CrossMark

Functional identity rather than functional diversity or species richness controls litter mixture decomposition in a subtropical forest

Guigang Lin · De-Hui Zeng

Abstract

Aims While growing evidence has shown consistently positive plant diversity effects on primary productivity, diversity effects on litter decomposition remain inconclusive. Our aim was to evaluate the relative importance of functional identity (FI), functional diversity (FD) and species richness (SR) for litter mixture decomposition and litter mixing effects.

Methods 32 mixtures of leaf litter from seven tree species were constructed by creating two independent gradients of FD and SR. Decomposition of these mixtures was measured using laboratory microcosms. Moreover, component litter was separated from mixtures to assess species-specific responses to mixing.

Results FI but not FD or SR significantly influenced litter mixture decomposition. Six and nine litter mixtures separately exhibited synergistic and antagonistic non-additive effects with litter mixing effects ranging from −8.97% to 16.82%, which did not significantly relate to FD or SR. Mass loss of two fast-decomposing species was inhibited and that of two out of five slow-decomposing species was accelerated by the presence of other species. Chemical traits of a given component species and trait differences between this species and its neighbors significantly influenced its response to litter mixing.

Conclusions These results suggest that relationship between FD and litter mixing effect is far from generalizable and highlight that analyzing species-specific responses to mixing is useful in exploring mechanisms underlying interactions among component litter.

Keywords Carbon quality · Functional diversity · Functional identity · Litter mixing effect · Species richness · Subtropical forest

G. Lin · D.-H. Zeng
CAS Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China

G. Lin · D.-H. Zeng (✉)
Daqinggou Ecological Station, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China
e-mail: zengdh@iae.ac.cn

Introduction

Increasing human-induced loss of biodiversity worldwide has raised concerns about its consequences on ecosystem functioning (Ceballos et al. 2015; Soliveres et al. 2016). While growing evidence has shown the consistently positive effects of plant diversity on primary production (e.g. Liang et al. 2016), plant diversity effects on litter decomposition are still difficult to predict (Cardinale et al. 2011; Frainer et al. 2015). Given the significant role of litter decomposition in providing nutrients for plant growth and releasing photosynthetically fixed carbon (C) into atmosphere (Aerts 1997), it is critical to explore mechanisms underlying diversity

effects on litter decomposition to fully understand the consequences of biodiversity loss on ecosystem functioning.

To accurately predict plant diversity effects, it should be known which measures of diversity most influence litter mixture decomposition (Frainer et al. 2015; Lecerf et al. 2011). Plant diversity can be measured in terms of either the number of species present or the extent of differences in functional traits among species in a community (Laliberté and Legendre 2010). As the commonly used metric in representing plant diversity, species richness was found to have idiosyncratic effects on litter decomposition in terrestrial ecosystems (Cardinale et al. 2011). The rationale behind the poor predictability of species richness may be that litter functional traits rather than its taxonomic identity affect decomposition (Scherer-Lorenzen 2008; Tardif and Shipley 2015). Therefore, trait-based approach has increasingly been used to understand and predict plant diversity effects on litter decomposition (Finerty et al. 2016; García-Palacios et al. 2017).

For functional traits, both their mean values (i.e. functional identity) and variability (i.e. functional diversity), which are two complementary components representing functional property of communities, could potentially influence litter mixture decomposition (Finerty et al. 2016). Functional identity of litter mixtures can be represented by community-weighted mean trait values, which are reformulated from mass-ratio hypothesis (Grime 1998; Tardif and Shipley 2013). This hypothesis assumes either the absence of interspecific interactions or the counterbalance between positive and negative interactions among component litter (Grime 1998; Tardif and Shipley 2015). Based on this assumption, litter mixture decomposition can be simply calculated as the abundance-weighted decomposition of its component litter (Tardif and Shipley 2013). Although functional identity has been found to be the main driver of litter mixture decomposition, observed decomposition rates of litter mixtures are commonly either faster or slower than those expected from mass-ratio hypothesis, indicating the presence of litter mixing effects (Cardinale et al. 2011; Hättenschwiler et al. 2005). These effects, although not large themselves, have been shown to have significant effects on estimated nitrogen supply to trees during forest succession (Finzi and Canham 1998) and cause errors in predicting litter mixture decomposition according to mass-ratio hypothesis (Tardif and Shipley 2015). To explain the magnitude

and direction of litter mixing effects, several mechanisms have been proposed including nutrient transfer among component litter, complementary resource use and the influences of secondary metabolites (Hättenschwiler et al. 2005). Despite the variety of these mechanisms, the essential prerequisite of mixing effects is proposed to be the variations among component litter in terms of functional traits rather than taxonomic identity of litter species (Scherer-Lorenzen 2008; Tardif and Shipley 2015). However, experimental evidence for this proposition is inconclusive, with significant relationships between functional diversity and litter mixing effects being found in some studies (Lecerf et al. 2011; Tardif and Shipley 2015) but not in others (Barantal et al. 2011; Frainer et al. 2015). Therefore, whether functional diversity can explain variations in litter mixing effects remains controversial. Furthermore, species richness and functional diversity are unarguably linked, but very few studies have isolated the effects of functional diversity from those of species richness (Tobner et al. 2016).

