How to manage degraded monoculture plantations in South China: a perspective from reciprocal litter transplant experiment

Zhongyu Sun, Yuhui Huang, Long Yang, Qinfeng Guo, Meili Wen, Jun Wang & Nan Liu

ONLINE FIRST

Landscape and Ecological Engineering

ISSN 1860-1871

Landscape Ecol Eng
DOI 10.1007/s11355-020-00414-x

Springer

Landscape and Ecological Engineering
https://doi.org/10.1007/s11355-020-00414-x

ORIGINAL PAPER

How to manage degraded monoculture plantations in South China: a perspective from reciprocal litter transplant experiment

Zhongyu Sun[1] · Yuhui Huang[2] · Long Yang[1] · Qinfeng Guo[3] · Meili Wen[1] · Jun Wang[4] · Nan Liu[4]

Received: 9 June 2019 / Revised: 2 February 2020 / Accepted: 5 February 2020

Abstract

Litter decomposition, an important component of nutrient cycling, is often one of the limiting factors for the development of monoculture tree plantations for restoration, and how to improve the litter decomposition rate remains as a major challenge. To help resolve this issue, we developed a mixed-litter transplantation approach to improve the litter decomposition and nutrient cycling in *Schima superba*, *Cunninghamia lanceolata*, *Eucalyptus urophylla*, and *Acacia mangium* monoculture plantations in China. The monospecific leaf litters of the four species were collected and their possible two-, three- and four-species combinations were transplanted between plantations. We examined the influences of home/away field, litter species richness, and litter composition on litter decomposition during 24 months treatment. A significant effect of litter composition on litter decomposition (Duration × Composition effect) was detected in *E. urophylla* plantation. The influence of litter richness on litter decomposition was significant in *A. mangium* plantation (Duration × Richness effect). The litter of *C. lanceolata* and *A. mangium* had a distinct home-field advantage, while the litter of *S. superba* had a distinct away-field advantage in decomposition. We observed a positive relationship between richness and litter decomposition in *C. lanceolate* plantation. The effect of Duration × Species Interaction on litter decomposition, was significant in *E. urophylla* plantation, indicating a non-additive effect. Litter decomposition in *E. urophylla* plantation could be explained by idiosyncratic model, and the rivet model may be appropriate to illustrate the litter decomposition in *A. mangium* plantation. Finally, since the litter decomposition in degraded *A. mangium* plantations had a distinct home-field advantage and was significantly affected by litter richness, transplanting mixed litters of neighboring plantations may be beneficial to improve its litter decomposition rate. Transplanting of *S. superba* litters due to the distinct home-field advantage to neighboring plantations such as *E. urophylla* plantation whose litter decomposition is significantly affected by litter composition, may be an effective management method for improving litters decomposition.

Keywords Litter mixture · Litter decomposition · Away-field advantage · Non-additive effect · Rivet hypothesis · Plantation management and reconstruction

Introduction

China has the world's largest plantation resource (Brockerhoff et al. 2008; Piao et al. 2009). Especially in South China, large monoculture plantations of native or exotic species were created for ecological restoration or industrial utilization in the middle of the twentieth century (Peng 2003). These plantations provided high-quality ecosystem services at multiple scales in the early stages (Peng et al. 2009). The abandoned bare land turned to green, and the soil conditions improved rapidly after the afforestation. Through the years, however, some monoculture plantations began to perform poorly in terms of ecosystem function, displaying degradation of soil fertility and declines in productivity (Zhu and Li 2007). The declines in litter decomposition and nutrient cycling efficiency have been suggested to be among the major causes (Chen et al. 2004; Wang et al. 2007). Generally in such degraded plantations, large amounts of litter accumulate on the ground due to the slow decomposition

---

Zhongyu Sun and Yuhui Huang contributed equally to this work.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11355-020-00414-x) contains supplementary material, which is available to authorized users.

✉ Long Yang
yanglong@gdas.ac.cn

Extended author information available on the last page of the article

rate, and the accumulated litter may further hinder nutrient cycling and species regeneration (Barlow et al. 2007). Thus, the restoration of ecosystem function lags behind the restoration of ecosystem structure. Many restoration projects did not consider the factors of decomposers and detritivores while restoring the vegetation. At the early stages of restoration, there is relatively little litter on the surface. Although there were few decomposers and detritivores present, the small amounts of litter could decompose via the leaching of rain. However, mature trees meant greater amounts of litter on the ground, and eventually this amount was beyond the capacity of the existing decomposers and detritivores. The remnant litter influences the microclimate in such a way as to hinder nutrient cycling and species regeneration. The community structure of decomposers and detritivores may have also been affected (Li et al. 2004; Xu et al. 2005). These events have caused the degradation of monoculture plantations. Therefore, how to accelerate litter decomposition is a major issue in managing these degraded monoculture plantations.

Accelerating the decomposition of remnant litter may be an effective method of ameliorating the degradation of monoculture plantations. The transplantation of litter, based on the "away-field advantage" theory, provides one potential approach (Chomel et al. 2015). Previous studies have indicated that the litter decomposition of some species is accelerated within a foreign environment in comparison to the native area because the microenvironment of the foreign area may be more suitable for the decomposition of the litter of those species. Ecologically important decomposer species may also move to the away field to exploit the litter. This in turn stimulates the activity of microscopic organisms, resulting in rapid decomposition. This phenomenon has been described as an "away-field advantage" (Gholz et al. 2000; Mahaney 2010; Chapman et al. 2011). Ayres et al. (2009a) found that eight of 35 studies of litter transplantation showed an "away-field advantage". However, to date the effects and potential applications of the "away-field advantage", such as the possibility of using litter transplantation to accelerate litter decomposition in degraded plantations, has rarely been studied. In contrast, most of the previous studies concerned the "home-field advantage (HFA)" phenomenon, i.e., litter decomposes faster in its original habitat than in foreign habitats (Vivanco and Austin 2008; Chomel et al. 2015; Li et al. 2017). Some studies have indicated that the specificity of soil organisms was the primary cause of the home- or away-field advantage (Ayres et al. 2009b). The decomposition duration, litter quality and adjustability of soil organisms determined the strength of the advantage (Zha et al. 2012). Nevertheless, the mechanisms of home- or away-field advantages have remained unclear.

In addition to the away-field advantage, litter decomposition may also benefit from appropriate litter species richness and species interactions. The influence of litter species richness on litter decomposition can be classified as non-additive (positive or negative) and additive (Zero-effect) (Hättenschwiler et al. 2005; Chapman and Koch 2007; Madritch and Cardinale 2007). Gartner et al. (2004) concluded that 108 out of 162 leaf mixtures exhibited non-additive mass loss; 94 out of 123 leaf mixtures exhibited non-additive nutrient dynamics; 55% and 65% of leaf mixtures exhibited non-additive patterns in the respective abundance and activity of decomposers. When a positive effect exists, the mixture of different litters will accelerate the litter decomposition depending on litter composition and quality measures including N concentration, C/N ratio, P concentration, C/P ratio, and lignin concentration (Taylor et al. 2007, Giesselmann et al. 2010, Ge et al. 2013). The mixed litters also provide a better physical and chemical environment for the decomposer community and indirectly improve the litter decomposition through decomposer activities (Hansen 1999; Nilsson et al. 1999; Hector et al. 2000). Therefore, a mixed-litter strategy is a potential approach for the acceleration of litter decomposition in degraded monoculture plantations.

