Tree litter identity and predator density control prey and predator demographic parameters in a Mediterranean litter-based multi-trophic system

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Abstract

Plant litter decomposition is an essential process of ecosystem functioning, driven by a complex soil food web. The identity and density of the predators, as well as the quality and quantity of litter, could conjointly affect the strength of trophic interactions within a soil food web. Pine and oak are dominant tree species in temperate and Mediterranean forests and, although they exhibit distinct litter characteristics, no previous study attempted to decipher how these two litters can affect a litter-based multi-trophic system with varying predator density. Using a microcosm experiment, we aimed at understanding how different densities of a predatory Acari (*Stratiolaelaps scimitus*) and two Mediterranean litter species (*Quercus pubescens* and *Pinus halepensis*) may impact the demographic parameters of the predatory Acari, its Collembola prey (*Folsomia candida*) and the fungal biomass associated with litter. We did not observe any interactive effect of litter identity and predator density on both predator and prey demographic parameters. Survival and fecundity rates of the predator and its prey decreased at high predator density. However, demographic parameters of the predator and its prey were differentially affected by litter identity, with greater prey demographic parameters in *Quercus* litter and, in the opposite, greater predator demographic parameters in *Pinus* litter, probably due to differences in physical characteristics providing more or less refuge for the prey. We also observed a higher increase in fungal biomass in *Pinus* compared to *Quercus* litter, i.e. the litter with the fungivorous Collembola abundance reduced by the predatory Acari. Litter identity could thus strongly regulate these tri-trophic interactions (Fungi – fungivorous Collembola – predatory Acari) in forest ecosystems. Finally, the implications of our findings could be important as the distribution area of oak and pine forests may be altered in response to climate change with then potentially strong cascading effects on soil organisms and the processes they drive.

Keywords

Acari; Collembola; Forest ecosystem; Litter traits; Plant-soil interaction; Predator-prey interaction.

1. Introduction

Plant litter decomposition is an essential process in terrestrial ecosystem functioning, as it affects the rate of carbon and nutrient cycling (Wardle, 2002; Bardgett, 2005; Berg and Laskowski, 2005), soil fertility (Scheu et al., 2005; Gobat et al., 2013) and plant performance (Poveda et al., 2005). Litter decomposition is governed by environmental conditions (e.g. humidity, temperature, soil pH; Aerts, 1997; Chapin et al., 2002; Gobat et al., 2013), litter quality (i.e. physical and chemical characteristics of litter; Meentemeyer, 1978; Aber et al., 1990; Aerts, 1997), and soil organisms (i.e. composition, biomass and activity: Persson, 1989; Bardgett, 2005; Berg and Laskowski, 2005). Mesofauna is an important group of soil organisms, which largely contributes to litter decomposition, particularly through interactions with soil microorganisms (Lussenhop, 1992; Kliromonos and Kendrick, 1995; Rihani et al., 1995; Wardle and Lavelle, 1997; Kandeler et al., 1999; Scheu et al., 2005).

Predatory Acari regulate Collembola communities through top-down control (Koehler, 1999; Schneider and Maraun, 2009; Wissuwa et al., 2012; Thakur et al., 2015; Thakur et al., 2017). Collembola, known as fungivore organisms (Lussenhop, 1992; Chahartaghi et al., 2005; Buse and Filser, 2014), regulate abundance, diversity, activity and dispersal of microbial communities (Filser, 2002; Berg and Laskowski, 2005; Scheu et al., 2005), which in turn affect leaf litter mineralization (Berg and Laskowski, 2005; Gobat et al., 2013). These trophic interactions regulate cycling of essential elements such as carbon and nitrogen during litter decomposition (Kaspari and Yanoviak, 2009; Schmitz et al., 2010; Gobat et al., 2013; Thakur et al., 2015).

The second type of control driving the soil food web, i.e. bottom-up control, is determined by the quantity and quality of litter. This could affect microbial biomass and diversity (Hättenschwiler and Vitousek, 2000; Chomel et al., 2014; Santonja et al., 2017) and, by cascading effects, fungivorous organisms (Asplund et al., 2015; Thakur and Eisenhauer, 2015; Santonja et al., 2017; Santonja et al., 2018), predator organisms (Vucic-Pestic et al., 2010; Kalinkat et al., 2013; Santonja et al., 2017), and finally the efficiency of decomposition process (Vivanco and Austin, 2008; Santonja et al., 2017).

Several previous studies assessing the relative importance of top-down (i.e. by soil predators) and bottom-up (i.e. by plant litter quality and quantity) controls on the soil food web focused on temperate ecosystems (Ponsard et al., 2000; Kalinkat et al., 2013; Thakur and Eisenhauer, 2015; Thakur et al., 2015). For example, regarding the top-down control, Thakur et al. (2015) observed a negative effect of increasing *Hypoaspis aculeifer* (i.e. predatory Acari) density on the survival rate of *Folsomia candida*, *Proisotoma minuta* and *Sinella curviseta* (i.e. Collembola preys) by using herbaceous plant litter. In contrast, regarding the bottom-up control, Kalinkat et al. (2013) reported a decrease in consumption rate of a predator centipede (*Lithobius mutabilis*) on its Collembola prey (*Heteromurus nitidus*) according to the increase of litter quantity (*Fagus sylvatica*). Pine and oak are dominant tree species that structure both temperate and Mediterranean forests (Ellenberg, 2009; Quézel and Médail, 2003). Although oak leaves and pine needles are known to be chemically and structurally different (Santonja et al., 2015a, 2015b), no previous study attempted to decipher how these two litter types can affect a litter-based multi-trophic system with varying predator density.

