

Leaf litter decomposition in *Pinus massoniana* monoculture and mixed plantation with *Castanopsis fissa* in a subtropical area of China

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Abstract We measured the rates of *Pinus massoniana* needle litter decomposition mixed with different proportions of *Castanopsis fissa* leaf litter in *P. massoniana* monoculture and *P. massoniana* mixed with *C. fissa* forests, which are the typical forest of the subtropical zone of China. The broadleaved species on sites could naturally promote the degradation of litter and mineralization of carbon and nitrogen, which results in faster nutrient return and enhanced productivity. But it is not well known how specific species influence the decomposition processes of each other in mixtures. In this paper, there were 4 types of litter mixtures, which referred to the mass ratio of *P. massoniana* leaf to *C. fissa* leaf in the mixtures: 1:1, 3:2, 7:3, and 1:0. We placed 4 types of litterbags in the two forest types for an over 12-month experiment. We applied the litterbag technique for this experiment. The main results were: 1. *P. massoniana* leaf litter (1:0) decomposed faster in the mixed forest than in monoculture. 2. The mixed leaf litter (1:1, 3:2, 7:3) decomposed faster than the monoculture *P. massoniana* litter, moreover, the 1:1 type decomposed the fastest. 3. The mixture effects on needle litter decomposition changed during decomposition process, the antagonistic mixture effects of 1:1 and 7:3 could be found in the first six months in the mixed and monoculture stands, the non-additive synergistic litter mixture effects dominated after 9 months. The results showed that broadleaff litter could promote the decomposition of conifer litter, and the decomposition of litter was faster in the mixed forest than in the monoculture coniferous forest. It also shows that keeping a suitable proportion of broad-leaved tree species in coniferous monoculture forest is beneficial to the nutrient cycle and the tree's growth.

Keywords: mixed leaf litter, decomposition, coniferous monoculture, broadleaved species, subtropical area.

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Introduction

Litter decomposition represents a fundamental process that dictates the carbon flux between the biosphere and the atmosphere (Gartner & Cardon, 2004; Chapin et al., 2011; Handa et al., 2014; Zhou et al., 2020). Moreover, it releases approximately 10 times more carbon into the atmosphere compared to anthropogenic fossil fuel combustion (Prentice et al., 2001; Srivastava et al., 2009; Cardinale et al., 2011). Numerous studies have been conducted on the decomposition of litter from single tree species (Lin et al., 2015; Smith et al., 2024; Zhao et al., 2024), whereas in natural conditions, litter typically decomposes in mixed forms (Gartner et al., 2004). Therefore, there is a growing consensus among scholars regarding the decomposition process and mechanism of mixed litter (Prescott et al., 2000; Bonanomi et al., 2010; Li et al., 2017; Zeng et al., 2024), further revealing the interspecific relationships in tree species mixtures.

In forest ecosystems, differences in species composition on a site could influence the composition and activity of the soil microbial community through alteration of microclimate, production of litter, interactions with herbivores, production of root exudates, and interactions with root symbiotic organisms such as mycorrhizal fungi (Prescott & Grayson, 2013). As such, the decomposition process of litter is altered by the characteristics of vegetation and the interactions of ecological processes (Ayres et al., 2009). Particularly, when litter from distinct species is mixed, the decomposition environment undergoes alteration (Wardle, 2003).

Nutrients or specific secondary metabolites may transfer among different litter types, thereby impacting the abundance and activity of decomposers (Gessner et al., 2010). These alterations may give rise to mixed effects in litter decomposition. When the decomposition rate and nutrient release of mixed litter surpass the predicted values derived from single-litter decomposition, the mixed effect is manifested as a facilitation effect; conversely, it demonstrates

an inhibitory effect. In forest mixtures, there are latent interactions among different species during litter decomposition, which was introduced previously by Staaf (1980) and Seastedt (1984). Mixed leaf litter from different species often decomposed differently than the decomposition of litter from the individual species (Chapman & Newman, 2010).

Mixed litter decomposition processes are affected by species richness and species identity within the mixture (Gartner & Cardon, 2004; Hooper et al., 2005; Schindler & Gessner, 2009). Previous results showed that mixtures of leaf litter often induced synergistic or antagonistic non-additive effects on litter decomposition (Gartner & Cardon, 2004; Hättenschwiler & Gasser, 2005; Srivastava, 2009; Handa et al., 2014; Trogisch et al., 2016). Chapman and Koch (2007) indicated that the decay of mixed coniferous litter was faster by up to 50% than expected, with individual coniferous litter of those mixtures degrading to a rate 85 % faster than expected, because the existence of litter from various species in litter bags may draw a more varied and probably more active microbial community (Gartner & Cardon, 2004).

The results of two- or three-species litter mixtures of *Quercus robur*, *Ulmus laevis*, and *Acer negundo* showed that litter mixtures had both additive and non-additive features on litter mass (Ágoston-Szabó et al., 2017). The research of Zheng et al. (2017) in a temperate forest illustrated that the mixing litter did not show non-additive effects on litter mass loss.

Despite the extensive research, it is not well known how specific species influence the decomposition processes of each other in mixtures (Prescott et al., 2000). Besides, it is unclear whether the non-additive mixture effects showed the time effect on decomposition (Prescott et al., 2000). Furthermore, the previous studies (Prescott et al., 2004; Smith et al., 2024; Zhao et al., 2024) have largely focused on the effects of the species mixture diversity on decomposition and have rarely studied the effects of species mixtures with different mass ratios on decomposition.

In Guangdong Province, the most dominant plantation is *Eucalyptus* spp. (1.83×10^6 ha), followed by *Cunninghamia lanceolata* and *Pinus massoniana* (7.74×10^5 ha) (Lin et al., 2025).