Following previous studies, we hypothesized that litter transplantation with an appropriate mixed-litter strategy would improve the litter decomposition and nutrient cycling in degraded monoculture plantations, thus aiding in restoration. In this study, we designed a litter transplantation experiment to test the effects of decomposition habitat, litter species richness, and litter composition on litter decomposition in four degraded monoculture tree plantations, i.e., *Schima superba*, *Cunninghamia lanceolata*, *Eucalyptus urophylla*, *and Acacia mangium* in South China. The four species were commonly used to restore degraded slopes in South China, mostly due to their high growth rates. This study focused on the following issues: (1) Does the litter decomposition rate benefit from the away-field advantage effect? (2) How do the litter species richness and composition influence litter decomposition? (3) What types of litter transplantation and litter mixtures can we use to restore monoculture plantations?

Materials and methods

Study area

The study was conducted at the Heshan National Field Research Station of Forest Ecosystems (112° 50′ E, 22° 34′ N) located in Heshan City, Guangdong, China. This station, 40 ha in size, is one of the stations of the Chinese Ecological Research Network (CERN). The area has a south subtropical monsoon climate, with a mean annual temperature of 22.6 °C, mean annual precipitation of approximately 1700 mm, and annual radiation of

4350.5 $MJm^{-2}a^{-1}$. Located on red laterite soil, the climax plant community is a low subtropical monsoon evergreen broad-leaved forest that includes species of *Lauraceae*, *Euphorbiaceae*, and *Fagaceae.* As a result of serious and long-term human disturbance, however, the soil has been severely eroded, and the original vegetation has almost completely disappeared. Four experimental, single-species plantations of *Schima superba*, *Cunninghamia lanceolata*, *Eucalyptus urophylla*, *and Acacia mangium* were established at the station in 1984 to restore the degraded, hilly land. The four plantations in this study, each occupying approximately 3 ha, are adjacent to each other near Heshan city, Guangdong province, China. The original geographical conditions were considered as identical bare ground. *S. superba* and *C. lanceolata* are native species, and *E. urophylla*and *A. mangium* originated from Australia (Supporting Table S1). In recent years, all plantations have grown slowly, and seedling regeneration of the dominant species has decreased. The plantations of *C. lanceolata* and *A. mangium* are in obvious states of degradation. The spacing between trees is three meters. The basic ecological and environmental conditions in the four kinds of forest plantations are listed in Table 1. The "home" and "away" fields differ in light penetration, litter mass, soil bulk density, and soil exchangeable potassium. The light penetration was significantly lower in *S. superba* forest and the litter mass was significantly lower in *E. urophylla* forest. The soil bulk density was significantly different among *S. superba*, *C. lanceolate*, and *A. mangium* plantations. The soil exchangeable potassium in *E. urophylla* was significantly lower than in the other three forests.

Litter quality assessment

The leaf litter used in this study was obtained from the four single-species plantations. Fresh leaf litter of the four species was collected in 10 litter traps (1 m × 1 m) in each plantation, and the chemical characteristics of the litter, i.e., the content of carbon (C), nitrogen (N), phosphorus (P), and lignin, were measured. Litter samples were digested with 1:1 $K_2Cr_2O_7$, and H_2SO_4 and then titrated with $FeSO_4$ to determine total C content (Graça et al. 2005). For the measurements of total N and total P, the litter samples were digested by H_2SO_4 with a 12:1 mixture of K_2SO_4 and $CuSO_4$ and then analyzed by flow injection analyzer QuikChem 8000 Series FIA (Wu et al. 2009; Ye et al. 2009). Lignin was measured following Van Soest (Graça et al. 2005).

Decomposition experiment

After being air-dried for 15 days, the leaf litter was placed in litter bags (20 cm × 20 cm; 2-mm × 2-mm openings; 18 g of the air-dried litter per bag). There were four types of single-species litter bags (for *S. superba* (S), *C. lanceolata* (C), *E. urophylla* (E), or *A. mangium* (A) and 11 types of mixtures: S + C, S + E, S + A, C + E, C + A, E + A, S + C+E, S + C+A, S + E+A, C + E+A, and S + C+E + A (see Figure S1 and Table S2). The mass of each species in each litter bag was equal to 18 g divided by the number of species in the litter bag. The 15 types of litter bags were treated as a group and three groups were deployed in three plots (10 m × 10 m) at each of the four plantations; thus a total of 45 (15 bags each plot × 3 plots) litter bags were placed in three plots as

Table 1 Ecological and environmental characteristics of the four 30-year-old monoculture plantations planted with *S. superba*, *C. lanceolata*, *E. urophylla*, and *A. mangium*, respectively

Characteristic	*S. superba*	*C. lanceolata*	*E. urophylla*	*A. mangium*	References
Average height (m)	16.7 ± 0.4c	15.0 ± 0.6d	22.0 ± 0.6a	18.3 ± 0.7b	This study
Average DBH (cm)	18.3 ± 1.1ab	16.0 ± 1.4b	20.2 ± 2.1a	19.7 ± 2.0a	This study
Canopy cover (%)	40.0 ± 15.0a	45.0 ± 13.1a	29.3 ± 5.2a	60.6 ± 2.2a	Wang et al. (2009)
Light penetration (%)	9.35 ± 2.18b	23.27 ± 4.24a	12.42 ± 2.07ab	22.71 ± 3.94a	Wang et al. (2009)
Litter mass (g/m^2)	877 ± 107a	741 ± 134ab	361 ± 38b	1124 ± 134a	Wang et al. (2009)
SBD (g/cm^3)	1.54 ± 0.07a	1.25 ± 0.07c	1.40 ± 0.07b	1.39 ± 0.10b	Wang et al. (2009)
SOM (g/kg)	1.55 ± 0.10a	1.57 ± 0.11a	1.38 ± 0.01a	1.57 ± 0.36a	Wang et al. (2009)
SHN (mg/kg)	101.27 ± 5.89a	100.21 ± 4.32a	105.82 ± 8.13a	120.25 ± 1.85a	Wang et al. (2009)
SEK (mg/kg)	111.60 ± 17.18ab	99.57 ± 5.32ab	67.47 ± 1.92b	122.20 ± 10.48a	Wang et al. (2009)
SAP (mg/kg)	1.82 ± 0.40a	2.32 ± 0.93a	1.97 ± 1.04a	1.97 ± 0.58a	Wang et al. (2009)
Total PLFAs (ng/g)	7003.10 ± 1466.92a	5979.69 ± 2219.38a	7288.89 ± 1888.11a	7190.31 ± 1466.92a	Sun et al. (2014)
Bacteria (%)	80	90	76	81	Sun et al. (2014)
Fungi (%)	10	9	10	10	Sun et al. (2014)

Values are mean ± SD. Means within rows sharing the same letter are not significantly different ($P < 0.05$)

DBH diameter at breast height, *SBD* soil bulk density, *SOM* soil organic matter, *SHN* soil hydrolyzed nitrogen, *SEK* soil exchangeable potassium, *SAP* soil available phosphorus, *Total PLFAs* total phospholipid fatty acids in surface soil (0–5 cm depth) three duplicated treatments. The three plots were located at the top, middle and bottom of the slope in the plantations. The interval was approximately 80 m. After the understory vegetation was cleared from the plots in April 2013, a total of 360 litter bags (4 plantations × 3 plots per plantation × 15 types of litter bags × 2 collection times) were placed on the soil surface. Each litter bag was tagged with a small PVC slice. All litterfalls not in the litter bags were cleared every 2 weeks to avoid the effects from non-experimental factors. The litter bags were collected after 6 months, 12 months and 24 months, and the litter mass loss was measured. After 6 months, 12 months and 24 months, one litter bag of each treatment was opened, and the decomposing leaves in the litter bags were carefully removed with tweezers. The leaf litter was cleaned with distilled water and oven-dried to a constant weight. The litter mass loss was calculated by subtracting the remaining dry mass from the initial dry mass to obtain the percentage of mass loss.

