (Webb, Ackerly & Kembel, 2008; Supporting Information Figure S2). This mega-tree included taxa both at the family and genus levels, and our resulting tree was well resolved for most of the internal nodes (92 of 116). Ages of 29 nodes in our tree were obtained from literature (Supporting Information Table S2) and subsequently used to calibrate the tree under a birth–death model with the BEAST 1.5.4 (Drummond & Rambaut, 2007) and the POLYTOMYRESOLVER script (Kuhn, Mooers & Thomas, 2011). We also used this procedure to simultaneously resolve polytomies and generate many independent trees in such a way that topological and chronological uncertainty could be included in subsequent analyses. To ensure chain convergence, we generated 11,112 phylogenetic trees and discarded the first 25%. We randomly selected five phylogenetic trees for subsequent analyses, as we did for fungi, bacteria and archaea (see details below). Further details about this procedure can be found in Verdú and Pausas (2013).

2.3 | Soil sampling and sample analysis

Surface soil samples (0–5 cm) from the 150 transects were collected with a hand shovel after removing the surface layer that included ashes (for burned plots), litter, mosses and stones. Along each transect, one composite sample was taken that consisted of 10 regularly distributed subsamples of c. 100 g. Samples were transported into an isothermal icebox to the laboratory, sieved (<2 mm) and kept at 5°C. Soil moisture content (gravimetric humidity), pH and electrical conductivity (EC) were analysed with standard procedures as in Goberna et al. (2012). Total C (TC) and N (TN) were determined by dry combustion at 500°C using a TruSpec C/N analyser (Leco Corp., MI, USA). Total organic C (TOC) was also quantified after a 55°C acidic (HCl) treatment of the samples, and total inorganic C

estimated as the difference between TC and TOC. Ammonium N (NH_4^+-N) and nitrate N (NO_3^--N) were quantified spectrophotometrically using the Nessler's reagent (0.09 M solution of K_2HgI_4 in 2.5 M KOH) and after reducing it to NO_2^--N.

To assess the adequacy of our paired samples, we checked that the contents of total inorganic C did not significantly differ between pairs of burned and unburned transects ($t_{71} = 0.77$, $p = 0.44$). Total inorganic C, mainly corresponding to carbonates in our study soils, is not expected to be affected by fire unless temperature exceeds 1,000°C (Certini, 2005).

2.4 | DNA extraction and sequence processing

Soil DNA was extracted from c. 0.25 g soil with the PowerSoil DNA Isolation Kit (MO BIO Laboratories, Carlsbad, CA, USA). DNA quality was checked by electrophoresis in 1% agarose gels run in 0.5× Tris–acetate–EDTA buffer. Amplifications of fungal ITS region were performed using the ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS4R (5′-TCCTCCGCTTATTGATATGC-3′) primers (Gardes & Bruns, 1993; White, Bruns, Lee & Taylor, 1990). Amplifications of the bacterial and archaeal 16S rRNA gene were performed using the universal prokaryotic primers 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 806R (5′-GGACTACVSGGGTATCTAAT-3′; Caporaso et al., 2012). Each sample contained a unique 8-nucleotide barcode in its 5′ end. A single-step 30 cycle PCR was performed using HotStarTaq Plus Master Mix Kit (Qiagen, Valencia, CA, USA) under the following conditions: denaturation at 94°C for 3 min, followed by 28 cycles of denaturation at 94°C for 30 s, annealing at 53°C for 40 s, and elongation at 72°C for 1 min, and a final elongation step at 72°C for 5 min. PCR products from all samples were mixed in equal concentrations and purified using Agencourt Ampure beads (Agencourt Bioscience Corporation, MA, USA). Pyrosequencing was performed by MR DNA (Shallowater, TX, USA) using Roche 454 FLX titanium instruments and reagents, and following manufacturer's instructions.

2.5 | Sequence analysis and phylogeny reconstruction

Fungal ITS amplifications produced 1,649,877 DNA sequences. Primers and barcodes were trimmed and short sequences (<150 bp) removed. Sequences with homopolymers exceeding 6 bp, and those with ambiguous base calls were removed. The sequence processing workflow included denoising, chimera and singleton removal. Operational taxonomic units (OTUs), defined at an identity level of 97%, were taxonomically classified using BLAST and the UNITE database v.7 (Kõljalg et al., 2013). After this initial processing, 1,080,311 sequences were grouped into 6,620 OTUs. The OTU × transect community matrix, initially constructed from absolute read counts, was standardized by dividing the abundance of each OTU between the total number of reads *per* transect. In order to reconstruct the fungal phylogeny, we first constructed a genus-level tree from the literature that included all possible fungal genera, families, orders, classes or phyla found in our study (Supporting Information Figure S3). Then, OTUs were grafted into this tree according to their taxonomic information. Tree branch lengths were estimated from 42 dated nodes obtained from the literature, as for plants (Supporting Information Table S3). In order to resolve the polytomies, 580 trees were generated with BEAST after running the POLYTOMYRESOLVER script. Five phylogenetic trees were randomly selected after removing the first 143 trees (25% of burnin), which were used for subsequent analyses. As fungal ITS region is highly variable within and between species (Nilsson, Kristiansson, Ryberg, Hallenberg & Larsson, 2008), we tested the robustness of our results after delimiting fungal OTUs at a cut-off of 99% sequence similarity. Postfire recovery in richness, phylogenetic α and β diversity, as well as relative abundance of main phyla, remained the same (data not shown).

