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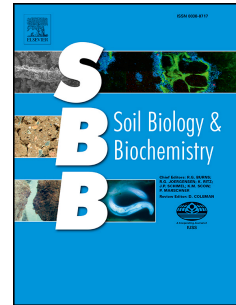
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1 **Title:** Soil biota response to experimental rainfall reduction depends on the dominant tree  
2 species in mature Northern Mediterranean forests

3

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18

19 **Abstract**

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

44 area (SLA) and water holding capacity (WHC) as drivers of soil biota parameters. Finally, the  
45 study highlights that within the same Mediterranean region, climate change could differently  
46 alter the soil organisms inhabiting the litter layer and their contributions to the decomposition  
47 process depending on the tree species and soil biota group considered.

48

49 **Keywords:** climate change; Mediterranean forest; mesofauna; microorganism; plant-soil  
50 (below-ground) interactions; soil biota.

51

## 52 **1. Introduction**

53 Litter is one of the basal elements of a food web that controls nutrient turnover, carbon  
54 sequestration and the overall ecosystem functioning (Wall et al., 2012; Gobat et al., 2013).  
55 Among soil biota, mesofauna (mainly Collembola and Acari) drives many biotic interactions  
56 which are fundamental for structuring the soil food web and decomposing leaf litter. Firstly,  
57 microbi-detrivore organisms (e.g., Collembola and Oribatid Acari) participate directly to the  
58 micro-fragmentation of leaf litter, but also control microbial communities through grazing and  
59 dispersing spores and mycelium (Berg and Laskowski, 2005; Chahartaghi et al., 2005; Scheu  
60 et al., 2005; Anslan et al., 2016). Secondly, predators (e.g., Mesostigmatid and some  
61 Prostigmatid Acari) regulate microbi-detrivore organisms by feeding on them (Koehler,  
62 1999; Schneider and Maraun, 2009; Thakur et al., 2015) and then indirectly control the leaf  
63 litter decomposition.

64 Chemical and physical characteristics of the leaf litter strongly control soil mesofauna  
65 demographic parameters and interactions (Hättenschwiler et al., 2005; Chomel et al., 2016;  
66 Santonja et al., 2018; Aupic-Samain et al., 2019). Under the specific Mediterranean climatic  
67 conditions (summer drought and episodic drying/rewetting cycles; Larcher, 2000; Sardans and  
68 Peñuelas, 2013; Gauquelin et al., 2018), trees generally produce sclerophyllous leaves

69 (Coûteaux et al., 1995) characterized by high lignin concentration (Tian et al., 1992; Gallardo  
70 and Merino, 1993), low specific leaf area (Wright et al., 2005; Pallardy, 2010) and high  
71 diversity and concentration of specialized metabolites (i.e., terpene and phenolic compounds;  
72 Macchioni et al., 2003; Fernandez et al., 2009). These particular characteristics of  
73 Mediterranean trees could potentially lead to distinct litter quality control over soil mesofauna  
74 compared to the other temperate forests for which litter nutrient contents (e.g., C, N and P) are  
75 frequently reported as key drivers of soil mesofauna demographic parameters (Jandl et al.,  
76 2003; Martinson et al., 2008; Jacob et al., 2009; Maaroufi and De Long, 2020). However, to  
77 our knowledge, only few studies investigated this effect of litter quality on soil mesofauna in  
78 Mediterranean forests (e.g., Barba et al., 2016; Santonja et al., 2017; Aupic-Samain et al.,  
79 2019), necessitating deeper investigation to improve our mechanistic understanding of such  
80 relationships.

81         Among terrestrial biomes, Mediterranean ecosystems are recognized as being the most  
82 sensitive to climatic change (Sala et al., 2000; Schröter et al., 2005). Regional climate models  
83 for the Mediterranean Basin predict a warming of 3.4°C and a decrease of annual  
84 precipitations by 30% for the end of the 21<sup>st</sup> century, which will result in an intensification of  
85 summer drought events (Giorgi and Lionello, 2008; IPCC, 2013; Polade et al., 2014).  
86 Therefore, by decreasing water availability, climate change in Mediterranean ecosystems may  
87 have a direct negative impact on soil microorganisms (e.g., Sardans and Peñuelas, 2010;  
88 Talmon et al., 2011) and mesofauna (e.g., Tsiafouli et al., 2005; Santonja et al., 2017). In  
89 addition, climate change may indirectly impact microbial and mesofaunal communities by  
90 altering litter quality and quantity produced by plants as climatic conditions strongly control  
91 plant growth and survival and consequently leaf and litter traits (Wright et al., 2005; Sardans  
92 and Peñuelas, 2007; Rodriguez-Ramirez et al., 2017). Indeed, previous studies reported that  
93 experimental decrease in water conditions implies lower nutrient content (Chen et al., 2013;

94 Santonja et al., 2019) and higher specialized metabolite content (Hernández et al., 2004;  
95 Munné-Bosch and Peñuelas, 2004) with potential negative cascading effects on soil biota  
96 (Allison et al., 2013; García-Palacios et al., 2016a; Santonja et al., 2019). In addition, oaks  
97 and pines are dominant tree genera that structure both temperate and Mediterranean forests  
98 (Ellenberg, 1988; Quézel and Médail, 2003). As oak and pine forests exhibit different  
99 microclimatic and soil properties (e.g., pH, soil type, humus forms; Table 1; Gauquelin et al.,  
100 2016) as well as chemically and structurally different litters (oak leaves vs. pine needles;  
101 Aupic-Samain et al., 2019; Santonja et al., 2015), we could expect that climate change may  
102 distinctly affect soil biota in these two forest types. However, our current understanding of  
103 soil biota responses to climate change drivers in Mediterranean oak and pine forests is still  
104 limited by a lack of studies addressing conjointly the relative contributions of environmental  
105 conditions and leaf litter quality and both direct and indirect effects of climate change on  
106 these organisms.