In this context, we designed a microcosm experiment in order to evaluate how shifts in both predator density and litter identity could alter the tri-trophic interactions between fungi, fungivorous Collembola and predatory Acari in Mediterranean forests. Top-down control on soil food web was assessed by manipulating the density of predator (i.e. no predator, low,

moderate and high abundances) by a predatory Acari (*Stratiolaelaps scimitus* Womersley). Litter identity control on soil food web was assessed by using two litter types: *Quercus pubescens* Willd. leaves and *Pinus halepensis* Mill. needles. More precisely, we tested how these two types of control could affect the demographic parameters (i.e. survival and fecundity rates, size and biomass) of the predatory Acari (*S. scimitus*) and its Collembola prey (*Folsomia candida* Willem). We also followed the fungal biomass changes during the experiment. According to previous studies, we first hypothesized a negative effect of increasing predator density on the prey demographic parameters. Secondly, we hypothesized a higher negative effect of predator presence on the prey demographic parameters with *P. halepensis* compared to *Q. pubescens* litter, as a litter exhibiting a large surface (i.e. *Q. pubescens* in the present study) could provide more refuges for the prey compared to a litter exhibiting a lower surface (i.e. *P. halepensis* in the present study) (Santonja et al., 2018).

2. Material and methods

2.1. Soil and litter collection

Soil and plant litter material of *Quercus pubescens* Willd. and *Pinus halepensis* Mill. were harvested in two natural forest sites. For both locations, the climate is defined as Mediterranean with high temperatures and low rainfall during summer, while winter is mild and humid.

The first study site is located in the Luberon Natural Regional Park (43°45′34.26″N; 5° 17′57.84″E), in Provence, SE France. It is an oak forest dominated by downy oak (*Q. pubescens*) at 650 m above sea level developed on a calcosol with S horizon according to the French pedologic referential (Baize and Girard, 1998). The second study site is located in the departmental forest of Font-Blanche (43° 14’ 25’’ N; 5° 40’ 40’’ E) in Provence, SE France. It

is a pine forest of Aleppo pine (*P. halepensis*) at 425 m above sea level developed on a rendosol according to the French pedologic referential (Baize and Girard, 1998).

In the two forests, soil cores (5 cm diameter × 5 cm depth) were harvested in January 2016 and disposed into Berlese-Tullgren funnels during 12 days to remove the bulk of mobile soil animals. Then soil cores were sieved (2 mm mesh) and frozen twice during 48 h to remove the remaining soil fauna, in particular immobile forms (eggs, pupae). Soil samples were autoclaved twice (24 h between the two cycles with 1 atm at 121 °C) in order to eliminate soil microorganisms (Alef and Nannipieri, 1995; Trevors, 1996; Fernandez et al., 2013). Soil samples from oak and pine forests were characterized by similar pH (6.05 ± 0.34 *vs.* 5.7 ± 0.1, respectively; t = -2.8, P = 0.100), percentage of organic matter (23.9 ± 0.8 *vs.* 25.5 ± 0.1, respectively; t = 1.9, P = 0.187) and nitrogen concentration (31.5 ± 1.0 *vs.* 32.0 ± 0.5 $mg.g^{-1}$, respectively; t = 0.4, P = 0.682).

Leaf litter of *Q. pubescens* and needle litter of *P. halepensis* were randomly sampled in February 2016 on the forest floor, in order to collect litter already conditioned by fungi. Litter samples were dried at room temperature for 24 h and frozen at -18 °C for 48 h in order to remove fauna. This method of defaunation has been previously used efficiently to remove soil fauna with a minimal effect on the microbial community (Poll et al., 2007; Thakur et al., 2015; Thakur et al., 2017). Samples of both litter species were stored in a dark room at ambient temperature until the start of the experiment, except 8 aliquotes of litter which were frozen at -72 °C, lyophilized for 72 h and ground into powder prior to chemical and fungal analyses of initial conditions.

2.2. Mesofauna collection

The experiment was conducted using two well-represented invertebrate groups from the leaf litter of Mediterranean oak and pine forests: Acari as the predator and Collembola as the

prey (Poinsot-Balaguer and Kabakibi, 1987; Chomel et al., 2014; Santonja et al., 2017; Thibaud, 2017). Due to i) the difficulty to distinguish easily several species from a same genus in the field, such as for example *F. candida* and *Folsomia fimetaria* that coexist together *in natura*, ii) the high number of individuals necessary to perform the experiment (i.e. 960 Collembola and 152 Acari individuals), and iii) the necessity to not use arthropod individuals adapted to live in *Quercus* or in *Pinus* litter, we decided to use naive individuals of Acari and Collembola from laboratory rearings representative of the dominant orders (i.e. Mesostigmata and Entomobryomorpha, respectively) encountered in Mediterranean forest litter (Chomel et al., 2014; Santonja et al., 2017; personal observations).

Stratiolaelaps scimitus (Acari: Laelapidae) was selected as predatory Acari. *S. scimitus* is an ubiquitous species (Karg, 1998) known as predator of Collembola (Koehler, 1999; Schröder et al., 2015; Thakur et al., 2017). Individuals were reared in plastic boxes (5.5 cm diameter × 7 cm height) containing a flat mixture of plaster of Paris and activated charcoal in 9:1 ratio, permanently water saturated. Acari individuals were fed with individuals of *Folsomia candida* (Collembola: Isotomidae) and *Sinella coeca* Schött. (Collembola: Entomobryidae).