The 16S rRNA amplifications produced 2,547,644 sequences, which were processed as the ITS DNA sequences. After initial processing, 1,280,728 sequences were grouped into 7,003 bacterial OTUs and 38,503 sequences into 26 archaeal OTUs. OTUs were taxonomically classified using BLASTN and a curated database based on GREENGENES, RDPII and NCBI (DeSantis et al., 2006) and aligned with PYNAST (Caporaso, Bittinger et al., 2010) in QIIME 1.9.1 (Caporaso, Kuczynski et al., 2010). We constructed a separated OTU × transect abundance matrix for bacteria and archaea, and calculated relative abundance as above. We corrected the relative abundances based on the estimated number of 16S rRNA gene copies (Kembel, Wu, Eisen & Green, 2012). Bacterial and archaeal phylogenies were separately reconstructed using RAXML 8.2.4 (Stamatakis, 2014) on the Cipres Portal (http://www.phylo.org), using the maximum-likelihood algorithm with 1,000 bootstraps. A constrained topology at the phylum level, and at the class level for Proteobacteria, was used for all monophyletic clades in accordance with the SILVA database (Release 123, Quast et al., 2013). To account for the uncertainty of the phylogenetic reconstruction from short DNA sequences, five independent phylogenetic trees were constructed for bacteria and archaea.

2.6 | Diversity metrics and phylogenetic composition

Plant richness was calculated as the sum of species *per* transect. Fungal, bacterial and archaeal richness was estimated by an individual-based multinomial model using QIIME, in order to reduce the bias due to the differential sequencing depth across samples. This model samples without replacement at a given sampling depth as in Colwell et al. (2012).

Phylogenetic α diversity of plants, fungi, bacteria and archaea was calculated as the abundance-weighted standardized mean phylogenetic distance ($_{std}$MPD) with the picante package for R (Kembel et al., 2010):

$$\text{Phylogenetic } \alpha \text{ Diversity } (P\alpha D) = {}_{std}\text{MPD} = (\text{MPD}_{obs} - \text{MPD}_{rand})/\text{sd\_MPD}_{rand}$$

where MPD_{obs} is the mean pairwise phylogenetic distance of species or OTUs *per* transect, MPD_{rand} is the mean ($n = 999$) of the community phylogenetic distance after randomly shuffling the distance

matrix labels of all the species or OTUs, and sd_MPD$_{rand}$ is the standard deviation of MPD$_{rand}$ (Webb et al., 2002). Positive values of $_{std}$MPD indicate that the community is composed by organisms more distantly related than expected by chance, whereas negative values indicate the opposite situation. Plant cover and OTU relative abundance matrices were used to weight the $_{std}$MPD of above- and belowground communities, respectively.

Fire-driven changes in the phylogenetic composition (i.e., phylogenetic β diversity) were evaluated between paired burned and unburned transects (see above) using UniFrac distances (Lozupone & Knight, 2005). In order to have an estimate of the natural compositional similarity that occurs under unburned conditions, we also calculated phylogenetic β diversities for pairs of unburned transects within each site. Weighted UniFrac distances were calculated using the GUNIFRAC package in R (Chen, 2012).

2.7 | Statistical analysis

In order to test the effects of geographic distance on both soil abiotic properties and community composition, Mantel correlograms were run using the VEGAN package for R (Oksanen et al., 2015). Transects were used as the general unit of observation. Correlograms were only calculated between unburned transects to avoid the potential confounding effect in the burned plots caused by the time elapsed since fire at short sampling distances. The composition of plant, fungal, bacterial or archaeal communities as well as several soil abiotic variables was spatially autocorrelated (Supporting Information Figure S4).

We tested the existence of short-term fire effects by comparing soil properties, species richness and phylogenetic α and β diversities between plots that had burned 0–3 years ago and their unburned transects through paired *t* tests in R.

To estimate the postfire recovery of all variables, we used the difference (Δ) between the value of each variable in paired burned and unburned transects, or directly the value from phylogenetic β diversity, as the dependent variable and time since fire as the fixed effect variable in a Bayesian generalized linear model (GLM). Spatial autocorrelation was accounted for in the model by incorporating the geographic distance matrix between transects as a random effect variable as in Stone, Nee and Felsenstein (2011). The models were run with the help of the MCMCglmm package for R (Hadfield, 2010). We calculated the average recovery times for all variables by interpolation or extrapolation through the equation of the fitted model.