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

119 biomass and mesofaunal abundance due to a decrease in leaf/ needle litter quality (e.g.,  
120 increased specialized metabolite content) and iv) soil biota will be more sensitive to reduced  
121 precipitation in oak compared to pine forests where soil biota is already conditioned by more  
122 constraining environmental conditions (e.g., litter content).

123

## 124 **2. Materials and Methods**

125

### 126 **2.1. Study site**

127 The study was concurrently set up in three Mediterranean experimental sites (Table 1).  
128 The first is the Oak Observatory at the “Observatoire de Haute Provence” (O<sub>3</sub>HP) located in  
129 the Luberon Natural Regional Park (43°45'34.26"N; 5°17'57.84"E), in Provence, SE France  
130 (Gauquelin et al., 2011). This oak forest is dominated by deciduous downy oak (*Quercus*  
131 *pubescens* Willd.). The second site is located in the Puéchabon State Forest (43°44'30" N;  
132 3°35'40" E) in Occitanie, SE France (Misson et al., 2010). This oak forest is dominated by the  
133 evergreen holm oak (*Quercus ilex* L.). The third site is located in the departmental forest of  
134 Font-Blanche (43°14'25"N; 5°40'40"E) in Provence, SE France (Simioni, 2011). This is a  
135 mixed forest, but Aleppo pine (*Pinus halepensis* Mill.) is the most abundant species,  
136 contributing around 70% of the basal area. During the two years of field experiment, the mean  
137 annual precipitation ranged from 635.6 mm in the *P. halepensis* forest to 1020.9 mm in the *Q.*  
138 *ilex* forest, while the mean annual temperature ranged from 12.3°C in the *Q. pubescens* forest  
139 to 14.1°C in the *P. halepensis* forest (Supplementary Fig. S2).

140 In order to simulate the intensification of the summer drought period, each site is  
141 equipped with a rain exclusion device reducing approximately 30% of annual precipitation  
142 (similar to climatic models projection – A2 scenario; Giorgi and Lionello, 2008; IPCC, 2013).  
143 In the *Q. pubescens* forest the rain exclusion device consists of a 15 m × 20 m rainout-shelter



144 above the canopy which dynamically excluded precipitations by deploying automated shutters  
145 during rainfall events of the vegetation growing season (i.e., from spring to autumn)  
146 (Supplementary Fig. S2a). In the *Q. ilex* and *P. halepensis* forests the rain exclusion is  
147 performed by using fixed PVC gutters installed below the forest canopy, excluding about 30%  
148 at each rainfall event (Supplementary Fig. S2b and c). In each site, we compared control plots  
149 (natural drought - ND) and rain exclusion plots (amplified drought – AD) (Table 1 and  
150 Supplementary Fig. S1).

151

## 152 **2.2. Litter collection**

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

160

## 161 **2.3. Experimental design**

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

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

181

#### 182 **2.4. Initial litter characteristics**

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

186 Carbon (C) and nitrogen (N) concentrations were determined by thermal combustion  
187 on a Flash EA 1112 series C/N elemental analyzer (Thermo Scientific®, Waltham, MA,  
188 USA). Phosphorus (P) and cations, i.e., calcium (Ca), sodium (Na), potassium (K) and  
189 magnesium (Mg), were extracted from 80 mg of grounded litter with 8 ml of HNO<sub>3</sub> and 2 ml  
190 of H<sub>2</sub>O<sub>2</sub>. Then, samples were heated at 175 °C for 40 min using a microwave digestion system  
191 (Ethos One, Milestone SRL, Sorisole, Italy). After this mineralization step, every sample was  
192 adjusted to 50 ml with demineralized water. P concentration was measured colorimetrically  
193 using the molybdenum blue method (Grimshaw et al., 1989). 100  $\mu$ l of sample, 100  $\mu$ l of

194 NaOH, 50  $\mu$ l of mixed reagent (emetic tartrate and ammonium molybdate solution) and 50  $\mu$ l  
195 of ascorbic acid were mixed directly in a 96 well microplate. After 45 min at 40 °C, the  
196 reaction was completed, and P concentration was measured at 720 nm using a microplate  
197 reader (Victor, Perkin Elmer, Waltham, MA, USA). Cations concentrations were determined  
198 by atomic absorption spectrophotometer. Total phenolic compounds were measured  
199 colorimetrically by the adapted method of Peñuelas et al., (1996) using gallic acid as standard  
200 (expressed as equivalent acid gallic). 250 mg of litter sample were extracted in 20 ml of a 70  
201 % aqueous methanol solution, shaken for 1 h, and then filtered (0.45  $\mu$ m filter); 50  $\mu$ l of  
202 filtered extract were mixed with 200  $\mu$ l of saturated aqueous Na<sub>2</sub>CO<sub>3</sub> (to stabilize the color  
203 reaction), 1650  $\mu$ l of distilled water and 100  $\mu$ l Folin-Ciocalteu reagent (Folin and Denis,  
204 1915). After 30 min, the reaction was completed, and the concentration of phenolics was  
205 measured at 765 nm on a UV/Vis spectrophotometer (Thermo Scientific®, Waltham, MA,  
206 USA). Lignin, cellulose and hemicellulose as well as water soluble compounds (WSC)  
207 concentrations of initial litter materials were determined according to the Van Soest extraction  
208 protocol (Van Soest, 1963) using a fiber analyzer (Fibersac 24, Ankom, Macedon, NJ, USA).  
209 All concentrations were expressed in mg g<sup>-1</sup> of litter dry weigh.

