# Interactions between invertebrate and microbial communities in decomposing camphor and Masson pine litter varied with seasonal rainfall

Jun Li[1,2], Chenhui Chang[3,4], Wanqin Yang[1,*]

[1] *School of Life Science, Taizhou University, 1139# Shifu Avenue, Taizhou, Zhejiang 318000, China*

[2] *Key Laboratory of Cultivation and Protection for Non-Wood Forest Trees, Ministry of Education, Central South University of Forestry and Technology, No. 498, Shaoshan Road, Changsha, Hunan 410004, China*

[3] *Systems Ecology, Faculty of Science, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081HV Amsterdam, The Netherlands*

[4] *Institute of Ecology & Forestry, Sichuan Agricultural University, No.211, Huimin Road, Wenjiang District, Chengdu, Sichuan 611130, China*

Type of paper: Research article

*Corresponding author: Wanqin Yang, School of Life Science, 1139# Shifu Avenue, Taizhou, Zhejiang 318000, China

*E-mail addresses*: scyangwq@163.com

**Running Title** Interactions between invertebrate and microorganism in foliar litter

**Abstract**

To reveal the changes in the interactions between invertebrate and microbe in decomposing litter along with seasonal rainfall, litterbags containing camphor (*Cinnamomum longepaniculatum*) and Masson pine (*Pinus massoniana*) litter were respectively in-situ incubated on the floor of Masson pine and camphor mixed plantations in October 2013 in subtropical region of China. Different mesh sizes of litterbags were used to control the access of the invertebrate. The invertebrates were collected by funnel method, and microbial communities were measured by phospholipid fatty acid (PLFA) method after collecting the litterbag samples in slightly rainy season (SRS), micro rainy season (MRS), early rainy season (ERS) and rainy season (RS) during 2-yr decomposition. We found that the abundance and structure of microbial and invertebrate communities varied sharply with seasonal rainfall and tree species. Invertebrate exclusion generally decreased all types of microbial biomasses (the total microbial biomass, fungal biomass and bacterial biomass, Gram-positive bacterial biomass and Gram-negative bacterial biomass) in Masson pine needle litter, but generally increased these types of microbial biomasses in camphor foliar litter at most time. Invertebrate exclusion decreased the mass loss rate of Masson pine litter, but increased the mass loss rate of camphor litter. In conclusion, the interactions between invertebrates and microbial communities are significantly controlled by litter quality and the seasonal rainfall pattern, which could significantly drive the decomposition process of leaf litter.

**Keywords:** foliar litter species; phospholipid fatty acids (PLFA); bacteria; fungi;

subtropical regions

# 1. Introduction

Both invertebrates and microbes play crucial roles in litter decomposition (D. A. Wardle et al., 2004; Wood, Schlindwein, Soares, & Araujo, 2012), which is a key process in bioelement cycle and energy flow in forest ecosystem (Berg & Mcclaugherty, 2003). Generally, invertebrates are classified as predator, herbivore, fungivorous, bacterivorous and saprophage, each functioning on litter decomposition in different ways (Gräff, Berkus, & Köhler, 1997; Zwart et al., 1994). Microorganisms are the primary regulators of terrestrial carbon and nutrient cycling (Thomas W Crowther, Boddy, & Hefin Jones, 2012). They can degrade the foliar litter components using extracellular enzyme (Baerlocher, 1992; Berg & McClaugherty, 2014) and release inorganic matter to soil and improve litter palatability to the invertebrate (Dighton, White, & Oudemans, 2005; Suberkropp, 1998). Previous studies have indicated that soil invertebrate activity could increase nutrients level and stimulate microbial growth (Denton, Bardgett, Cook, & Hobbs, 1999; Saggar, Mercer, Hedley, & Yeates, 1999). However, some invertebrates may break the fungal hypha or feed on bacteria and fungi, thus decreasing the efficiency of litter decomposition (T. W. Crowther et al., 2013). Consequently, the invertebrate community can be closely correlated with microbial community and together regulate the decomposition process of foliar litter. Many studies have addressed the dynamics of invertebrate or microbial communities in soil and litter (Negussie et al., 2015; Svyrydchenko & Brygadyrenko, 2014). It is well-known that both soil invertebrates and microbes are sensitive to seasonal rainfall and temperature (Bouskill et al., 2013; Couteaûx, Bottner, & Berg, 1995; Pereira et al., 2019). However, less attention has been paid to the changes in the interactions between invertebrate and microbial communities in decomposing foliar litter with seasonal rainfall. Together, understanding the changes in invertebrate and the microbial communities and their interactions with seasonal rainfall and tree species is key to better revealing the mechanism of litter decomposition.

As important decomposers of litter decomposition, soil invertebrates and microorganisms can actively participate in litter decomposition (W. Wang, Yang, Bo, Liu, & Wu, 2015), and their contributions on decomposing process are strongly affected by environmental factors (Barnes et al., 2015). For instance, seasonal changes in abiotic factors such as sunlight, temperature, and rainfall could regulate the composition and abundance of decomposer communities (AlbariÑO, Villanueva, & Canhoto, 2008; Couteaûx et al., 1995; Moeed & Meads, 1986). However, there is no inconsistent conclusion about how seasonal rainfall affects the dynamics of invertebrate and microbial communities (Frith & Frith, 1990; Moeed & Meads, 1986; Wall et al., 2008), i.e. the mechanism on the effect of soil organism on litter decomposition remains uncertain. Lower moisture might limit microbial distributions and activities (Bouskill et al., 2013). For instance, Couteaûx et al. (1995) found that the microbial community became inactive under unfavourable moisture content. Pereira et al. (2019) addressed that the reduction of rainfall gives slight effects on Actinobacteria and bacterial abundance, but significantly increases the abundance of soil fungal communities in the Mediterranean forests. Although numerous studies have investigated the changes in the activity and structure of invertebrate or microbial community with the seasons (Allison et al., 2013; Yoshida, Takito, Soga, & Hijii, 2013), little is known about how the interactions between invertebrate and microbial communities in decomposing litter change in accordance with seasonal rainfall.

Previous studies have demonstrated that foliar litter species exert great bottom-up effect on decomposition (Frouz, Roubíčková, Heděnec, & Tajovský, 2015; Walker et al., 2014; D. A. Wardle et al., 2004). The chemical composition of litter determines the structure and species composition of biotic community present in decomposing litter (Wardle & Lavelle, 1997). In general, the invertebrate tends to inhabit at high-quality litter (Iii, Ostertag, & Cowie, 2011). However, some microbes, such as the Gram-negative bacteria, prefer to easily decomposed litter, whereas the Gram-positive bacteria are adapted to decomposition-resistant litter (Nottingham, Griffiths, Chamberlain, Stott, & Tanner, 2009; Suzuki, Grayston, & Prescott, 2013). Many studies have addressed the effects of litter quality on the invertebrate or the microbial community (Cleveland et al., 2014; Fernandes, Duarte, Cássio, & Pascoal, 2015; Ferreira & Chauvet, 2011; Leroy & Marks, 2006), but little attention has been given to the changes in the interaction between invertebrate and microbial communities in decomposing litter with tree species.

We therefore hypothesized that both invertebrate and microbial communities in decomposing litter and their interactions would vary greatly with the seasonal rainfall and tree species, and consequently drive the litter decomposition. To test these hypotheses, we conducted a litter decomposition experiment in the subtropical forest region in the upper reaches of the Yangtze River. Litterbags containing foliar litter of camphor (*Cinnamomum longepaniculatum*) and Masson pine (*Pinus massoniana*), two representative tree species in the region, were respectively in-situ incubated on the floor of camphor and Masson pine plantations. The structure and composition of invertebrate and the microbial communities in decomposing litter during different seasonal rainfall periods in two years were measured by the funnel and phospholipid fatty acid (PLFA) methods. The objectives of this study are to understand (1) the variation in the structure of microbial and invertebrate communities in decomposing litter with seasonal rainfall and foliar litter species, and (2) the changes in the interactions between invertebrate and microbial communities in decomposing litter with seasonal rainfall and foliar litter species.

## 2. Materials and methods

### 2.1. Site description

In-situ litter decomposition experiment was conducted in the Masson pine and camphor mixed plantation situated in Gao County, Sichuan Province (104°32′-104°34′E, 28°34′-28°36′N; 412-567 m.a.s.l.), which is located in the upper reaches of the Yangtze River and the southern margin of the Sichuan Basin (Justine et al., 2015). The climate is subtropical, sub-humid monsoon with an annual precipitation of 1021 mm. The mean annual temperature is 18.1°C, with the lowest and highest temperature of 7.8°C (January) and 36.8°C (July) respectively. Masson pine and camphor are two representative afforestation tree species in this region and are widely planted in monoculture or mixed culture. More details about the species composition of the understory plant community see Justine et al. (2015). The soil type is mountain yellow earth with a mean thickness of 40-60 cm, from soil horizons down to parent material. Soil pH is 4.3±0.4. The content of total organic carbon, total nitrogen content, and the total phosphorus content are 16.3±1.5 g/kg, 0.7±0.1 g/kg, and 2.0±0.3 g/kg, respectively (W. Wang, Yang, Tan, Liu, & Fuzhong, 2013).

### 2.2. Experimental design and sampling

Foliar litters of Masson pine and camphor were collected from the plantation in October 2013, and then air-dried at room temperature until equilibrium mass. For each foliar litter species, 10-g dried litter samples were enclosed in 20 cm×20 cm nylon litterbags with two types of mesh sizes (0.04 mm on both sides, and 0.04 mm at bottom side and 3 mm on top side). The litter bags with 0.04 mm on both sides prevented soil invertebrate from entering the litterbags (invertebrate excluded), whereas the other type of litter bags allowed for the access of the invertebrate (invertebrate included) (Crutsinger, Sanders, & Classen, 2009; Zwahlen, Hilbeck, & Nentwig, 2007). We selected three homogeneous plots (10 m×10 m) within the plantation to carry out leaf litter decomposition experiment. In November 2013, 576 litterbags (2 litterbag types × 2 foliar litter species × 3 plots × 6 replicates × 8 sampling dates) were incubated on the forest floor after removing the litter and weeds on the soil surface.