Folsomia candida was selected as prey species. This is a parthenogenetic and ubiquitous Collembola known as fungivorous and frequently used in laboratory experiment (Fountain and Hopkin, 2005; Staaden et al., 2011; Schröder et al., 2015; Thakur et al., 2017). Individuals were reared in plastic boxes (5.5 cm diameter × 7 cm height) containing a flat mixture of plaster of Paris and activated charcoal in a ratio 9:1, permanently water saturated. Individuals were fed *ad libitum* with dry yeast pellets (Arkopharma®). To synchronize the age of the organisms, oviposition was stimulated by placing adults on a new breeding substrate (Fountain and Hopkin, 2005). After oviposition, adults were removed and the eggs hatched 3-4 days later. To ensure that the population was as homogeneous as possible, eggs were placed in a large container and juveniles were fed for the first time altogether.

All the organisms were kept at 95-100% humidity at 20 °C (± 1 °C) and were starved 48 h before start of the experiment.

2.3. Experimental setup

2.3.1. Microcosm preparation

Plastic boxes (5.5 cm diameter × 7 cm height) were used as microcosms for the experiment. The bottom of the microcosms was covered by a cotton pad to keep humidity constant and to prevent organism loss. The top of the microcosms was covered by a nylon net (33 µm mesh). Each microcosm was filled with 12 g (dry mass) of autoclaved soil coming from the respective forests and 1 g (dry mass) of associated leaf litter cut into pieces 2 cm length × 0.5 cm width for oak leaves and 2 cm length for pine needles. We acknowledge that this cutting method differs from natural conditions, but we were constrained to use plant material cut into smallest pieces in the microcosms. As the specific leaf area of *Q. pubescens* and *P. halepensis* litter used in our experiment were respectively 174.15 cm^2 g^{-1} and 108.20 cm^2 g^{-1} (Table 1), the litter area available for prey and predator to interact were respectively 1741.5 mm^2 and 1082.0 mm^2 for 1 g of litter. Fifteen ml of distilled water was added to both soils.

2.3.2. Experimental procedures

We tested the effects of two litter species (*Q. pubescens* or *P. halepensis*) and four predator densities (no predator, low, moderate and high abundances) on the respective tri-trophic interactions between fungi, fungivorous Collembola and predatory Acari. Control samples were added in order to estimate the effects of the two litter species on fungal biomass in the absence of soil fauna. Each combination was replicated 8 times and then led to the

construction of 80 microcosms, i.e. 2 litter species × (4 predator densities + 1 treatment without fauna) × 8 replicates.

Except for the treatment without fauna, 30 individuals of the Collembola *F. candida* were added in all treatments (i.e. no predator, low, moderate and high predator densities) 7 days after the start of the experiment. In order to allow prey acclimation to leaf litter habitat, individuals of the Acari *S. scimitus* were added 14 days after the start of the experiment according to four predator densities: 0, 3, 6 or 10 individuals per microcosm, corresponding to no predator, low, moderate and high predator densities, respectively. Every two days, one ml of distilled water was added to each microcosm (Cragg and Bardgett, 2001; Schneider and Maraun, 2009).

2.4. Demographic parameters of mesofauna

After 4 weeks, litter and soil from the microcosms were disposed separately in Berlese-Tullgren funnels for 45 to 60 min. Juveniles and adults of *S. scimitus* and *F. candida* were extracted and counted. To collect and count remaining individuals, litter was observed under a stereomicroscope and soil was flooded with tap water and gently stirred before counting floating animals. The remaining litter samples were frozen at -72 °C, lyophilized for 72 h and ground into powder, prior to chemical analyses and fungal biomass determination.

Four demographic parameters were measured at the end of the experiment:

(i) survival rate of adults (100 × number of individuals at the end of the experiment / number of individuals at the start of the experiment),

(ii) fecundity rate (100 × number of juveniles at the end of the experiment / number of adults at the end of the experiment),

(iii) individual size of adults using a stereomicroscope connected with a camera (Stereomicroscope VWR, 10×) and the ToupView software,

(iv) individual biomass of adults frozen at -18 °C, lyophilized during 72 h and weighed (dry mass).

2.5. Litter characteristics

Initial litter quality was determined from four subsamples of each litter species (*Q. pubescens* and *P. halepensis*). Carbon and N concentrations were determined by thermal combustion on a Flash EA 1112 series C/N elemental analyzer (Thermo Scientific®, Waltham, MA, USA). Phosphorus (P) concentration was measured colorimetrically using the molybdenum blue method (Grimshaw et al., 1989). Eight ml of $HN0_3$ and 2 ml of H_2O_2 were added to 80 mg of ground litter sample and heated at 175 °C for 40 min using a microwave digestion system (Ethos One, Milestone SRL, Sorisole, Italy). After this mineralization step, every sample was adjusted to 50 ml with demineralized water. 100 µl of sample, 100 µl of NaOH, 50 µl of mixed reagent (antimony potassium 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). Lignin concentration was determined according to the Van Soest extraction protocol (Van Soest and Wine, 1967) using a fiber analyzer (Fibersac 24, Ankom, Macedon, NJ, USA). Total Folin phenolics were measured colorimetrically by the adapted method of Peñuelas et al. (1996) using gallic acid as a standard. 0.25 g litter sample was dissolved in 20 ml of a 70% aqueous methanol solution, shaken for 1 h, and then filtered (0.45 µm filter); 50 µl of the filtered extract was then mixed with 100 µl Folin-Ciocalteu reagent (Folin and Denis, 1915), 200 µl of saturated aqueous Na_2CO_3 (to stabilize the color reaction), and 1650 µl of distilled water. 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). To determine the water