Calculation of home-field advantage (HFA)

The home-field advantage (HFA) was calculated as follows (Ayres et al. 2009a):

$$\mathrm{ADH}_i = \mathrm{HDD}_i - \mathrm{ADD}_i - \mathrm{H} \tag{1}$$

$$\mathrm{HDD}_i = \left(\mathrm{D}_{\mathrm{iI}} - \mathrm{D}_{\mathrm{jI}}\right) + \left(\mathrm{D}_{\mathrm{iI}} - \mathrm{D}_{\mathrm{kI}}\right) + \left(\mathrm{D}_{\mathrm{iI}} - \mathrm{D}_{\mathrm{lI}}\right) \tag{2}$$

$$\mathrm{ADD}_i = \left(\mathrm{D}_{\mathrm{iJ}} - \mathrm{D}_{\mathrm{jJ}}\right) + \left(\mathrm{D}_{\mathrm{iK}} - \mathrm{D}_{\mathrm{kK}}\right) + \left(\mathrm{D}_{\mathrm{iL}} - \mathrm{D}_{\mathrm{lL}}\right) \tag{3}$$

$$\mathrm{H} = \left(\mathrm{HDD}_{\mathrm{i}} + \mathrm{HDD}_{\mathrm{j}} + \mathrm{HDD}_{\mathrm{k}} + \mathrm{HDD}_{\mathrm{l}}\right) / (\mathrm{N} - 1) \tag{4}$$

Where ADH_i is the additional decomposition at home for species i; i, j, k, and l are litters derived from the four plant species; I, J, K, and L are the areas dominated by species i, j, k, and l, respectively; D is the decomposition rate; and HDD and ADD represent home decomposition difference and away decomposition difference, respectively. H represents the mean home performance for all four species; and N is the total number of species (i.e., four in this study). If $ADH_i > 0$, litter from species i decomposed faster than expected when at home (i.e., there was an HFA); if $ADH_i = 0$, there was no HFA; and if $ADH_i < 0$, litter decomposition at home occurred slower than expected (i.e., there was an away-field advantage, AFA). We calculated ADH for each species in each plot. The "home-field" and "away-field" in this study were defined based on plantations type.

Statistical analyses

One-way analysis of variance (ANOVA) was performed to test the differences in ADH among different species and in litter mass loss after 24 months among 15 types of litter bags. Differences were considered to be significant if $P < 0.05$ and the Duncan test was used for post hoc multiple comparisons. General linear regression was used to describe the relationship between litter richness and remaining litter mass (%) in each of the four plantations. Two-way ANOVAs were then used to examine the effects of site, home vs. away, and the interactions on litter mass loss. When all single-species treatments were treated as one group and all multiple-species treatments were treated as the other group, and *T*-tests were used to examine the differences between the two groups. The effects of duration, site, treatment, and their interactions on litter mass loss were examined using three-way ANOVAs. Least significant difference (LSD) tests were used for post hoc multiple comparisons when an effect was significant at $\alpha = 0.05$ (Ball et al. 2008). ANOVAs were carried out to examine plot (three levels), duration (two levels), the presence of each litter species (two levels), and species interaction (SpInt, 11 levels) and their interactions on litter mass loss in the four plantations. The value of SpInt was used to test for non-additivity. Significant SpInt indicated significant non-additivity, while no significant SpInt indicated additivity. A nested model was used to detect the rivet hypothesis (Giesselmann et al. 2010). The rivet hypothesis suggests that increasing species richness can enhance ecosystem functions, while idiosyncratic response hypothesis suggests that species composition contributes more to ecosystem functions. The rivet hypothesis was supported if the relationship between time and litter richness was significant, and idiosyncratic response hypothesis was supported if the relationship between time and species components was significant. All statistical analysis was performed using SPSS16.0 for Windows software package.

Results

The influence of "away-field advantage" on litter decomposition

The ADH values of the four species showed that *S. superba* had a significant away-field advantage (ADH = − 36.17, Fig. 1). In contrast, *C. lanceolata* had a significant home-field advantage (ADH = 24.38). *A. mangium* (ADH = 2.35) and *E. urophylla* (ADH = 0.31), did not show a significant home-field advantage. The values of ADH between *S. Superba* and *C. lanceolate* were significantly different.

The relationship between litter richness and litter decomposition

The litter richness and litter mass loss showed a significantly negative relationship in *C. lanceolata* plantation (Fig. 2).

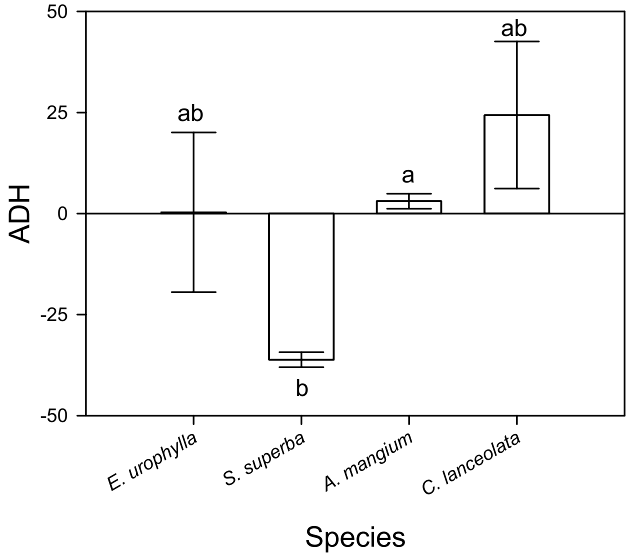

Fig. 1 Home- and away- field advantages of litters from *S. superba*, *E. urophylla*, *A. mangium*, and *C. lanceolata*. ADH is the additional decomposition at home. If $ADH_i > 0$, there was a HFA; and if $ADH_i < 0$, there was an AFA. Note: One way ANOVA and Duncan test were used. The columns with same letter means no significant difference between each other

But no significant relationship was observed between litter richness and litter mass loss in *S. superba*, *A. mangium,* and *E. urophylla* plantations.

The mean litter mass loss of multi-species was relatively higher than single-species in each plantation (Fig. 3). When all single-species bags treated as one group and all multi-species bags treated as the other group, the litter mass loss of multi-species also tended to be higher than that of single-species, but the difference was not significant (*T* test, $N = 4$ for single-species, $N = 11$ for multi-species, $P = 0.384$; Fig. 3).

