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Soil biota response to experimental rainfall reduction depends on the dominant tree species in mature northern Mediterranean forests

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ABSTRACT

Soil organisms play a major role on litter decomposition process and nutrient cycling in forest ecosystems. These organisms are extremely sensitive to environmental conditions such as soil temperature and moisture conditions which control their demographic parameters and activity. The ongoing climate change can therefore directly affect soil biota communities and the processes they drive. Besides, climate change can also indirectly affect soil biota by altering tree functional traits (e.g., N, Ca, Mg, water holding capacity) with cascading effects on the litter quality. The aim of this study was to determine the relative effects of increased drought and litter type on microbial biomass (bacteria and fungi) and mesofauna abundance (Collembola and Acari) in three experimental sites representative of the three main forests encountered in the northern part of the Mediterranean Basin (dominated by either *Quercus pubescens*, *Quercus ilex* or *Pinus halepensis*) where rainfall exclusion experiments were taking place. At each site, and in each precipitation treatment (natural and amplified drought plots), we collected and transplanted foliage litters (i.e., species × drought level). After two years, we reported a litter species effect: *Q. pubescens* litter presented consistently the higher abundance of all soil biota groups compared to *Q. ilex* and *P. halepensis* litters in each forest. Surprisingly, despite that the amplified drought treatment induced a modification of the litter quality, we did not reported an indirect reduced precipitation effect on soil biota parameters. While Oribatid Acari abundance decreased with amplified drought in all three forest types, the direct effects on the other soil biota groups were forest-dependent. In *P. halepensis* forest, amplified drought resulted in higher bacterial and fungal biomasses but lower Collembola abundance. In *Q. ilex* forest both Collembola and predatory Acari abundances decreased with amplified drought. In addition, the positive relationships between Collembola and Oribatida abundances and litter mass loss disappeared under amplified drought conditions in both *Q. ilex* and *P. halepensis* forests. These results suggest a key role played by Ca, Mg, specific leaf area (SLA) and water holding capacity (WHC) as drivers of soil biota parameters. Finally, the study highlights that within the same Mediterranean region, climate change could differently alter the soil organisms inhabiting the litter layer and their contributions to the decomposition process depending on the tree species and soil biota group considered.

1. Introduction

Litter is one of the basal elements of a food web that controls nutrient turnover, carbon sequestration and the overall ecosystem functioning (Wall et al., 2012; Gobat et al., 2013). Among soil biota, mesofauna (mainly Collembola and Acari) drives many biotic interactions which are fundamental for structuring the soil food web and decomposing leaf litter. Firstly, microbi-detritivore organisms (e.g., Collembola and Oribatid Acari) participate directly to the micro-fragmentation of leaf litter, but also control microbial communities through grazing and

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dispersing spores and mycelium (Berg and Laskowski, 2005; Chahartaghi et al., 2005; Scheu et al., 2005; Anslan et al., 2016). Secondly, predators (e.g., Mesostigmatid and some Prostigmatid Acari) regulate microbi-detritivore organisms by feeding on them (Koehler, 1999; Schneider and Maraun, 2009; Thakur et al., 2015) and then indirectly control the leaf litter decomposition.

Chemical and physical characteristics of the leaf litter strongly control soil mesofauna demographic parameters and interactions (Hättenschwiler et al., 2005; Chomel et al., 2016; Santonja et al., 2018; Aupic-Samain et al., 2019). Under the specific Mediterranean climatic conditions (summer drought and episodic drying/rewetting cycles; Larcher, 2000; Sardans and Peñuelas, 2013; Gauquelin et al., 2018), trees generally produce sclerophyllous leaves (Coûteaux et al., 1995) characterized by high lignin concentration (Tian et al., 1992; Gallardo and Merino, 1993), low specific leaf area (Wright et al., 2005; Pallardy, 2010) and high diversity and concentration of specialized metabolites (i.e., terpene and phenolic compounds; Macchioni et al., 2003; Fernandez et al., 2009). These particular characteristics of Mediterranean trees could potentially lead to distinct litter quality control over soil mesofauna compared to the other temperate forests for which litter nutrient contents (e.g., C, N and P) are frequently reported as key drivers of soil mesofauna demographic parameters (Jandl et al., 2003; Martinson et al., 2008; Jacob et al., 2009; Maaroufi and De Long, 2020). However, to our knowledge, only few studies investigated this effect of litter quality on soil mesofauna in Mediterranean forests (e.g., Barba et al., 2016; Santonja et al., 2017; Aupic-Samain et al., 2019), necessitating deeper investigation to improve our mechanistic understanding of such relationships.

Among terrestrial biomes, Mediterranean ecosystems are recognized as being the most sensitive to climatic change (Sala et al., 2000; Schröter et al., 2005). Regional climate models for the Mediterranean Basin predict a warming of 3.4 °C and a decrease of annual precipitations by 30% for the end of the 21st century, which will result in an intensification of summer drought events (Giorgi and Lionello, 2008; IPCC, 2013; Polade et al., 2014). Therefore, by decreasing water availability, climate change in Mediterranean ecosystems may have a direct negative impact on soil microorganisms (e.g., Sardans and Peñuelas, 2010; Talmon et al., 2011) and mesofauna (e.g., Tsiafouli et al., 2005; Santonja et al., 2017). In addition, climate change may indirectly impact microbial and mesofaunal communities by altering litter quality and quantity produced by plants as climatic conditions strongly control plant growth and survival and consequently leaf and litter traits (Wright et al., 2005; Sardans and Peñuelas, 2007; Rodriguez-Ramirez et al., 2017). Indeed, previous studies reported that experimental decrease in water conditions implies lower nutrient content (Chen et al., 2013; Santonja et al., 2019) and higher specialized metabolite content (Hernández et al., 2004; Munné-Bosch and Peñuelas, 2004) with potential negative cascading effects on soil biota (Allison et al., 2013; García-Palacios et al., 2016a; Santonja et al., 2019). In addition, oaks and pines are dominant tree genera that structure both temperate and Mediterranean forests (Ellenberg, 1988; Quézel and Médail, 2003). As oak and pine forests exhibit different microclimatic and soil properties (e.g., pH, soil type, humus forms; Table 1; Gauquelin et al., 2016) as well as chemically and structurally different litters (oak leaves *vs.* pine needles; Aupic-Samain et al., 2019; Santonja et al., 2015), we could expect that climate change may distinctly affect soil biota in these two forest types. However, our current understanding of soil biota responses to climate change drivers in Mediterranean oak and pine forests is still limited by a lack of studies addressing conjointly the relative contributions of environmental conditions and leaf litter quality and both direct and indirect effects of climate change on these organisms.