In monoculture coniferous forests, the forest growth depends largely on this feedback of nutrients through litter decomposition (Mo et al., 1996), since the quantity of nutrients entering the ecosystem, each year is frequently low (Aber & Mellilo, 1991; Schlesinger, 1997) and the soil is normally poor. Researchers have recommended maintaining deciduous species naturally in sites (Li et al., 2017; Pan et al., 2020; Prescott, 2024), as the benefits of deciduous species are faster litter decomposition and carbon and nitrogen mineralization, leading to faster nutrient return and increased productivity (Prescott et al., 2000). The replacement of *Pinus massoniana* monocultures with mixed plantations containing native species, such as *Castanopsis fissa*, occurred with natural succession and was considered a method of compensating for soil nutrient deficiency (Yang et al., 2010).

Our main goal was to study how different litter mixtures influence the decomposition in forests. Therefore we investigated the following hypotheses: 1) whether the forest ecosystem still has the “home-field advantage” effect on mixture litter decomposition; 2) whether different mixing ratios of forest species affect the litter decomposition.

Material and methods

Research area

The field sites were located within the Dinghu

Mountain National Nature Reserve (23°09'21" N, 112°30'39" E) in Guangdong Province, China. The topography is low hilly, with the altitude below 1000 m. This area has a humid monsoon climate, with a mean annual precipitation of 1678 mm, 80% of the precipitation occurs during the wet season (April to September) (Zhou et al., 2011). The mean annual temperature is 21.4 °C, the average temperatures in the coldest month (January) and the warmest month (July) are 12.6°C and 28.0°C, respectively (Liu et al., 2025). The soil type is lateritic red soil, with a 50 - 80 cm soil depth.

The general information of the study plots is shown in Table 1.

We set up three plots in a nearly 60-year-old *P. massoniana* monoculture and three plots in an over 70-year-old mixed *P. massoniana* and *C. fissa* forest, respectively. The plot size was: 30 × 30 m. The minimum distance between adjacent plots was 30 m.

The dominant species of monoculture stand is *P. massoniana*, which basal area at breast height (BA) accounts for 92% of the stand (Table 2), with the remainder consisting of *Eucalyptus urophylla* × *E. grandis*, *Litsea cubeba*, *Mallotus paniculatus*, *Melicope pteleifolia*, and *Schima superba*. The understory layer was composed by 14 species in the shrub layer and 26 species in the herb layer, was abundant with *Alchomea trewioides*, *Clerodendrum fortunatum*, *Embbliia ribes*, *Ficus variolosa*, *Mallotus paniculatus*, *Melastoma candidum*, *Melicope pteleifolia*, *Psychotria asiatica*, *Dicranopteris pedata*, and *Mussaenda pubescens*. In the *C. fissa* and *P. massoniana* mixed forest, the first species contributes to 83% of the total

Table 1 The general information of two forest types.

| Factor | <i>P. massoniana</i> | <i>P. massoniana</i> and <i>C. fissa</i> |
|--|----------------------|--|
| Stand age /year | 50–60 | 70–80 |
| Altitude /m | 58 | 51 |
| Slope (°) | 22 | 23 |
| Slope aspect | Southeast | Southeast |
| Density /(trees·ha ⁻¹) | 475±25 | 712±12 |
| Diameter at breast height /cm | 24.9±1.2 | 17.5±1.4 |
| Tree height /m | 10±0.2 | 9±0.2 |
| Canopy density /% | 77 | 91 |
| Soil type | Lateritic red soil | Lateritic red soil |
| Soil pH | 3.15 | 3.02 |
| Soil bulk density /(g·cm ⁻³) | 1.48±0.03 | 1.42±0.03 |
| Soil natural water content /% | 26.13±1.1 | 26.77±1.0 |

basal area, followed by *P. massoniana* at 13%, alongside other species including *Litsea cubeba*, *Mallotus paniculatus*, and *Melicope pteleifolia*. The understory layer contained 23 species in the shrub layer and 29 species in the herb layer, mainly consisting of *C. fissa*, *Cryptocarya concinna*, *Ficus variolosa*, *Ixora chinensis*, *Melicope pteleifolia*, *Psychotria asiatica*, *Schefflera heptaphylla*, *Blechnum orientale*, *Dicranopteris pedata*, and *Mussaenda pubescens*.

Experimental design and litterfall collection

The decomposition of leaf litter was studied from March 2016 to March 2017, using the litterbag technique (Bocock & Gilbert 1957). Fresh *P. massoniana* needles and *C. fissa* leaves were collected from the OL (fresh leaf litter) layer of the forest floor in January and February 2016 (during the dry season in Guangdong Province). All the fresh leaves were oven-dried at 65 °C until constant weight (Prescott et al., 2017). The substrates were placed in 20 cm × 20 cm size polyethylene mesh bags, which with 1.8 mm mesh size, that could allow the smaller detritivorous soil fauna occurring at the site enter (Lin et al. 2015). The litter bags were placed between the OL and OF (fermentation layer) layers of the forest floor in the plots.

The four types of litter bag referred to 4 different ratios of *P. massoniana* leaves to *C. fissa* leaves:

- 1:1 composed 10 g *P. massoniana* leaves and 10 g *C. fissa* leaves;

- 3:2 composed 12 g *P. massoniana* leaves and 8 g *C. fissa* leaves;

- 7:3 composed 14 g *P. massoniana* leaves and 6 g *C. fissa* leaves;

- 1:0 composed 20 g *P. massoniana* leaves and 0 g *C. fissa* leaves.