The relationship between litter composition and litter decomposition

Litter quality measures for *S. superba*, *C. lanceolata*, *E. urophylla*, and *A. mangium* are shown in Table 2. The initial N and lignin contents in leaf litter of *S. superba* and *A. mangium* were higher than in the other two species. *A. mangium* had the highest C (55.5%) and lignin (57.7%) content. *E. urophylla* had the highest C/N (63) and lignin/N (51) ratios. The P content in leaves of *S. superba* and *C. lanceolata* were higher than in the other two species. The decomposition results of all groups are shown in Fig. 4. In the *S. superba* plantation, the mixed litters of *E. urophylla* and *A. mangium* presented the highest litter loss. In the *C. lanceolate* plantation, the mixed litters of

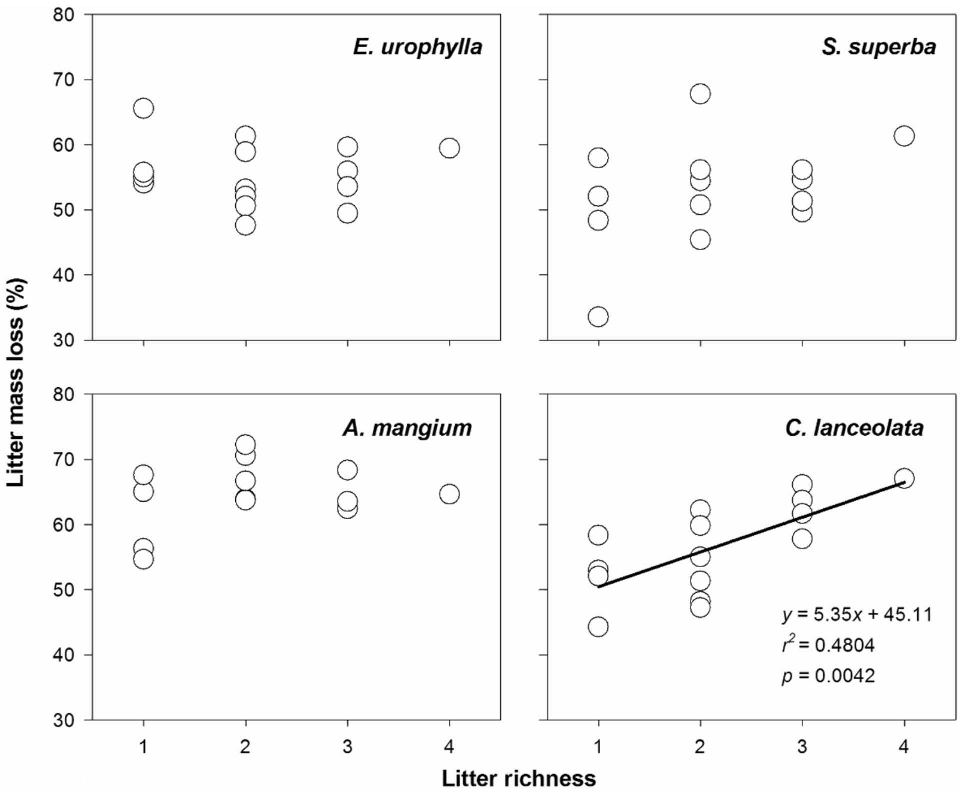

Fig. 2 The relationship between litter richness and litter mass loss (in 24 months) in *S. superba, E. urophylla*, *A. mangium*, and *C. lanceolata* forest plantations in South China

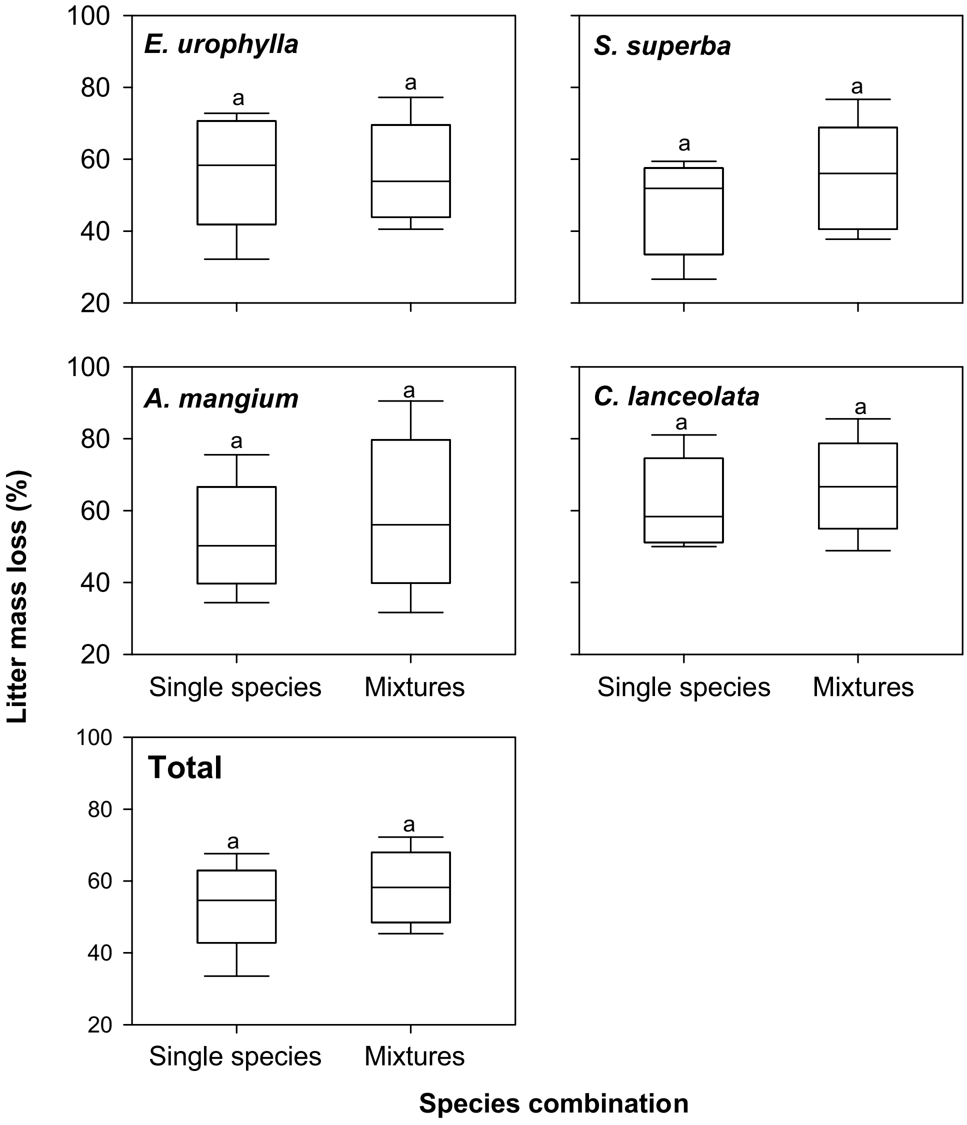

Fig. 3 Litter mass loss (in 24 months) in single- vs. multiple-species litter bags in *S. superba, C. lanceolata*, *E. urophylla*, and *A. mangium* plantations, and the averaged values across all four plantations in South China. Data analysis was conducted by *T* test method. The boxes with same letter means no significant difference between each other

Table 2 The initial chemical traits of fresh leaf litter of *S. superba*, *C. lanceolata*, *E. urophylla*, and *A. mangium*