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

216

## 217 ***2.5. Mesofauna extraction and identification***

218 Mesofauna was extracted from one litterbag using the Tullgren funnel method for 10  
219 days (Berlese, 1905). Collected arthropods were stored in 70 % ethanol, counted by using a  
220 binocular microscope and separated between Collembola and Acari, with different suborders  
221 for the latter: Oribatid, Mesostigmatid and Prostigmatid Acari (Gisin, 1960; Hopkin, 1997).  
222 Collembola and Oribatid Acari were assigned as microbi-detritivores and Mesostigmatid and  
223 Prostigmatid Acari as predators (Coleman et al., 2004; Donoso et al., 2013; Crotty et al.,  
224 2014; Santonja et al., 2017).

225

## 226 **2.6. Litter mass loss estimation**

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

229

## 230 **2.7. PLFA analyses**

231 Since, the phospholipid fatty acids (PLFA) are essential components of all living cells  
232 (Tollefson and McKercher, 1983; Zelles, 1999) with a wide structural diversity (Zelles, 1997;  
233 Tornberg et al., 2003), we used PLFA as biomarkers of litter microbial communities. The  
234 PLFA were extracted from freeze-dried ground litter according to the method from Buyer and  
235 Sasser (2012) with modifications. Four ml of Bligh–Dyer extractant containing 4  $\mu$ l of 1,2-  
236 dinonadecanoyl-sn-glycero-3-phosphocholine (C19:0; Avanti® Polar lipids, Inc.) as internal  
237 standard were added to 0.5 g of samples. Lipids separation was performed by solid-phase  
238 extraction (SPE) on Phenomenex® (Strata SI-1 with 50 mg of silica, 55  $\mu$ m, 70 Å). The  
239 resulting fatty acid methyl ester (FAMES) were analysed by gas-chromatography/mass-  
240 spectrometry (GC-MS) on an Agilent 7890 system equipped with an MSD5977A Network  
241 mass detector, an ALS7693 automatic injector and an HP5-MS apolar column (30 m  $\times$  0.25  
242 mm  $\times$  0.25  $\mu$ m; J&W Agilent Technologies) and MassHunter software. Qualitative analysis

243 of FAMES resulted by retention time comparison via FAMES mixture (range between C4 to  
244 C24). The total PLFA concentration was used as measure of the total microbial biomass,  
245 while fungal and bacterial biomasses were estimates through PLFA markers summed  
246 (Frostegård and Bååth, 1996). Biomasses were expressed in  $\mu\text{g g}^{-1}$  dw of litter. Among the 24  
247 identified PLFAs in the samples, 12 microbial specific PLFAs were analysed. The fatty acids  
248 i15:0, a15:0, i16:0 and i17:0 were used as biomarkers for Gram-positive bacteria; 16:1 $\omega$ 7,  
249 18:1 $\omega$ 7 and cy19:0 were used as biomarkers of Gram-negative bacteria; 15:0, 17:0 were used  
250 as general bacterial markers and 19:1 $\omega$ 8 were used as biomarkers of methane oxidizing  
251 bacteria (Frostegård et al., 1993). The total bacterial PLFA biomass was calculated by adding  
252 Gram-positive, Gram-negative and general bacterial biomarkers while 18:2 $\omega$ 6,9 was used as a  
253 biomarker of fungi (Bååth and Anderson, 2003; Klamer and Bååth, 2004).

254

## 255 **2.8. Statistical analysis**

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

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

265 Four-way analyses of variance (ANOVA), followed by Tukey tests for post-hoc  
266 pairwise comparisons, were used to test the effects of forest site, litter species identity,  
267 precipitation treatment, litter type and their interactions on the 5 soil biota parameters

268 previously log-transformed: abundances of Collembola, Oribatida, and predator and  
269 biomasses of bacteria and fungi. The full models were then simplified to determine the most  
270 parsimonious models using the *dredge* function of *MuMIn* package (Barton, 2016), an  
271 established model selection procedure with both forward and backward selection algorithms,  
272 which ranks all candidate models (all possible combinations of the initial explanatory  
273 variables included in the full model) based on the lowest Akaike Information Criterion (AIC).  
274 Thus, litter type treatment initially included in the full models, was never retained in the most  
275 parsimonious models.

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

279

### 280 **3. Results**

281

#### 282 **3.1. Initial litter characteristics**

283 The PCA (Fig. 2) and PERMANOVA (Pseudo- $F_{\text{litter species}} = 42.5$ ,  $P = 0.001$ ) revealed a  
284 considerable variation of initial litter quality between the three plant species. The first axis of  
285 the PCA (43 % of the variance explained) discriminated leaves of *Q. pubescens* from leaves  
286 of *Q. ilex* with higher SLA, Mg and lower Na and lignin contents in the former. The second  
287 axis of the PCA (34 % of the variance explained) distinguished *P. halepensis* from the two  
288 *Quercus* species, with a higher WSC concentration and, on the opposite, lower WHC, Ca and  
289 hemicellulose concentrations in the former. In addition, PERMANOVA revealed an effect of  
290 litter type (i.e., leaves or needles collected from trees in ND or AD plots; Pseudo- $F_{\text{litter type}} =$   
291 3.3 ;  $P = 0.033$ ) indicating a modification of litter quality under amplified drought conditions,  
292 as well as an interaction between litter species and litter type (Pseudo- $F_{\text{litter species} \times \text{litter type}} =$