In total, 504 litterbags were placed in the field, 288 bags in *P. massoniana* forest (3 plots, 24 each litter mixture bags in one plot of each treatment), 216 bags in mixed stand (3 plots, 24 bags of 3 treatments, 1:1, 7:3, and 1:0 in each plot respectively). We sampled the litter bags every three months during the 12 month-period (from March 02 (the initial litter nutrients) in 2016 to March 13 in 2017), and we sampled 18 replicate samples per forest type (for each litter mixture type we took out 6 litterbags a time in each plot, we have 3 plots of each forest type), 4 times in total. The initial litter nutrients were determined by 6 samples, which were randomly taken out of *P. massoniana* or *C. fissa* leaf litter. To investigate the soil chemical characteristics, the soil was sampled using an 8 cm diameter soil corer: 16 cores were bulked by depth (0 - 5 cm, 5 - 10 cm, 10 - 20 cm, 20 - 30 cm, 30 - 40 cm, 40 - 60 cm) in each plot, to four composite samples per depth.

Following the collection of litterbags, soil particles and colonizing soil fauna were removed as much as possible. For the composed leaf mixtures, the constituent species were manually separated to determine the mass loss of each individual species within the mixture. Then, all the litter was oven-dried at 65°C to a constant weight. After removing root particles, mineral soil samples were dried at 40°C, milled and sieved (<2 mm). The total N

Table 2 Tree species composition of the two stands (mean ± standard error).

| Stand | Species | Height (m) | DBH (cm) | Abundance (trees/plot) | BA Percent (%) |
|---|---|------------|-----------|------------------------|----------------|
| <i>P. massoniana</i> monoculture | <i>Eucalyptus urophylla</i> × <i>E. grandis</i> | 7.70±0.9 | 16.30±3.1 | 5 | 3.69 |
| | <i>Litsea cubeba</i> | 4.5 | 4.5 | 1 | 0.05 |
| | <i>Mallotus paniculatus</i> | 8.0 | 11 | 1 | 0.34 |
| | <i>Melicope pteleifolia</i> | 4.75±1.3 | 7.15±0.5 | 2 | 0.28 |
| | <i>Pinus massoniana</i> | 11.38±0.6 | 29.91±1.5 | 37 | 92.00 |
| <i>C. fissa</i> and <i>P. massoniana</i> mixed forest | <i>Schima superba</i> | 9.29±1.2 | 13.67±1.5 | 7 | 3.64 |
| | <i>Castanopsis fissa</i> | 7.62±0.4 | 10.47±0.7 | 39 | 13.09 |
| | <i>Litsea cubeba</i> | 5.0 | 5.8 | 1 | 0.10 |
| | <i>Mallotus paniculatus</i> | 6.50±0.6 | 8.58±0.8 | 12 | 2.70 |
| | <i>Melicope pteleifolia</i> | 5.25±0.3 | 8.10±2.5 | 2 | 0.40 |
| | <i>Pinus massoniana</i> | 11.17±0.5 | 27.56±1.2 | 36 | 83.70 |

concentration was determined by the Kjeldahl method. Ca, K, Mg, and P concentrations were determined by atomic absorption spectroscopy (AAS Vario 6; Analytik Jena, Jena, Germany) after HNO₃ digestion (Heinrichs et al., 1986). Total C of the litter was determined using the oil-bath potassium dichromate titration method (Dong et al., 1996). The organic matter was determined by high temperature potassium dichromate oxidation followed by volumetric method. Fresh mineral soil samples were analyzed for pH in water using a 1:2.5 soil/water suspension using a glass electrode (pH meter, single rod assembly) (Meiwes et al. 1986).

Statistical analysis

Leaf litter mass loss was calculated as:

$$\text{mass loss (\%)} = ((m_0 - m_1)/m_0) \times 100 \quad (1)$$

where: m_0 represents the initial dry weight of individual species leaf litter, and m_1 refers to the dry weight of individual species leaf litter at harvest time. We calculated the decomposition rates as (Olson 1963):

$$k = -\ln(m/im)/t \quad (2)$$

with m is remaining dry mass at decomposition period t , im is the litter dry mass at time $t = 0$, and \ln is natural logarithm.

To compare the litter decomposition rates (k) between the different treatments, the percentage of the remaining litter dry mass, y , after decomposition time t , was calculated by the exponential function model proposed by Wieder & Land (1982):

$$y = e^{(-kt)} \quad (3)$$

For each mixture, the dry mass percentage of the remaining leaf litter after decomposed 0, 3, 6, 9, and 12 months fitted to a nonlinear

function and the decomposition rate (k) were estimated. To examine non-additive, synergistic or antagonistic of mixture effects of *C. fissa* litter on *P. massoniana* leaf litter mass loss at each decomposition period, the relative mixture effect (RME) was calculated as follows:

$$\text{RME (\%)} = ((m_{\text{obs}} - m_{\text{exp}})/m_{\text{exp}}) \times 100 \quad (4)$$

where m_{obs} is the observed mass loss of the *P. massoniana* leaf litter from mixed leaf litter and m_{exp} is the expected mass loss of the *P. massoniana* leaf litter, calculated as the mass loss of the *P. massoniana* leaf litter in the single species litter bags (Wardle et al. 1997). Deviations with the value of zero indicated non-additive effects, deviations with positive or negative values indicated synergistic or antagonistic effects, respectively.

There were two forest types (monoculture and mixed forest) and for litter types (ratio of mass composition of coniferous leaves to broad leaves: 1:1, 3:2, 7:3, and 1:0). Homoscedasticity was tested by the Fligner-Killeen test, and normality was tested by the Shapiro-Wilk test. Differences between 2 levels of forest and 4 levels of litter types were estimated by ANOVA ($P < 0.05$) or pairwise Wilcoxon test ($P < 0.05$). The decomposition time effects were tested by Wilks' Lambda test. All calculations and statistical tests were performed in R, version 4.2.2 (QUOTE: R Development Core Team 2022).