We explored the relationships between the postfire recovery in plant phylogenetic diversity, plant biomass, the soil conditions and the soil microbial phylogenetic diversity. To do this, we performed a series of Bayesian GLMs, whose directionality was posed based on a priori knowledge as follows.

First, to test whether the recovery of plant phylogenetic α diversity fosters plant biomass (Cadotte, 2013), we performed a GLM with ΔPlant PαD as independent and ΔPlant biomass as dependent variables including time since fire and the geographic distance matrix as random effects in the model (see above).

Second, we analysed the effects of plant biomass on soil conditions and vice versa, after reducing the variability of soil parameters through a principal component analysis (PCA) that included the differentials (Δ) of soil pH, TOC, TN, moisture, NO_3^--N, NH_4^+-N and EC between pairs of burned and unburned transects (Supporting Information Figure S5). We interpreted PC1 and PC2, respectively, (52% and 21% of total variance) as gradients of recovery of soil organic matter and mineral N (Supporting Information Figure S5). We analysed the effects of plant biomass on the postfire recovery of soil organic matter (PC1) as soil organic matter essentially comes from plant inputs (i.e., litter and exudates). In contrast, we analysed the effects of soil mineral N (PC2) on the postfire recovery of plant biomass, as the forms of mineral N available to plants are generated either by the combustion or by the microbial mineralization of organic N.

Finally, we analysed the effects of soil conditions on microbial phylogenetic α diversity and vice versa. As the vast majority of soil microbes are heterotrophic, and their contribution to the total pool of soil organic carbon is generally very low (<3% in nearby Mediterranean ecosystems, Goberna et al., 2012; Navarro-Cano et al., 2014), we evaluated whether the postfire recovery in soil organic matter (PC1) determines ΔFungal PαD, ΔBacterial PαD and ΔArchaeal PαD in three separate models. In contrast, as soil microbes are both consumers (e.g., heterotrophs) and producers of mineral N (e.g., nitrifying microbes), we tested the bidirectional relationship between the postfire recovery of soil mineral N (PC2) and microbial phylogenetic diversity.

3 | RESULTS

3.1 | Fire effects on plant communities

Fire significantly decreased aboveground plant cover and biomass (Figure 1 and Supporting Information Figure S6, Table 1). In particular, fire decreased the plant cover of main families under unburned conditions, which were dominated by *Fagaceae* (plant cover % ± *SE*, 29 ± 3%), *Poaceae* (28 ± 3%) and *Lamiaceae* (18 ± 1%; Supporting Information Figure S7). While the reductions in plant cover were large for *Fagaceae* (−21 ± 6%), *Poaceae* (−18 ± 5%) and *Pinaceae* (−17 ± 3%), those for *Lamiaceae* (−10 ± 6%), *Fabaceae* (+1 ± 3%) and *Cistaceae* (+2 ± 2%) were less pronounced or even increased after fire (Supporting Information Figure S7). Both plant cover and biomass significantly tended to recover with time after fire (plant Δcover postmean estimate [95% credible interval] = 4×10^{-3} [3×10^{-3}, 6×10^{-3}]; Δbiomass = 0.13 [0.03, 0.22]). Plant cover recovered after 17 years while the recovery of the plant biomass was not reached during the time spanned in the study, but extrapolated to 24 years.

Fire did not significantly alter richness but decreased the phylogenetic α diversity of plant communities (Figure 2a,b and Supporting Information Figure S8, Table 1). In addition, the plant phylogenetic β diversity between pairs of burned and unburned transects (shaded area, Figure 2c) was higher than that between unburned transects

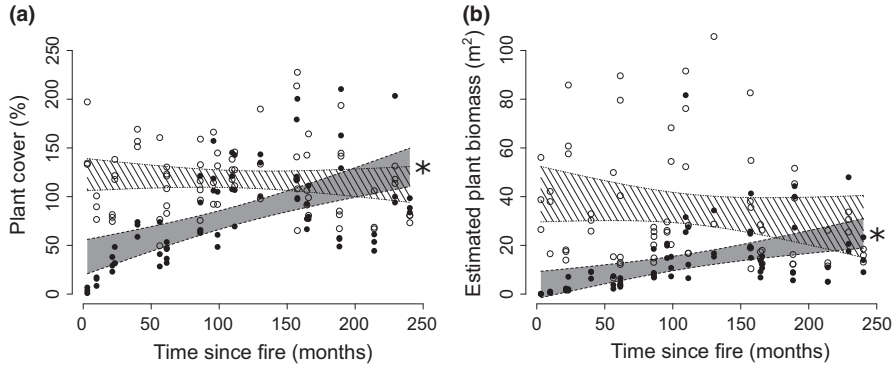

FIGURE 1 Postfire trends of (a) plant cover and (b) estimated biomass after fire. Filled circles indicate burned transects and unfilled circles unburned transects. Shaded and hatched areas show the confidence intervals of linear regressions among burned and unburned plots, respectively. Asterisks indicate the existence of a significant postfire temporal trend of the studied parameter measured as the paired difference (Δ) between burned and unburned transects ($p < 0.05$). See Section 3 for statistical details