293 2.4;  $P = 0.046$ ) indicating a modification of litter traits according to the tree species  
294 considered. AD induced an increase of Mg and Na for both oak species, a decrease of Ca  
295 content the three tree species (Supplementary Table S1). SLA and WHC decreased with AD  
296 for the two *Quercus* species but did not change for *P. halepensis* (Supplementary Table S1).  
297 Finally, AD induced an increase of leaf phenolic content for *Q. ilex* whereas no change was  
298 observed for *Q. pubescens* leaves and *P. halepensis* needles (Supplementary Table S1).

299

### 300 **3.2. Microbial community**

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

308

### 309 **3.3. Soil mesofauna**

310 We collected a total of 27 292 individuals of microarthropods from all the litterbags.  
311 Collembola were the most abundant microbi-detritivore arthropods (49 %), compared to  
312 Oribatida (39 %), while predatory Acari represented 12 % of the microarthropods community.  
313 As reported for microbial biomass, mesofaunal abundance varied according to litter species  
314 identity but was not affected by litter type (Table 2, Supplementary Fig. S3). The abundance  
315 of all mesofauna groups associated to *Q. pubescens* litter was always two times higher  
316 compared to *Q. ilex* and *P. halepensis* litters (Fig. 3c-e).

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

327

### 328 ***3.4. Relationships between soil biota parameters and litter mass loss***

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

335

## 336 **4. Discussion**

337 Our study highlighted that litter identity strongly controls soil biota in Mediterranean  
338 forests after a 24-month field litterbag experiment. In each of the three forest, *Q. pubescens*  
339 litter had consistently more abundance of all soil biota groups compared to *Q. ilex* and *P.*  
340 *halepensis* litters. Our results suggest a key role played by Ca, Mg, specific leaf area (SLA)  
341 and water holding capacity (WHC) as drivers of soil biota parameters. In addition, amplified



342 drought differently affects soil biota with an increase in microbial biomass and a decrease in  
343 soil fauna abundance. However, except for Oribatida Acari, negative effect of amplified  
344 drought were dependent on the forest considered. Surprisingly, amplified drought did not  
345 indirectly affect the soil biota by altering the tree litter quality.

346

#### 347 ***4.1. Effects of litter traits on soil biota***

348 We provided clear evidence that soil biota communities are strongly controlled by  
349 litter species identity, but we only partly confirm our first hypothesis of higher abundance of  
350 soil biota in oak compared to pine forests. More precisely, the abundance of all soil biota  
351 associated with *Q. pubescens* litter was higher compared to *Q. ilex* and *P. halepensis* litters,  
352 whatever the forest in which the litter decomposed. *Q. pubescens* leaves exhibited higher  
353 specific leaf area (SLA) and water holding capacity (WHC) compared to *Q. ilex* leaves and *P.*  
354 *halepensis* needles. Higher litter SLA has been reported to induce an increase in water  
355 availability (Castro-Díez et al., 1997; Makkonen et al., 2012, 2013) or in habitat structure for  
356 Collembola (Kalinkat et al., 2013; Santonja et al., 2018; Aupic-Samain et al., 2019). WHC is  
357 a physical trait corresponding to the litter ability to hold the water, which is necessary for soil  
358 biota development and activity (Pflug and Wolters, 2001; Makkonen et al., 2012, 2013;  
359 Santonja et al., 2017). In addition, *Q. pubescens* leaves also exhibited higher Ca and Mg  
360 concentrations than the two other litters. Ca positively affects fungal growth and activity  
361 (Eriksson et al., 1990; Jenkins and Suberkropp, 1995) and is a key constitutive of invertebrate  
362 cuticles (Cairns and Yan, 2009). Mg plays an important role in the growth and metabolic  
363 functions of microbial cells (Walker, 1994) and is an essential element for invertebrates  
364 required for enzymatic reactions, nerve connections or muscle function (National Research  
365 Council, 2005). Some previous studies identified these physical (SLA and WHC) and  
366 chemical (Ca and Mg) litter traits as important drivers of the litter decomposition process in

367 Mediterranean forests (García-Palacios et al., 2016a), which support our study demonstrating for  
368 the first time that these litter traits directly control soil biota in Mediterranean forests and then  
369 ecosystem processes. However, we acknowledge that soil biota parameters were analysed  
370 only at one sampling time in the present study (after 730 days of decomposition in litterbags),  
371 preventing an extrapolation to soil biota dynamics throughout litter decomposition time and  
372 necessitating additional experimentations to confirm our findings.

373

#### 374 ***4.2. Direct and indirect effect of precipitation treatment on soil biota***

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

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

392 while soil fauna abundance decreased under amplified drought in the three studied  
393 Mediterranean forests.