holding capacity (WHC), intact leaf litter samples were soaked in distilled water for 24 h, drained and weighed. The dry weight was determined after drying samples at 60 °C for 48 h. WHC was calculated as moist weight / dry weight × 100% (Santonja et al., 2015b). Specific leaf area (SLA) was determined by using the Image J software (https://imagej.nih.gov/ij/, MA, USA). SLA was calculated as the ratio between leaf area and leaf dry weight.

2.6. Fungal biomass

Fungal biomass was determined by quantifying ergosterol, which is a fungal membrane constituent considered as a good indicator of living fungal biomass (Gessner and Chauvet, 1993; Ruzicka et al., 2000). We measured the fungal biomass on both initial litter samples (i.e. 2 litter species × 8 replicates) and litter samples at the end of the experiment (i.e. 2 litter species × (4 predator densities + 1 treatment without fauna) × 8 replicates). Ergosterol was extracted from 50 mg of litter with 5 ml of an alcohol base (KOH/methanol 8 g l^{-1}) for 30 min and purified by solid-phase extraction on a Waters® (Milford, MA, USA) Oasis HLB cartridge (Gessner and Schmitt, 1996). The extract produced was purified and quantified by high-performance liquid chromatography (HPLC) on a Hewlett Packard series 1050 system running with HPLC-grade methanol at a flow rate of 1.5 ml min^{-1}. Detection was performed at 282 nm, and the ergosterol peak was identified based on the retention time of an ergosterol standard.

2.7. Statistical analysis

Statistical analyses were performed with R software (version 3.3.1). Significance was evaluated in all cases at $P < 0.05$. Prior to analyses of variance (ANOVA), normality and homoscedasticity of the residuals were checked using Shapiro-Wilk and Levene tests, respectively. When conditions were not met, data were analyzed by non-parametric Kruskal-Wallis tests.

Student *t*-tests were performed to compare initial litter characteristics.

Two-way ANOVAs, followed by Tukey tests for post hoc pairwise comparisons, were used to test the effects of litter identity (*Q. pubescens* et *P. halepensis*) and predator density (no predator, low, moderate and high), on two demographic parameters of *S. scimitus* (i.e. survival rate and size), and on all demographic parameters of *F. candida* (i.e. survival and fecundity rate, size and biomass). A Wilcoxon test was performed to test the effect of litter identity on the fecundity rate of *S. scimitus*. A Kruskal-Wallis test, followed by Dunn tests for post hoc pairwise comparisons, was performed to test the effect of predator density on the fecundity rate of *S. scimitus*.

Two-way ANOVAs, followed by Tukey tests for post hoc pairwise comparisons, were also used to test the effects of litter identity (*Q. pubescens* and *P. halepensis*) and fauna (fauna with no predator or low, moderate and high predator densities + treatment without fauna) on fungal biomass changes during the experiment. These changes were calculated as (final concentration - initial concentration) / (initial concentration) × 100%.

3. Results

3.1. Initial litter characteristics

Over the 7 initial litter characteristics, only 5 varied between the two litter species (Table 1). Carbon, phosphorus and lignin concentrations were 11%, 142% and 52% higher in *P. halepensis* compared to *Q. pubescens* litter (Table 1), respectively. On the opposite, WHC and SLA values were 44% and 61% higher with *Q. pubescens* litter compared to *P. halepensis* litter (Table 1), respectively.

3.2. Predator demographic parameters

Survival and fecundity rates of *S. scimitus* were 42% and 569% higher with *P. halepensis* litter compared to *Q. pubescens* litter (Table 2; Figs. 1a and 1c), respectively. The survival rate of *S. scimitus* was lower at high predator density compared to low and moderate predator densities (Table 2; Fig. 1b). Contrary to survival rate, the fecundity rate of *S. scimitus* was not significantly affected by the predator density (Table 2), despite the fact that we observed a trend to a decrease in fecundity rate with the increase in predator density (Fig. 1d). Litter identity and predator density did not affect significantly the body size (Table 2; Figs. 1e and 1f) and individual biomass (Table 2; Figs. 1g and 1h) of *S. scimitus*.

3.3. Prey demographic parameters

The survival rate of *F. candida* was 28% higher with *Q. pubescens* litter compared to *P. halepensis* litter (Table 2; Fig. 2a). The survival rate of *F. candida* was reduced in the presence of the predator and was lower at high predator density compared to the low and moderate predator densities (Table 2; Fig. 2b). The fecundity rate of *F. candida* was not affected by the litter identity (Table 2; Fig. 2c) and was higher at moderate predator density compared to the low and high predator densities (Table 2; Fig. 2d). *Q. pubescens* litter had a positive weak effect on the size of *F. candida* compared to *P. halepensis* (Table 2; Fig. 2e) but not on *F. candida* biomass (Table 2; Fig. 2g). Size and biomass of *F. candida* were not affected by predator density (Table 2; Figs. 2f and 2h).