Results

The characteristics of initial leaf litter and soil

The leaf litter of *C. fissa* concentration significant less carbon ($545.67 \pm 5.1 \text{ g}\cdot\text{kg}^{-1}$), and more N ($15.42 \pm 0.5 \text{ g}\cdot\text{kg}^{-1}$), K ($1.49 \pm 0.2 \text{ g}\cdot\text{kg}^{-1}$), Mg ($0.85 \pm 0.0 \text{ g}\cdot\text{kg}^{-1}$) concentrations than *P. massoniana* leaf litter (Table 3).

Table 3 Initial chemical quality of *C. fissa* and *P. massoniana* leaf litter (means of six replicates \pm standard error). Significant effects among the two species leaf litter are indicated by different lowercase letters.

| Concentration (g in $\cdot\text{kg}^{-1}$ dry mass) | <i>C. fissa</i> | <i>P. massoniana</i> |
|---|-------------------|----------------------|
| Carbon (C) | 545.67 \pm 5.1a | 578.18 \pm 1.0b |
| Nitrogen (N) | 15.42 \pm 0.5b | 8.60 \pm 0.5a |
| Phosphorus (P) | 0.36 \pm 0.0a | 0.31 \pm 0.0a |
| Potassium (K) | 1.49 \pm 0.2b | 0.65 \pm 0.0a |
| Calcium (Ca) | 7.52 \pm 0.3a | 7.47 \pm 0.2a |
| Magnesium (Mg) | 0.85 \pm 0.0b | 0.58 \pm 0.0a |

The P and Ca concentrations in the *C. fissa* leaf litter are higher than in the *P. massoniana* leaf litter, but insignificant.

The monoculture *P. massoniana* litter has highest C concentration ($578.18 \pm 0.00 \text{ g kg}^{-1}$) and C/N ratio (67.20 ± 0.00), and the 1:1 type litter has lowest C/N ratio (46.77 ± 0.02) (Table 4).

The mixed stand has higher soil organic matter at each depth than in the *P. massoniana* monoculture stand (Table 5), and higher organic matter, total nitrogen, total phosphorus concentrations at the surface soil (0 - 5 cm, and 5 - 10 cm), but not statistically significant. The soil of mixed stand is less acidity than of monoculture stand at 0 - 5 cm.

Responses of leaf litter mass loss to litter mixtures

The mass loss of litter type 1:0 (*P. massoniana*,

C. fissa) was lowest both in the mixed forest and monoculture forest compared to the other litter types after 12 months decomposition (Figure 1). The total mass loss of 1:1 ($28.64\% \pm 2.6$, $57.74\% \pm 2.7$, $78.90\% \pm 2.5$, $73.59\% \pm 3.1$) in the mixed forest was highest compared to the total mass of other litter types from June 2016 to March 2017, and the mass loss of *C. fissa* leaf litter from 1:1 was highest as well in the mixed forests. From March 2016 to December 2016, the mass loss of the total leaves of all litter mixtures, the broad leaves, and the coniferous leaves in the mixed forest increased sharply, however, from December 2016 to March 2017 their mass loss decreased. In the monoculture forest, only the mass loss of 1:0 decreased during the last three months decomposition (Figure 1).

Comparing the litter decomposition rate, the litter mixture of 1:1 decomposed significant faster

Table 4 Carbon (g kg^{-1}) and nitrogen (g kg^{-1}) concentrations and C/N ratios (\pm standard error) in the leaf litter mixtures before decomposition. Significant effects among different litter mixtures are indicated by different lowercase letters.

| | 1:1 | 3:2 | 7:3 | 1:0 |
|---------------------------------------|--------------------|--------------------|-------------------|--------------------|
| C ($\text{g} \cdot \text{kg}^{-1}$) | 561.92 \pm 0.02a | 565.17 \pm 0.04b | 568.3 \pm 0.10c | 578.18 \pm 0.00d |
| N ($\text{g} \cdot \text{kg}^{-1}$) | 12.01 \pm 0.00d | 11.33 \pm 0.01c | 10.66 \pm 0.02b | 8.60 \pm 0.00a |
| C/N | 46.77 \pm 0.02a | 49.87 \pm 0.04b | 53.32 \pm 0.11c | 67.20 \pm 0.00d |

Note: litter type: 1:1, 3:2, 7:3, 1:0 refer to the ratio of *P. massoniana* leaves to *C. fissa* leaves.

Table 5 The soil main chemical characteristics of the two forests (means of six replicates \pm standard error). Different letters indicate significant differences between monoculture forest and mixed forest at each depth ($P < 0.05$, pairwise Wilcoxon test).