394         Except for Oribatida Acari, the drought responses of the soil biota varied according to  
395 the forest type considered. In *P. halepensis* forest, we observed lower Collembola abundance  
396 but higher microbial biomass with the amplified drought treatment. Since Collembola are  
397 known to be microbial feeders (Maraun et al., 2003) and soil microbial communities to be  
398 drought-tolerant in Mediterranean ecosystems (Sherman et al., 2012; Curiel Yuste et al.,  
399 2014), higher microbial biomass under reduced precipitation could be the result of lower  
400 Collembola feeding activity on them. Moreover, specialized microorganisms species could  
401 also benefit on specific conditions from *P. halepensis* forest (higher specialized metabolites  
402 from *P. halepensis* litter) to proliferate at the expense of generalist species. In contrast, in *Q.*  
403 *ilex* forest we reported lower Collembola and predatory Acari abundances with amplified  
404 drought, but no differences in microbial biomass. Since Acari Mesostigmata and Prostigmata  
405 are active predators of Collembola (Koehler, 1999; Schneider and Maraun, 2009) and are  
406 more drought-tolerant than Collembola (Santonja et al., 2017), this finding could suggest that  
407 amplified drought in *Q. ilex* forest led to a negative cascading effect from Collembola to their  
408 predators. However, in *Q. pubescens* forest we observed no effect of reduced precipitation on  
409 Collembola, nor on their basale resource (microorganisms) and nor on their predators (Acari).  
410 An explanation may lie in the differences among the precipitation reduction set-ups used in  
411 three Mediterranean forests: precipitation reduction (~30%) in the *Q. pubescens* forest is  
412 concentrated in the summer months, as expected by the climatic models (IPCC, 2013; Polade  
413 et al., 2014), while in *Q. ilex* and *P. halepensis* forests, reduced precipitation is effective  
414 throughout the year. As sampling was done in winter, soil biota was likely able to recover  
415 from the amplified summer drought in *Q. pubescens* forest, given that precipitation patterns,  
416 and not only the amounts, could impact the soil biota. A previous assessment of the soil

417 microbial community associated to litter performed in the same *Q. ilex* forest in 2013 reported  
418 a significant decrease of their biomass under amplified drought (García-Palacios et al.,  
419 2016b), which was not significantly confirmed in December 2016 by the present study. In  
420 addition, Santonja et al., (2017) reported a negative effect of amplified drought on both  
421 Collembola and Oribatid Acari in the same studied *Q. pubescens* forest between 2012 and  
422 2013, while this negative effect was maintained only for Oribatid Acari for the present study.  
423 Such discrepancies among studies could be explained by a number of factors, among which  
424 are the year to year climatic differences, and the different sampling periods and methods. The  
425 experiment of Santonja et al., (2017) in the *Q. pubescens* forest was performed just after the  
426 installation of the rain exclusion device in 2011 while the present study was performed 5  
427 years later. As Oribatid Acari exhibit lower dispersal ability (Hopkin, 1997), lower fecundity  
428 rate (Houck, 2012) or higher habitat specialization (Wehner et al., 2016) than Collembola, we  
429 could also speculate why these Oribatid Acari are still negatively affected by amplified  
430 drought treatment after several years, while Collembola were able to adapt to the drier  
431 conditions. Finally, while increasing Collembola and Oribatida abundances were positively  
432 related to litter mass loss in *Q. ilex* and *P. halepensis* forests, amplified drought conditions  
433 suppressed these relationships. This last finding highlights that, in addition to the impact on  
434 soil biota demographic parameters, drier environmental conditions alter the contributions of  
435 soil organisms to the processes they drive in Mediterranean forests.

436

## 437 **5. Conclusion**

438 The focus of this study was to assess how litter quality and reduced precipitation drive  
439 soil biota in three Mediterranean forests. We provide clear evidence that soil biota  
440 communities are strongly controlled by litter traits with a common pattern for all taxonomic  
441 groups studied. *Q. pubescens* litter exhibited the highest microbial biomasses and mesofaunal

442 abundances in comparison to *Q. ilex* and *P. halepensis* litters whatever the forest in which the  
443 litter decomposed, likely due to a better microhabitat (SLA and WHC) as well as nutritive  
444 resource (Ca and Mg) conditions. Surprisingly, despite the amplified drought treatment  
445 inducing a modification of litter quality, we did not observe an indirect climate change effect  
446 on soil biota due to this intraspecific shift in litter quality. However, we observed a direct  
447 effect of amplified drought on soil biota and their contributions to the litter decomposition  
448 process with different response patterns depending on both the taxonomic group and the  
449 Mediterranean forest considered.

450

#### 451 **Author contributions**

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

455

#### 456 **Data accessibility**

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

459

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479

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764 **Tables**

765

766 **Table 1.** Main characteristics of the three studied forests. MAT and MAP correspond  
 767 respectively to the annual mean values of temperature and precipitation between 2008 and  
 768 2019 in natural precipitation (ND) and amplified drought (AD) plots (Supplementary Fig. S2).  
 769 These values did not significantly differ between the forest sites (One-way ANOVAs,  $F_{\text{site}} =$   
 770  $0.6$ ;  $P > 0.05$ ,  $F_{\text{site}} = 1.7$ ;  $P > 0.05$  and  $F_{\text{site}} = 1.8$ ;  $P > 0.05$  for MAT, MAP in ND plots and  
 771 MAP in AD plots, respectively).