TABLE 1 Short-term (0–3 years) fire effects on plant and soil microbial communities and soil parameters. *t* Tests ($df = 14$) comparing burned and unburned plots are shown. Significant differences ($p < 0.05$) between burned and unburned plots are indicated in bold

	Variable	Unburned plots	Burned plots	t_{14}	*p*
Plants	**Cover**	**1.21 ± 0.10**	**0.31 ± 0.06**	**−9.048**	**<0.001**
	Biomass	**37.4 ± 5.23**	**2.87 ± 0.85**	**−6.656**	**<0.001**
	Species richness	11.1 ± 0.60	10.4 ± 1.40	−0.577	0.573
	Phylogenetic α diversity	**1.70 ± 0.10**	**0.30 ± 0.20**	**−5.576**	**<0.001**
	Phylogenetic β diversity	**0.19 ± 0.02**	**0.38 ± 0.04**	**5.004**	**<0.001**
Fungi	**OTU richness**	**536 ± 23**	**454 ± 14**	**−2.844**	**0.013**
	Phylogenetic α diversity	**−2.29 ± 0.44**	**−0.50 ± 0.32**	**3.136**	**0.007**
	Phylogenetic β diversity	**0.29 ± 0.02**	**0.43 ± 0.03**	**3.532**	**0.003**
Bacteria	**OTU Richness**	**1621 ± 26**	**1492 ± 48**	**−3.442**	**0.004**
	Phylogenetic α diversity	**−3.06 ± 0.25**	**−2.14 ± 0.21**	**2.389**	**0.032**
	Phylogenetic β diversity	**0.12 ± 0.01**	**0.18 ± 0.01**	**4.394**	**<0.001**
Archaea	OTU Richness	10.9 ± 0.4	11.8 ± 0.5	1.370	0.192
	Phylogenetic α diversity	−1.68 ± 0.05	−1.76 ± 0.05	−1.555	0.142
	Phylogenetic β diversity	0.07 ± 0.01	0.08 ± 0.01	1.542	0.145
Soil parameters	**TOC (g/100 g)**	**13.8 ± 1.8**	**7.1 ± 0.4**	**−3.808**	**0.002**
	TN (g/100 g)	**0.8 ± 0.09**	**0.5 ± 0.04**	**−3.928**	**0.002**
	pH	**7.6 ± 0.08**	**8.0 ± 0.02**	**4.731**	**<0.001**
	Moisture (%)	**10.2 ± 1.0**	**5.5 ± 0.5**	**−5.652**	**<0.001**
	NO_3^--N (mg/kg)	**41 ± 13**	**94 ± 18**	**3.309**	**0.005**
	NH_4^+-N (mg/kg)	2.8 ± 0.9	2.5 ± 1.1	−0.132	0.897
	C/N ratio	**16.6 ± 0.6**	**13.7 ± 0.5**	**−3.470**	**0.004**
	EC (μS/cm)	235 ± 20	247 ± 18	0.673	0.512

Note. Plant cover is expressed as the fraction of the plot that is covered by one or more plant species. Note that the plant cover fraction can be >1 if there are overlapping canopies. Biomass is expressed as the total sum of the biomass per plant species.

(hatched area, Figure 2c, Table 1). That is, plant communities exposed to fire were more phylogenetically dissimilar to unburned plots than expected based on nondisturbed communities. Differences in plant richness, phylogenetic α and β diversities between burned and unburned plots were significantly reduced with time since fire (Δrichness = 0.02 [2.6×10^{-3}, 0.03]; $\Delta P\alpha D = 6.8 \times 10^{-3}$ [2.4×10^{-3}, 1.2×10^{-2}]; $P\beta D = -4.9 \times 10^{-4}$ [-9.5×10^{-4}, -9.5×10^{-5}]; asterisks in Figure 2). Plant phylogenetic α and β diversities were estimated to recover unburned levels on average after 20 and 32 years, respectively.