| Depth (cm) | Organic matter ($\text{g} \cdot \text{kg}^{-1}$) | | N ($\text{g} \cdot \text{kg}^{-1}$) | | P ($\text{g} \cdot \text{kg}^{-1}$) | | pH | | CEC ($\text{g} \cdot \text{kg}^{-1}$) | |
|------------|--|-------------------|---------------------------------------|-----------------|---------------------------------------|------------------|--------------------|-----------------|---|--------------------|
| | monoculture forest | mixed forest | monoculture forest | mixed forest | monoculture forest | mixed forest | monoculture forest | mixed forest | monoculture forest | mixed forest |
| 0-5 | 44.90 \pm 3.6a | 52.96 \pm 4.8a | 1.42 \pm 0.1a | 1.65 \pm 0.2a | 0.19 \pm 0.01a | 0.22 \pm 0.02a | 2.91 \pm 0.0a | 2.82 \pm 0.0a | 86.01 \pm 21.9a | 136.90 \pm 18.6a |
| 5-10 | 29.93 \pm 0.9a | 39.10 \pm 10.4a | 1.02 \pm 0.1a | 1.34 \pm 0.3a | 0.17 \pm 0.01a | 0.21 \pm 0.02a | 3.11 \pm 0.0a | 3.04 \pm 0.0a | 48.71 \pm 4.9a | 100.13 \pm 19.4a |
| 10-20 | 14.93 \pm 1.4a | 22.20 \pm 3.7a | 0.65 \pm 0.1a | 0.86 \pm 0.1a | 0.15 \pm 0.01a | 0.18 \pm 0.01a | 3.22 \pm 0.0a | 3.28 \pm 0.0a | 33.58 \pm 4.3a | 67.98 \pm 5.8a |
| 20-40 | 10.10 \pm 1.2a | 12.71 \pm 1.6a | 0.52 \pm 0.0a | 0.66 \pm 0.1b | 0.14 \pm 0.00a | 0.18 \pm 0.01a | 3.21 \pm 0.0a | 3.17 \pm 0.1a | 36.32 \pm 6.7a | 52.77 \pm 6.0a |
| 40-60 | 7.82 \pm 0.9a | 13.57 \pm 5.8b | 0.47 \pm 0.0a | 0.60 \pm 0.1b | 0.15 \pm 0.00a | 0.17 \pm 0.01a | 3.32 \pm 0.0a | 2.81 \pm 0.1a | 29.23 \pm 4.1a | 65.78 \pm 27.1a |

Table 6 Decomposition constants (k) (\pm standard error) in 12 months for individual leaf litter within mixtures and the mixed leaf litter. Significant effects among different litter types of broadleaves and coniferous leaves from the same stand are indicated by different lowercase letters, and significant effects among different litter types between different stands of broadleaves, conifer leaves, and litter mixtures, respectively, are indicated by upper case letters ($P < 0.05$, pairwise Wilcoxon test).

| Plot | type | Total mass loss (g) | | | k (month^{-1}) | | |
|--------------------|------|---------------------|----------------------|------------------|-----------------------------|----------------------|-----------------|
| | | <i>C. fissa</i> | <i>P. massoniana</i> | Litter mixture | <i>C. fissa</i> | <i>P. massoniana</i> | Litter mixture |
| Mixed forest | 1:1 | 8.56 \pm 0.3cC | 6.21 \pm 0.4bA | 14.77 \pm 0.6B | 0.21 \pm 0.0bB | 0.11 \pm 0.0aA | 0.14 \pm 0.0B |
| | 3:2 | - | - | - | - | - | - |
| | 7:3 | 3.72 \pm 0.4aA | 9.87 \pm 0.4cD | 13.59 \pm 0.5B | 0.21 \pm 0.0bB | 0.18 \pm 0.0bC | 0.12 \pm 0.0B |
| | 1:0 | - | 11.83 \pm 0.4dE | 11.83 \pm 0.4A | - | 0.12 \pm 0.0aB | 0.12 \pm 0.0B |
| Monoculture forest | 1:1 | 6.05 \pm 0.3bB | 6.48 \pm 0.2bA | 12.53 \pm 0.4B | 0.10 \pm 0.0aA | 0.10 \pm 0.0aA | 0.10 \pm 0.0A |
| | 3:2 | 5.12 \pm 0.3bB | 8.06 \pm 0.3cB | 13.18 \pm 0.3B | 0.27 \pm 0.0cC | 0.26 \pm 0.0dD | 0.10 \pm 0.0A |
| | 7:3 | 3.26 \pm 0.2aA | 9.38 \pm 0.3cB | 12.63 \pm 0.4B | 0.17 \pm 0.0bB | 0.16 \pm 0.0cC | 0.09 \pm 0.0A |
| | 1:0 | - | 10.98 \pm 0.3dD | 10.98 \pm 0.3A | - | 0.12 \pm 0.0bB | 0.12 \pm 0.0B |

Note: litter type: 1:1, 3:2, 7:3, 1:0 refers to the mass ratio of *P. massoniana* leaves to *C. fissa* leaves.

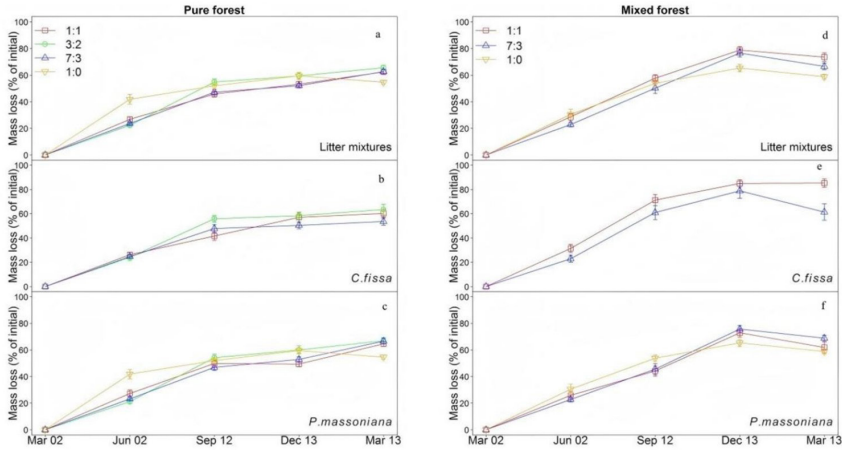


Figure 1 Leaf litter mass loss (% in initial mass) of total leaves in monoculture forest (a) and mixed forest (d), and single species (*C. fissa*, *P. massoniana*) leaf litter in the mixture litterbags in the monoculture (b, c) and mixed forests (e, f). Error bars are standard errors of estimates. The ratios of 1:1, 3:2, 7:3, and 1:0 refer to the ratios of the leaf litter mass of *P. massoniana* to *C. fissa*.

in the mixed forest ($k = 0.14$) whereas the litter mixture of 1:0 decomposed significant faster in the monoculture forest ($k = 0.12$) (Table 6). The litter mixture of 1:1, 7:3, and 1:0 decomposed faster in the mixed than in the monoculture forest. The broadleaves and coniferous leaves from 3:2 decomposed fastest in the monoculture stand compared to other leaves from other litter mixtures: $k = 0.27$, $k = 0.26$, respectively.