Characteristic	*S. superba*	*C. lanceolata*	*E. urophylla*	*A. mangium*
C (%)	52.1 ± 1.2a	50.6 ± 0.7b	53.8 ± 1.0a	55.5 ± 2.3a
N (%)	1.35 ± 0.05a	1.15 ± 0.24ab	0.85 ± 0.11b	1.31 ± 0.27a
P (%)	0.04 ± 0.01a	0.04 ± 0.01a	0.02 ± 0.01b	0.02 ± 0.01b
Lignin (%)	50.6 ± 8.9a	32.5 ± 3.4b	43.0 ± 8.7ab	57.7 ± 10.1a
C:*N*	38.6 ± 4.4b	44.0 ± 5.7b	63.3 ± 3.6a	42.4 ± 8.2b
Lignin: *N*	37.5 ± 6.8ab	28.3 ± 5.1b	50.6 ± 7.8a	44.0 ± 6.6a

Values are mean ± SD. Means within rows sharing the same letter are not significantly different ($P < 0.05$)

S. superba, *E. urophylla* and *C. lanceolate* decomposed the fastest. In the *E. urophylla* plantation, the litter of *A. mangium* showed the highest litter loss. In the *A. mangium* plantation, the mixed litters of *E. urophylla* and *A. mangium* decomposed the fastest. In addition, the Duration × SpInt effect was not significant, indicating that the mixing of species had an additive effect on mass loss in the *S. superba, C. lanceolata*, and *A. mangium* plantations (Table 3). In the *E. urophylla* forest, however, the strong interaction between duration and species interaction (Duration × SpInt, $P = 0.010$) indicated a non-additive effect (Table 3). The presence of each species in the four plantations had no effect on litter mass loss, except that the presence of *C. lanceolata* significantly affected mass loss in the *E. urophylla* planation. In the *S. superba* plantation, the interaction between duration and *A. mangium* was significant. In the *E. urophylla* plantation, the interaction

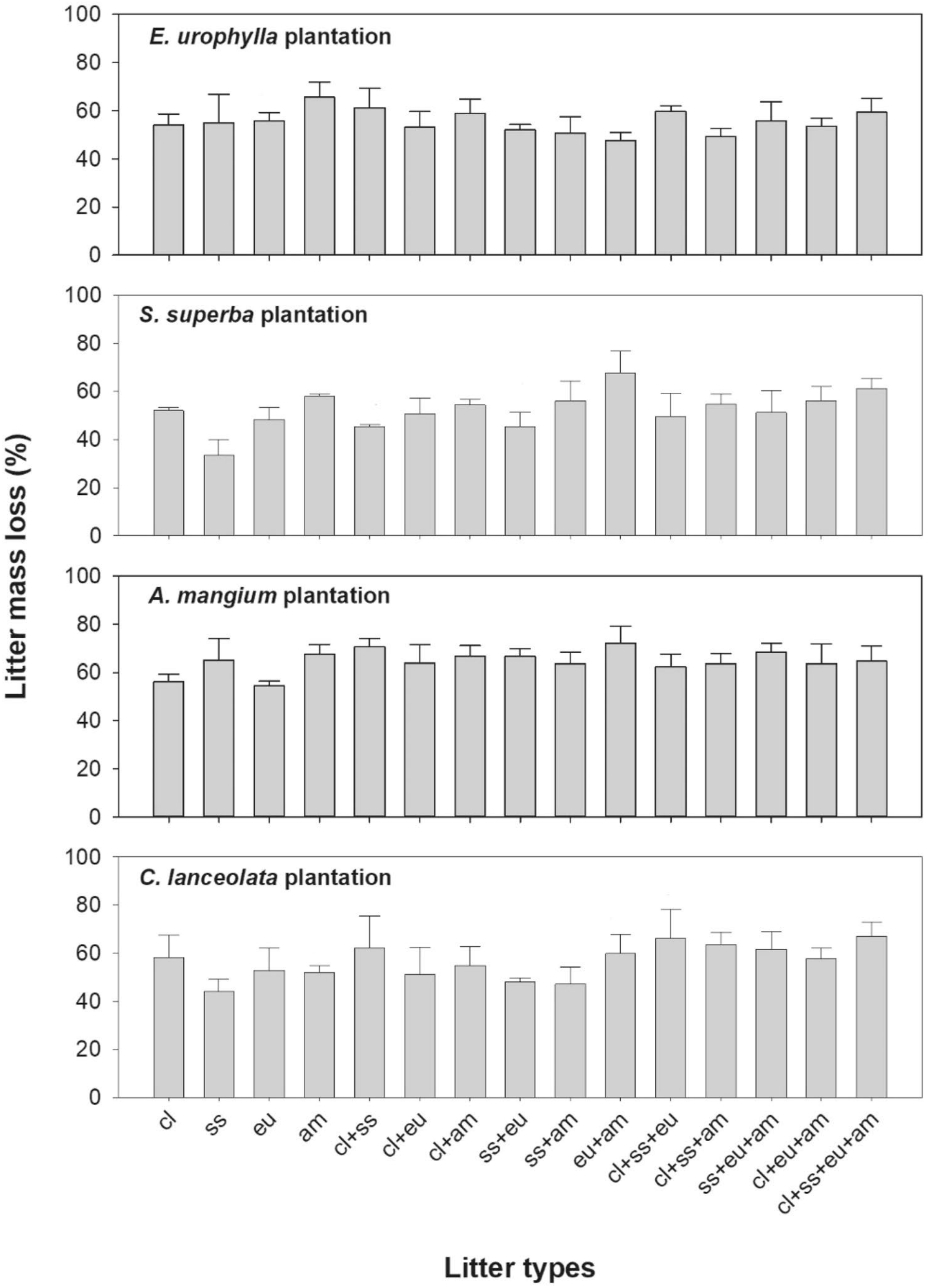

Fig. 4 Litter mass loss (in 24 months) of 15 types of litter bags, including four single-species, six two-species, four three-species and one four-species in *S. superba, C. lanceolata*, *E. urophylla*, and *A. mangium* plantations in South China. No significant differences were detected between groups (One way ANOVA, $N = 15$, $P = 0.05$)

between duration and *S. superba* or *C. lanceolata* significantly influenced litter mass loss (Table 3).

In the *S. superba* and *C. lanceolata* plantations, plot, duration, litter richness, composition, and their interactions had no effect on litter mass loss (Table 4). In the *E. urophylla* plantation, the effects of duration and the interaction between duration and litter composition on litter mass loss were significant. In the *A. mangium* plantation, duration and the interaction between duration and litter richness also significantly affected the litter mass loss (Table 4).