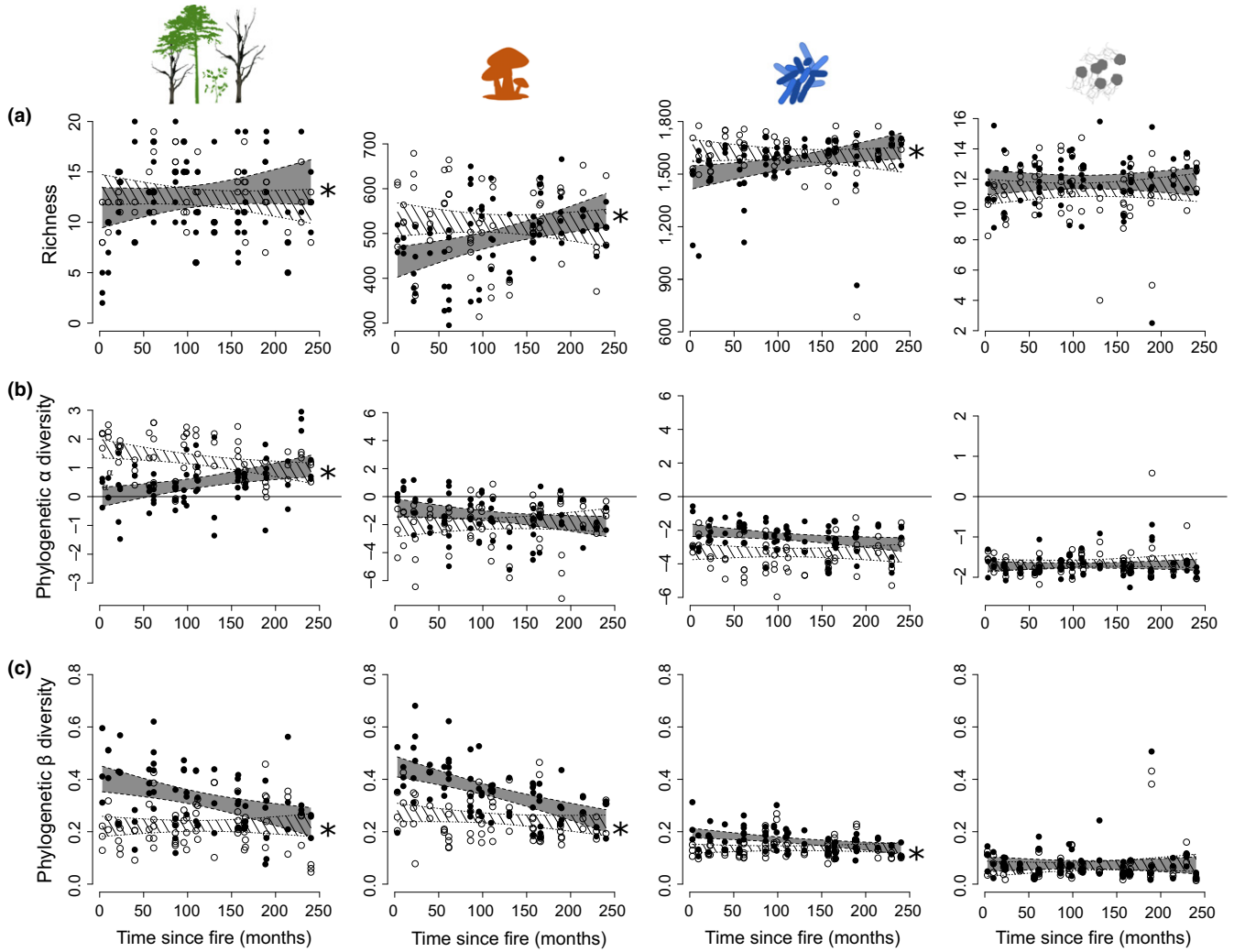

FIGURE 2 Postfire trends of (a) richness, (b) phylogenetic α diversity and (c) phylogenetic β diversity of plants, soil fungi, bacteria and archaea (from left to right). Filled circles indicate burned transects and unfilled circles unburned transects. In (a) and (b), shaded and hatched areas show the confidence intervals of linear regressions among burned and unburned plots, respectively. In (c), shaded areas indicate confidence intervals of the phylogenetic β diversity between each burned and unburned plot, and hatched areas between pairs of unburned transects. Asterisks indicate significant postfire temporal trends of the paired difference (Δ) between burned and unburned transects ($p < 0.05$). None of the temporal trends of unburned plots (i.e., hatched areas) were statistically significant. See Section 3 for statistical details. Silhouettes represent plant and soil fungal, bacterial and archaeal communities. Original images (from http://www.phylopic.org and http://www.silhouettevectorstock.com) have been slightly modified and are licensed for use either under the Public Domain Mark 1.0 (fungi) or under a Creative Commons Attirbution-ShareAlike 3.0 Unported licence (http://creativecommons.org/licenses/by-sa/3.0; pine, MM Tobias; bacteria and archaea, M Crook) [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Fire effects on soil conditions and microbial communities

Fire decreased soil TOC, TN, moisture and the C/N ratio, while it increased pH and NO_3^--N in the short term (Supporting Information Figure S9, Table 1). In the 20 years spanning our study, these initial changes only reverted for NO_3^--N and pH, whose unburned values recovered after approximately 12 and 18 years, respectively. Fire-driven changes in soil moisture decreased with time since fire, but they would require c. 21 years to reach the unburned level.