In this context, we set up a 2-year litter transplant experiment in the three main forests encountered in the northern part of the Mediterranean Basin (*Quercus pubescens*, *Quercus ilex* and *Pinus halepensis* dominated forests) in which we manipulated the amounts of precipitation (natural *vs.* amplified drought), the litter species identity (leaf/needle litters from the three tree species) and the litter type (litters collected from natural or amplified drought plots) in order to determine their relative effects on soil biota, including both microbial (bacteria and fungi) and mesofaunal (Acari and Collembola) communities. We hypothesized that i) microbial biomass and mesofaunal abundance associated with decomposing oak leaves are higher compared to pine needles due to lower amount of refractory compounds (e.g., specialized metabolites); ii) reduced precipitation directly decreases microbial biomass and mesofaunal abundance as water availability is a strong constraining environmental factor; iii) reduced precipitation indirectly decreases microbial biomass and mesofaunal abundance due to a decrease in leaf/needle litter quality (e.g., increased specialized metabolite content) and iv) soil biota will be more sensitive to reduced precipitation in oak compared to pine forests where soil biota is already conditioned by more constraining environmental conditions (e.g., litter content).

Table 1
Main characteristics of the three studied forests. MAT and MAP correspond respectively to the annual mean values of temperature and precipitation between 2008 and 2019 in natural precipitation (ND) and amplified drought (AD) plots (Supplementary Fig. S2). These values did not significantly differ between the forest sites (One-way ANOVAs, $F_{site} = 0.6$; $P > 0.05$, $F_{site} = 1.7$; $P > 0.05$ and $F_{site} = 1.8$; $P > 0.05$ for MAT, MAP in ND plots and MAP in AD plots, respectively).

Forests	*Quercus pubescens* Willd.	*Quercus ilex* L	Mixed *Pinus halepensis* Mill.
Sites	Oak Observatory at the Observatoire de Haute Provence (O3HP)	Puéchabon	Font-Blanche
Location	430 56′ 115″ N, 050 42′ 642″ E	43° 44′ 29″N, 3°35′ 45″E	43°14′27″ N, 5°40′45″ E
Altitude a.s.l. (m)	650	270	425
MAT (°C)	12.6	14.0	13.7
MAP ND (mm)	866.3	955.4	605.0
MAP AD (mm)	639.5	698.9	441.6
Soil type	pierric calcosol	rhodo-chromic luvisol	leptosol
Soil texture	clay	clay loam	clay
Soil pH	6.76	6.6	6.8
Surface rocks cover (%)	23	75	50
Dominant tree species	*Quercus pubescens* Willd	*Quercus ilex* L.	mixed *Pinus halepensis* Mill./ *Quercus ilex* L.
Other dominant plant species	*Acer monspessulanum* L *Cotinus coggygria* Scop.	*Buxus sempervirens* L. *Phyllirea latifolial* L. *Pistacia terebinthus* L. *Juniperus oxycedrus* L.	*Quercus coccifera* L. *Phyllirea latifolia* L.
Tree density (stems/ha)	3503	4500	3368
Forest structure	even-age (70 years)	even-age (74 years)	uneven-age (61 years)
Type of rain exclusion system	Dynamic system: moving roof device	Permanent system: PVC gutters	Permanent system: PVC gutters
Rain exclusion system dimensions (m2)	300	140	625
Rain exclusion device installation	2012	2003	2009

2. Materials and methods

2.1. Study site

The study was concurrently set up in three Mediterranean experimental sites (Table 1). The first is the Oak Observatory at the "Observatoire de Haute Provence" (O_3HP) located in the Luberon Natural Regional Park (43°45′34.26″N; 5°17′57.84″E), in Provence, SE France (Gauquelin et al., 2011). This oak forest is dominated by deciduous downy oak (*Quercus pubescens* Willd.). The second site is located in the Puéchabon State Forest (43°44′30″ N; 3°35′40″ E) in Occitanie, SE France (Misson et al., 2010). This oak forest is dominated by the evergreen holm oak (*Quercus ilex* L.). The third site is located in the departmental forest of Font-Blanche (43°14′25″N; 5°40′40″E) in Provence, SE France (Simioni, 2011). This is a mixed forest, but Aleppo pine (*Pinus halepensis* Mill.) is the most abundant species, contributing around 70% of the basal area. During the two years of field experiment, the mean annual precipitation ranged from 635.6 mm in the *P. halepensis* forest to 1020.9 mm in the *Q. ilex* forest, while the mean annual temperature ranged from 12.3 °C in the *Q. pubescens* forest to 14.1 °C in the *P. halepensis* forest (Supplementary Fig. S2).

In order to simulate the intensification of the summer drought period, each site is equipped with a rain exclusion device reducing approximatively 30% of annual precipitation (similar to climatic models projection – A2 scenario; Giorgi and Lionello, 2008; IPCC, 2013). In the *Q. pubescens* forest the rain exclusion device consists of a 15 m × 20 m rainout-shelter above the canopy which dynamically excluded precipitations by deploying automated shutters during rainfall events of the vegetation growing season (i.e., from spring to autumn) (Supplementary Fig. S2a). In the *Q. ilex* and *P. halepensis* forests the rain exclusion is performed by using fixed PVC gutters installed below the forest canopy, excluding about 30% at each rainfall event (Supplementary Figs. S2b and c). In each site, we compared control plots (natural drought - ND) and rain exclusion plots (amplified drought – AD) (Table 1 and Supplementary Fig. S1).

2.2. Litter collection

Freshly abscised leaves and needles of *Q. pubescens*, *Q. ilex* and *P. halepensis* were collected in ND and AD plots over the litterfall period in 2014. For that, litter traps were used during the abscission period that occurred from June to September for the needles (*P. halepensis*) and from October to November for the leaves (*Q. ilex* and *Q. pubescens*). Immediately after collection, the leaves/needles were air dried at room temperature and stored until the beginning of the experiment. Several aliquots of senescent leaves or needles were also frozen at −20 °C, freeze-dried for 72 h and ground prior to chemical analyses.

2.3. Experimental design

Plant litter decomposition was studied over 730 days using the litterbags method (Swift et al., 1979). In December 2014, 10 g (in equivalent dry weight) of senescent leaves or needles of either *Q. pubescens*, *Q. ilex* and *P. halepensis* collected from trees either in ND or AD plots were placed in a 4-mm mesh litterbag (20 × 20 cm) designed to allow colonization by microbes and mesofauna. Litter transplants were made between each site for the three species considered, i.e., a litter bag containing the litter of each species placed on each forest site, under the two precipitation conditions, i.e., ND and AD (see Fig. 1).