3.4. Fungal biomass

Fungal biomass increased in both litter species during the experiment (Fig. 3). However, fungal biomass increased at rate two times higher in *P. halepensis* litter compared to *Q. pubescens* litter ($F = 13.51$, $P < 0.001$; Fig. 3a). Contrary to litter identity, predator density did not affect fungal biomass changes ($F = 1.63$, $P > 0.05$; Fig. 3b).

4. Discussion

4.1. Predator density control

In agreement with our first hypothesis, we observed an effect of increasing predator density on both the survival and fecundity rates of *F. candida*. Firstly, the survival rate of *F. candida* was higher in the absence of a predator. Secondly, when predators were present, a lower survival rate was observed at the highest predator density compared to the two other densities. These results are in accordance with previous studies that also highlighted a negative effect of increasing density of predatory Acari on the survival rate of their prey in temperate ecosystems (Schneider and Maraun, 2009; Thakur et al., 2015). Interestingly, the strong negative impact of high predator density on *F. candida* survival rate was concomitant to a strong negative impact on *S. scimitus* survival rate. This low survival rate of the predator at high initial density could be due to starvation induced by the lower availability of prey abundance and/or by predator cannibalism (Polis, 1981), which has been previously observed for *Stratiolaelaps* (Berndt et al., 2003; Thakur et al., 2015).

Surprisingly, we observed an increase in the fecundity rate of *F. candida* when the predator density was moderate. Thakur and Eisenhauer (2015) also reported a greater growth rate of a Collembola population (*Proisotoma minuta*) with a high density of predatory Acari in a temperate grassland litter-based system (i.e. 4 prey individuals per predator individual), which is located between our moderate (i.e. 5 prey individuals per predator individual) and our high predator density (i.e. 3 prey individuals per predator individual). A trade-off between survival and reproduction of Collembola could explain these interesting results. In the present study, at moderate predator density, the increase in the fecundity rate of Collembola compensated the reduction in their survival rate. This increase in the number of Collembola juveniles at moderate

predator density led to higher prey availability and then to higher survival rate of the predatory Acari compared to the high predator density. On the contrary, the high density of predatory Acari did not lead to a better fecundity rate of Collembola. This key finding suggests that when conditions become too restrictive for the prey (i.e. at high predator density in our study), prey individuals try to survive rather than to invest in reproduction whatever the litter type, leading to strong negative feedback for both prey and predator populations.

Finally, even if shifts in Collembola abundance among the different predator densities were significant, we observed no effect of predator density on fungal biomass changes during the experiment. Previous studies also reported an absence of predator density effect on microorganisms (McLean et al., 1996; Mikola and Setälä, 1998a; Laakso and Setälä, 1999; Sackett et al., 2010). For example, Mikola and Setälä (1998b) observed a negative effect of the presence of a predatory nematode on microbivorous nematode with no cascading effect on microbial biomass after 21 weeks of experiment. Laakso and Setälä (1999) also reported that the presence of a predatory Acari (Mesostigmata) reduced the abundance of microbi-detritivorous organisms with no cascading effect on microbial biomass after 38 weeks of experiment. For both experiments, the absence of cascading effect on microbial biomass according to the presence/absence of a predator was explained by the fact that the microbial communities are able to mitigate grazing effects of microbivorous species (Nematode or Collembola) by increasing and accelerating their turnover rates (Mikola and Setälä, 1998a, 1998b). Additionally, despite the fact that the effect was not significant, we observed a trend to higher fungal biomass when solely the fungivorous Collembola were present compared to the treatments with no fauna or with predator presence (Fig. 3). In fact, the presence of microbivorous species is also known to stimulate or sustain microbial growth by changing the microbial environment (Visser, 1985; Wolters, 1991; Cragg and Bardgett, 2001) and by

dispersing spores and mycelium (Anslan et al., 2016), thus also mitigating the negative effect of their grazing.

4.2. Litter identity control

In agreement with our second hypothesis, *F. candida* was also strongly affected by litter identity, as survival rate and body size of *F. candida* were higher with *Q. pubescens* litter compared to *P. halepensis* litter. In strong contrast to *F. candida*, survival and fecundity rates of predatory Acari were higher with *P. halepensis* litter than with *Q. pubescens* litter. As hypothesized, litter physical characteristics could be responsible to this shift in the outcome of prey-predator interaction, as the specific leaf area of *P. halepensis* needles was 61% lower compared to *Q. pubescens* leaves. Indeed, *P. halepensis* needles provided less refuge for prey to escape their predator, leading to higher suppression of Collembola individuals by predatory Acari. This result comforts the recent finding of Santonja et al. (2018) that pointed out a higher predation effect of a predatory centipede (Lithobiidae) on *F. candida* abundance following the decrease in specific leaf area of European oak (*Quercus robur*) litter, i.e. at an intraspecific level. Previous studies also reported the importance of habitat structure as an important driver of prey-predator interactions by influencing encounter probabilities between Collembola and their predators (Vucic-Pestic et al., 2010; Kalinkat et al., 2013). For example, Kalinkat et al. (2013) observed that an increase of litter quantity resulted in more available refuges for a Collembola prey (*H. nitidus*), leading to a decrease in consumption rate by its centipede predator (*L. mutabilis*). Vucic-Pestic et al. (2010) also showed a decrease in consumption rate by spiders (*Pardosa lugubris)* on Collembola (*H. nitidus*) in presence of moss (*Polytrichum formosum*), highlighting the importance of refuges for the prey. In the present study, in addition to the importance of i) litter presence (Vucic-Pestic et al., 2010), ii) litter quantity (Kalinkat et al., 2013), iii) litter physical traits at an intraspecific level (Santonja et al., 2018), we

demonstrated the key importance of litter identity (*Quercus vs. Pinus*) as a regulating factor of predator-prey interactions in a Mediterranean leaf litter system. However, evidence from our laboratory experiment should be confirmed with a field experiment taking into account more complex conditions (e.g. distinct litter decomposition stages, several prey and predator species).