Discussion

The home-field and away-field advantages of litter decomposition in degraded monoculture plantations

In this study, HFA was detected in three of the four subtropical plantations, i.e., those with *C. lanceolate*, *A. mangium* and *E. urophylla*. These HFA effects were greater than those reported by Veen et al. (2015) and Ayres et al. (2009a). In contrast, a strong away-field advantage was detected in

Table 3 ANOVA statistics for the effects of duration, plot, species interaction (SpInt), the presence of each litter species (*S. superba, C. lanceolata*, *E. urophylla*, and *A. mangium*), and their interactions on litter mass loss in four plantations in South China

Source	*d.f.*	*F*	*P*
S. superba plantation			
Plot	2	2.274	0.219
Duration	2	4.055	0.109
SpInt	10	1.171	0.364
S. superba	1	0.991	0.424
C. lanceolata	1	1.738	0.318
E. urophylla	1	2.558	0.251
A. mangium	1	2.243	0.273
Plot × duration	4	2.984	**0.023**
Duration × *S. superba*	2	0.447	0.668
Duration × *C. lanceolata*	2	1.108	0.414
Duration × *E. urophylla*	2	0.312	0.748
Duration × *A. mangium*	2	8.581	**0.036**
Duration × SpInt	20	1.038	0.445
C. lanceolata plantation			
Plot	2	0.656	0.555
Duration	2	5.646	0.068
SpInt	10	1.010	0.468
S. superba	1	0.245	0.670
C. lanceolata	1	0.340	0.619
E. urophylla	1	0.617	0.515
A. mangium	1	1.333	0.368
Plot × duration	4	8.119	**0.000**
Duration × *S. superba*	2	3.872	0.116
Duration × *C. lanceolata*	2	4.563	0.093
Duration × *E. urophylla*	2	0.055	0.947
Duration × *A. mangium*	2	0.554	0.613
Duration × SpInt	20	1.094	0.392
E. urophylla plantation			
Plot	2	23.626	0.060
Duration	2	167.837	**0.000**
SpInt	10	1.494	0.213
S. superba	1	5.194	0.150
C. lanceolata	1	39.007	**0.025**
E. urophylla	1	3.386	0.207
A. mangium	1	0.090	0.792
Plot × duration	4	0.194	0.940
Duration × *S. superba*	2	12.641	**0.019**
Duration × *C. lanceolata*	2	8.645	**0.035**
Duration × *E. urophylla*	2	0.256	0.786
Duration × *A. mangium*	2	0.465	0.658
Duration × SpInt	20	2.362	**0.010**
A. mangium plantation			
Plot	2	3.702	0.243
Duration	2	109.427	**0.000**
SpInt	10	0.984	0.488
S. superba	1	0.338	0.620
C. lanceolata	1	3.718	0.194
E. urophylla	1	1.079	0.409
A. mangium	1	8.175	0.105
Plot × Duration	4	0.277	0.891
Duration × *S. superba*	2	0.412	0.688
Duration × *C. lanceolata*	2	3.064	0.156
Duration × *E. urophylla*	2	0.361	0.717
Duration × *A. mangium*	2	3.172	0.151
Duration × SpInt	20	1.469	0.149

Table 4 ANOVA statistics for the effects of plot, Duration, litter richness, litter species composition, and their interactions on litter mass loss in four plantations in South China

Source	*d.f.*	*F*	*P*
S. superba plantation			
Plot	2	1.694	0.349
Duration	2	3.650	0.127
Richness	2	0.205	0.822
Composition	8	1.857	0.142
Duration × richness	4	0.853	0.531
Duration × composition	16	1.010	0.475
C. lanceolata plantation			
Plot	2	0.672	0.557
Duration	2	5.646	0.068
Richness	2	2.705	0.181
Composition	8	0.589	0.773
Duration × richness	4	0.800	0.558
Duration × composition	16	1.179	0.334
E. urophylla plantation			
Plot	2	3.681	0.223
Duration	2	167.837	**0.000**
Richness	2	0.371	0.712
Composition	8	2.250	0.080
Duration × richness	4	0.730	0.596
Duration × composition	16	2.712	**0.008**
A. mangium plantation			
Plot	2	0.484	0.662
Duration	2	109.074	**0.000**
Richness	2	0.514	0.633
Composition	8	1.349	0.291
Duration × richness	4	4.510	**0.036**
Duration × composition	16	0.973	0.506

The rivet hypothesis is supported if Duration × richness is significant ($P < 0.05$). If Duration × composition is significant ($P < 0.05$), the idiosyncratic response hypothesis is supported (Giesselmann et al. 2010) the *S. superba* plantation. Generally, HFA of one species is closely related to the litter quality in away sites (Veen et al. 2015). When the litter quality differed, especially in the N: P ratios of the home and away fields, the HFA of the litters was higher. This phenomenon has been termed the "substrate quality-matrix quality interaction (SMI)" (Freschet et al. 2012; Perez et al. 2013). However, HFA in our study was not determined by the differences in litter quality between home–home and away sites, but rather was inversely related to the litter quality of the selected species, i.e., litter with lower quality had a higher HFA. Low-quality litter usually contains complex chemicals, including lignin, cellulose, and hemicelluloses, and is generally recalcitrant. These litters may select local soil organisms that are able to use them as sources of carbon, energy, and nutrients, resulting in a greater HFA (Ayres et al. 2009a, b). *S. superba* litter, which had a high quality, showed a significant away-field advantage. The main reason may be that the soil animal and microbial community in the away field facilitated litter decomposition due to the variations in litter structure and chemistry (Ayres et al. 2009b). A novel litter with different litter quality may contain resources that have been limiting for the microbial community; and such litter could be complementary for the detritivores. The differences in soil animals and microbes between home and away fields thus needs further study.

Effects of litter richness and composition on litter decomposition in degraded monoculture plantations

The effects of litter species richness on litter decomposition vary among studies and there is no consensus regarding how litter species richness may affect the litter decay rate (Hättenschwiler et al. 2005; Ball et al. 2008). In our study, no significant relationship between richness and litter decomposition was observed in *E. urophylla*, *S. superba*, and *A. mangium* plantations, but a significantly positive relationship exists in *C. lanceolata* plantation. This may indicate that the influence of litter richness on litter decomposition depends the tree species in the monoculture plantations. Vivanco and Austin (2008) found that tree species identity would alter forest litter decomposition through long-term plant-environment and interspecific interactions (Vivanco and Austin 2008). After more than 30 years' natural development, every monoculture plantation has created a specific habitat condition for growth and nutrient cycling, including temperature, soil chemical-physical characteristics, soil microbes and soil animals, which together influence the relationship between litter richness and decomposition. Meanwhile, the non-additivity was only significant in the *E. urophylla* plantation. The additive or non-additive effect is influenced by chemical components of the mixed litters such as the contents of C, N, P, and phenolics (Hector et al. 2000; Sun et al. 2009; Meier and Bowman 2010; Chen et al. 2011, 2017). Our results indicate that the tree species in the monoculture plantation may determine the additive or non-additive effect of mixed litters. The heterogeneity of habitat, nutrients, and microorganisms created by different tree species during 30 years may be the direct reason (Hättenschwiler et al. 2005; Kominoski et al. 2009; Kubartová et al. 2009; Yan et al. 2010).

Several hypotheses or models have been developed to describe the effects of species richness and species identity on litter decomposition. Two such hypotheses are the rivet hypothesis and the idiosyncratic response hypothesis (Ehrlich and Ehrlich 1988; Lawton 1994; Giesselmann et al. 2010). The rivet hypothesis emphasizes the role of species richness, while the idiosyncratic hypothesis emphasizes the role of species composition. Many studies have shown that the relationship between litter species diversity and litter decomposition follows the idiosyncratic hypothesis (Gartner and Cardon 2004; Ball et al. 2008; Giesselmann et al. 2010). In our study, different models seemed to function in different plantations. The idiosyncratic model may better describe the litter decomposition in the *E. urophylla* forest because of the Comopsition × Duration significant effect on litter decomposition (Table 4). In the *A. mangium* forest, litter richness significantly affected decomposition (Table 4), suggesting that the rivet model may be appropriate. Based on the rivet hypothesis, the litter species may show niche complementarity and positive interactions with each other in the *A. mangium* forest (Zhang and Zhang 2002). In *S. superba* and *C. lanceolate* plantations, no significant idiosyncratic or rivet effect was found in this study, implying that the litter decomposition in these two plantations may be influenced by multiple factors.