Effects of litter mixtures on *P. massoniana* leaf litter decomposition

The effects of *C. fissa* leaf litter on *P. massoniana* leaf litter decomposition varied, which is decided by decomposition time. In addition, the mixture effects were significantly affected by decomposition time in both monoculture and mixed forests (Wilks' Lambda for the Time effect, $p < 0.001$ ***) (Table 7). In the monoculture forests, the mass loss of *P. massoniana* leaf litter from the litter mixture of 3:2 (B) was faster than the *P. massoniana* leaf litter from 1:0 during the decomposition time of 6 months, 9 months, and 12 months (Figure

2 b, c, d); the mass loss of conifer leaf litter from the litter mixture of 1:1(A) and 7:3 (C) was slower during the first 9 month (Figure 2 a, b, c); during the last 3 decomposition months (Figure 2 d) the mass loss of *P. massoniana* leaf litter from the 3 litter mixtures was stimulated by the mixture, and the mean RME = + 27.05% (Table 7). In the mixed forests, the mass loss of *P. massoniana* leaf litter from the litter mixture of 1:1 (A) and 7:3 (C) was slower than the *P. massoniana* leaf litter from 1:0 in the decomposition time of 3 months (Figure 2 e) and 6 months (Figure 2 f), and faster in the 9 (Figure 2 g) and 12 months (Figure 2 h), with the mean REM of + 25.23% and + 16.99%, respectively.

***P. massoniana* leaf litter decomposition in individual species litterbags**

Leaf litter mass loss of *P. massoniana* in individual species litterbags (1:0 type) increased with decomposition time was characterized by an initial faster rate, followed by a slower rate for both decomposition sites (Figure 3). Mass loss

Table 7 The soil main chemical characteristics of the two forests (means of six replicates ± standard error). Different letters indicate significant differences between monoculture forest and mixed forest at each depth ($P < 0.05$, pairwise Wilcoxon test).

| Time (month) | Monoculture forest | | Mixed forest | | | |
|--------------|--------------------|-------------------------------|----------------------------|----------|-------------------------------|---------------------------|
| | mean RME | Time | Litter type | mean RME | Time | Litter type |
| 3 | -29.97% | | | -7.70% | | |
| 6 | -4.37% | $p < 0.001$ ***, $df = 44$ | $p = 0.073$, $df = 88$ | -19.44% | $p < 0.001$ ***, $df = 18$ | $p = 0.42$, $df = 18$ |
| 9 | -12.75% | | | +25.23% | | |
| 12 | +27.05% | | | +16.99% | | |

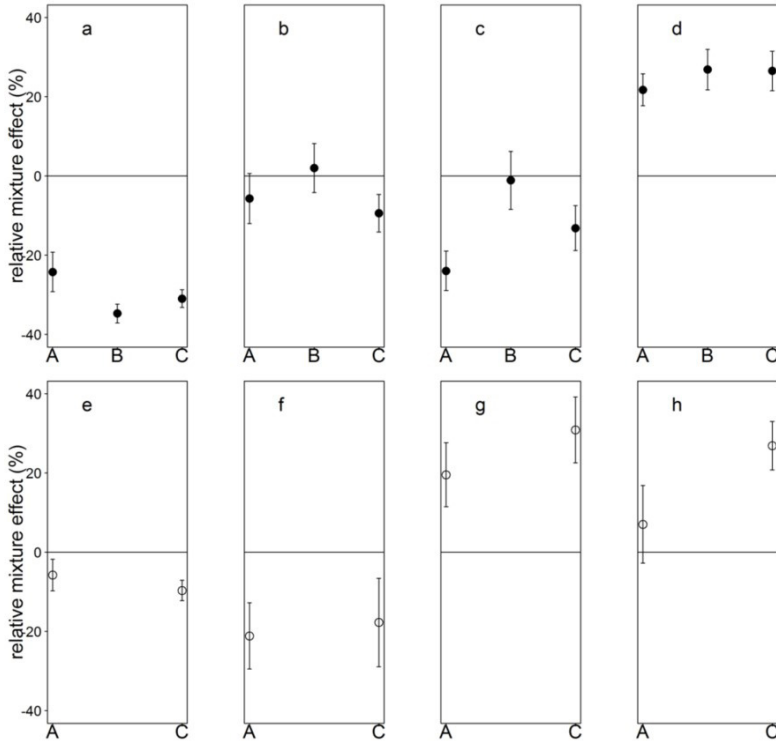


Figure 2 Mean relative mixture effects (\pm se) on *P. massoniana* leaf litter mass loss for three different litter mixtures in *P. massoniana* monoculture forests, and two different litter mixtures in *P. massoniana* and *C. fissa* mixed forests (the ratio of *P. massoniana* to *C. fissa*: A: 1:1, B: 3:2, C: 7:3) decomposed (a) (e) 3 months, (b) (f) 6 months, (c) (g) 9 months, (d) (h) 12 months. Closed and pen circles indicate the different litter mixtures in the monoculture forests and mixed forests, respectively.