Finally, fungal biomass was also strongly affected by the litter identity. Both initial fungal biomass and fungal biomass increase during the experiment were higher with *P. halepensis* litter compared to *Q. pubescens* litter. The higher carbon concentration and the twice higher phosphorus concentration in *P. halepensis* compared to *Q. pubescens* initial litter could be responsible for the stronger increase in fungal biomass observed during the experiment. Indeed, carbon (Meidute et al., 2008) and phosphorus (Enríquez et al., 1993; Wardle et al., 2004) are essential elements for microbial growth. Additionally, bacteria, in particular actinomycete, are also important colonizers of decaying litter (Hättenschwiler and Vitousek, 2000; Gobat et al., 2013) that could compete with fungi for C resource (Lloyd and Lockwood, 1966, Weller, 1988; Romani et al., 2006). The higher C and lignin contents of *P. halepensis* compared to *Q. pubescens* litter probably favored fungi that are able to degrade recalcitrant compounds, such as lignin, compared to bacteria that mainly depends on the availability of more simple compounds (Moorhead and Sinsabaugh, 2006). Despite this higher fungal biomass associated with *P. halepensis* litter, we did not observe an increase in fecundity, survival, size or biomass of the fungivorous Collembola. These results suggest that the predatory Acari exhibited a higher top-down control on its prey with this litter compared to the *Q. pubescens* litter.

5. Conclusion

Our study highlighted for the first time the importance of both predator density and litter identity as drivers of tri-trophic interactions (Fungi – fungivorous Collembola – predator Acari)

in a Mediterranean forest litter system. We found that survival and fecundity rates of the predator and its prey were significantly reduced at high predator density. Interestingly, the demographic parameters of the predator and its prey strongly differed according to litter identity. The higher specific leaf area of *Q. pubescens* litter could explain the lower top-down control of the predator on its prey, leading to a reduction of predator and, on the opposite, an increase of prey survival. Based on the results of our microcosm experiment, the implications of our findings could be important under climate change as the distribution area of *Q. pubescens* may become scarcer and, in opposite, that of *P. halepensis* may increase in response to a drier climate (Gaucherel et al., 2008; Sanchez de Dios et al., 2009), with then potentially strong cascading effects on soil organisms and the processes they drive (e.g. litter decomposition and nutrient cycling). In consequence, the litter habitat modifications mediated by a potential replacement of oak by pine forests would amplify the predatory control of Collembola populations and, in opposite, decrease the control of fungal population by the fungivorous Collembola.

Author contributions

MS and VB designed the experiment. AAS, CL and MS performed the experiment. AAS and MS analyzed the data. AAS, VB, CL, CF and MS wrote the manuscript.

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Tables

Table 1. Initial litter characteristics of the two litter species used in this study. Values are means ± SE. All percentages are on a dry mass basis. Separated *t*-tests were performed for every initial litter characteristic. *T-values* and associated *P*-values (with the respective symbols * for $P < 0.05$, ** for $P < 0.01$, and *** for $P < 0.001$) are indicated. Water Holding Capacity, SLA = Specific Leaf Area.

	Q. pubescens	*P. halepensis*	*t-test*
C (%)	47.09 ± 0.19	52.37 ± 0.79	6.46***
N (%)	1.18 ± 0.06	1.01 ± 0.03	2.39
P (‰)	0.19 ± 0.01	0.46 ± 0.04	7.03***
Lignin (%)	19.85 ± 1.08	30.18 ± 0.73	7.91***
Phenolics (%)	5.90 ± 0.88	7.10 ± 0.22	1.32
WHC (%)	154.50 ± 3.41	106.93 ± 2.99	10.49***
SLA ($cm^2\ g^{-1}$)	174.15 ± 3.35	108.20 ± 6.70	8.80***

Table 2. Output of analyses of variance testing for the effects of litter identity and predator density on demographic parameters of *Stratiolaelaps scimitus* and *Folsomia candida* (except for fecundity rate of *S. scimitus* for which the results of Wilcoxon and Kruskal-Wallis tests for litter identity and predator density effects are reported, respectively). d.f. = degrees of freedom, %SS = percentage of sums of squares. *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.