Using "away-field advantage" and "non-additive effects" to manage the degraded monoculture plantations in South China

Litter transplantation experiments are designed to validate the relationship between species diversity and litter decomposition as an ecosystem function. This study suggests that litter transplantation could be used in the management of degraded monoculture plantations in subtropical China. In some degraded monoculture plantations, litter transplantation could increase litter decomposition and nutrient cycling. Taking the monoculture *A. mangium* plantation as an example, the deep litter layer inhibits nutrient cycling and seedling recruitment, thus causing degradation (Wang et al. 2009). This study showed that *S. superba* litter had a significant away-field advantage (57.5%), especially in *A. mangium* plantation (Fig. 4). At the same time, the litter of *E. urophylla* + *A. mangium* decayed the fastest in the *S. superba* plantation. This indicates that transferring *S.*

superba litter to the *A. mangium* plantation and placing *E. urophylla* + *A. mangium* litter in the *S. superba* plantation is a potential way to accelerate the nutrient cycling of degraded plantations. This study also shows that the litter of *A. mangium* decomposed the fastest in the *E. urophylla* plantation, suggesting that transplanting the *A. mangium* litter to the *E. urophylla* plantation is a potential way of improving the function of large areas of *E. urophylla* plantations in South China. However, the litter-transplantation method needs to create a minimum functional area that includes the *S. superba*, *E. urophylla* and *A. mangium* plantations, else the litter-transplantation method will be difficult to realize. As a result, the reconstruction of large areas of *E. urophylla* plantations and building an appropriate "minimum functional area" may be the first step. The minimum functional area can ensure the feasibility of the litter-transplantation method, and this should be considered at the beginning of monoculture plantation reconstruction in South China.

The results of the mixed-litter decomposition suggest a mixed plantation prospect for the reconstruction of the degraded monoculture plantations in South China. Generally, the mixed-species plantations had higher biomass (Khanna 1997), a higher nutrient cycling rate (Santos et al. 2017), higher soil organic carbon (Forrester et al. 2013), and greater microbial biomass and activity (Bini et al. 2013). Our results showed that the mixed litters of *A. mangium* and *E. urophylla* decomposed the fastest in the *A. mangium* plantation. At the same time, the litter of *A. mangium* had the highest decomposition rate in the *E. urophylla* plantation. This indicates that a mixed plantation of *A. mangium* and *E. urophylla* may be an appropriate choice when the government reconstructs the large areas of *E. urophylla* plantations in South China.

Conclusion

Litter decomposition is an important component of nutrient cycling. A large number of monoculture plantations for restoration purpose in China show standstill, even degradation in ecosystem functions because of the thick litter accumulation. Thus, how to accelerate the litter decomposition is a major challenge. Our mixed-litters transplanting experiment showed that the species used for monoculture plantations played an important role in the relationship between litter composition/richness and litter decomposition. In *E. urophylla* plantation, Composition × Duration shows a significant effect on litter decomposition while litter richness significantly affected decomposition in *A. mangium* plantation. The litter of *C. lanceolata* had a significant home-field advantage, while *S. superba* had a significant away-field advantage in decomposition. The non-additive effect was only significant in *E. urophylla* plantation. Based on the significant away-field advantage and non-additive effects, transplanting the litter of *S. superba* would improve the *A. mangium* plantation, and creating an *A. mangium* + *E. urophylla* mixed plantation was suggested as a potential strategy for the reconstruction of large areas of *E. urophylla* in South China.

Acknowledgements This research was funded by the National Natural Science Foundation of China (Nos. 31770473, 31400380, 41301582), Science and technology projects of Guangdong Province (2018B030324002), and GDAS' Special Project of Science and Technology Development (2017GDASCX-0805, 2018GDASCX-0101, 2020GDASYL-20200302001). We thank our colleagues at the Heshan National Field Research Station of Forest Ecosystems, especially Hai Ren, Weijun Shen, Zhian Li, Shenglei Fu, Guoyi Zhou and Zhanfeng Liu, for helpful suggestions, and Yongbiao Lin, Xingquan Rao and Zhipeng Chen for field assistance. We would like to thank LetPub (http://www.letpub.com) for providing linguistic assistance during the preparation of this manuscript.

Author contributions ZS, LY, YH conceived and designed the research; ZS, YH, LY, JW, NL performed the experiments; YH, SZ analyzed the data; ZS, YH, YL, MW, QG contributed reagents/materials/analysis tools; ZS, YH, LY wrote and edited the manuscript.

References

Ayres E, Steltzer H, Berg S, Wall DH (2009a) Soil biota accelerate decomposition in high-elevation forests by specializing in the breakdown of litter produced by the plant species above them. J Ecol 97:901–912

Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N, Parton WJ, Moore JC, Wall DH (2009b) Home-field advantage accelerates leaf litter decomposition in forests. Soil Biol Biochem 41:606–610

Ball BA, Hunter MD, Kominoski JS, Swan CM, Bradford MA (2008) Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. J Ecol 96:303–313

Barlow J, Gardner TA, Ferreira LV, Peres CA (2007) Litterfall and decomposition in primary, secondary and plantation forests in the Brazilian Amazon. Forest Ecol Manag 247:91–97

Bini D, Figueiredo AF, Silva MCP, Vasconcellos RLdF, Cardoso EJBN (2013) Microbial biomass and activity in litter during the initial development of pure and mixed plantations of *Eucalyptus grandis* and *Acacia mangium*. Rev Bras Cienc Solo 37:76–85

Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? Biodivers Conserv 17:925–951

Chapman SK, Koch GW (2007) What type of diversity yields synergy during mixed litter decomposition in a natural forest ecosystem? Plant Soil 299:153–162

Chapman SK, Samantha K, Feller IC (2011) Away-field advantage: mangrove seedlings grow best in litter from other mangrove species. Oikos 120:1880–1888

Chen SL, Wang SL, Chen CY (2004) Degradation mechanism of Chinese fir plantation. Chin J Appl Ecol 15:1953–1957

Chen F, Hua Z, Yang B, Ouyang Z, Kai Z, Yi X (2011) The decomposition of coniferous and broadleaf mixed litters significantly changes the carbon metabolism diversity of soil microbial communities in subtropical area, southern China. Acta Ecol Sin 31:3027–3035

Chen YC, Ma SQ, Sun J, Wang XD, Cheng GW, Lu XY (2017) Chemical diversity and incubation time affect non-additive responses of soil carbon and nitrogen cycling to litter mixtures from an alpine steppe soil. Soil Biol Biochem 109:124–134

Chomel M, Guittonny-Larchevêque M, DesRochers A, Baldy V (2015) Home field advantage of litter decomposition in pure and mixed plantations under boreal climate. Ecosystems 18:1014–1028

Ehrlich P, Ehrlich A (1988) Extinction: the causes and consequences of the disappearance of species. Random House USA Inc, New York

Forrester DI, Pares A, O'Hara C, Khanna PK, Bauhus J (2013) Soil organic carbon is increased in mixed-species plantations of *Eucalyptus* and nitrogen-fixing *Acacia*. Ecosystems 16:123–132