The effects of fire on the belowground communities were group-dependent. Archaea, which belonged mainly to *Crenarchaeota* (99 ± 0.3%) under unburned conditions, were resistant to fire as shown by the similar values in burned and unburned plots for all diversity metrics during the whole study period (Figure 2 and Supporting Information Figure S8, Table 1). However, fire initially decreased both fungal and bacterial richness (Figure 2a and Supporting Information Figure S8, Table 1). Richness recovered with time since fire (fungi = 0.56 [0.14, 0.93]; bacteria = 0.98 [0.56, 1.45]), and differences between burned and unburned plots diminished after 13 years (Figure 2a and Supporting Information

Figure S8). Fire provoked an initial increase in the phylogenetic α diversity of both fungi and bacteria, contrarily to plants (Figure 2b and Supporting Information Figure S8). The phylogenetic α diversity of fungal and bacterial communities tended to decrease with time since fire, but changes were not significant during the study period (fungi = -3.9×10^{-3} [-1.3×10^{-2}, 4.6×10^{-3}]; bacteria = -3.3×10^{-3} [-8.2×10^{-3}, 1.3×10^{-3}]). Both fungal and bacterial communities exposed to recent fires showed higher phylogenetic β diversity than expected based on the variability of nondisturbed communities (Figure 2c, Table 1). The phylogenetic β diversity between burned and unburned plots decreased significantly with time since fire (fungi = -8.7×10^{-4} [-1.2×10^{-3}, -5.8×10^{-4}]; bacteria = -2.5×10^{-4} [-4.0×10^{-4}, -1.2×10^{-4}]). Both fungal and bacterial communities recovered their prefire phylogenetic β diversity after 19 years. Compositional changes within fungi resulted from increases in *Ascomycota*, which altered the balance between *Ascomycota* (% DNA sequences ± *SE*, 52 ± 2%) and *Basidiomycota* (47 ± 2%) after recent fires (Supporting Information Figure S7). Fire did not alter in the short term the relative abundance of main bacterial phyla, that is *Actinobacteria* (27 ± 0.9%) followed by *Proteobacteria* (22 ± 0.4%), *Planctomycetes* (21 ± 0.5%) and *Acidobacteria* (9 ± 0.5%), although significant decreases in *Actinobacteria* and *Proteobacteria*, and increases in *Acidobacteria* were found after 5 years (Supporting Information Figure S7).

3.3 | Linkages between above- and belowground communities

To test our hypothesis, we performed sequential Bayesian GLMs, whose main results are schematized in Figure 3. First, we confirmed that the postfire increase in plant phylogenetic α diversity leads to the recovery of plant biomass (postmean = 9.3 [3.0, 15.35]). Further, the recovered plant biomass partly accounted for the amelioration of soil organic matter as reflected by its significant positive effect on the first axis (PC1) of a PCA performed on soil abiotic parameters (0.02 [0.006, 0.04]). Changes in soil PC2, which we interpreted as a gradient of recovery of mineral N, did not impact plant biomass (−4.0 [−9.5, 2.5]; Figure 3; Supporting Information Figure S5). Finally, we detected that postfire changes in the soil organic matter drove the recovery of soil fungal and bacterial phylogenetic α diversity, while that of archaeal phylogenetic α diversity was unrelated to the shifts in soil organic C or mineral N (PC1 = 0.01 [−0.03, 0.06]; PC2 = 0.02 [−0.04, 0.08]). In particular, both fungal and bacterial phylogenetic α diversity significantly decreased to prefire levels with soil organic C (fungi = −0.3 [−0.6, −0.07]; bacteria = −0.4 [−0.5, −0.2]), while PC2 did not explain shifts in fungal or bacterial PαD (fungi = 0.27 [−0.19, 0.72]); bacteria = −0.02 [−0.38, 0.29]). Changes in microbial PαD did not also significantly explain PC2 (fungi = 0.07 [−0.03, 0.18]; bacteria = −0.07 [−0.23, 0.12]; archaea = 0.20 [−0.31, 0.71]; Figure 3).