		Survival rate			Fecundity rate			Individual size			Individual biomass		
	d.f.	%SS	*F*-value	*P*-value	%SS	*F*-value	*P*-value	%SS	*F*-value	*P*-value	%SS	*F*-value	*P*-value
S. scimitus													
Litter (L)	1	26.21	21.02	***		14.48	***	0.00	0.01		5.87	2.79	
Predation (P)	2	20.19	8.10	**		3.75		4.41	1.00		1.86	0.44	
L × P	2	1.21	0.49					2.55	0.58		8.24	1.96	
Residuals	42	52.39						93.04			84.03		
F. candida													
Litter (L)	1	12.59	16.85	***	0.07	0.06		6.77	4.96	*	0.00	0.00	
Predation (P)	3	43.95	59.62	***	27.68	7.86	***	8.21	2.01		5.29	1.15	
L × P	3	1.63	0.73		6.52	1.85		8.57	2.09		9.02	1.97	
Residuals	56	41.83			65.73			76.45			85.69		

Figure legends

Fig. 1. Effects of litter identity (a, c, e, g) and fauna treatment (b, d, f, h) on survival rate (a, b), fecundity rate (c, d), individual size (e, f) and individual biomass (g, h) of *Stratiolaelaps scimitus*. Values are means ± SE; n = 32 and 16 for litter identity and predator density treatments, respectively. Different letters denote significant differences between treatments with a < b. LP = Low Predator density, MP = Moderate Predator density, HP = High Predator density.

Fig. 2. Effects of litter identity (a, c, e, g) and fauna treatment (b, d, f, h) on survival rate (a, b), fecundity rate (c, d), individual size (e, f) and individual biomass (g, h) of *Folsomia candida*. Values are means ± SE; n = 32 and 16 for litter identity and predator density treatments, respectively. Different letters denote significant differences between treatments with a < b < c. NP = No Predator, LP = Low Predator density, MP = Moderate Predator density, HP = High Predator density.

Fig. 3. Effects of litter identity (a) and fauna treatment (b) on fungal biomass changes during the experiment. Values are means ± SE; n = 32 and 16 for litter identity and fauna treatments, respectively. Different letters denote significant differences between treatments with a < b. NF = No Fauna, NP = No Predator, LP = Low Predator density, MP = Moderate Predator density, HP = High Predator density.

Fig. 1.

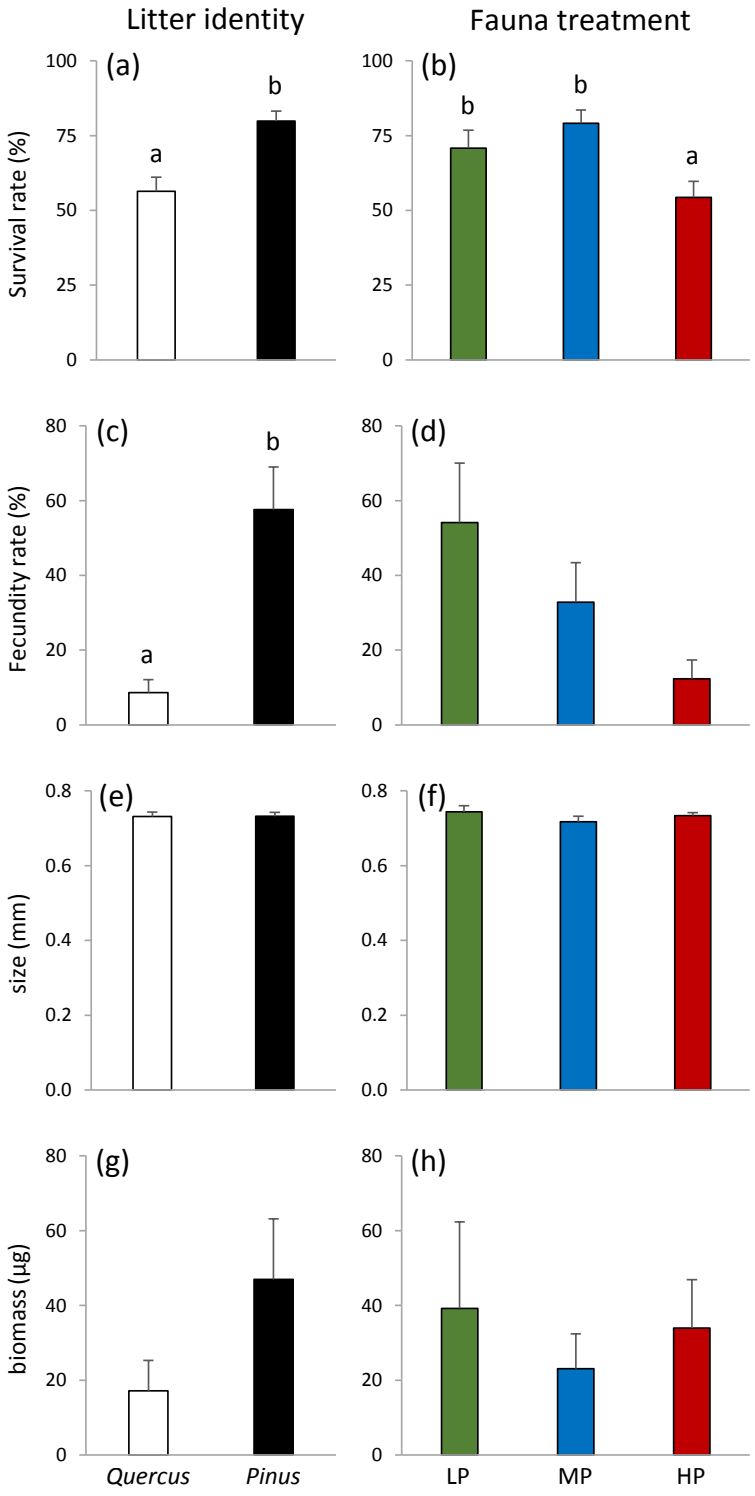

Litter identity
Fauna treatment
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Survival rate (%)
Fecundity rate (%)
size (mm)
biomass (µg)
a
b
b
b
a
a
b
100
75
50
25
0
80
60
40
20
0.8
0.6
0.4
0.2
0.0
Quercus
Pinus
LP
MP
HP

Fig. 2.