Thus, the experiment consisted in 36 treatment combinations corresponding to 3 forest sites (*Q. pubescens*, *Q. ilex* and *P. halepensis* forests) × 3 litter species (*Q. pubescens*, *Q. ilex* and *P. halepensis*) × 2 litter types (litters collected from ND or AD plots) × 2 precipitation treatments (ND and AD) (Fig. 1). Each modality had 5 replicates for a total of 180 litterbags. Litterbags were placed perpendicularly to the gutters system in *Q. ilex* and *P. halepensis* forests and under the rain exclusion device in the *Q. pubescens* forest by using 5 transects (i.e., 5 replicates of the 6 litterbag modalitites) equidistant from each other (1 m distance between the 5 transects and 0.6 m between the 6 litterbags). Transects were oriented E-W. They were placed on the ground after the removal of the litter layer and fixed to the soil with galvanized nails to prevent movement by animals or wind. The litter layer was then replaced over the litterbags. In December 2016, i.e., after 730 days of decomposition, all the litterbags were harvested and sealed in plastic bags to prevent the further loss of biological material.

2.4. Initial litter characteristics

Initial litter quality of the three litter species (*Q. pubescens, Q. ilex* and *P. halepensis*) collected from the two precipitation treatments (ND and AD) was determined from five samples.

Carbon (C) and nitrogen (N) concentrations were determined by thermal combustion on a Flash EA 1112 series C/N elemental analyzer (Thermo Scientific®, Waltham, MA, USA). Phosphorus (P) and cations, i.e., calcium (Ca), sodium (Na), potassium (K) and magnesium (Mg), were extracted from 80 mg of grounded litter with 8 ml of $HN0_3$ and 2 ml of H_2O_2. Then, samples were heated at 175 °C for 40 min using a microwave digestion system (Ethos One, Milestone SRL, Sorisole, Italy).

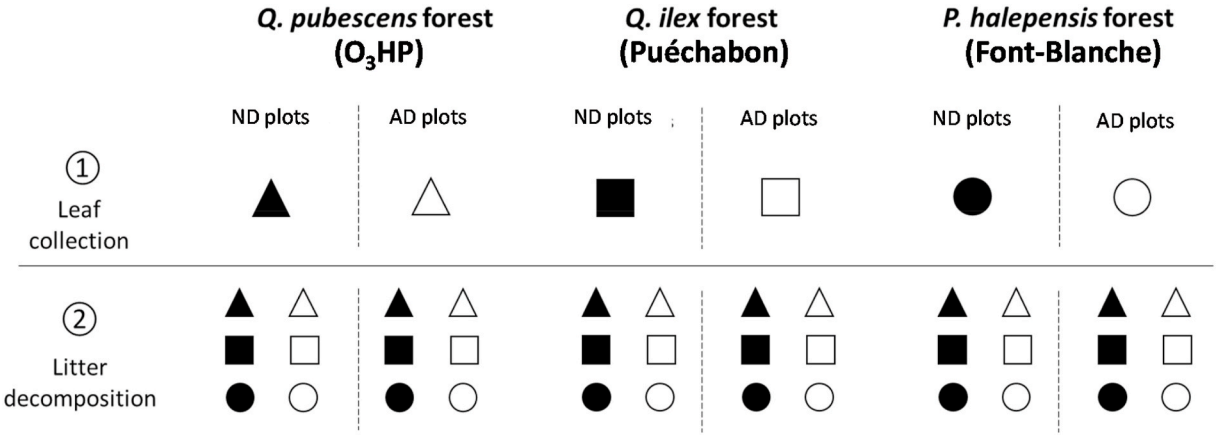

Fig. 1. Schematic design of the field experiment. First, we collected senescent leaves or needles in three forest sites (*Quercus pubescens* forest, *Quercus ilex* forest or *Pinus halepensis* forests) according to the two precipitation treatments (natural or amplified drought plots). Second, we performed a 2-year litter decomposition experiment using the two litter types of the three litter species placed in the two precipitation treatments of the three forests. ND = natural and AD = amplified drought.

After this mineralization step, every sample was adjusted to 50 ml with demineralized water. P concentration was measured colorimetrically using the molybdenum blue method (Grimshaw et al., 1989). 100 µl of sample, 100 µl of NaOH, 50 µl of mixed reagent (emetic tartrate and ammonium molybdate solution) and 50 µl of ascorbic acid were mixed directly in a 96 well microplate. After 45 min at 40 °C, the reaction was completed, and P concentration was measured at 720 nm using a microplate reader (Victor, Perkin Elmer, Waltham, MA, USA). Cations concentrations were determined by atomic absorption spectrophotometer. Total phenolic compounds were measured colorimetrically by the adapted method of Peñuelas et al. (1996) using gallic acid as standard (expressed as equivalent acid gallic). 250 mg of litter sample were extracted in 20 ml of a 70% aqueous methanol solution, shaken for 1 h, and then filtered (0.45 µm filter); 50 µl of filtered extract were mixed with 200 µl of saturated aqueous Na_2CO_3 (to stabilize the color reaction), 1650 µl of distilled water and 100 µl Folin-Ciocalteu reagent (Folin and Denis, 1915). After 30 min, the reaction was completed, and the concentration of phenolics was measured at 765 nm on a UV/Vis spectrophotometer (Thermo Scientific®, Waltham, MA, USA). Lignin, cellulose and hemicellulose as well as water soluble compounds (WSC) concentrations of initial litter materials were determined according to the Van Soest extraction protocol (Van Soest, 1963) using a fiber analyzer (Fibersac 24, Ankom, Macedon, NJ, USA). All concentrations were expressed in mg g^{-1} of litter dry weigh.

To determine the Water Holding Capacity (WHC), intact leaf or needle were soaked in distilled water for 24 h, drained and weighed. The dry weight was determined after drying the samples at 60 °C for 48 h. WHC was calculated as (moist weight/dry weight) × 100 and expressed in % (Santonja et al., 2015). Specific Leaf Area (SLA) was calculated as the ratio between leaf area (determined by using the Image J software; https://imagej.nih.gov/ij/, MA, USA) and dry weight and was expressed in cm^2 g^{-1} of dry weigh.

2.5. Mesofauna extraction and identification

Mesofauna was extracted from one litterbag using the Tullgren funnel method for 10 days (Berlese, 1905). Collected arthropods were stored in 70% ethanol, counted by using a binocular microscope and separated between Collembola and Acari, with different suborders for the latter: Oribatid, Mesostigmatid and Prostigmatid Acari (Gisin, 1960; Hopkin, 1997). Collembola and Oribatid Acari were assigned as microbi-detritivores and Mesostigmatid and Prostigmatid Acari as predators (Coleman et al., 2004; Donoso et al., 2013; Crotty et al., 2014; Santonja et al., 2017).