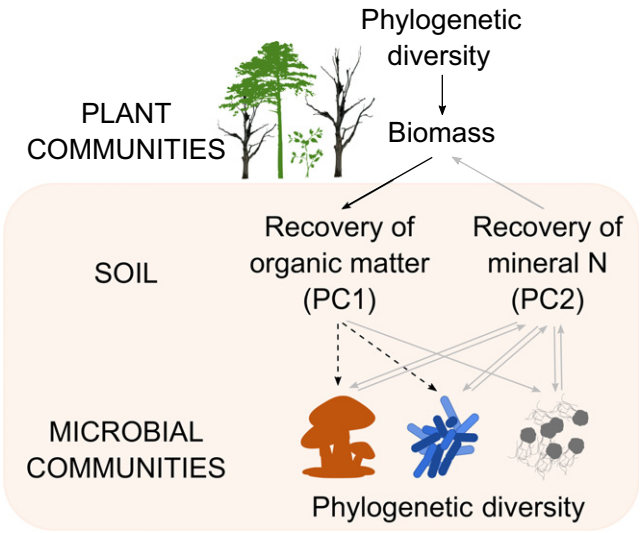

FIGURE 3 The recovery of plant phylogenetic diversity after fire significantly fosters plant biomass, which in turn ameliorates soil organic matter (PC1). The recovery of soil organic matter leads to a reduction in the fungal and bacterial phylogenetic α diversity. Black arrows indicate significant effects of Bayesian GLMs, with either positive (solid lines) or negative effects (dotted lines). Grey arrows indicate nonsignificant effects. Silhouettes represent plant and soil fungal, bacterial and archaeal communities as in Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

4 | DISCUSSION

Our results showed that fire had opposing effects on plant and soil microbial (fungal and bacterial) phylogenetic α diversity, while it did not alter archaeal diversity. By favouring evolutionarily related fire-prone species, fire reduced plant phylogenetic α diversity which was restored after two decades. These shifts triggered the recovery of soil organic matter that, in turn, drove the community reassembly of soil microbes. Fungal and bacterial phylogenetic α diversity, which increased in the short term after fire as a result of an altered competitive hierarchy, decreased with time since fire although more than two decades are necessary to return to predisturbance conditions.

Fire did not change the richness but altered the composition of plant communities, lowering their phylogenetic α diversity by favouring closely related plants. The resprouting of adult plants and the rapid emergence of seedlings from the seed bank after fire can explain the unaltered levels of plant richness, which can even increase due to the colonization by new species (Keeley, Bond, Bradstock, Pausas & Rundel, 2012). Similar species richness after fire can be obtained with different species composition and consequently, with different phylogenetic diversity, which tend to decrease in plant communities since fire favours the evolutionarily conserved seeder phenotype that is present in a few families (Verdú & Pausas, 2007). Here, we found a reduction in phylogenetic diversity to levels indistinguishable from the random expectation. In Mediterranean ecosystems, this pattern has been attributed to the combination of two

counteracting strategies, that is those of seeders belonging to a few families and resprouters spread across several families, that respectively push towards low and high phylogenetic diversities finally generating a random phylogenetic pattern (Verdú et al., 2009). Our results are in line with this explanation as seeders were slightly affected (*Lamiaceae*) or even favoured (*Cistaceae* and *Fabaceae*) by fire, while resprouters (*Fagaceae* and *Poaceae*) were harmed but not excluded from the community. Plant phylogenetic diversity significantly increased with time after fire, reaching the unburned level after c. 20 years. Such an increment has been attributed to the nurse effect of pioneer seeders that facilitate the recruitment of late-successional evolutionarily distant species (Verdú et al., 2009). At later stages, facilitation can turn into competition, further increasing the phylogenetic diversity of plant communities (Castillo, Verdú & Valiente-Banuet, 2010). In the long term, however, the prolonged absence of disturbance could favour the dominance of few highly competitive species declining the phylogenetic diversity of plant communities (Verdú et al., 2009). Experimental evidence shows that phylogenetically diverse plant assemblages produce higher biomass through species complementarity (Cadotte, 2013). Similarly, we found that the postfire increase in plant phylogenetic α diversity significantly drives plant productivity in terms of biomass, and this has further reflection on soil processes.