772

Forests	<i>Quercus pubescens</i> Willd.	<i>Quercus ilex</i> L.	Mixed <i>Pinus halepensis</i> Mill.
Sites	Oak Observatory at the Observatoire de Haute Provence (O <sub>3</sub> HP)	Puéchabon	Font-Blanche
Location	43° 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	<i>Quercus pubescens</i> Willd.	<i>Quercus ilex</i> L.	mixed <i>Pinus halepensis</i> Mill. / <i>Quercus ilex</i> L.
Other dominant plant species	<i>Acer monspessulanum</i> L. <i>Cotinus coggygria</i> Scop.	<i>Buxus sempervirens</i> L. <i>Phyllirea latifolia</i> L. <i>Pistacia terebinthus</i> L. <i>Juniperus oxycedrus</i> L.	<i>Quercus coccifera</i> L. <i>Phyllirea latifolia</i> 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 (m <sup>2</sup> )	300	140	625
Rain exclusion device installation	2012	2003	2009

773

774

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

782

	df	Bacteria		Fungi		Collembola		Oribatida		Predator	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
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	*

783

784

785 **Table 3.** Matrix of Spearman correlations between litter mass loss after 24 months of  
 786 decomposition and the 4 soil biota directly involved in the decomposition process (bacteria,  
 787 fungi, Collembola and Oribatida) according to forest site and precipitation treatment. Values  
 788 in this matrix can range from -1.0 to 1.0, with 1.0 indicating perfectly correlated variables and  
 789 -1.0 indicating perfectly negative correlations. Significant correlations are indicated with the  
 790 respective symbols \*\*\* for  $P < 0.001$ , \*\* for  $P < 0.01$ , \* for  $P < 0.05$  and *ms* for  $P < 0.07$ . ND  
 791 = natural drought and AD = amplified drought.

792

	<i>Q. pubescens</i> forest		<i>Q. ilex</i> forest		<i>P. halepensis</i> 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 <sup>ms</sup>	0.11	0.53**	0.19	0.36*	0.09
Oribatida	0.10	-0.08	0.61***	0.29	0.45**	0.34 <sup>ms</sup>

793

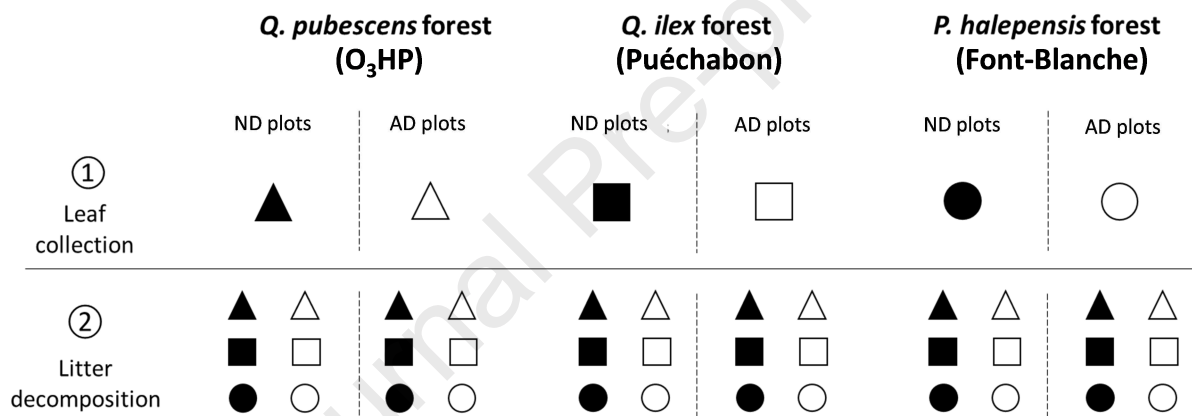
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795 **Figures**

796

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

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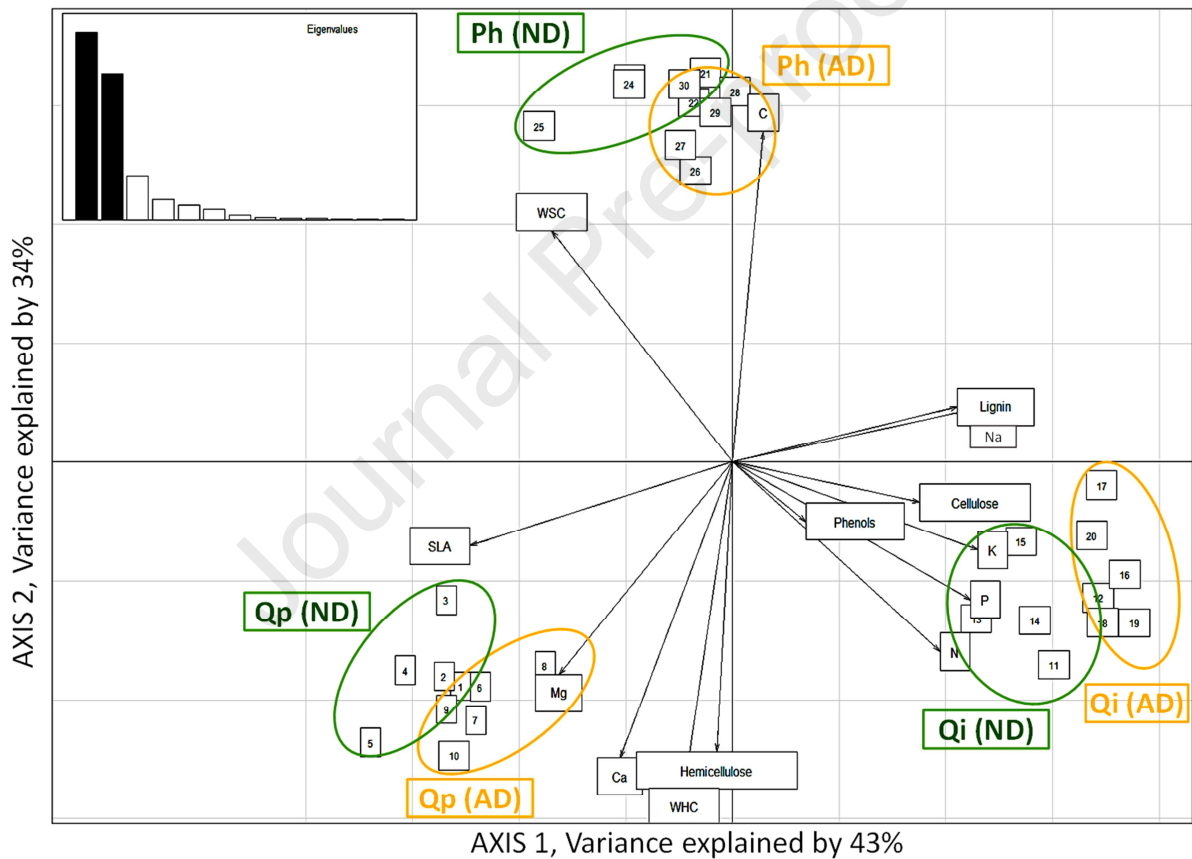