Based on historical precipitation records of Laifu town of Gao County, China, the litterbags were retrieved in the slightly rainy season (SRS; November 1-December

24), micro rainy season (MRS; December 25-March 7), early rainy season (ERS; March 8-June 15), and the rainy season (RS; June 16-October 31) from 2013 to 2014. Three litterbags collected from each plot and transported to the lab were used to collect and identify the invertebrate; three litterbags of each treatment were put into the icebox, transported to the lab, and used for PLFA extraction (stored at -70 ℃).

The air temperature was recorded every two hours using data loggers (iButton DS1923-F5, Maxim/Dallas Semiconductor, Sunnyvale, USA), and the precipitation data were obtained from an online Chinese Weather Database (http://sc.weather.com.cn/qxfw/index.shtml) (Fig. S.1).

## 2.3. The invertebrate and the microbial organism extraction

The invertebrates in the litterbags were extracted by the Tullgren method (Crossley & Blair, 1991) for 4 days and then collected in 90% ethanol. All the invertebrates were identified into genus level, if possible, with the guidance of the book Pictorial keys to the soil animals of China (Wenying, 1998) using stereomicroscope (Leica, EZ4HD). The list of the invertebrate collected in our study and the abundance data were shown in Table S.1 and S.2. Losing of last sampling litter weight data results in the individual density of the invertebrate cannot be computed.

The PLFA bioindicators obtained in this study were presented in Table S.3 using the nomenclature of Frostegård, Tunlid, and Bååth (1993). The single extraction method modified by White, Davis, Nickels, King, and Bobbie (1979) was used for the total lipids. A 1 (±0.0050) gram freeze-dried and ground foliar litter sample was used for PLFA determination according to the method mentioned by Chang et al. (2019). More details see the website https://www.protocols.io/view/extraction-of-plfa-from-wood-debris-ixmcfk6.

### 2.4. Data analysis

Decomposition regression model of foliar litter (Olsen, 1963):

$$Y = a e^{-kt} \qquad \text{Equation 1}$$

*Y* is the residual rate of foliar litter. *a* is the fitting parameter. *t* is the days of decomposition. *k* is the decomposition constant.

Time to loss 50% mass loss:

$$T_{0.5} = \ln 0.5 / (-k) \qquad \text{Equation 2}$$

Time to loss 95% mass loss:

$$T_{0.95} = \ln 0.05 / (-k) \qquad \text{Equation 3}$$

Nonparametric test with a significance level of 0.05 was used to compare the total microbial biomass, bacterial biomass, fungal biomass, ratio of fungal to bacterial biomass, Gram-positive ($G^+$) bacterial biomass, Gram-negative ($G^-$) bacterial biomass, ratio of $G^+$ to $G^-$ bacterial biomass, and the individual density of the invertebrate between foliar litters of tree species and among different seasonal rainfall periods, respectively. Spearman’s correlation coefficient was calculated to determine the significance of correlations between invertebrate individual density and microbial biomass, between invertebrate individual density and litter mass loss, and between microbial biomass and litter mass loss using the two-tailed test with significance levels of 0.01 and 0.05. Principal co-ordinates analysis (PCoA) and Permutational MANOVA (Permanova) based on Bray-Curtis distance were used to evaluate the effect of foliar litter species, invertebrate and seasonal rainfall pattern on microbial PLFA. Partial Least Squares Discriminant Analysis (PLS-DA) was used to measure the contribution of foliar litter species and invertebrate on microbial PLFA structure in different seasonal rainfall periods. Correlation heatmaps between invertebrate and microbial communities, and PCoA and PLS-DA were performed using OmicShare tools, a free online platform for data analysis (http://www.omicshare.com/tools). The Nonparametric test and Spearman's correlation were carried out with R program (version 4.3.5).

## 3. Results

### 3.1. Abundance and individual density of invertebrate community

The total abundance (Fig. 1a) and individual density (Fig. 1b) of invertebrate community in decomposing litter were significantly (*P* <0.05) affected by seasonal rainfall and foliar litter species. The abundance and individual density of invertebrate community increased from the first SRS to the second SRS in decomposing Masson pine litter, and then decreased from the second SRS to second RS. The highest individual density occurred in the second SRS, while the lowest occurred in the first and second MRS in decomposing camphor litter. Regardless of foliar litter species, the invertebrate community in decomposing litter was dominated by Prostigmata, Isotomidae, Oribatida and Anystidae (Table S.1).

3.2. Effects of invertebrate exclusion on total microbial biomass

The effects of invertebrate exclusion on total microbial biomass in foliar litter varied greatly with seasonal rainfall periods and tree species (Fig. 2). The total microbial biomass in foliar litters of all the treatments all changed with the seasonal rainfall, and the peaks depended on decomposing years. In the first decomposition year, higher total microbial biomass was observed in SRS and MRS compared with the other rainfall seasons, while in the second year, higher total microbial biomass was observed in RS or ERS. The opposite response of total microbial biomass to invertebrate exclusion was observed between Masson pine and camphor litters (Fig. 2). Invertebrate exclusion increased the total microbial biomass in decomposing camphor litter, but decreased the total microbial biomass in decomposing Masson pine litter. Moreover, for Masson pine litter, invertebrate exclusion gave stronger negative effects on total microbial biomass in MRS of the first decomposition year, and that in SRS of the second decomposition year. For camphor litter, invertebrate exclusion gave stronger effects on the total microbial biomass in RS.

3.3. Effects of invertebrate exclusion on fungal and bacterial biomass

Fungal biomass, bacterial biomass and the ratio of fungal to bacterial biomass in decomposing litter varied greatly with the seasonal rainfall, and the responses of these indexes to invertebrate exclusion varied greatly with foliar litter species (Fig. 3). The highest fungal biomass in the two species litters was observed in the dry season (SRS), whereas the lowest value was found in the RS. The variations in bacterial biomass in two foliar litters showed the same pattern with total microbial biomass. In both foliar litter species, the highest ratio of fungal to bacterial biomass was observed in the first SRS, and the ratio was less than 0.1 at other periods.

The effects of the invertebrate exclusion on fungal and bacterial biomass and their ratio also changed with seasonal rainfall and foliar litter species (Fig. 3c). Invertebrate exclusion significantly decreased the fungal and bacterial biomass in the first MRS and the second SRS in Masson pine litter, but significantly ($P$ <0.05) increased the bacterial biomass in the second RS in camphor litter. However, the effects of invertebrate exclusion on fungal biomass depended greatly on seasonal rainfall and tree species. On the whole, invertebrate exclusion significantly increased the ratio of fungi to bacterial biomass in dry season, but slightly decreased the ratio of fungal to bacterial biomass.

### 3.4. Effects of invertebrate exclusion on G+ and G- bacterial biomass

Seasonal rainfall had strong effects on $G^+$ bacterial biomass, $G^-$ bacterial biomass, and the ratio of $G^+/G^-$ bacterial biomass in both species of foliar litter (Fig. 4). Higher $G^+$ bacterial biomass in two foliar litters was observed in the second RS, while lower value was found in the first ERS, RS and the second SRS. Higher $G^-$ bacterial biomass in two foliar litter was found in the first SRS and the second RS, while lower value was detected in the first ERS and RS during the whole incubation years. Except SRS, the ratio of $G^+/G^-$ bacterial biomass in both species of foliar litter was significantly higher in the second decomposition year than that in the first year (Fig. 4c).

Tree species and seasonal rainfall pattern regulated the effects of invertebrate exclusion on $G^+$ and $G^-$ bacterial biomass and their ratios (Fig. 4). Invertebrate exclusion significantly decreased the $G^+$ bacterial biomass in the first MRS and the $G^-$ bacterial biomass in the first MRS, the second SRS and MRS in decomposing Masson pine litter, but increased $G^+$ bacterial biomass during the second RS and $G^-$ bacterial biomass in the first RS and the second ERS in decomposing camphor foliar litter. $G^-$ bacterial biomass in decomposing litter was more susceptible to invertebrate exclusion than $G^+$ bacterial biomass.

3.5. Changes in microbial community structure

Principal Co-ordinates Analysis (PCoA) and Permutational MANOVA (Permanova) showed that seasonal rainfall (*P*<0.001) was the predominant factor affecting the microbial community structure (Fig. 5). Foliar litter species gave significant (*P*=0.038) effect on microbial community structure. Microbial community composition in SRS differed significantly from that in other three seasonal rainfall periods.

The results of PLS-DA showed the species of foliar litter and invertebrate exclusion both gave significant effect on microbial community structure (Fig. S.2 and Fig. S.3), and the former showed a stronger effect than the latter. It is worth noting that the biomass of 16:1ω9c, the bioindicator of the $G^-$ bacteria, was markedly affected by foliar litter species and invertebrate exclusion during the decomposition process.

### 3.6. Changes in interactions between microbial and invertebrate communities

Spearman's correlation indicated that significant effects of invertebrate exclusion on microbial communities changed with foliar litter species and seasonal rainfall pattern (Table 1). During the first decomposition year, invertebrate individual density was significantly negatively correlated with all parameters of microbial biomass except the F/B and the G+/G- in Masson pine litter; invertebrate individual density was significantly and negatively correlated with all parameters of microbial biomass except the F/B in camphor litter. No significant correlations were observed between invertebrate individual density and microbial PLFA in litter of tree species during the second decomposition year.