Apart from functional diversity, analyzing species-specific responses to litter mixing has also been suggested to be a useful complementary tool to explore mechanisms underlying interactions among component litter species within mixtures (Hättenschwiler et al. 2005). This is because patterns of interspecific interactions can be obscured by whole mixture analyses if the positive responses of some component litter are balanced by the negative responses of others within litter mixtures (Barantal et al. 2011; Lin et al. 2013). For example, nutrient (e.g. nitrogen) transfer from high-quality litter to low-quality litter through passive or active means may accelerate the decomposition of low-quality litter (Handa et al. 2014; Mao et al. 2016), while the high concentrations of secondary metabolites (e.g. lignin) of low-quality litter could decrease the decomposition rates of high-quality litter (Gessner et al. 2010). Therefore, if these two mechanisms work in parallel, interactions among component litter cannot be detected just through analyzing functional diversity of litter mixtures. Unfortunately, most of the previous studies have focused on decomposition rates of whole mixtures, neglecting species-specific responses to litter mixing (Hättenschwiler et al. 2005; Lecerf et al. 2011).

Although previous studies have frequently reported plant diversity effects on litter mixture decomposition, most of these studies were conducted in temperate ecosystems and involved a low number of species (Gartner

and Cardon 2004; Trogisch et al. 2016). In the present study, 32 different mixtures of leaf litter from seven common subtropical tree species varying widely in chemical traits were used to examine the relative effects of functional identity, functional diversity and species richness on litter mixture decomposition and litter mixing effects during one year laboratory incubation. To achieve this, two independent gradients were created with the first gradient being species richness levels and the second gradient being a series of litter mixtures under each species richness level over which functional diversity varied widely, which can orthogonally separate the effects of functional diversity and species richness (Tobner et al. 2014). Additionally, component litter was separated from litter mixtures to identify species-specific responses. Based on this novel experimental design, we specifically tested the following hypotheses: (1) functional identity could be the main factor driving litter mixture decomposition and functional diversity could be useful in explaining litter mixing effects; and (2) high-quality litter could decrease and low-quality litter could increase their decomposition rates in mixtures relative to decomposing alone.

Materials and methods

Material collection and preparation

Leaf litter and soil samples used for laboratory incubation were collected from Heshan National Field Research Station of Forest Ecosystems (22°41′ N, 112°54′ E) located in Guangdong Province, South China. Detailed information about this study site can be found in Li et al. (2001) and Zhang et al. (2012). Freshly fallen leaf litter of seven broad-leaved tree species was collected using litter traps during October to November 2014 (Table 1). Among these seven tree species, five (*Cinnamomum burmannii*, *Sterculia lanceolata*, *Michelia macclurei*, *Schima superba* and *Machilus chinensis*) were collected from a secondary forest. Leaf litter of *Acacia mangium* and *A. crassicarpa* was collected from monoculture plantations, which were planted on degraded land neighboring to this secondary forest to improve soil fertility in 1984 (Li et al. 2001). The inclusion of these two N-fixing trees was to increase variations in functional traits among litter species and test their potential effects on decomposition of other species. Care was taken to exclude leaf litter with any

signs of insect herbivory, fungal attack or atypical color. After removing petioles, leaf litter was dried at 65 °C to constant mass and divided into two subsamples. One subsample used for laboratory incubation was chopped into pieces (4 cm × 4 cm) to avoid size effects on litter decomposition. The other subsample was milled (< 0.25 mm) to measure initial chemical traits. Meanwhile, soils at the depth of 0–10 cm were sampled from several random locations of a *Eucalyptus citriodora* plantation at our study site. This was done to avoid any potential effects of home field advantage on litter decomposition (Ayres et al. 2009). All soil samples were thoroughly mixed and sieved to pass a 2 mm mesh to remove roots and other debris. Soil samples were then stored at 4 °C until incubation. These soils had the following characteristics: organic C of 15.50 g·kg^{-1}, total N of 1.50 g·kg^{-1} and pH of 3.91 (Zhang et al. 2012).