Freschet GT, Aerts R, Cornelissen JHC (2012) Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. J Ecol 100:619–630

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246

Ge X, Zeng L, Xiao W, Huang Z, Geng X, Tan B (2013) Effect of litter substrate quality and soil nutrients on forest litter decomposition: a review. Acta Ecol Sin 33:102–108

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biol 6:751–765

Giesselmann UC, Martins KG, Brändle M, Schädler M, Marques R, Brandl R (2010) Diversity and ecosystem functioning: litter decomposition dynamics in the Atlantic rainforest. Appl Soil Ecol 46:283–290

Graça MAS, Bärlocher F, Gessner MO (2005) Methods to study litter decomposition. Springer, Dordrecht

Hansen RA (1999) Red oak litter promotes a microarthropod functional group that accelerates its decomposition. Plant Soil 209:37–45

Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol S 36:191–218

Hector A, Beale AJ, Minns A, Otway SJ, Lawton JH (2000) Consequences of the reduction of plant diversity for litter decomposition: effects through litter quality and microenvironment. Oikos 90:357–371

Khanna PK (1997) Comparison of growth and nutrition of young monocultures and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii*. Forest Ecol Manag 94:105–113

Kominoski JS, Hoellein TJ, Kelly JJ, Pringle CM (2009) Does mixing litter of different qualities alter stream microbial diversity and functioning on individual litter species? Oikos 118:457–463

Kubartová A, Ranger J, Berthelin J, Beguiristain T (2009) Diversity and decomposing ability of saprophytic fungi from temperate forest litter. Microb Ecol 58:98–107

Lawton JH (1994) What Do Species Do in Ecosystems? Oikos 71:367–374

Li ZA, Zou B, Ding Y, Cao Y (2004) Key factors of forest litter decomposition and research progress. Chin J Ecol 23:77–83

Li YB, Li Q, Yang JJ, Lü XT, Liang WJ, Han XG, Bezemer TM (2017) Home-field advantages of litter decomposition increase with increasing N deposition rates: a litter and soil perspective. Funct Ecol 31:1792–1801

Madritch MD, Cardinale BJ (2007) Impacts of tree species diversity on litter decomposition in northern temperate forests of Wisconsin, USA: a multi-site experiment along a latitudinal gradient. Plant Soil 292:147–159

Mahaney WM (2010) Plant controls on decomposition rates: the benefits of restoring abandoned agricultural lands with native prairie grasses. Plant Soil 330:91–101

Meier CL, Bowman WD (2010) Chemical composition and diversity influence non-additive effects of litter mixtures on soil carbon and nitrogen cycling: implications for plant species loss. Soil Biol Biochem 42:1447–1454

Nilsson MC, Wardle DA, Dahlberg A (1999) Effects of plant litter species composition and diversity on the boreal forest plant-soil system. Oikos 86:16–26

Peng S (2003) Study and application of restoration ecology in tropical and subtropical China. Science Press, Beijing

Peng SL, Hou YP, Chen BM (2009) Vegetation restoration and its effects on carbon balance in Guangdong Province, China. Restor Ecol 17:560–561

Perez G, Aubert M, Decaëns T, Trap J, Chauvat M (2013) Home-field advantage: a matter of interaction between litter biochemistry and decomposer biota. Soil Biol Biochem 67:245–254

Piao S, Fang J, Ciais P, Peylin P, Huang H, Sitch S, Wang T (2009) The carbon balance of terrestrial ecosystems in China. Nature 458:1009–1013

Santos FM, Chaer GM, Diniz AR, Balieiro FDC (2017) Nutrient cycling over five years of mixed-species plantations of Eucalyptus and Acacia on a sandy tropical soil. Forest Ecol Manag 384:110–121

Sun XF, Huang JH, Wang M, Han XG (2009) Responses of litter decomposition to biodiversity manipulation in the Inner Mongolia grassland of China. Biodiv Sci 17:397–405

Sun ZY, Ren H, Schaefer V, Guo QF, Wang J (2014) Using ecological memory as an indicator to monitor the ecological restoration of four forest plantations in subtropical China. Environ Monit Assess 186:8229–8247

Taylor BR, Mallaley C, Cairns JF (2007) Limited evidence that mixing leaf litter accelerates decomposition or increases diversity of decomposers in streams of eastern Canada. Hydrobiologia 592:405–422

Veen GF, Freschet GT, Ordonez A, Wardle DA (2015) Litter quality and environmental controls of home-field advantage effects on litter decomposition. Oikos 124:187–195

Vivanco L, Austin AT (2008) Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. J Ecol 96:727–736

Wang Q, Wang S, Fan B, Yu X (2007) Litter production, leaf litter decomposition and nutrient return in *Cunninghamia lanceolate* plantations in south China: effect of planting conifers with broadleaved species. Plant Soil 297:201–211

Wang J, Ren H, Yang L, Duan W (2009) Establishment and early growth of introduced indigenous tree species in typical plantations and shrubland in South China. For Ecol Manag 258:1293–1300

Wu XR, Ye XS, Zhao ZQ (2009) Comparison of determining the soil total nitrogen concentration with a continuous flow injection analyzer and Kjeldahl method. J Huazhong Agric Univ 28:560–563

Xu GL, Zhou GY, Mo JM, Zhou XY, Peng SJ (2005) The response of soil fauna composition to forest restoration in Heshan. Acta Ecol Sin 25(7):1670–1677

Yan HY, Xi GU, Shen H (2010) Microbial decomposition of forest litter: a review. Chin J Ecol 29:1827–1835

Ye XS, Wu XR, Zhao ZQ (2009) Comparison of determining the soil total phosphorus concentration by continuous flow injection analyzer and traditional analysis methods. Res Explor Lab 28:560–563

Zha TG, Zhang ZQ, Sun G, Wang GM, Yun XQ, Wang YK, Liu Y (2012) Home-field advantage of litter decomposition and its soil biological driving mechanism: a review. Acta Ecol Sin 32:7991–8000

Zhang Q, Zhang D (2002) Biodiversity and ecosystem functioning: recent advances and controversies. Chin Biodivers 29:60–64

Zhu J, Li F (2007) Forest degradation/decline: research and practice. Chin J Appl Ecol 18:1601–1609

Affiliations

Zhongyu Sun[1] · Yuhui Huang[2] · Long Yang[1] · Qinfeng Guo[3] · Meili Wen[1] · Jun Wang[4] · Nan Liu[4]

Zhongyu Sun
sunzhyu_lzu@126.com

Yuhui Huang
huangyh@sinogaf.cn

Qinfeng Guo
qfgguofs@gmail.com

Meili Wen
wenml@gdas.ac.cn

Jun Wang
wxj@scib.ac.cn

Nan Liu
liunan@scib.ac.cn

[1] Key Lab of Guangdong for Utilization of Remote Sensing and Geographical Information System, Guangzhou Institute of Geography, Guangzhou 510070, China

[2] Guangdong Provincial Key Laboratory of Forest Culture, Protection and Utilization, Guangdong Academy of Forestry, Guangzhou 510520, China

[3] Eastern Forest Environmental Threat Assessment Center, USDA FS, Research Triangle Park, NC 27709, USA

[4] CAS Engineering Laboratory for vegetation Restoration on Islands and Coastal Zones, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China