During the first decomposition year, Prostigmata and Isotomidae in Masson pine litter were significantly and negatively correlated with $G^+$ bacterial biomass and fungal biomass; Entomobrya was significantly negatively correlated with Gram-positive bacterial biomass while positively correlated with 16:1ω5t; Oribatida was negatively correlated with bacterial and fungal biomass (Fig. 6a). In camphor litter, Prostigmata and Oribatida were significantly and negatively correlated with bacterial and fungal biomass; Isotomidae was significantly and negatively correlated with bacterial biomass (Fig. 6b). During the second decomposition year, Anystidae in Masson pine litter was significantly and negatively correlated with $G^+$ bacterial biomass (Fig. 6c). In camphor litter, Liacarus was significantly and negatively correlated with $G^+$ bacterial biomass; Malaconothrus was positively correlated with bacterial biomass (Fig. 6d).

According to Fig. 2-4 and Table S.5, the interactions between invertebrate and microbial communities in decomposing litter varied greatly with seasonal rainfall pattern and tree species. The weakest interactions between invertebrate and microbial communities were found in the ERS both for the two tree species. In Masson pine, the strongest interactions were in the MRS during the first year while in the SRS during the second year; in camphor litter, the strongest interactions were in the RS during two decomposition years.

Spearman's correlations of litter mass loss with invertebrate individual density and microbial parameters depended greatly on tree species and seasonal rainfall pattern (Table 2). In the first decomposition year, Masson pine litter mass loss was significantly and negatively correlated with all types of microbial biomasses. Similarly, camphor litter mass loss was significantly and negatively correlated with microbial parameters except $G^+/G^-$ bacterial biomass. Invertebrate individual density was significantly and positively correlated with Masson pine litter loss during the first decomposition year.

## 4. Discussion

The results supported our hypotheses that the structure of invertebrate and microbial communities, and their interactions varied greatly with seasonal rainfall patterns and tree species. Our results also indicated that the effects of invertebrate exclusion on microbial community structure depended greatly on seasonal rainfall pattern and tree species, and in turn affected the litter decomposition process.

### 4.1 Interactions between invertebrate and microbial communities in decomposing litter

Both microorganism and invertebrate play active roles in decomposing litter, but the relative contribution to litter decomposition depends greatly on their interactions (Straalen & Gestel, 1997). In this study, both positive and negative relationships were found between invertebrate and microbial communities, of which varied with tree species and seasonal variations. These results were consistent with Cole, Staddon, Sleep, and Bardgett (2004), who have concluded that soil fauna can have positive, negative or neutral effects on microbial properties. In general, the invertebrate tends to compete with the microorganism for resources and habitats in foliar litter (Scheu, Ruess, & Bonkowski, 2005). Some invertebrates also feed on bacteria or fungus (Griffiths & Caul, 1993; Sohlenius, 1980). Some studies have showed that the actions of some invertebrates led to nutrient releases from decomposing litter, thus enriching the microbial community (Ball, Bradford, & Hunter, 2009; Piatek, Munasinghe, Peterjohn, Adams, & Cumming, 2009; Kathryn B Piatek, Prinith Munasinghe, William T Peterjohn, Mary Beth Adams, & Jonathan R Cumming, 2010; K. B Piatek, P Munasinghe, W. T Peterjohn, M. B Adams, & J. R Cumming, 2010). As a consequence, the interactions between soil organisms were often determined by predation intensity, resource richness, soil biological community structure and nutrients (Scheu et al., 2005).

### 4.2 Dynamics of microbial and invertebrate communities and their interactions varied with seasonal rainfall pattern

Our result indicated that seasonal rainfall was the predominant factor affecting the dynamics of microbial community, which was consistent with previous study (Zhao, Wu, Yang, Tan, & He, 2016). We further found the highest biomass values of total microorganism, fungi, bacteria, G+ and G- bacterial biomass occurred from slightly rainy season (SRS) to micro rainy season (MRS) in the first decomposition year, which is consistent with the findings that the soil microbial biomass decreased with increasing incubation temperature (Wu, Yu, Wang, Ding, & Xu, 2010). As decomposition proceed, microbial biomass and composition in foliar litter is strongly affected by the decreases in labile compounds and the increases in recalcitrant compounds (Sauvadet, Chauvat, Brunet, & Bertrand, 2017; Sauvadet, Chauvat, Fanin, Coulibaly, & Bertrand, 2016). At the early period of decomposition, microbial biomass gradually increased in abundance owing to the high amount of labile constituents derived from the fresh foliar litter (Boer, Folman, Summerbell, & Boddy, 2005). In this study, the large amount of precipitation leached many nutrients in the rainy season (RS), and at the early stage of litter decomposition, fungi dominated the microbial community, which was consistent with the results by Harley (1971), who have demonstrated that fungi are the main primary colonizers of fresh foliar litter. That is, fungi break foliar litter down into fragments, thus providing an increased surface area to which bacteria can adhere (Lin, Liu, Yan, & Hai, 2004). Fungi tend to be most active in winter (Bewley & Parkinson, 1985; Parkinson, Domsch, & Anderson, 1978). Thus, higher fungal biomass was detected in the slightly rainy season. However, the total microbial biomass, bacterial biomass, $G^+$ bacterial biomass, and the ratio of $G^+/G^-$ bacterial biomass gradually increased from the slightly rainy season to the rainy season in the second decomposition year. It is worth noting that the increase of $G^+$ bacterial biomass accounted for the primary proportion of total biomass and bacterial biomass. In general, the ratio of $G^+/G^-$ bacterial biomass is known as an indicator of nutrient content (Kourtev, Ehrenfeld, & Häggblom, 2003). Many studies have shown that $G^+$ bacteria are better able to utilize refractory substances (Schutter & Dick, 2001), while $G^-$ bacteria prefer labile carbon sources (Kramer & Gleixner, 2006; Nottingham et al., 2009; Waldrop & Firestone, 2004). Together, the structures of microbial community in decomposing litter are strongly changed by the consumption of labile components.

Similar to the microorganism, the invertebrate was also strongly affected by seasonal rainfall. The abundance and individual density of invertebrate community gradually increased from the first slightly rainy season to the second slightly rainy season, which was similar to the results of a study by Liu, Yang, Wu, Tan, and Wang (2014). Many studies have suggested that temperature and precipitation are the key factors influencing the dynamics of invertebrate community (David & Gillon, 2009; S. Wang, Ruan, & Bing, 2009). In this study, the environment with higher temperature and humidity occurred in the rainy season, which was more suitable for the invertebrate (Gongalsky et al., 2008; González & Seastedt, 2000).

Bardgett and Putten (2014) have reviewed that soil organisms vary over timescales. In our study, the interactions between invertebrate and microbial communities varied sharply with seasonal rainfall in the subtropical planation, which had barely been reported before. During the first winter (from the first slightly rainy season to the first micro rainy season), although there was much fresh foliar litter, a small quantity of the invertebrate, whose activity was limited by the low temperatures, needed time to garrison into foliar litter. As time passed, the temperatures and precipitation increased, and the foliar litter released large amounts of nutrients due to invertebrate fragmentation, microbial decomposition, and rainfall leaching. Thus, the invertebrate became active again, and invertebrate individual density gradually increased in the first early rainy season (ERS) and rainy season, which was similar to the results by Xu, Kuster, Günthardt-Goerg, Dobbertin, and Li (2012). In the first rainy season, strong leaching and resource consumption utilized by soil organisms and plants, might lead to competitive relationships between invertebrate and microbial communities. This result is verified by increasing abundance and individual density of invertebrate community (Fig. 1) and decreasing biomass of 16:1ω7c and 16:1ω9c when the invertebrate existed (Table S.5 and Fig. 4). As the litter decomposition proceed, individual density and microbial biomass only changed slightly in the second slightly rainy season. It is likely that new fresh foliar litter provides more resources for soil organisms and week disturbance of lighter rainfall, and brings relative stable microenvironments. During the second slightly rainy season, the invertebrate gave stronger effects on the microbial community. To be more precise, presence of the invertebrate increased the biomass of $G^-$ bacteria, other bacteria and fungi (Table S.5 and Fig. 4). The increase of $G^-$ bacterial biomass reflected the occurrence of more newly unstable carbon sources. Many studies have reported that $G^-$ bacteria typically live on substances with relatively unstable carbon sources (Kramer & Gleixner, 2006; Nottingham et al., 2009; Waldrop & Firestone, 2004). Therefore, there might be interactive relationships between invertebrate and microbial communities. Although new freshly foliar litter covered on the surface, it was hard to pour in the litter bag due to the small pore diameter. Thus, microbial biomass especially G+ bacterial biomass gradually increased with increasing temperature after the second slightly rainy season, while invertebrate individual density decreased. It is likely that there were refractory substances that account for a relatively large proportion from the second micro rainy season to the rainy season. Moreover, the variations of microbial biomass in the second decomposition year were significantly different between Masson pine and camphor litter, implying that foliar litter species would dramatically affect the dynamics of invertebrate and the microbial communities and their interactions.

### 4.3 The effects of foliar litter species on microbial and invertebrate communities and their interactions

Litter quality determined by tree species is a critical factor affecting the soil organisms (Saetre & Bååth, 2000; X. Wang, Yu, Zhou, & Fu, 2016). Although there were many differences in litter quality between Masson pine and camphor (Table S.6), similar correlations of litter mass loss with microbial biomass (negative) and invertebrate individual density (positive) were observed in both tree species (Table 2), implying that seasonal changes in rainfall and temperature are also key drivers of litter decomposition besides litter quality. In this study, the dynamics of microbial biomass in decomposing litter varied markedly with tree species (Fig. 2-5, Table S.4).

Similarly, significant differences of invertebrate community in litterbags were observed between Masson pine and camphor litter, implying litter quality dominates the structure and composition of invertebrate community in decomposing litter.