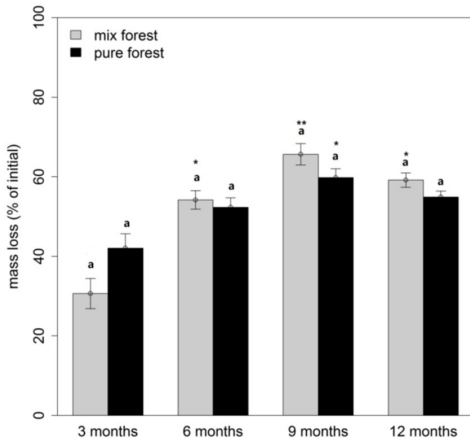


Figure 3 Leaf litter mass loss (% of initial \pm se) of *P. massoniana* incubated 3, 6, 9, and 12 months in single species litterbags (*P. massoniana* to *C. fissa* refers to 1:0) in the monoculture forests and mixed forests. Different lowercase letters indicate significant differences between monoculture forest and mixed forest at each incubated time ($P < 0.05$, pairwise Wilcoxon test). “**” indicates significant differences among incubated time in the mixed forest and monoculture forest, respectively (* $P < 0.05$, ** $P < 0.01$ pairwise Wilcoxon test).

in the mixed forest averaged $30.7\% \pm 3.8\%$ after decomposed 3 months, and significantly increased to $54.2\% \pm 2.3\%$ from the first decomposition period to the second decomposition period, then significantly increased to $65.7\% \pm 2.7\%$ in the third decomposition period, but remarkable, did not further increase until the fourth decomposition time ($59.2\% \pm 1.8\%$) (Wilks' Lambda for the Time effect, $P = 0.008$). We found differences but not significant in mean decomposition rate constants ($k \text{ year}^{-1}$) between the mixed forest and monoculture forest ($P = 0.534$) and mean k -value was higher in the monoculture forests ($1.47 \pm 0.07 \text{ year}^{-1}$).

The Partial Least Squares (PLS) regression model including the litter quality parameters, the concentration of C, Ca, K, Mg, N, P, and C/N, C/N/P explained 41.31% and 46.01% of variation among mean k -values in the mixed forest and monoculture, respectively. In the mixed forest, the initial concentration

of C, K, and P was positively related to the decomposition rate, the initial concentration of Mg, N, C/N, and C/N/P was negatively related to the decomposition rate. The initial concentrations of C, Ca, K, Mg, and P were negatively related to the decomposition rate in the monoculture stands; the initial concentration of N, C/N, and C/N/P related to the decomposition rate in the *P. massoniana* monoculture negatively (Figure 4).

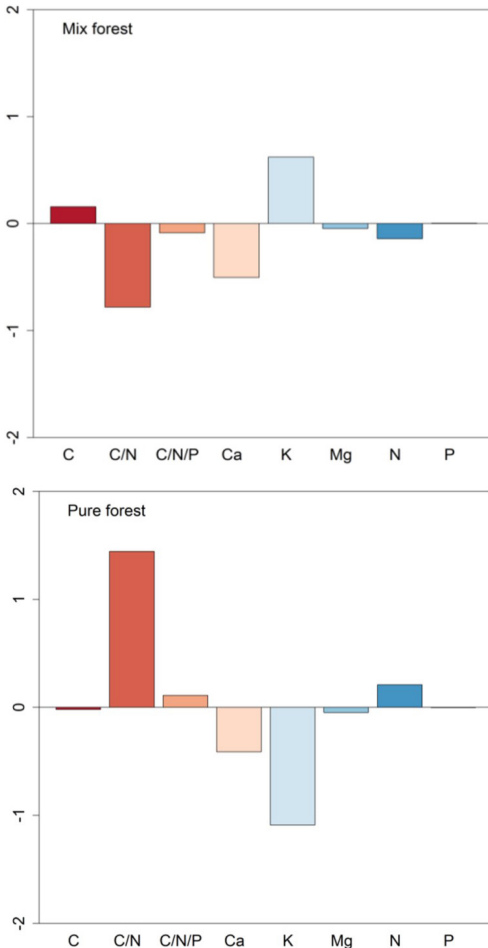


Figure 4 Results of Partial Least Squares (PLS) regression analysis indicated the variables of importance of projection (VIP) estimating the relative importance of initial concentrations of carbon (C), calcium (Ca), potassium (K), magnesium (Mg), nitrogen (N), phosphorus (P), the ratio of C to N (C/N), and the ratio of C to N to P (C/N/P) in litter, explaining variation of decomposition rate constants (k year⁻¹) of the *P. massoniana* leaf litter in single species litterbags in the mixed forest and *P. massoniana* monoculture stand.

Discussions

Single species litter decomposition

The mass loss of the individual species leaf litter of *P. massoniana* was faster in the *P. massoniana* forests only in the first three months, from the sixth to twelfth months was slower than in the mixed forest, and significantly higher in the third month (Figure 3). That could be explained by plant litter generally decomposes faster at the site from which it was from (the ‘home-field advantage’ - HFA; Gholz et al. 2000), because of the existence of special microbial communities and soil enzyme that can decompose specific litter (Ayres et al. 2009, He et al. 2016). Later on (from the sixth month, Figure 3), the coniferous litter decomposed faster in the mixed forest likely due to the differences in microclimatic conditions (He et al. 2016), including higher diversity of decomposer communities, and the forest environments keeps the decomposing material wetter than in the monoculture forests (Bai et al. 2023).

The results showed the positive correlation between N concentration and mass loss in the *P. massoniana* monoculture (Figure 4). That would be caused by the substrate N concentration was positively related to a labile C fraction, or negatively correlated with some factors that inhibited decomposition, or with other nutrient that was limiting litter decomposition (Hobbie 2006, Berg et al. 1991, Berg 2006) indicated a significant negative relationship between N concentration and lignin decomposition across seven litter types. Furthermore, the microorganisms involved in litter decomposition in this case had to rely on the initial N concentration of leaf litter largely (Melillo et al. 1982). While the correlation of the initial concentration of N and the decomposition rates was inverse in the mix forests which was negative (Figure 4). In the study of (Melillo et al. 1982) also showed the decomposition constants (k) correlated to the initial nitrogen concentration, with the correlation coefficient -0.05. (Aber et al. 1991) have demonstrated an inverse relationship between the litter mass loss and the nitrogen concentration. Additionally,

Berg (2000) found a negative relationship between N concentration and the litter mass loss appeared during the late stages of litter decomposition.