2.6. Litter mass loss estimation

After mesofauna extraction, the litter samples were freeze-dried (Lyovac GT2) for 72 h and the remaining dry mass (%) after 730 days of decomposition was calculated.

2.7. PLFA analyses

Since, the phospholipid fatty acids (PLFA) are essential components of all living cells (Tollefson and McKercher, 1983; Zelles, 1999) with a wide structural diversity (Zelles, 1997; Tornberg et al., 2003), we used PLFA as biomarkers of litter microbial communities. The PLFA were extracted from freeze-dried ground litter according to the method from Buyer and Sasser (2012) with modifications. Four ml of Bligh–Dyer extractant containing 4 µl of 1,2-dinonadecanoyl-sn-glycero-3-phodphocholine (C19:0; Avanti® Polar lipids, Inc.) as internal standard were added to 0.5 g of samples. Lipids separation was performed by solid-phase extraction (SPE) on Phenomenex® (Strata SI-1 with 50 mg of silica, 55 µm, 70 Å). The resulting fatty acid methyl ester (FAMEs) were analysed by gas-chromatography/mass-spectrometry (GC-MS) on an Agilent 7890 system equipped with an MSD5977A Network mass detector, an ALS7693 automatic injector and an HP5-MS apolar column (30 m × 0.25 mm × 0.25 µm; J&W Agilent Technologies) and MassHunter software. Qualitative analysis of FAMEs resulted by retention time comparison via FAMEs mixture (range between C4 to C24). The total PLFA concentration was used as measure of the total microbial biomass, while fungal and bacterial biomasses were estimates through PLFA markers summed (Frostegård and Bååth, 1996). Biomasses were expressed in µg g^{-1} dw of litter. Among the 24 identified PLFAs in the samples, 12 microbial specific PLFAs were analysed. The fatty acids i15:0, a15:0, i16:0 and i17:0 were used as biomarkers for Gram-positive bacteria; 16:1ω7, 18:1ω7 and cy19:0 were used as biomarkers of Gram-negative bacteria; 15:0, 17:0 were used as general bacterial markers and 19:1ω8 were used as biomarkers of methane oxidizing bacteria (Frostegård et al., 1993). The total bacterial PLFA biomass was calculated by adding Gram-positive, Gram-negative and general bacterial biomarkers while 18:2ω6,9 was used as a biomarker of fungi (Bååth and Anderson, 2003; Klamer and Bååth, 2004).

2.8. Statistical analysis

Statistical analyses were performed using a combination of univariate and multivariate techniques with R software (version 3.3.1). Statistical significance was evaluated in all cases at $P < 0.05$. Normality and homoscedasticity of the residuals were checked using Shapiro-Wilk and Levene tests, respectively.

To analyse the differences of the initial characteristics of the three litter species (*Q. pubescens, Q. ilex* and *P. halepensis*) and the two litter types (leaves or needles collected from trees in ND or AD plots) we performed a Principle Component Analysis (PCA) followed by pairwise tests with permutational multivariate analyses of variance (PERMANOVA; Anderson, 2005) using the *adonis* function of the *vegan* package (Oksanen et al., 2007, 2013).

Four-way analyses of variance (ANOVA), followed by Tukey tests for post-hoc pairwise comparisons, were used to test the effects of forest site, litter species identity, precipitation treatment, litter type and their interactions on the 5 soil biota parameters previously log-transformed: abundances of Collembola, Oribatida, and predator and biomasses of bacteria and fungi. The full models were then simplified to determine the most parsimonious models using the *dredge* function of *MuMIn* package (Barton, 2016), an established model selection procedure with both forward and backward selection algorithms, which ranks all candidate models (all possible combinations of the initial explanatory variables included in the full model) based on the lowest Akaike Information Criterion (AIC). Thus, litter type treatment initially included in the full models, was never retained in the most parsimonious models.

Finally, Spearman correlations were performed to link litter mass loss after 24 months of decomposition to the 4 soil biota directly involved in the decomposition process (bacteria, fungi, Collembola and Oribatida).

3. Results

3.1. Initial litter characteristics

The PCA (Fig. 2) and PERMANOVA (Pseudo-$F_{\text{litter species}} = 42.5$, $P = 0.001$) revealed a considerable variation of initial litter quality between the three plant species. The first axis of the PCA (43% of the variance explained) discriminated leaves of *Q. pubescens* from leaves of *Q. ilex* with higher SLA, Mg and lower Na and lignin contents in the former. The second axis of the PCA (34% of the variance explained) distinguished *P. halepensis* from the two *Quercus* species, with a higher WSC concentration and, on the opposite, lower WHC, Ca and hemicellulose concentrations in the former. In addition, PERMANOVA revealed an effect of litter type (i.e., leaves or needles collected from trees in ND or AD plots; Pseudo-$F_{\text{litter type}} = 3.3$; $P = 0.033$) indicating a modification of litter quality under amplified drought conditions, as well as an