We found a negative relationship between microbial biomass and invertebrate abundance in decomposing litter. Even so, it is difficult to conclude that microbial biomass in decomposing litter decreases with the increase of invertebrate density and abundance. In fact, the interactions between invertebrate and microbial communities might be regulated by many biotic and abiotic factors such as seasonal hydrothermal dynamics and litter quality. Previous studies have indicated that the higher value of C/N, C/P and lignin content and the lower N content are, the more restricted activities of the microorganism are in foliar litter, and then the more slowly foliar litter decomposes (Moore et al., 1999; Taylor, Parkinson, & Parkinson, 1989). In this study, the ratios of C/N and C/P, and lignin content in Masson pine litter were higher than those in camphor litter, and N content was the opposite (Table S.6). Invertebrate exclusion promoted the decomposition of Masson pine litter, but dramatically lowered the decomposition of camphor litter (Table 3). The result might be attributed to that the microorganism is the predominant decomposer in foliar litter (Ayres, Dromph, & Bardgett, 2006). In this study, invertebrate exclusion sharply decreased the microbial biomass in decomposing Masson pine litter, increased the microbial biomass in camphor litter during two decomposition years (Fig. 2-4). Thereby, we speculate that the invertebrate benefits microbial growth and proliferation in Masson pine litter by breaking into or digesting the foliar litter, and excreting liable substrate for microbes, while the invertebrate could decrease the microbial biomass and activity by preying on bacteria and fungi. Briefly, the positive or negative interaction between invertebrate and microbial communities runs the decomposition of leaf litter, and the contribution of invertebrate to litter decomposition depends greatly on tree species and season.

## 5. Conclusion

The dynamics of microbial and invertebrate communities, and their interactions in decomposing litter were strongly affected by tree species and seasonal rainfall. In general, positive, negative and neutral correlations between invertebrate and microbial communities were observed, depending on seasonal rainfall pattern and foliar litter species, which determine the richness and structure of soil invertebrate and microbial communities. Invertebrate exclusion significantly slowed down the rate of decomposition process by decreasing the microbial biomass in Masson pine litter, while promoted the rate of decomposition process by increasing the microbial biomass in camphor litter. Regardless of tree species, the weakest interactions were observed in the early rainy season. In Masson pine litter, the strongest interactions were found in the micro rainy season of the first decomposition year, while that in the slightly rainy season during the second decomposition year. In camphor litter, the strongest interactions were in the rainy season during the two year decomposition. Further studies should deeply explore the effects of litter functional traits on microbial and invertebrate communities, and their interactions.

## Acknowledgement

This work was supported by the National Natural Science Foundation of China [grant numbers 31570445, 31570601, 31270498]

## Conflicts of interest statement

The co-authors of the manuscript have no conflicts of interest related to this study

# Reference

AlbariÑO, R., Villanueva, V., & Canhoto, C. (2008). The effect of sunlight on leaf litter quality reduces growth of the shredder *Klapopteryx kuscheli*. *Freshwater Biol., 53*(9), 1881-1889. doi:10.1111/j.1365-2427.2008.02016.x

Allison, S. D., Ying, L., Claudia, W., Goulden, M. L., Martiny, A. C., Treseder, K. K., & Martiny, J. B. H. (2013). Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology, 94*(3), 714-725. doi:10.1890/12-1243.1

Ayres, E., Dromph, K., & Bardgett, R. (2006). Do plant species encourage soil biota that specialise in the rapid decomposition of their litter? *Soil Biology and Biochemistry, 38*(1), 183-186. doi:10.1016/j.soilbio.2005.04.018

Baerlocher, F. (1992). Research on aquatic hyphomycetes: historical background and overview. In *The Ecology of Aquatic Hyphomycetes* (pp. 1-15). Berlin: Springer.

Ball, B. A., Bradford, M. A., & Hunter, M. D. (2009). Nitrogen and phosphorus release from mixed litter layers is lower than predicted from single species decay. *Ecosystems, 12*(1), 87-100. doi:10.1007/s10021-008-9208-2

Bardgett, R. D., & Putten, W. H., Van Der. (2014). Belowground biodiversity and ecosystem functioning. *Nature, 515*(7528), 505-511. doi:10.1038/nature13855

Barnes, P., Throop, H., Archer, S., Breshears, D., McCulley, R., & Tobler, M. (2015). Sunlight and soil–litter mixing: Drivers of litter decomposition in drylands. In U. Lüttge & W. Beyschlag (Eds.), *Progress in Botany* (pp. 273-302). Switzerland: Springer.

Berg, B., & Mcclaugherty, C. (2003). *Plant Litter*. Berlin: Springer.

Berg, B., & McClaugherty, C. (2014). *Plant Litter. Decomposition, Humus Formation, Carbon Sequestration* (3rd ed.). Berlin: Springer Verlag.

Bewley, R. J. F., & Parkinson, D. (1985). Bacterial and fungal activity in sulfur dioxide polluted soils. *Can. J. Microbiol., 31*(1), 13-15. doi:10.1139/m85-003

Boer, W. D., Folman, L. B., Summerbell, R. C., & Boddy, L. (2005). Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews, 29*(4), 795-811. doi:10.1016/j.femsre.2004.11.005

Bouskill, N., Lim, H., Borglin, S., Salve, R., Wood, T., Silver, W., & Brodie, E. (2013). Pre-exposure to drought increases the resistance of tropical forest soil bacterial communities to extended drought. *ISME J, 7*(2), 384-394. doi:10.1038/ismej.2012.113

Chang, C., Wu, F., Wang, Z., Tan, B., Cao, R., Yang, W., & Cornelissen, J. H. C. (2019). Effects of epixylic vegetation removal on the dynamics of the microbial community composition in decaying logs in an alpine forest. *Ecosystems, 22*(7), 1478-1496.

Cleveland, C. C., Reed, S. C., Keller, A. B., Nemergut, D. R., O'Neill, S. P., Ostertag, R., & Vitousek, P. M. (2014). Litter quality versus soil microbial community controls over decomposition: a quantitative analysis. *Oecologia, 174*(1), 283-294. doi:10.1007/s00442-013-2758-9

Cole, L., Staddon, P. L., Sleep, D., & Bardgett, R. D. (2004). Soil animals influence microbial abundance, but not plant–microbial competition for soil organic nitrogen. *Functional Ecology, 18*(5), 631-640. doi:10.2307/3599317

Couteaûx, M.-M., Bottner, P., & Berg, B. (1995). Litter decomposition, climate and liter quality.

*Trends in Ecology & Evolution, 10*(2), 63-66. doi:10.1016/S0169-5347(00)88978-8

Crossley, D. A., & Blair, J. M. (1991). A high-efficiency, “low-technology” Tullgren-type extractor for soil microarthropods. *Agr. Ecosyst. Environ., 34*(1), 187-192. doi:10.1016/0167-8809(91)90104-6

Crowther, T. W., Boddy, L., & Hefin Jones, T. (2012). Functional and ecological consequences of saprotrophic fungus–grazer interactions. *ISME J, 6*(11), 1992-2001.

Crowther, T. W., Stanton, D. W., Thomas, S. M., A'Bear, A. D., Hiscox, J., Jones, T. H., . . . Boddy, L. (2013). Top-down control of soil fungal community composition by a globally distributed keystone consumer. *Ecology, 94*(11), 2518-2528. doi:10.1890/13-0197.1

Crutsinger, G. M., Sanders, N. J., & Classen, A. T. (2009). Comparing intra-and inter-specific effects on litter decomposition in an old-field ecosystem. *Basic and Applied Ecology, 10*(6), 535-543. doi:10.1016/j.baae.2008.10.011

David, J. F., & Gillon, D. (2009). Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. *Glob. Change Biol., 15*(1), 156–165. doi:10.1111/j.1365-2486.2008.01711.x

Denton, C. S., Bardgett, R. D., Cook, R., & Hobbs, P. J. (1999). Low amounts of root herbivory positively influence the rhizosphere microbial community in a temperate grassland soil. *Soil Biology and Biochemistry, 31*(1), 155-165.

Dighton, J., White, J., & Oudemans, P. (2005). *The fungal community: its organization and role in the ecosystem* (3rd ed.). Boca Raton: Taylor & Francis.

Fernandes, I., Duarte, S., Cássio, F., & Pascoal, C. (2015). Plant litter diversity affects invertebrate shredder activity and the quality of fine particulate organic matter in streams. *Mar. Freshwater Res., 66*(5), 449-458. doi:10.1071/MF14089

Ferreira, V., & Chauvet, E. (2011). Future increase in temperature more than decrease in litter quality can affect microbial litter decomposition in streams. *Oecologia, 167*(1), 279-291. doi:10.1007/s00442-011-1976-2

Frith, D., & Frith, C. (1990). Seasonality of litter invertebrate populations in an australian upland tropical rain forest. *Biotropica., 22*, 181. doi:10.2307/2388411

Frostegård, Å., Tunlid, A., & Bååth, E. (1993). Phospholipid fatty acid composition, biomass, and activity of microbial communities from two soil types experimentally exposed to different heavy metals. *Appl. Environ. Microb., 59*(11), 3605-3617.

Frouz, J., Roubíčková, A., Heděnec, P., & Tajovský, K. (2015). Do soil fauna really hasten litter decomposition? A meta-analysis of enclosure studies. *Eur. J. Soil Biol., 68*, 18–24. doi:10.1016/j.ejsobi.2015.03.002

Gongalsky, Konstantin, B., Persson, Tryggve, Pokarzhevskii, & Andrei, D. (2008). Effects of soil temperature and moisture on the feeding activity of soil animals as determined by the bait-lamina test. *Appl. Soil Ecol., 39*(1), 84-90. doi:10.1016/j.apsoil.2007.11.007

González, G., & Seastedt, T. R. (2000). Comparison of the abundance and composition of litter fauna in tropical and subalpine forests. *Pedobiologia, 44*(5), 545-555. doi:10.1078/s0031-4056(04)70070-0

Gräff, S., Berkus, M., & Köhler, G. A. R. (1997). Metal accumulation strategies in saprophagous and phytophagous soil invertebrates: a quantitative comparison. *BioMetals, 10*(1), 45-53.