The results of our study are also consistent with (Wardle et al. 2002, Schaefer et al. 1985), who did not observe a positive relationship between decomposition and N concentration. (Li et al. 2017) studied the effects of broadleaf litter mixture on decomposition in subtropical area of China and found that the decomposition rate was negatively correlated with initial N concentration and N:P ratio. Other studies (Zheng et al. 2017, Fang et al. 2007) found the N addition had a depressed effect on litter decomposition. This may be because the relatively abundant of exogenous nitrogen is available to the microorganisms participated in litter decomposition, then initial nitrogen concentration of the litter may not perform as great an influence on decomposition rate. The higher exogenous N may induce the higher microbe in the litter, which could more efficiently immobilise N and consume the soluble C in the litter, and further retard litter decomposition. Due to the microbial immobilisation of resources when the litter has poor quality, which retards the decomposition processes (Berg & Staaf 1980). This explanation is supported by our experiment results that the N concentrations in the mineral soil in the mix forests were higher than in the monoculture forests (Table 4).

Litter mixture effects

Mixture leaf litter from different tree species may impact the decomposition rate additively or non-additively. When the decomposition rate of individual species litter is not affected by another litter species existing in the mixture, purely additive effect occurs. In forest ecosystem, mixed leaf litter from species with different substrate quality and leaf structure changes the chemical environment and alters the total litter surface physically where decomposition is occurring (Gartner & Cardon 2004, Hector et al. 2000). These changes can also affect decomposer

abundance and activity (Wardle et al. 2003) or improve microclimatic conditions in mixture (Makkonen et al. 2012). In our study, leaf litter mixture effects on decomposition rate changed during decomposition process (Srivastava et al. 2009, Lecerf et al. 2011), the antagonistic mixture effects of 1:1 and 7:3 could be found in the first six months in the mix and monoculture forests, the non-additive of synergistic litter mixture effects dominated after 9 months (Figure 2). A proper explanation for the antagonistic mixture effects on decomposition rate at the early stage could be the chemical heterogeneity of structural and secondary litter compounds, which could influence the interactions between plants and microorganisms and outweigh the effects of the other functional characteristics in mixed litter, drives the litter decomposition (Chomel et al. 2016). Another possible explanation is that the litter mixture effects could be driven by the combination of complementary resources from litter species meets the requirements of the different microbial communities (Vos et al. 2013).

The leaf litter of the two species in our study had contrasting N concentrations (Table 2), *P. massoniana* in the mixtures with N-rich neighbors, during the decomposition the translocation of nutrients occurred, from good- to poor- quality litter releasing decomposition of the poor quality litter from nutrient limitation (Trogisch et al. 2016). High - quality litter is considered to have a high N concentration and a low C:N ratio (Berg & McLaugherty 2008). Litter of higher quality decomposes faster, initial litter quality is regarded as the controlling factor of decomposition at the local scale (Hobbie 2006, Setiawan et al. 2016). High N promotes the feeding activities of soil fauna by increasing fauna abundance (Porre et al., 2020). Besides, the higher carbon/nitrogen ratio (C/N) or higher lignin content reduces the availability and activity of microbial enzymes to carbohydrates. These change the corresponding strategies of microbial communities for refractory compounds, then increase the physical and chemical barriers during the litter decomposition process (Bhatnagar et al. 2018, García-Palacios

et al. 2017).

Antagonistic and synergistic effects in litter mixtures appeared at different incubation time and among different mixture types, indicating that the N transfer among the two leaf litters, and the different mixture ratio control the available N concentration. This is corresponding with some previous studies, which found that synergistic effects in litter mixtures turn stronger and more frequent as decomposition progresses, depending on the improved leaf litter quality and increased microbe diversity and activity at the last stage of decomposition (Liu et al. 2007, Chen et al. 2013, Wu et al. 2013). The study of Schimel & Hättenschwiler (2007) showed that litter mixture effects varied with decomposition time, which were detected after one year for legume litter and two years for conifer litter. Montané et al. (2013) demonstrated that the important mechanism for synergistic effects in litter mixtures was nutrient transmigration. Butenschoen et al. (2014) also found that the non-additive effects in litter mixtures prevailed after 6 months of decomposition. These are contrary to some other findings, which indicate that the positive effects of high-quality litter on decomposition rate in litter mixtures have been often emphasized, and synergistic effects are more common than antagonistic effects (Gartner & Cardon 2004, Hättenschwiler & Gasser 2005, Cuchietti et al. 2014).

Conclusions

The results of this study indicated that, *Pinus massoniana* leaf litter decomposed faster in the mixed forest than in the monoculture, and the mixed leaf litter decomposed faster than the pure *P. massoniana* litter. Moreover, the 1:1 type decomposed the fastest. The mixture effects on needle litter decomposition changed during the decomposition process. There were antagonistic mixture effects at the early decomposition stage. both Non-additive or synergistic litter mixture effects at the late decomposition stage. The results showed that broadleaf litter could promote the decomposition of conifer litter, and the

decomposition of litter was faster in the mixed forest than in the monoculture coniferous forest. According to the results, maintaining a suitable proportion of broad-leaved tree species in the coniferous monoculture forest is beneficial to the nutrient cycle and tree growth.

Conflict of interest

The authors declare no financial or personal interests could influence the work presented in this paper.

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