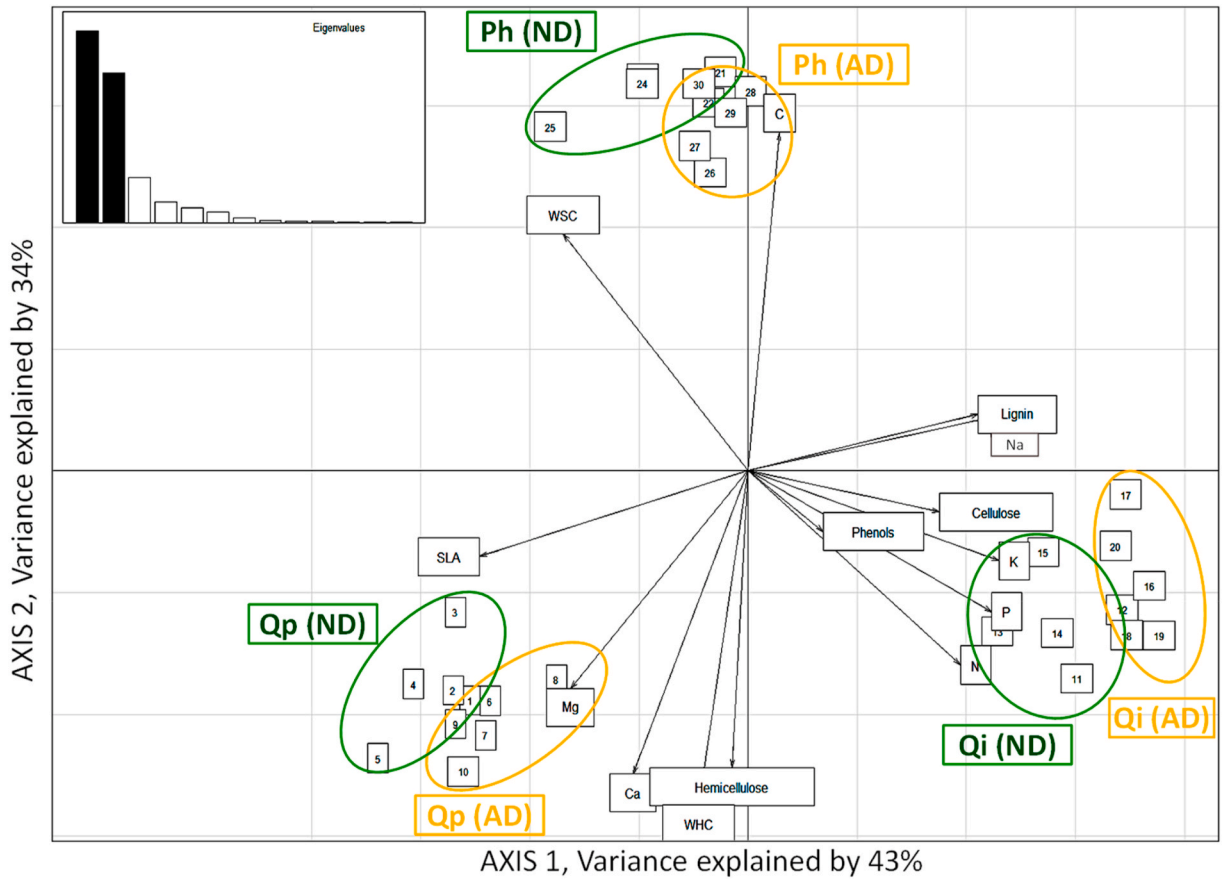

Fig. 2. Principal Component Analysis (PCA) based on the 13 initial litter traits (arrows), arranged by litter species identity (*Quercus pubescens*, *Quercus ilex* and *Pinus halepensis*) and litter type (leaves/needles collected from trees in ND or AD plots) showed by colored circles. Qp = *Q. pubescens*, Qi = *Q. ilex*, Ph = *P. halepensis*, ND = natural and AD = amplified drought, WSC= Water Soluble Compounds, C = Carbon, SLA= Specific Leaf Area, Mg = Magnesium, Ca = Calcium, WHC = Water Holding Capacity, N = Nitrogen, P = Phosphorous, and Na = Sodium.

interaction between litter species and litter type (Pseudo-$F_{\text{litter species} \times \text{litter type}} = 2.4$; $P = 0.046$) indicating a modification of litter traits according to the tree species considered. AD induced an increase of Mg and Na for both oak species, a decrease of Ca content the three tree species (Supplementary Table S1). SLA and WHC decreased with AD for the two *Quercus* species but did not change for *P. halepensis* (Supplementary Table S1). Finally, AD induced an increase of leaf phenolic content for *Q. ilex* whereas no change was observed for *Q. pubescens* leaves and *P. halepensis* needles (Supplementary Table S1).

3.2. Microbial community

Bacterial and fungal biomasses were respectively 16% and 15% higher in *Q. pubescens* litter compared to the two other litters (Table 2; Fig. 3a and b) and were not affected by the litter type (i.e., leaves or needles collected from trees in ND or AD plots, Supplementary Fig. S3). The effect of AD on microbial biomass was dependent on the forest considered (significant forest × precipitation interaction, Table 2). AD treatment had no effect on the fungal or bacterial biomasses in the *Q. pubescens* or *Q. ilex* forests, but increased them by 29% in the *P. halepensis* forest (Fig. 4a and b).

3.3. Soil mesofauna

We collected a total of 27 292 individuals of microarthropods from all the litterbags. Collembola were the most abundant microbi-detritivore arthropods (49%), compared to Oribatida (39%), while predatory Acari represented 12% of the microarthropods community.

As reported for microbial biomass, mesofaunal abundance varied according to litter species identity but was not affected by litter type

Table 2
Effects of the forest type (*Quercus pubescens*, *Quercus ilex* and *Pinus halepensis* forests), litter species identity, precipitation treatment (natural *vs.* amplified drought), and their interactions on microbial (bacterial and fungal biomasses) and mesofaunal (Collembola, Oribatida, and predator abundances) parameters. d.f. = degrees of freedom. *F*-values and associated *P*-values (with the respective symbols * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$) are indicated. Litter type treatment was initially included in the full models but it was never retained in the most parsimonious models.

		Bacteria		Fungi		Collembola		Oribatida		Predator	
	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Forest (F)	2	2.9		3.3	*	16.9	***	10.8	***	29.0	***
Species (S)	2	7.6	***	7.5	***	12.0	***	20.2	***	6.9	**
Precipitation (P)	1	0.9		1.5		4.6	*	11.9	***	0.2	
F × S	4	2.5		2.4							
F × P	2	3.4	*	3.4	*	6.1	**	2.1		4.1	*