Griffiths, B., & Caul, S. (1993). Migration of bacterial-feeding nematodes, but not protozoa, to decomposing grass residues. *Biol. Fert. Soils, 15*, 201-207. doi:10.1007/BF00361612

Harley, J. L. (1971). Fungi in Ecosystems. *Journal of Applied Ecology, 59*(3), 653-668. doi:10.2307/2258131

Iii, W. M. M., Ostertag, R., & Cowie, R. H. (2011). Macro-invertebrates accelerate litter decomposition and nutrient release in a Hawaiian rainforest. *Soil Biology and Biochemistry, 43*(1), 206-211. doi:10.1016/j.soilbio.2010.10.005

Justine, M. F., Wanqin, Y., Fuzhong, W., Bo, T., Muhammad, K., & Yeyi, Z. (2015). Biomass stock and carbon sequestration in a chronosequence of *Pinus massoniana* plantations in the upper reaches of the Yangtze river. *Forests, 6*(10), 3665-3682. doi:doi.org/10.3390/f6103665

Kourtev, P. S., Ehrenfeld, J. G., & Häggblom, M. (2003). Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biology and Biochemistry, 35*(7), 895–905. doi:10.1016/s0038-0717(03)00120-2

Kramer, C., & Gleixner, G. (2006). Variable use of plant- and soil-derived carbon by microorganisms in agricultural soils. *Soil Biology and Biochemistry, 38*(11), 3267–3278. doi:10.1016/j.soilbio.2006.04.006

Leroy, C. J., & Marks, J. C. (2006). Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. *Freshwater Biol., 51*(4), 605-617. doi:10.1111/j.1365-2427.2006.01512.x

Lin, B., Liu, Q., Yan, W. U., & Hai, H. E. (2004). Advances in the studies of forest litter. *Chin. J. Ecol., 23*(1), 60-64. doi:10.1088/1009-0630/6/5/011

Liu, R., Yang, W., Wu, F., Tan, B., & Wang, W. (2014). Soil fauna community structure and diversity during foliar litter decomposition in the subalpine/alpine forests of western Sichuan. *Chinese Journal of Applied & Environmental Biology, 20*(3), 499-507. doi:10.3724/SP.J.1145.2014.09045

Moeed, A., & Meads, M. J. (1986). Seasonality of litter-inhabiting invertebrates in two native-forest communities of Orongorongo Valley, New Zealand. *NEW Zeal. J. Zool., 13*(1), 45-63. doi:10.1080/03014223.1986.10422645

Moore, T., Trofymow, J. A., Taylor, B., Prescott, C., Camiré, C., Duschene, L., . . . Zoltai, S. (1999). Litter decomposition rates in Canadian forests. *Glob. Change Biol., 5*(1), 75-82. doi:10.1046/j.1365-2486.1998.00224.x

Negussie, A., Degerickx, J., Norgrove, L., Achten, W. M., Hadgu, K. M., Aynekulu, E., & Muys, B. (2015). Effects of accession, spacing and pruning management on in-situ leaf litter decomposition of *Jatropha curcas* L. in Zambia. *Biomass Bioenerg., 81*, 505-513. doi:10.1016/j.biombioe.2015.08.004

Nottingham, A. T., Griffiths, H., Chamberlain, P. M., Stott, A. W., & Tanner, E. V. J. (2009). Soil priming by sugar and leaf-litter substrates: a link to microbial groups. *Appl. Soil Ecol., 42*(3), 183-190. doi:10.1016/j.apsoil.2009.03.003

Olsen, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology, 44*, 322-331.

Parkinson, D., Domsch, K. H., & Anderson, J. P. E. (1978). Die entwicklung mikrobieller biomassen im organischen horizont eines fichtenstandortes. *Oecol. Plant., 13*, 355-366.

Pereira, S., Burešová, A., Kopecky, J., Mádrová, P., Aupic-Samain, A., Fernandez, C., . . . Mareckova, M. (2019). Litter traits and rainfall reduction alter microbial litter decomposers: the evidence from three Mediterranean forests. *FEMS Microbiology Ecology, 95*(12), fiz168. doi:10.1093/femsec/fiz168

Piatek, K. B., Munasinghe, P., Peterjohn, W. T., Adams, M. B., & Cumming, J. R. (2009). Oak contribution to litter nutrient dynamics in an Appalachian forest receiving elevated nitrogen and dolomite. *Can. J. Forest Res., 39*(5), 936-944(939). doi:10.1139/X09-028

Piatek, K. B., Munasinghe, P., Peterjohn, W. T., Adams, M. B., & Cumming, J. R. (2010). A decrease in oak litter mass changes nutrient dynamics in the litter layer of a central hardwood forest. *Northern Journal of Applied Forestry, 27*(3), 97-104.

Piatek, K. B., Munasinghe, P., Peterjohn, W. T., Adams, M. B., & Cumming, J. R. (2010). A decrease in oak litter mass changes nutrient dynamics in the litter layer of a central hardwood forest. *North J. Appl. For., 27*(3), 97-104. doi:10.1007/s11056-010-9197-9

Saetre, P., & Bååth, E. (2000). Spatial variation and patterns of soil microbial community structure in a mixed spruce–birch stand. *Soil Biology and Biochemistry, 32*(7), 909-917. doi:10.1016/s0038-0717(99)00215-1

Saggar, S., Mercer, C., Hedley, C., & Yeates, G. (1999). Increase in $^{14}$C-carbon translocation to the soil microbial biomass when five species of plant-parasitic nematodes infect roots of white clover. *Nematology, 1*(3), 295-300.

Sauvadet, M., Chauvat, M., Brunet, N., & Bertrand, I. (2017). Can changes in litter quality drive soil fauna structure and functions? *Soil Biology and Biochemistry, 107*(April 2017), 94-103. doi:10.1016/j.soilbio.2016.12.018

Sauvadet, M., Chauvat, M., Fanin, N., Coulibaly, S., & Bertrand, I. (2016). Comparing the effects of litter quantity and quality on soil biota structure and functioning: application to a cultivated soil in Northern France. *Appl. Soil Ecol., 107*, 261-271. doi:10.1016/j.apsoil.2016.06.010

Scheu, S., Ruess, L., & Bonkowski, M. (2005). Interactions between microorganisms and soil micro- and mesofauna. In B. F & V. A (Eds.), *Microorganisms in Soils: Roles in Genesis and Functions* (Vol. 3, pp. 253-275). Berlin: Springer.

Schutter, M., & Dick, R. (2001). Shifts in substrate utilization potential and structure of soil microbial communities in response to carbon substrates. *Soil Biology and Biochemistry, 33*(11), 1481-1491. doi:10.1016/s0038-0717(01)00057-8

Sohlenius, B. (1980). Abundance, biomass and contribution to energy flow by soil nematodes in terrestrial ecosystems. *Oikos, 34*, 186-194. doi:10.2307/3544181

Straalen, N. M. v., & Gestel, C. A. M. v. (1997). Soil invertebrates and micro-organisms. In P. Calow (Ed.), *Handbook of Ecotoxicology* (pp. 251-277): Blackwell Scientific Publications.

Suberkropp, K. (1998). Microorganisms and organic matter decomposition. In R. Naiman & R. Bilby (Eds.), *River ecology and management: lessons from the Pacific coastal ecoregion* (Vol. 120-143). New York: Springer.

Suzuki, Y., Grayston, S. J., & Prescott, C. E. (2013). Effects of leaf litter consumption by millipedes (*Harpaphe haydeniana*) on subsequent decomposition depends on litter type. *Soil Biology and Biochemistry, 57*, 116–123. doi:10.1016/j.soilbio.2012.07.020

Svyrydchenko, A. O., & Brygadyrenko, V. V. (2014). Trophic preferences of *Rossiulus kessleri* (Diplopoda, Julidae) for the litter of various tree species. *Folia Oecol., 41*(2), 202-212.

Taylor, B., Parkinson, D., & Parkinson, W. (1989). Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology, 70*(1), 97-104. doi:10.2307/1938416

Waldrop, M. P., & Firestone, M. K. (2004). Microbial community utilization of recalcitrant and simple carbon compounds: impact of oak-woodland plant communities. *Oecologia, 138*(2), 275-284. doi:10.1007/s00442-003-1419-9

Walker, D., Lawrence, B., Esterline, D., Graham, S., Edelbrock, M., & Wooten, J. (2014). A metagenomics-based approach to the top-down effect on the detritivore food web: a salamanders influence on fungal communities within a deciduous forest. *Ecol Evol, 4*(21), 4106-4116. doi:10.1002/ece3.1259

Wall, D., Bradford, M., St. John, M., Trofymow, J., Behan-Pelletier, V., Bignell, D., . . . Zou, X. (2008). Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Glob. Change Biol., 14*(11), 2661-2677. doi:10.1111/j.1365-2486.2008.01672.x

Wang, S., Ruan, H., & Bing, W. (2009). Effects of soil microarthropods on plant litter decomposition across an elevation gradient in the Wuyi Mountains. *Soil Biology and Biochemistry, 41*(5), 891-897. doi:10.1016/j.soilbio.2008.12.016

Wang, W., Yang, W., Bo, T., Liu, R., & Wu, F. (2015). Effects of soil fauna to nitrogen and phosphorus releases during litter decomposition at different phenological stages in the subtropical evergreen broad-leaved forest in Sichuan Basin. *Scientia Silvae Sinicae, 51*(1), 1-11. doi:10. 11707 /j. 1001-7488. 20150101

Wang, W., Yang, W., Tan, B., Liu, R., & Fuzhong, W. U. (2013). The dynamics of soil fauna community during litter decomposition at different phenological stages in the subtropical evergreen broad-leaved forests in Sichuan basin. *Acta Ecologica Sinica, 33*(18), 5737-5750. doi:10.5846/stxb201305301244

Wang, X., Yu, S., Zhou, L., & Fu, S. (2016). Soil microbial characteristics and the influencing factors in subtropical forests. *Acta Ecologica Sinica, 36*(1), 8-15. doi:10.1016/j.chnaes.2015.12.004

Wardle, & Lavelle. (1997). Linkages between soil biota, plant litter quality and decomposition. In G. Cadish & K. Giller (Eds.), *Driven by Nature Plant Litter Quality & Decomposition* (pp. 107-123). Wallingford: CAB International.