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805

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

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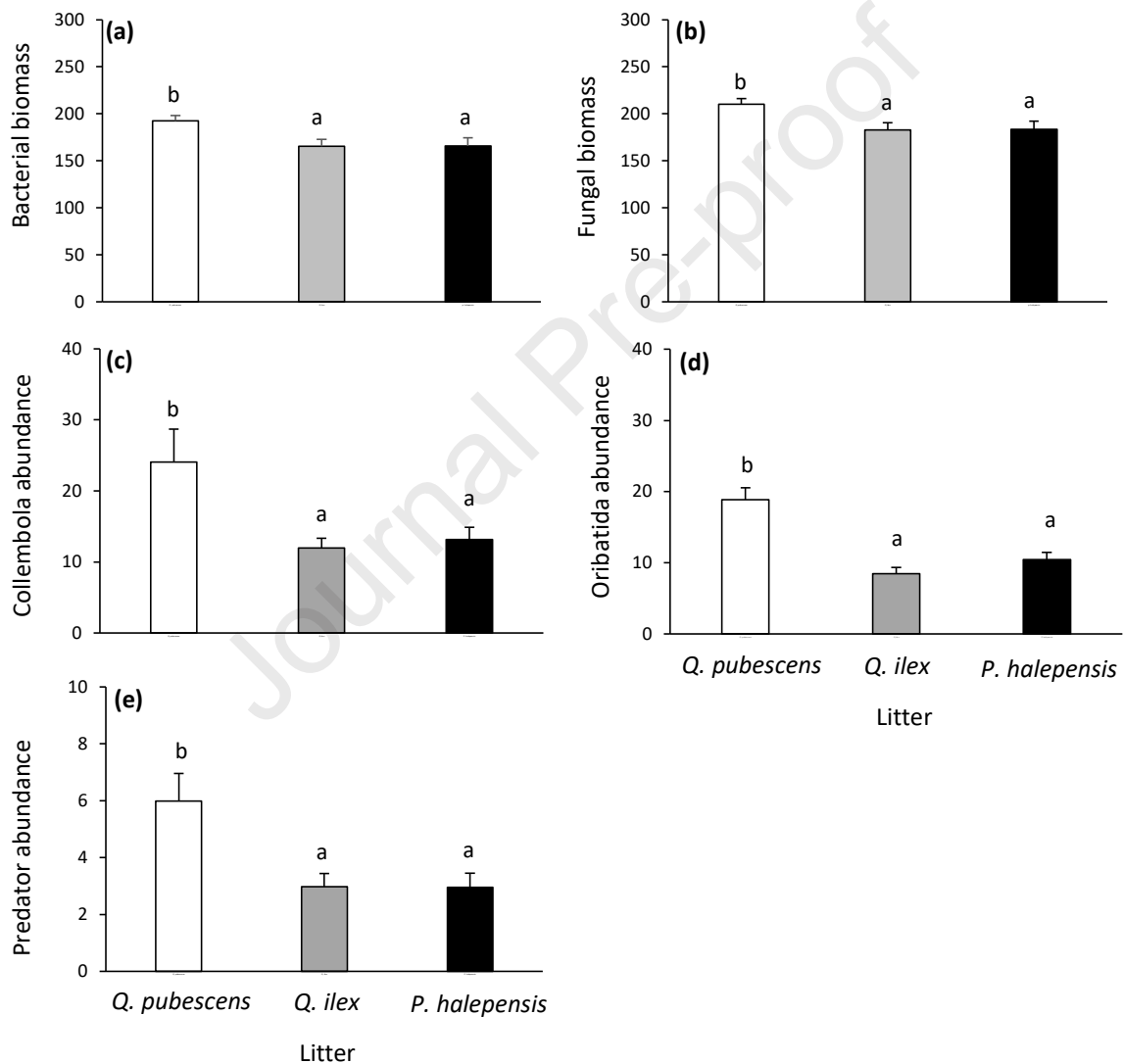


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815

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

821



822

823



824 **Fig. 4.** Bacterial biomass (a), fungal biomass (b), Collembola abundance (c) and predator

825 abundance (d) according to the forest type and the precipitation treatment (Table 2). Values