Main fire-induced changes in soil abiotic parameters included the reduction in organic substances and moisture, and a pulse in mineral nitrogen as has been widely reported in the literature (Certini, 2005). These parameters are major determinants of soil microbial composition and diversity in postfire scenarios (Goberna et al., 2012; Hart et al., 2005; Liu et al., 2015; Mikita-Barbato et al., 2015; Pérez-Valera et al., 2017). Belowground microbial communities exposed to fire showed specific responses that were group-dependent. Soil archaea were nonresponsive to fire in terms of richness, composition or phylogenetic diversity, suggesting that they are highly resistant both to heating and to the concomitant changes in soil parameters. In a previous study searching for immediate fire effects on soil microbiota in Mediterranean ecosystems, we detected shifts in archaeal diversity 1 day after fire that recovered as soon as 1 week later (Goberna et al., 2012). However, studies in other ecosystems point to shifts in archaeal communities that persist for at least 2 years (Mikita-Barbato et al., 2015). Fungal and bacterial communities showed parallel responses to fire, in spite of their enormous physiological and ecological differences such as heat tolerance or response to changes in organic compounds that suggest that fungi could be more sensitive to fire than bacteria (Cairney & Bastias, 2007; Hart et al., 2005; Mataix-Solera et al., 2009). Specifically, fire decreased richness, altered the community composition, and increased the phylogenetic α diversity of both fungal and bacterial communities. This is consistent with multiple studies that report fire-driven reductions in soil microbial richness (Ferrenberg et al., 2013; Kipfer, Egli, Ghazoul, Moser & Wohlgemuth, 2010; Pérez-Valera et al., 2017; Rincón et al., 2014; Smith, Kishchuk & Mohn, 2008; Visser, 1995; Xiang et al., 2014, 2015), although contrasting patterns have been also reported (Buscardo et al., 2014; Hamman, Burke & Stromberger, 2007; Holden, Gutierrez & Treseder, 2013; Rincón & Pueyo, 2010; Shen, Chen & Lewis, 2016; Sun et al., 2015). In Mediterranean ecosystems, the increment in phylogenetic α diversity has also been observed both for fungal and bacterial communities. Rincón et al. (2014) reported this trend in soil ectomycorrhizal fungi as consequence of the predominance of *Ascomycetes* after fire, which we also detected when targeting the whole fungal community. Fire-resistant *Ascomycetes* show rapid fruiting, stimulated growth and spore germination due to heating (Cairney & Bastias, 2007; Dix & Webster, 1995; Reazin, Morris, Smith, Cowan & Jumpponen, 2016; Smith et al., 2017), as well as lower sensitivity to dry conditions compared to *Basidiomycetes* (Rayner & Boddy, 1997; cited in Nordén, Götmark, Ryberg, Paltto & Allmér, 2008) making *Ascomycetes* more competitive under postfire conditions. Such a shift in the competitive hierarchies, together with the competition among postfire fungi (Dix & Webster, 1995), could explain the increase phylogenetic α diversity in the fungal community. In bacteria, we also attributed the increase in phylogenetic α diversity after an experimental fire to a shift in the competitive hierarchies (Pérez-Valera et al., 2017). Similarly, the fire-induced reduction in organic resources here detected can diminish the competitiveness of dominant taxa from entire clades that have high relative fitness under carbon-enriched conditions (Goldfarb et al., 2011), leading to an increased phylogenetic α diversity. This is supported by the fire-induced reduction in the relative abundance of both *Proteobacteria* and *Actinobacteria*, lineages that possess high competitive abilities for organic carbon substrates (Goldfarb et al., 2011). In addition, the alleviation of such a biotic filter sets the conditions for a stronger competition between closely related taxa with similar niches, for example fast-growing bacteria that benefit from the pulse in mineral N, which would further increase the phylogenetic diversity of the bacterial community (Mayfield & Levine, 2010).

The decreasing phylogenetic trends in α diversity of soil microbes with time since fire contrast with the tendency of plant phylogenetic α diversity to increase after disturbance. The main driver of the recovery of microbial phylogenetic α diversity was the restoration of soil organic matter supplied by an increasingly productive and phylogenetically diverse plant community. These results suggest that the evolutionarily related microbial taxa that dominate under high soil fertility recover their competitive strength as communities reassemble. Despite the opposing patterns in phylogenetic α diversity of above- and belowground communities, phylogenetic β diversity showed a consistent response for plants, fungi and bacteria. We detected a significant increase in the phylogenetic turnover of all groups in the short term after the wildfires under study. Others have reported a strong community turnover following intense fires and highlighted their potential to promote spatial patchiness and thus β diversity (Reazin et al., 2016). Phylogenetic turnover across all biological domains recovered prefire levels after two decades. Therefore, we can speculate that, even under the current accelerated fire regimes (Pausas & Fernández-Muñoz,

2012), our studied communities had enough time to recover. Further studies are needed to corroborate these results in other ecosystems, as ours are restricted to Mediterranean ecosystems and specific environmental conditions. The resilience of plant and soil microbes to current fire regimes guarantees the conservation of the old evolutionary legacy represented by all the biological domains in the tree of life. However, the increasing rates of disturbance the Earth is now facing could dramatically reduce the resilience of these biological lineages by eroding the phylogenetic diversity from which the communities are reassembled (Tan et al., 2012).

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DATA ACCESSIBILITY

DNA sequences: European Nucleotide Archive accession: http://www.ebi.ac.uk/ena/data/view/PRJEB13469 and http://www.ebi.ac.uk/ena/data/view/PRJEB13853. RData object containing phylogenetic trees of archaea, bacteria, fungi and plants: Dryad https://doi.org/10.5061/dryad.240t21v

AUTHORS' CONTRIBUTIONS

E.P.V., M.G. and M.V. designed the study. All authors collected field data, performed and discussed analyses. E.P.V., M.G. and M.V. wrote the manuscript and J.A.N.C. contributed to revisions.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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