Wardle, D. A., Bardgett, R. D., Klironomos, J. N., Setälä, H., Van Der Putten, W. H., & Wall, D. H. (2004). Ecological linkages between aboveground and belowground biota. *Science, 304*(5677), 1629-1633. doi:10.1126/science.1094875

Wenying, Y. (1998). *Pictorical keys to soil animals of China*. Beijing: Science Press.

White, D., Davis, W., Nickels, J., King, J., & Bobbie, R. (1979). Determination of the sedimentary microbial biomass by extractible lipid phosphate. *Oecologia, 40*(1), 51-62. doi:10.1007/BF00388810

Wood, C. T., Schlindwein, C. C. D., Soares, G. L. G., & Araujo, P. B. (2012). Feeding rates of *Balloniscus sellowii* (Crustacea, Isopoda, Oniscidea): the effect of leaf litter decomposition and its relation to the phenolic and flavonoid content. *Zookeys, 24*(176), 231-245. doi:10.3897/zookeys.176.1940

Wu, Y., Yu, X., Wang, H., Ding, N., & Xu, J. (2010). Does history matter? Temperature effects on soil microbial biomass and community structure based on the phospholipid fatty acid (PLFA) analysis. *J. Soil Sediment., 10*(2), 223-230. doi:10.1007/s11368-009-0118-5

Xu, G. L., Kuster, T. M., Günthardt-Goerg, M. S., Dobbertin, M., & Li, M. H. (2012). Seasonal exposure to drought and air warming affects soil Collembola and Mites. *Plos One, 7*(8), e43102. doi:10.1371/journal.pone.0043102

Yoshida, T., Takito, Y., Soga, M., & Hijii, N. (2013). Responses of litter invertebrate communities to litter manipulation in a Japanese conifer plantation. *Acta. Oecol., 51*(8), 74–81. doi:10.1016/j.actao.2013.06.003

Zhao, Y., Wu, F., Yang, W., Tan, B., & He, W. (2016). Variations in bacterial communities during foliar litter decomposition in the winter and growing seasons in an alpine forest of the eastern Tibetan Plateau. *Can. J. Microbiol., 62*(1), 35-48. doi:10.1139/cjm-2015-0448

Zwahlen, C., Hilbeck, A., & Nentwig, W. (2007). Field decomposition of transgenic Bt maize residue and the impact on non-target soil invertebrates. *Plant and Soil, 300*(1-2), 245-257. doi:10.1007/s11104-007-9410-6

Zwart, K. B., Burgers, S. L. G. E., Bloem, J., Bouwman, L. A., Brussaard, L., Lebbink, G., . . . Ruiter, P. C. D. (1994). Population dynamics in the belowground food webs in two different agricultural systems. *Agr. Ecosyst. Environ., 51*(1-2), 187-198.

**Table 1** Spearman's correlation coefficients between individual density of invertebrate and three types of microbial biomass, ratios of F/B and $G^{+}/G^{-}$, in decomposing foliar litter of Masson pine and camphor with invertebrate included. TB, Total microbial biomass; FB, Fungal biomass; BB, Bacterial biomass; F/B, The ratio of fungus to bacteria biomass; $G^{+}$, Gram-positive bacteria biomass; $G^{-}$, Gram-negative bacteria biomass; $G^{+}/G^{-}$. The ratio of Gram-positive bacteria to Gram-negative bacteria biomass.

| Sampling year | Species | TB | FB | BB | F/B | G+ | G- | G+/G- |
|---|---|---|---|---|---|---|---|---|
| First year | Masson pine | -0.797** | -0.844** | -0.727** | -0.314 | -0.690* | -0.643* | -0.366 |
| | Camphor | -0.671* | -0.657* | -0.671* | -0.004 | -0.832** | -0.636* | -0.732** |
| Second year | Masson pine | 0.533 | 0.287 | 0.500 | 0.050 | 0.102 | 0.250 | -0.068 |
| | Camphor | 0.017 | -0.035 | 0.017 | 0.116 | -0.301 | 0.433 | -0.519 |

Significant relationship at $P < 0.05$ and $P < 0.01$ level were indicated with *and **, respectively.

**Table 2** Spearman's correlation coefficients between litter mass loss and three types of microbial biomass, ratios of F/B and $G^+/G^-$, and individual density of invertebrate in decomposing foliar of Masson pine and camphor with invertebrate included. TB, Total microbial biomass; FB, Fungal biomass; BB, Bacterial biomass; F/B, The ratio of fungus to bacteria biomass; $G^+$, Gram-positive bacteria biomass; $G^-$, Gram-negative bacteria biomass; $G^+/G^-$. The ratio of gram-positive bacteria to gram-negative bacteria biomass.

| Sampling year | Species | TB | FB | BB | F/B | G+ | G- | G+/G- | Individual density |
|---|---|---|---|---|---|---|---|---|---|
| First year | Masson pine | -0.804** | -0.847** | -0.657* | -0.436 | -0.599* | -0.692* | -0.085 | 0.881** |
| | Camphor | -0.762** | -0.832** | -0.762** | -0.749** | -0.657* | -0.790** | -0.424 | 0.566 |
| Second year | Masson pine | -0.233 | 0.122 | -0.200 | 0.109 | -0.170 | -0.150 | 0.288 | 0.083 |
| | Camphor | -0.217 | 0.044 | -0.217 | 0.187 | -0.301 | 0.000 | -0.100 | 0.133 |

Significant relationship at $P < 0.05$ and $P < 0.01$ level were indicated with *and **, respectively

**Table 3** The regression models, decomposition constant (k), time to 50% mass loss ($T_{0.5}$), time to 95% mass loss ($T_{0.95}$) of foliar litter decomposition of Masson pine and camphor.

| Species | Invertebrate treatment | Regression models | *k* | $T_{0.5}$ (years) | $T_{0.95}$ (years) |
|---|---|---|---|---|---|
| Masson pine | Included(+) | $Y=110.30e^{-0.539t}$, $r^2=0.847$, $P<0.001$ | 0.539 | 1.29 | 3.54 |
| | Excluded(-) | $Y=105.10e^{-0.479t}$, $r^2=0.610$, $P<0.001$ | 0.479 | 1.45 | 4.91 |
| Camphor | Included(+) | $Y=97.05e^{-0.363t}$, $r^2=0.751$, $P<0.001$ | 0.363 | 1.91 | 3.99 |
| | Excluded(-) | $Y=103.76e^{-0.473t}$, $r^2=0.920$, $P<0.001$ | 0.473 | 1.47 | 3.26 |

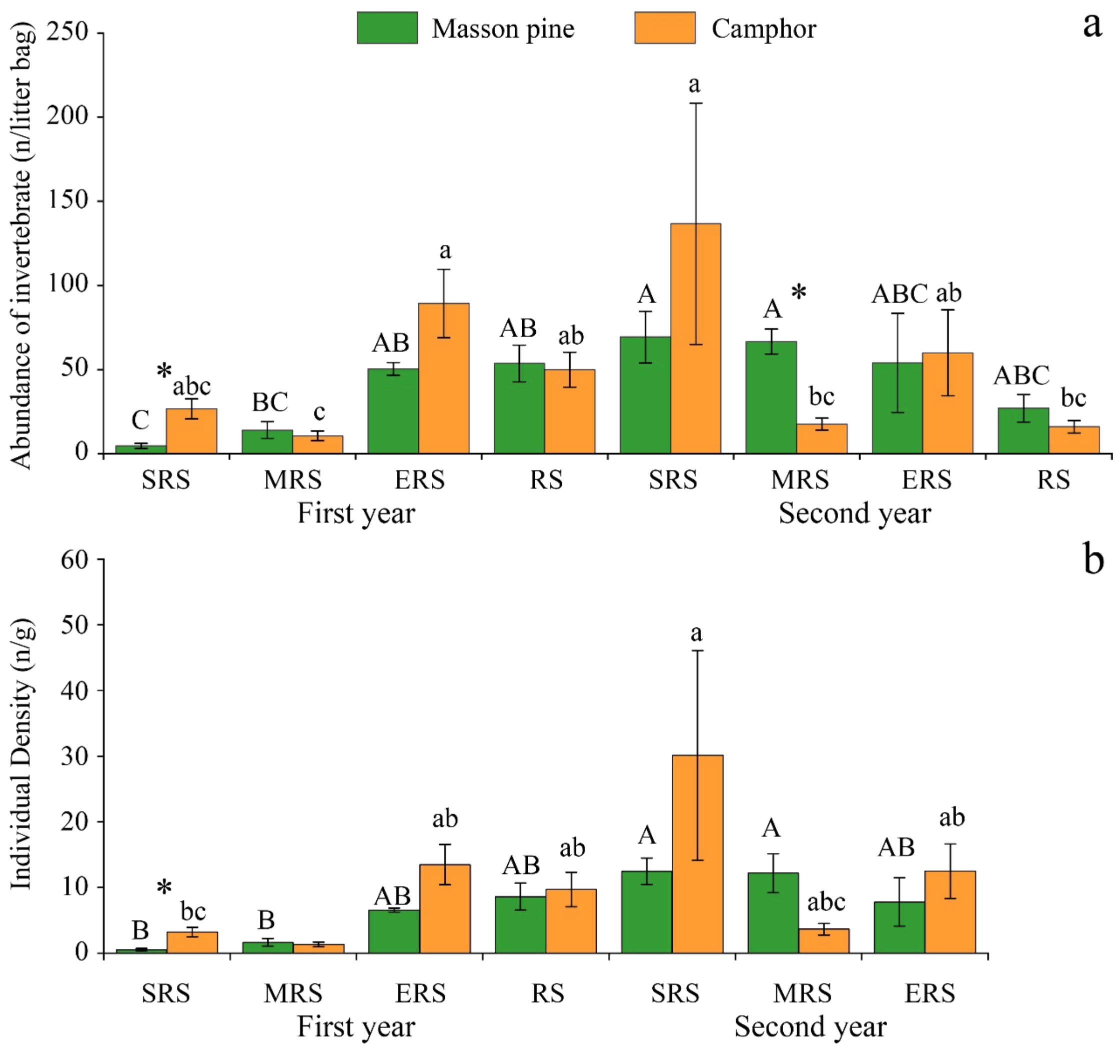


**Figure 1** Variation of total abundance (a) and individual density (b) of invertebrate in decomposing foliar litter of Masson pine and camphor in slight rainy season (SRS), micro rainy season (MRS), early rainy season (ERS), and rainy season (RS) during the first and second year of decomposition. Error bars represent the standard errors of the mean values (N=3). * indicates the significant difference between different tree species ($P$<0.05). Different capital letters and lowercase letters over the error bars indicate the significant differences ($P$ <0.05) among different seasonal rainfall periods in Masson pine and camphor foliar litter, respectively.

