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Short communication

Forest soil microbial functional patterns and response to a drought and warming event: Key role of climate–plant–soil interactions at a regional scale

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ABSTRACT

Little is known about how spatial and environmental patterns structure soil microbial activities. We investigated, on 47 soil samples collected in Mediterranean forests, the net and interaction effects of climatic-geographic and edaphic variables as well as vegetation cover and composition on soil microbial community-level physiological profiles (CLPPs) assessed by Microresp™. The effects of these variables were also analyzed on CLPP response to an experimental drought treatment. CLPPs were shown to be mainly driven by climate–plant–soil and plant–soil interactions; even after drought treatment, there was a decrease in microbial activity but no change in CLPPs. Our findings highlight the robustness of these relationships, which need to be assessed within different ecosystems considering various spatial scales to reliably predict climate change effects on terrestrial ecosystems.

It remains difficult to predict the responses of plant and microbial community relationships to climate change (Bardgett et al., 2008), partly due to lack of knowledge about the deterministic factors of the soil microbial functional patterns directly linked to ecosystem processes (Green et al., 2008; Griffiths et al., 2011). Focusing on Mediterranean forest ecosystems, particularly vulnerable to increased length of summer drought and frequency of heatwaves (IPCC, 2007), the aims of our study were first to assess the environmental surrogates driving soil microbial community-level physiological profiles (CLPPs), and then to determine the robustness of their relationships with environmental surrogates after an experimental *ex situ* hard "drought" event, like those that occur in Mediterranean regions.

The study area, about 7000 km^2 (long 4°5′–6°2′ E, lat 43°4′, 43°5′ N), is situated in an area of limestone-based soil in Provence, Southeastern France, with a Mediterranean climate (severe summer drought and mild humid winters). Forests are mixed stands of *Pinus halepensis* Mill., *Quercus ilex* L. and *Quercus pubescens* Willd. 47 soils were sampled across the area, covering a bioclimatic gradient (Fig. S1) during the 2010 summer drought period, when extreme heatwave events are likely to occur. On each plot (20 m × 20 m), 12 subsamples from the upper soil horizon (0–5 cm) were systematically cored along 3 transects (5, 10 and 15 m from the border), with 4 subsampling points on each transect at 4, 8, 12 and 16 m. All subsamples of the same plot were pooled to obtain a composite sample. Samples were then sieved at 2 mm, air-dried (due to the length of the sampling period, one month) and stored until analysis.

Soils were rewetted to 70% water holding capacity (WHC) (identified in pre-testing as optimal value to increase basal respiration in our 47 soils while conserving their variability, as against 30% and 50% WHC, *data not shown*) and incubated at 25 °C for eight days to standardize and equilibrate them before Time 0 (T0) analysis (Goberna et al., 2005). T0 CLPPs were determined by Microresp™ measuring substrate-induced respirations (SIR) on eight substrates, glucose (gluc), sucrose (suc), trehalose (treha), D+ cellobiose (cello), glycine (gly), caffeic acid (caff), ellagic acid (ella) and catechol (cat), following the adapted protocol of Campbell et al. (2003). Briefly, our aim being to compare SIRs of soils subjected to the same solution of substrate instead of their absolute rate of mineralization, we used the lowest water content among our samples to determine concentration of C substrate solutions; solutions were adjusted to pH = 7, a mean value of soil pH (Table 1), both to minimize chemical artifacts due to carbonate-derived CO_2 release and to avoid any

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Table 1
Descriptive statistics of the climatic–geographic (CG) and edaphic (EDA) variables. Soil texture is presented for informative purposes as a percentage of soil samples.

CG variables	Unit	Minimum	Maximum	Mean	Median	Std	Abbr
Elevation	m	30	770	387	370	189	elev
Becker light-climate index	(–)	0.24	1.34	0.93	1.00	0.28	ikr
Mean annual rainfall	mm	530	1088	736	700	117	annrain
Summer rainfall	mm	58	175	109	110	29	sumrain
Mean annual temperature	°C	9.30	14.80	12.38	12.30	1.34	anntemp
Cumulated elevation direction south south east	hm	0	3600	1516	1200	1098	elevcumsse
Distance to the sea direction south south east	km	1	86	44	50	24	distsea
Cumulated elevation direction west south west	hm	0	1700	589	500	437	elevcumwsw
Distance to the sea direction west south west	km	1	75	37	38	22	distseawsw
Distance to the ridge	m	0	3050	276	75	598	distridge