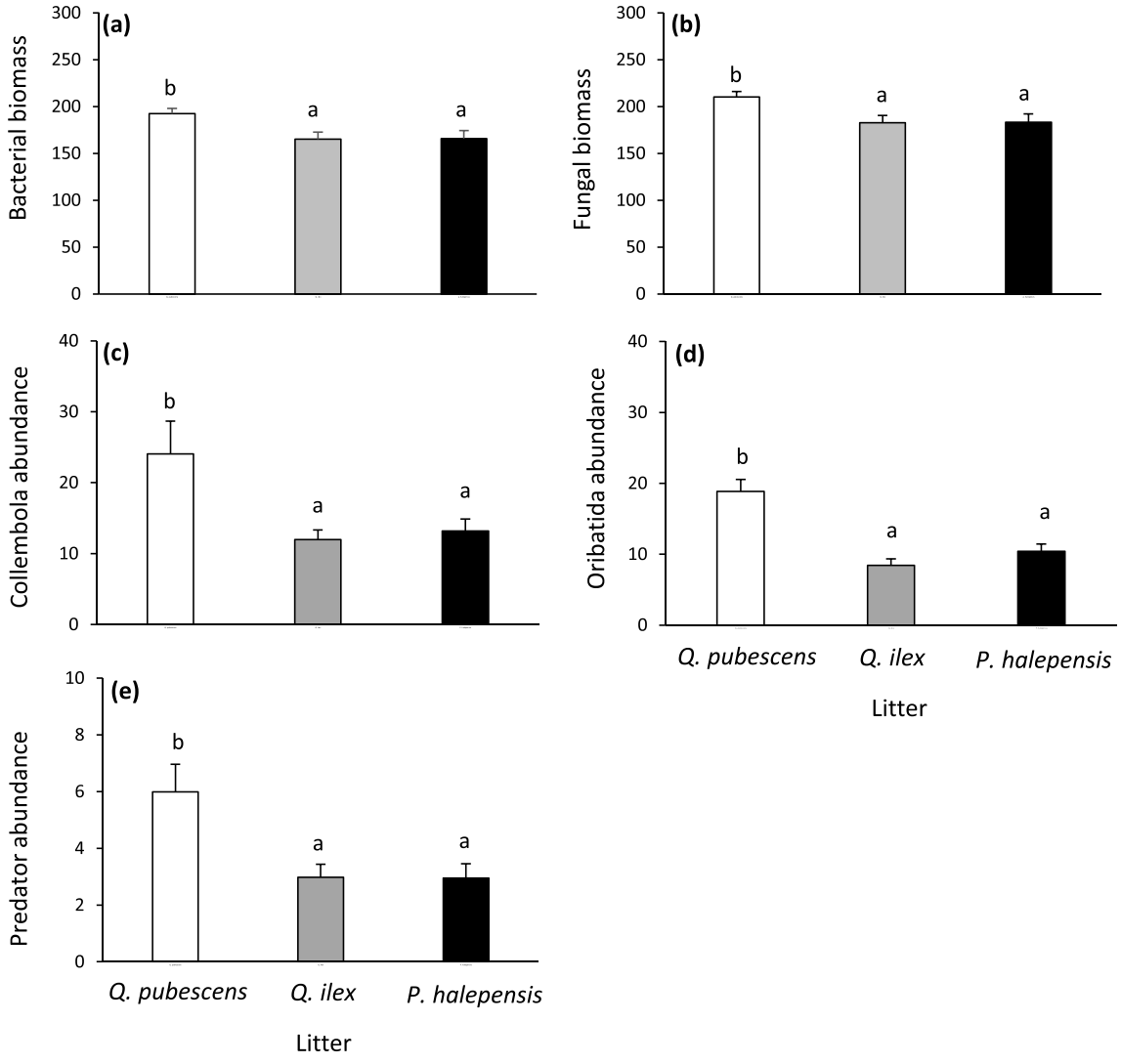

Fig. 3. Effects of litter species identity on bacterial biomass (a), fungal biomass (b), Collembola abundance (c), Oribatida abundance (d) and predator abundance (e). Values are means ± SE; n = 60. Microbial biomass is expressed as μg. g litter^{-1} and mesofauna abundance as nb of individuals. g litter^{-1}. Different letters denote significant differences between treatments from ANOVA analysis with a < b.

(Table 2, Supplementary Fig. S3). The abundance of all mesofauna groups associated to *Q. pubescens* litter was always two times higher compared to *Q. ilex* and *P. halepensis* litters (Fig. 3c–e).

Except for Oribatid Acari, forest type and precipitation treatment interactively affected Collembola and predator abundances (significant forest × precipitation interaction, Table 2). AD treatment did not affect Collembola abundance in *Q. pubescens* forest but decreased Collembola abundance by 46% and 48% in *Q. ilex* and *P. halepensis* forests, respectively. Consequently, the Collembola abundance was similar level across the three Mediterranean forests under AD treatment (Fig. 4c). The AD treatment had a significant effect only in the *Q. ilex* forest, with a 50% decrease of the predator abundance (Fig. 4d). Finally, Oribatid Acari abundance was respectively 87% and 62% higher in *Q. ilex* forest compared to *Q. pubescens* and *P. halepensis* forests (Fig. 5a) and was reduced by 33% under AD conditions in the three forest types (Fig. 5b).

3.4. Relationships between soil biota parameters and litter mass loss

While Collembola and Oribatida abundances were positively correlated with litter mass loss under ND condition in both *Q. ilex* and *P. halepensis* forests (Table 3), these relationships disappeared under AD conditions. Collembola abundance was only marginally correlated with litter mass loss under ND treatment in *Q. pubescens* forest (Table 3), and this trend also disappeared under drier conditions. Finally, fungal biomass was positely related to litter mass only in *Q. ilex* forest under AD conditions (Table 3).

4. Discussion

Our study highlighted that litter identity strongly controls soil biota in Mediterranean forests after a 24-month field litterbag experiment. In each of the three forest, *Q. pubescens* litter had consistently more abundance of all soil biota groups compared to *Q. ilex* and *P. halepensis* litters. Our results suggest a key role played by Ca, Mg, specific leaf area (SLA) and water holding capacity (WHC) as drivers of soil biota parameters. In addition, amplified drought differently affects soil biota with an increase in microbial biomass and a decrease in soil fauna abundance. However, except for Oribatida Acari, negative effect of amplified drought were dependent on the forest considered. Surprisingly, amplified drought did not indirectly affect the soil biota by