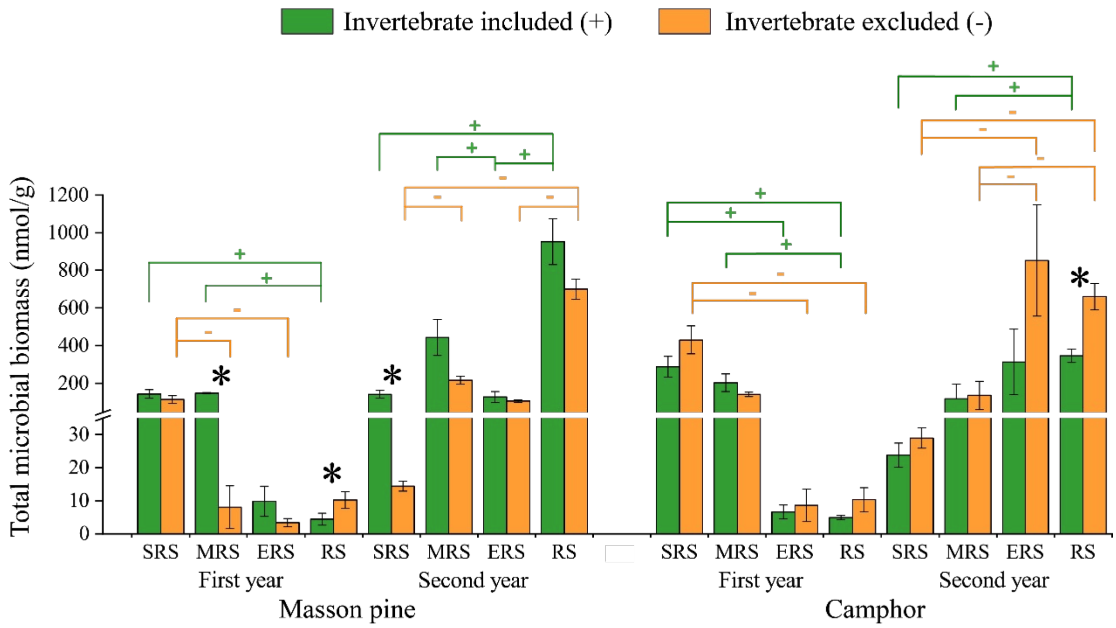


**Figure 2** The comparison of total microbial biomass in decomposing foliar litter of Masson pine and camphor between invertebrates included (+) and excluded (-) in slight rainy season (SRS), micro rainy season (MRS), early rainy season (ERS) and rainy season (RS).

Error bars represent the standard errors of the mean values (N=3). * indicates the significant difference ($P$<0.05) in total microbial biomass between Masson pine and camphor. + and - indicates the significant difference ($P$<0.05) pairwise comparison between different seasonal rainfall periods in the invertebrate included and invertebrate excluded treatment, respectively.

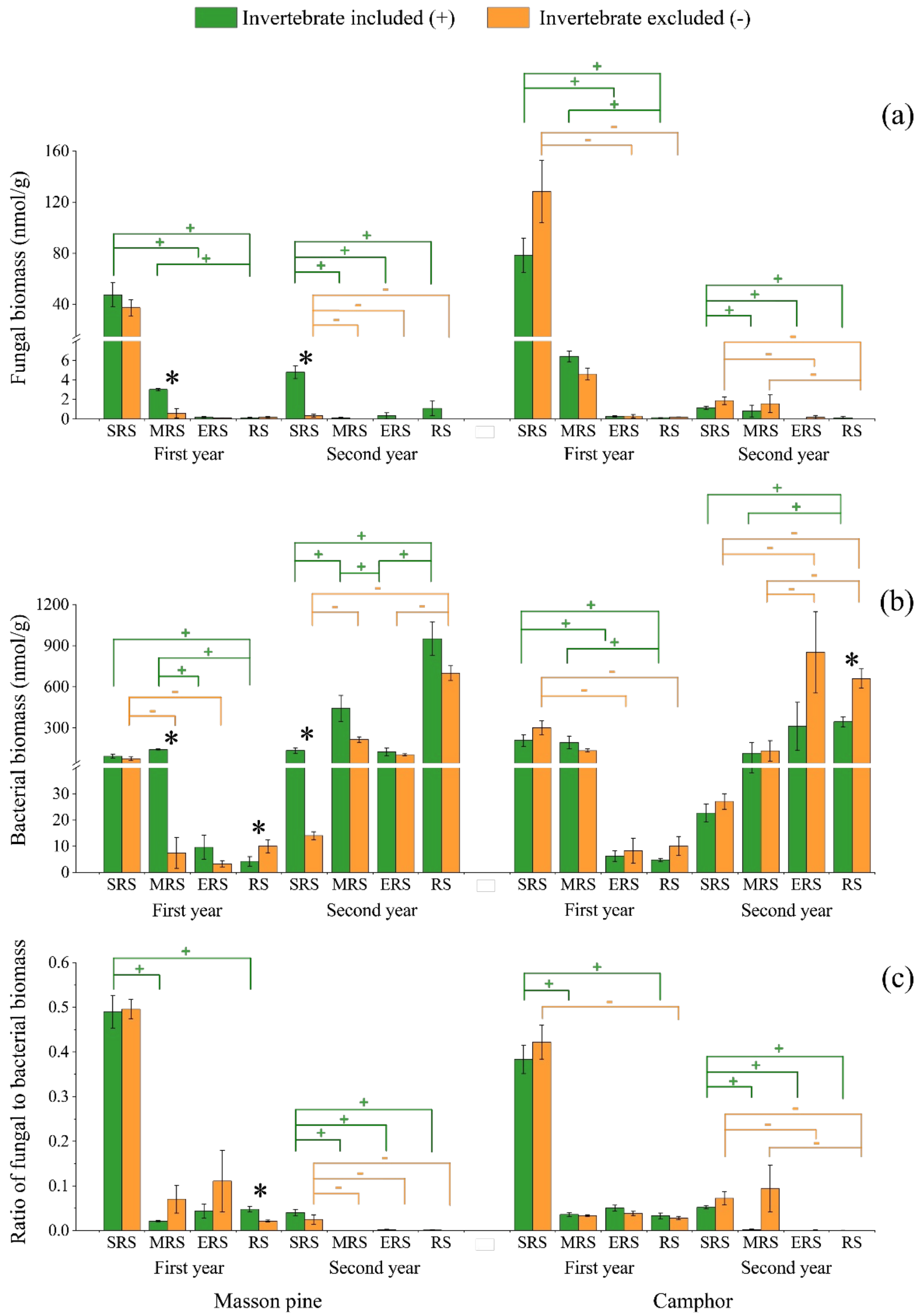


**Figure 3** The comparison of fungal biomass (a), bacterial biomass (b) and ratio of fungal to bacterial biomass (c) in decomposing foliar litter of Masson pine and camphor between invertebrates included (+) and excluded (-) in slight rainy season (SRS), micro rainy season (MRS), early rainy season (ERS) and rainy season (RS).

Error bars represent the standard errors of the mean values (N=3). * indicates the significant difference (*P*<0.05) between Masson pine and camphor. + and - indicates the significant difference (*P*<0.05) pairwise comparison between different seasonal rainfall periods in the invertebrate included and invertebrate excluded treatment, respectively.