EDA variables	Unit	Minimum	Maximum	Mean	Std	Abbr
Parent rock outcrops on the plot	%	0.00	65.00	4.90	13.40	proc
Total soil depth	cm	20.00	150.00	83.94	36.05	depth
Stones on litter ratio	(–)	0.01	0.15	0.05	0.06	st/lit
Coarse fragments in the topsoil	%	0.00	62.50	26.78	23.37	cofr
Number of fine roots (<2 mm) in the topsoil	/dm2	1.50	15.00	13.82	2.80	roots
pH value	(–)	6.43	7.58	7.16	0.29	pH
Calcium Carbonate content	g/100 g dry matter	0.00	45.73	13.82	12.63	CaCO3
Organic Carbon content	g/100 g dry matter	3.20	21.53	11.31	4.46	Corg
Total Nitrogen content	g/100 g dry matter	0.10	0.93	0.48	0.19	Ntot
Organic Carbon on total Nitrogen ratio	(–)	14.48	32.19	24.16	4.65	Corg_N
Water holding capacity of sieved soil	g/100 g dry matter	39.31	161.60	96.35	25.99	WHC
Water holding capacity based on soil texture	mm/cm	1.30	1.95	1.71	0.19	whcst
Soil texture (Based on the silt, sand, clay fractions of soil samples)	% of soil samples	Silty–clayey		51.06		
		Sandy–silty		19.15		
		Sandy–silty–clayey		29.79		

Abbr: abbreviation; Std: standard deviation.

substrate-pH effect on microbial communities (Bérard et al., 2011). After T0 measurements, samples were dried for ten days at 50 °C, to obtain "stressed" samples (ST), rewetted and maintained at 70% WHC, 25 °C for eight days. Simultaneously, 47 "unstressed" samples (NS), already subjected to the standardization conditions, were maintained at 70% WHC, 25 °C throughout. SIRs on both "NS" and "ST" samples were measured in the same way as at T0.

Organic carbon (Corg) and total nitrogen (Ntot) contents, Corg_N ratio, pH and water holding capacity (WHC), variables constitutive of the EDA compartment, were determined via the usual procedure for soil physicochemical analyses (Forster, 1995). Climatic and geographic variables (CG compartment) presented in Table 1, vegetation composition and structure of each plot (VEG compartment, list of species given Table S1), as well as other EDA variables (Table 1) are based on data from Vennetier et al. (2008) and Vennetier and Ripert (2009).

Before statistical analyses, SIRs on each substrate and each sample were standardized by scaling (subtracting the mean SIR of all soils on all substrates, then dividing by the standard deviation). RDA sets combining selected variables from the various compartments and derived adjusted R^2 values, followed by both variance partitioning analysis and Monte Carlo permutation tests, were used to assess both their relative impact and their interactions on T0 CLPPs and on their responses to drought. Effects of each compartment (individual effect) were thus broken down into real individual effect (net effect) and effect through their interactions (interaction effect), and synthesized through Venn diagrams. It was not possible to statistically test the significance of the interaction effect. T0, NS and ST CLPPs were compared through PCA. Two-way ANOVA followed by Tukey LSD *post hoc* tests were performed to assess the effects of interaction between drought treatment (T0, NS, ST) and type of substrate. CLPP response to drought was assessed by

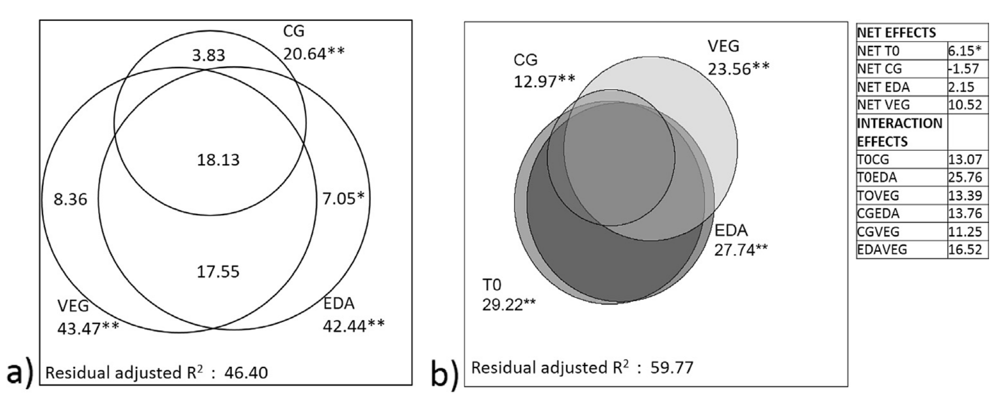

Fig. 1. a), b): Venn diagram of the individual, interaction and net effects of **a)** the various environmental compartments Climatic-geographic (CG), Edaphic (EDA) and Vegetation (VEG) on initial CLPPs (T0); Adjusted R-squared for each part of the circles are indicated with result of Monte–Carlo permutation test *p* value significance (*p* values are not shown; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$). **b)** The various environmental compartments Climatic-geographic (CG), Edaphic (EDA) and Vegetation (VEG), and initial CLPP (T0) on CLPP responses to drought; adjusted R-squared of individual effects are indicated on the diagram with their significance level **: $p < 0.01$; net effects and interaction effects are indicated near the diagram with their significance level (*: $p < 0.05$). The squares represent 100% of variance explained. Significance of the impact due to interactions could not be tested.