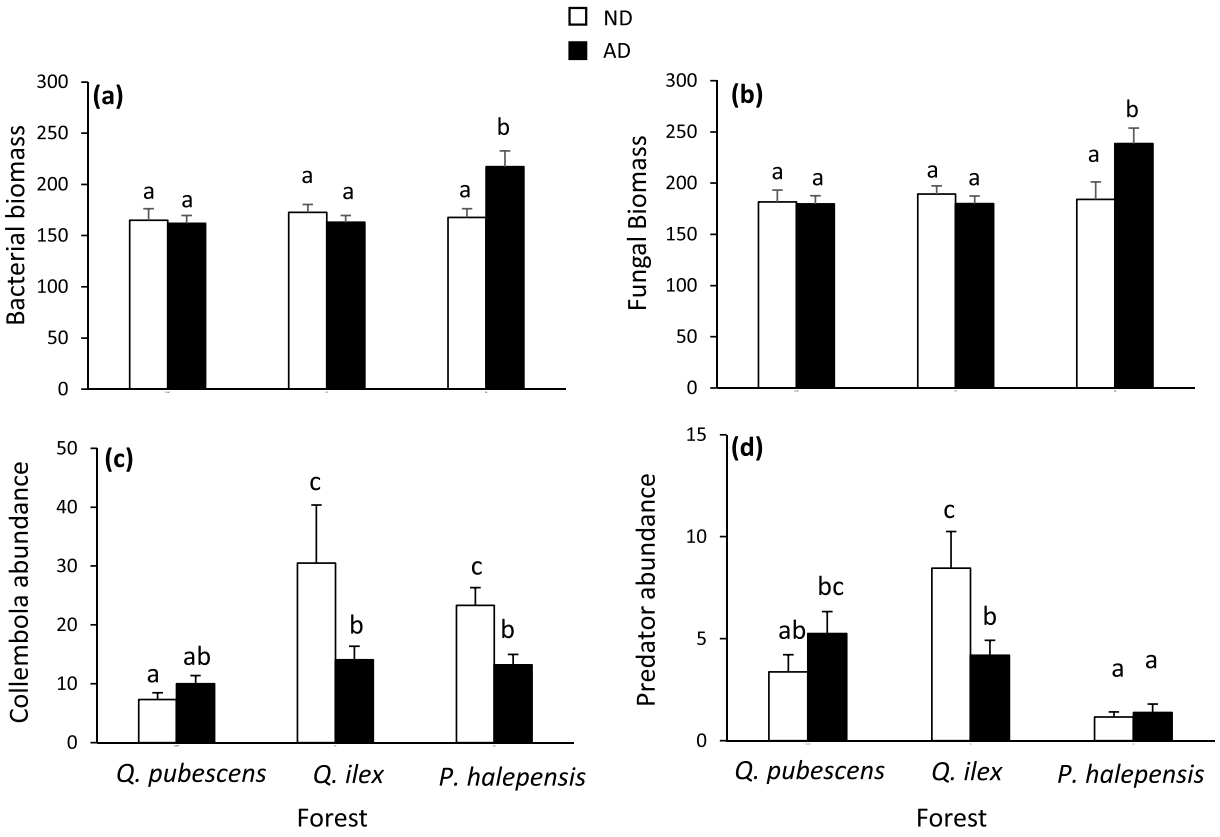

Fig. 4. Bacterial biomass (a), fungal biomass (b), Collembola abundance (c) and predator abundance (d) according to the forest type and the precipitation treatment (Table 2). Values are means ± SE; n = 30. Microbial biomass is expressed as μg. g litter^{-1} and mesofauna abundance as nb of individuals.g litter^{-1}. Different letters denote significant differences between treatments from ANOVA analysis with a < b < c. ND = natural and AD = amplified drought.

altering the tree litter quality.

4.1. Effects of litter traits on soil biota

We provided clear evidence that soil biota communities are strongly controlled by litter species identity, but we only partly confirm our first hypothesis of higher abundance of soil biota in oak compared to pine forests. More precisely, the abundance of all soil biota associated with *Q. pubescens* litter was higher compared to *Q. ilex* and *P. halepensis* litters, whatever the forest in which the litter decomposed. *Q. pubescens* leaves exhibited higher specific leaf area (SLA) and water holding capacity (WHC) compared to *Q. ilex* leaves and *P. halepensis* needles. Higher litter SLA has been reported to induce an increase in water availability (Castro-Díez et al., 1997; Makkonen et al., 2012, 2013) or in habitat structure for Collembola (Kalinkat et al., 2013; Santonja et al., 2018; Aupic-Samain et al., 2019). WHC is a physical trait corresponding to the litter ability to hold the water, which is necessary for soil biota development and activity (Pflug and Wolters, 2001; Makkonen et al., 2012, 2013; Santonja et al., 2017). In addition, *Q. pubescens* leaves also exhibited higher Ca and Mg concentrations than the two other litters. Ca positively affects fungal growth and activity (Eriksson et al., 1990; Jenkins and Suberkropp, 1995) and is a key constitutive of invertebrate cuticles (Cairns and Yan, 2009). Mg plays an important role in the growth and metabolic functions of microbial cells (Walker, 1994) and is an essential element for invertebrates required for enzymatic reactions, nerve connections or muscle function (National Research Council, 2005). Some previous studies identified these physical (SLA and WHC) and chemical (Ca and Mg) litter traits as important drivers of the litter decomposition process in Mediterraean forests (García-Palacios et al., 2016a), wich support our study demonstrating for the first time that these litter traits directly control soil biota in Mediterranen forests and then ecosystem processes. However, we acknowledge that soil biota parameters were analysed only at one sampling time in the present study (after 730 days of decomposition in litterbags), preventing an extrapolation to soil biota dynamics throughout litter decomposition time and necessiting additional experimentations to confort our findings.

4.2. Direct and indirect effect of precipitation treatment on soil biota

We confirmed our second hypothesis that decreasing precipitation directly affects of soil biota biomass and abundance. Conversely, we did not evidence an indirect effect of amplified drought on soil biota mediated by a shift in litter quality at intraspecific level (Fig. 2), in contrast to our third hypothesis. In a climate change context, these findings clearly highlight that reduced water availability prevails the intraspecific shift in litter quality due to plant water stress as a major driver of soil biota communities in our Mediterranean forests.

In temperate forest ecosystems, bacteria and fungi are often positively correlated with soil water availability (e.g., Pflug and Wolters, 2001; Taylor and Wolters, 2005; Lensing and Wise, 2007). In Mediterranean ecosystems, in contrast, the regular summer droughts could have select adapted phenotypes among microbial species (Criquet et al., 2000; Curiel Yuste et al., 2014; Pereira et al., 2019), leading to only weak or an absence of drought effect on soil bacterial and fungal communities (Wilkinson et al., 2002. Sherman et al., 2012; Curiel Yuste et al., 2014). In addition, higher mortality and lower fecundity rates were reported for both Collembola and Acari under drier condition, due to altered physiological processes (Holmstrup et al., 2001; Houck, 2012; Poinsot-Balaguer and Barra, 1991), species behavior (Verhoef and van Selm, 1983) or predator-prey interaction (Santonja et al., 2017). Consistently with these previous studies, microbial biomass was not negatively affected, while soil fauna abundance decreased under