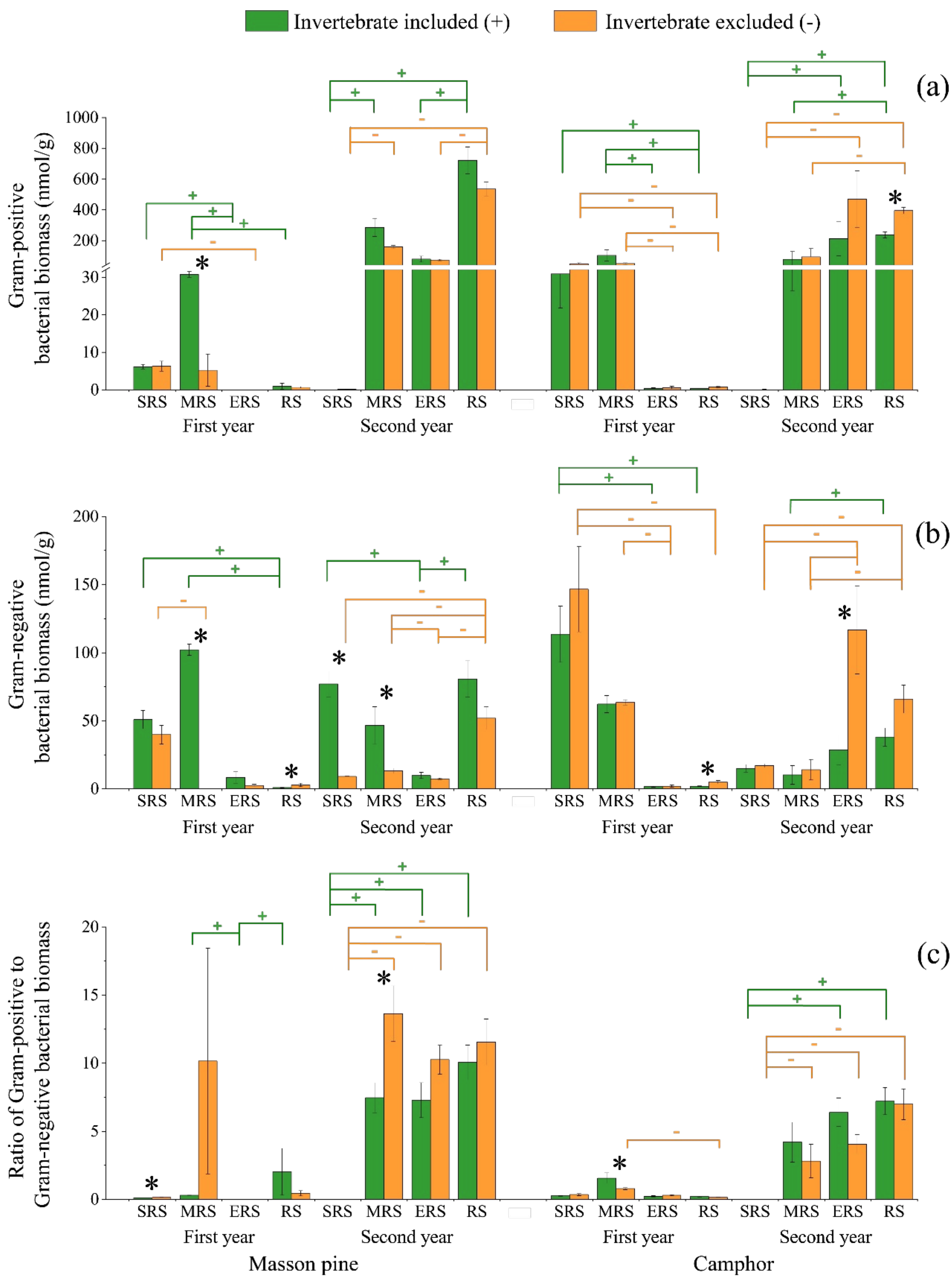


**Figure 4** The comparison of Gram-positive bacterial biomass (a), Gram-negative bacterial biomass (b) and ratio of Gram-positive to Gram-negative bacterial biomass (c) in decomposing foliar litter of Masson pine and camphor between invertebrates included (+) and excluded (-) in slight rainy season (SRS), micro rainy season (MRS), early rainy season (ERS) and rainy season (RS).

Error bars represent the standard errors of the mean values (N=3). * indicates the significant difference ($P$<0.05) between Masson pine and camphor. + and - indicates the significant difference ($P$<0.05) pairwise comparison between different seasonal rainfall periods in the invertebrate included and invertebrate excluded treatment, respectively.

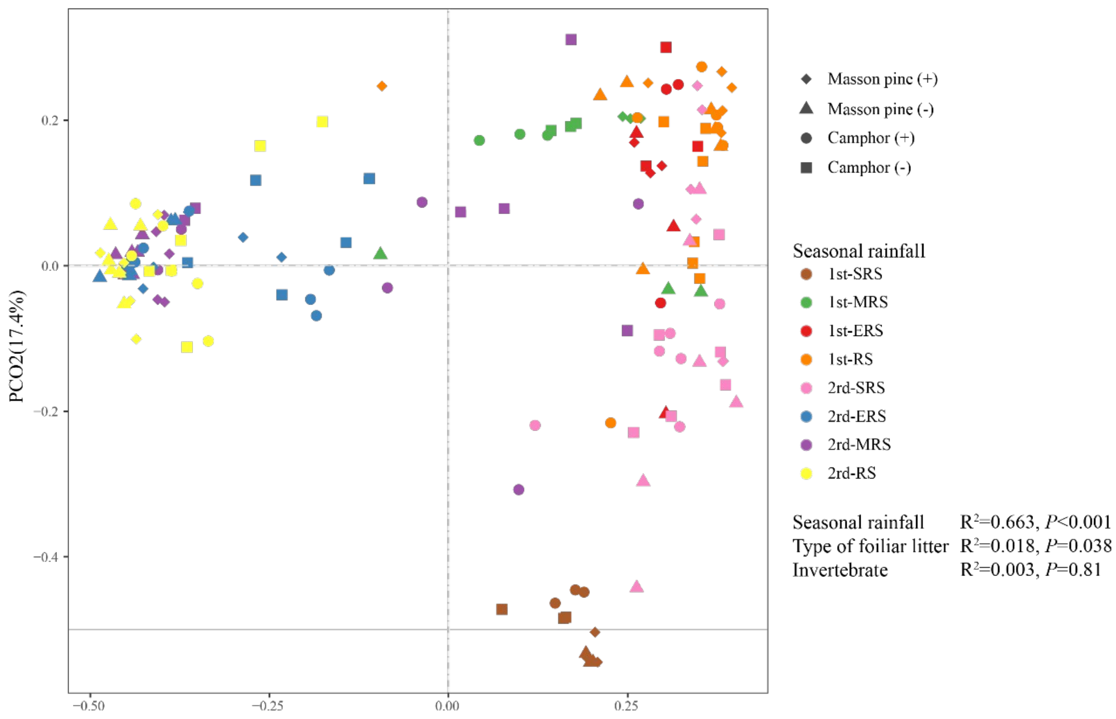


**Figure 5** Principal Co-ordinates Analysis (PCoA) of microbial community in decomposing foliar litter of Masson pine and camphor during the two sampling years based on Bray-Curtis distance. + and - indicates invertebrate included and excluded, respectively. Value of $R^2$ and $P$ were calculated using Permutational MANOVA (Permanova).

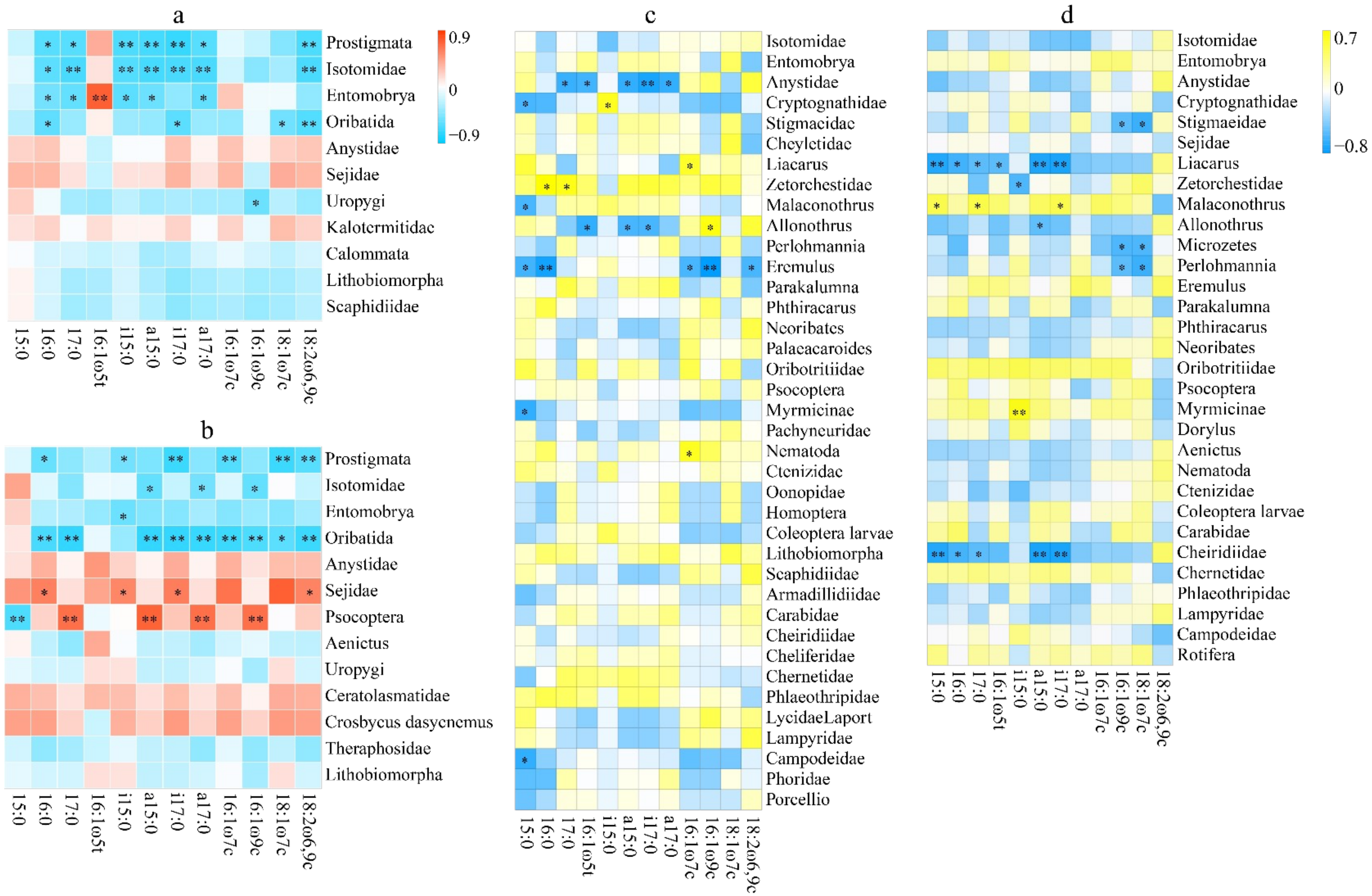


**Figure 6** Correlation heatmap based on Spearman correlation coefficients with two-tail test of PLFA bioindicators and invertebrate observed in foliar litter of Masson pine and camphor during the first year (a) and (b) and second year (c) and (d) of decomposition. * and ** indicate the significant correlation between invertebrate and PLFA at 0.05 level and 0.01 level, respectively.