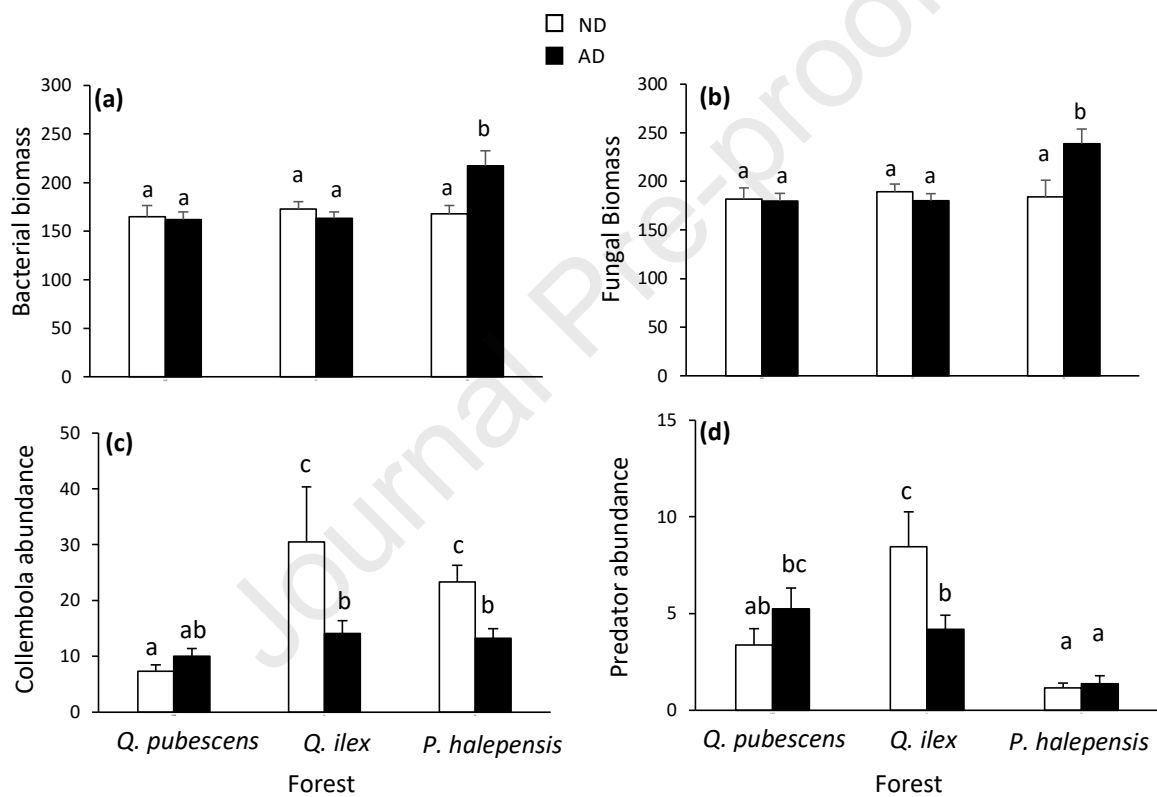
826 are means  $\pm$  SE; n= 30. Microbial biomass is expressed as  $\mu\text{g. g litter}^{-1}$  and mesofauna

827 abundance as nb of individuals.g litter<sup>-1</sup>. Different letters denote significant differences

828 between treatments from ANOVA analysis with  $a < b < c$ . ND = natural and AD = amplified

829 drought.

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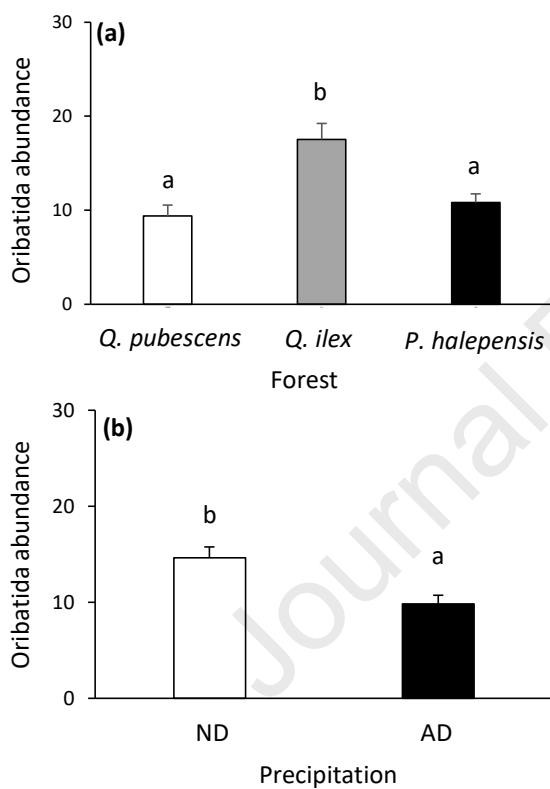


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832

833 **Fig. 5.** Effect of (a) forest site (*Quercus pubescens* forest in white, *Quercus ilex* forest in grey  
834 and *Pinus halepensis* forest in black) and (b) precipitation treatment (ND plot in white and  
835 AD plot in black) on Oribatida abundance. Values are means  $\pm$  SE; n = 60 for (a) and n = 90  
836 for (b). Abundance is expressed as nb of individuals.g litter<sup>-1</sup> and  $\mu$ g. g litter<sup>-1</sup>, respectively.  
837 Different letters denote significant differences between treatments with a < b. ND = natural  
838 and AD = amplified drought.

839



840

## Highlights

- Chemical (Ca, Mg) and physical (WHC, SLA) litter characteristics drive soil biota.
- Drier conditions lead to higher microbial biomass but lower mesofauna abundance.
- Drier conditions alter plant litter quality without cascading effect on soil biota.
- Drier conditions suppress soil fauna-litter decomposition efficiency relationships.

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**Conflict of interest:** The authors declare that they have no conflict of interest.

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