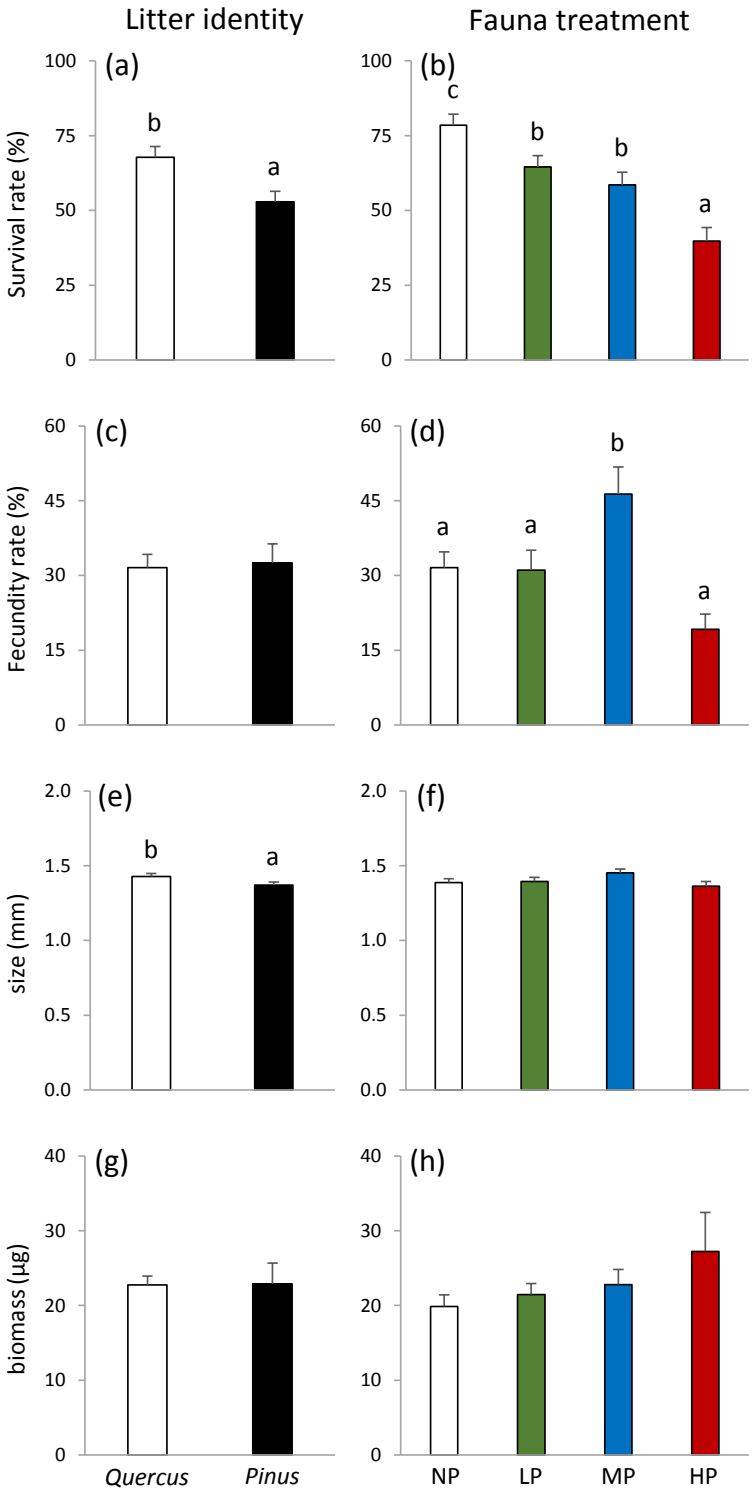
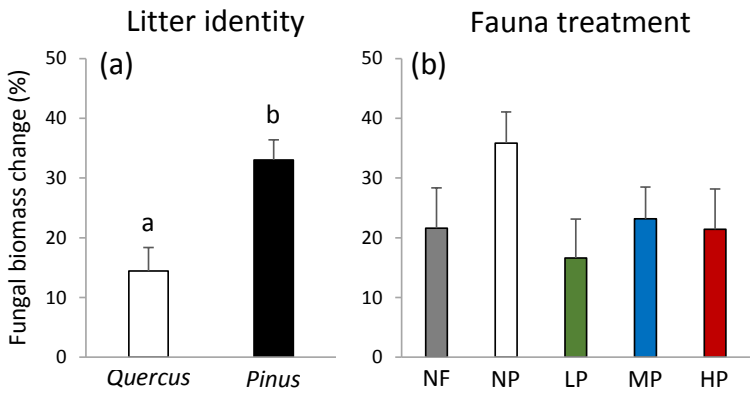

Litter identity
Fauna treatment
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Survival rate (%)
Fecundity rate (%)
size (mm)
biomass (µg)
Quercus
Pinus
NP
LP
MP
HP

Fig. 3.


Litter identity
Fauna treatment
(a)
(b)
Fungal biomass change (%)
50
40
30
20
10
0
a
b
Quercus
Pinus
NF
NP
LP
MP
HP