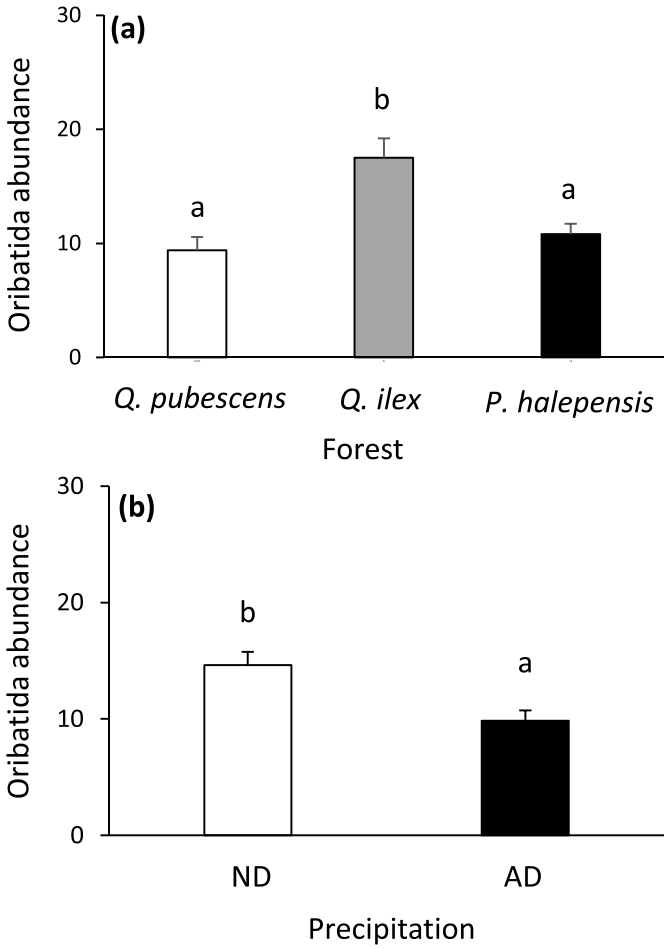

Fig. 5. Effect of (a) forest site (*Quercus pubescens* forest in white, *Quercus ilex* forest in grey and *Pinus halepensis* forest in black) and (b) precipitation treatment (ND plot in white and AD plot in black) on Oribatida abundance. Values are means ± SE; n = 60 for (a) and n = 90 for (b). Abundance is expressed as nb of individuals.g litter^{-1} and µg. g litter $^{-1}$, respectively. Different letters denote significant differences between treatments with a < b. ND = natural and AD = amplified drought.

Table 3
Matrix of Spearman correlations between litter mass loss after 24 months of decomposition and the 4 soil biota directly involved in the decomposition process (bacteria, fungi, Collembola and Oribatida) according to forest site and precipitation treatment. Values in this matrix can range from −1.0 to 1.0, with 1.0 indicating perfectly correlated variables and −1.0 indicating perfectly negative correlations. Significant correlations are indicated with the respective symbols *** for $P < 0.001$, ** for $P < 0.01$, * for $P < 0.05$ and *ms* for $P < 0.07$. ND = natural drought and AD = amplified drought.

	Q. pubescens forest		*Q.* ilex forest		*P. halepensis* forest	
	ND	AD	ND	AD	ND	AD
Bacteria	−0.10	−0.13	−0.14	0.29	−0.17	0.10
Fungi	−0.10	−0.18	−0.14	0.42*	−0.18	0.07
Collembola	0.34 *ms*	0.11	0.53**	0.19	0.36*	0.09
Oribatida	0.10	−0.08	0.61***	0.29	0.45**	0.34 *ms*

amplified drought in the three studied Mediterranean forests.

Except for Oribatida Acari, the drought responses of the soil biota varied according to the forest type considered. In *P. halepensis* forest, we observed lower Collembola abundance but higher microbial biomass with the amplified drought treatment. Since Collembola are known to be microbial feeders (Maraun et al., 2003) and soil microbial communities to be drought-tolerant in Mediterranean ecosystems (Sherman et al., 2012; Curiel Yuste et al., 2014), higher microbial biomass under reduced precipitation could be the result of lower Collembola feeding activity on them. Moreover, specialized microorganisms species could also benefit on specific conditions from *P. halepensis* forest (higher specialized metabolites from *P. halepensis* litter) to proliferate at the expense of generalist species. In contrast, in *Q. ilex* forest we reported lower Collembola and predatory Acari abundances with amplified drought, but no differences in microbial biomass. Since Acari Mesostigmata and Prostigmata are active predators of Collembola (Koehler, 1999; Schneider and Maraun, 2009) and are more drought-tolerant than Collembola (Santonja et al., 2017), this finding could suggest that amplified drought in *Q. ilex* forest led to a negative cascading effect from Collembola to their predators. However, in *Q. pubescens* forest we observed no effect of reduced precipitation on Collembola, nor on their basale resource (microorganisms) and nor on their predators (Acari). An explanation may lie in the differences among the precipitation reduction set-ups used in three Mediterranean forests: precipitation reduction (~30%) in the *Q. pubescens* forest is concentrated in the summer months, as expected by the climatic models (IPCC, 2013; Polade et al., 2014), while in *Q. ilex* and *P. halepensis* forests, reduced precipitation is effective throughout the year. As sampling was done in winter, soil biota was likely able to recover from the amplified summer drought in *Q. pubescens* forest, given that precipitation patterns, and not only the amounts, could impact the soil biota. A previous assessment of the soil microbial community associated to litter performed in the same *Q. ilex* forest in 2013 reported a significant decrease of their biomass under amplified drought (García-Palacios et al., 2016), which was not significantly confirmed in December 2016 by the present study. In addition, Santonja et al. (2017) reported a negative effect of amplified drought on both Collembola and Oribatid Acari in the same studied *Q. pubescens* forest between 2012 and 2013, while this negative effect was maintained only for Oribatid Acari for the present study. Such discrepancies among studies could be explained by a number of factors, among which are the year to year climatic differences, and the different sampling periods and methods. The experiment of Santonja et al. (2017) in the *Q. pubescens* forest was performed just after the installation of the rain exclusion device in 2011 while the present study was performed 5 years later. As Oribatid Acari exhibit lower dispersal ability (Hopkin, 1997), lower fecundity rate (Houck, 2012) or higher habitat specialization (Wehner et al., 2016) than Collembola, we could also speculate why these Oribatid Acari are still negatively affected by amplified drought treatment after several years, while Collembola were able to adapt to the drier conditions. Finally, while increasing Collembola and Oribatida abundances were positively related to litter mass loss in *Q. ilex* and *P. halepensis* forests, amplified drought conditions suppressed these relationships. This last finding highlights that, in addition to the impact on soil biota demographic paramaters, drier environmental conditions alter the contributions of soil organisms to the processes they drive in Mediterranean forests.

5. Conclusion

The focus of this study was to assess how litter quality and reduced precipitation drive soil biota in three Mediterranean forests. We provide clear evidence that soil biota communities are strongly controlled by litter traits with a common pattern for all taxonomic groups studied. *Q. pubescens* litter exhibited the highest microbial biomasses and mesofaunal abundances in comparison to *Q. ilex* and *P. halepensis* litters whatever the forest in which the litter decomposed, likely due to a better microhabitat (SLA and WHC) as well as nutritive resource (Ca and Mg) conditions. Surprisingly, despite the amplified drought treatment inducing a modification of litter quality, we did not observe an indirect climate change effect on soil biota due to this intraspecific shift in litter quality. However, we observed a direct effect of amplified drought on soil biota and their contributions to the litter decomposition process

with different response patterns depending on both the taxononomic group and the Mediterranean forest considered.

Author contributions

VB and CF designed the experiment. AAS, SP, CL, MS, CF and VB performed the experiment. AAS and MS analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and discussion and gave final approval for publication.

Data accessibility

Upon acceptance of this manuscript, the data supporting this article will be available from the Dryad Digital Repository.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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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.2020.108122.

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