Litter chemistry analysis

Eight chemical traits suggested to influence litter decomposition were determined at the species level, including three indices of proximate C fractions (organic soluble fraction (OSF), acid soluble fraction (ASF) and acid insoluble fraction (AIF)), and concentrations of C, N, phosphorous (P), calcium (Ca) and manganese (Mn) (Berg et al. 2017; Hobbie et al. 2006; Meier and Bowman 2008). C and N concentrations were measured by a Vario Microcube elemental analyzer (Elementar, Germany). For P, Ca and Mn concentrations, litter samples were digested in HF and HClO$_4$ solution and then analyzed by an ICP-MS analyzer (PerkinElmer, USA). Proximate C fractions were determined by a series of extractions (Meier and Bowman 2008; Ryan et al. 1990). In brief, milled samples were successively extracted by acetone and methanol. OSF was calculated as the difference in weights between original and extracted samples. Residues from the first extraction were separated into ASF and AIF by sulphuric acid digestion. The compound types represented by each C fraction are: OSF: soluble fats, simple sugars and soluble phenolics; ASF: cellulose, hemi-cellulose and starch; AIF: lignin, condensed tannins and cutin (Ryan et al. 1990).

Experimental design and laboratory incubation

A total of 39 treatments were created in this study, including seven single-species and 32 litter mixture treatments. For the establishment of litter mixtures, a

Table 1 Initial leaf litter chemical traits of the studied seven tree species

Species	C (%)	N (%)	P (mg·g^{-1})	Ca (mg·g^{-1})	Mn (mg·g^{-1})	OSF (%)	ASF (%)	AIF (%)
Cb	46.94	1.40	1.14	18.61	0.14	23.68	49.29	27.03
Sl	42.49	1.08	0.60	33.10	0.47	17.05	54.02	28.92
Mm	49.31	0.96	0.31	10.06	0.29	37.37	33.36	29.27
Ss	49.39	0.99	0.20	7.21	0.69	35.32	37.84	26.84
Mc	51.08	0.81	0.36	7.22	0.11	37.56	28.79	33.65
Am	50.27	1.73	0.40	6.36	0.15	25.87	28.08	46.05
Ac	51.01	1.24	0.16	4.32	0.11	28.34	26.92	44.74

Cb, *Cinnamomum burmannii*; Sl, *Sterculia lanceolata*; Mm, *Michelia macclurei*; Ss, *Schima superba*; Mc, *Machilus chinensis*; Am, *Acacia mangium*; Ac, *Acacia crassicarpa*. OSF, organic soluble fraction; ASF, acid soluble fraction; AIF, acid insoluble fraction

novel experimental design was conducted to orthogonally separate the effects of species richness (SR) and functional diversity (FD) on litter mixture decomposition and litter mixing effects, which was similar to the method described by Tobner et al. (2014). Specifically, two independent gradients were created. The first gradient was the setting of SR levels. Six SR levels from two- to seven-species mixtures were established. The second gradient was the setting of a series of litter mixtures under each SR level over which FD varied widely. For two- to five-species mixtures, six litter mixture treatments per SR level were established over a FD gradient based on the two following processes (24 treatments). First, all possible mixtures of two- to five-species were respectively arranged along the gradient of functional dispersion (FDis). FDis is a component of FD describing the mean distance of component species in multidimensional trait space to the centroid of species mixtures (Laliberté and Legendre 2010). This index was calculated using species mean values of the eight chemical traits we measured in leaf litter before performing the incubations. Second, mixtures with the first three highest and the first three lowest FDis values were selected at each SR level. In addition, we also included all possible six-species mixtures (7 treatments) and one seven-species mixture (1 treatment). The selected litter mixtures and their FDis values are shown in Table 2.

Laboratory microcosms were used to determine litter decomposition and mixing effects according to the method described by Lin et al. (2013). A total of 156 microcosms (39 treatments × 4 replicates) were constructed by filling plastic cups (6 cm in diameter and 10 cm in height) with 100 g field-moist soils. Two grams of single-species litter or litter mixtures (containing equal dry mass of component litter) were placed on soil surface of microcosms with litter and soils separated by 2 mm nylon mesh. Microcosms were watered to achieve 65% of soil water-holding capacity. After that, microcosms were sealed with perforated adherent films which can reduce water loss but allow gaseous exchange, and then weighed. Microcosms were incubated in laboratory incubators under dark conditions, and constant temperature (25 °C) and relative humidity (80%). During incubation, soil moisture was maintained at 65% of soil water-holding capacity by weighing microcosms every two weeks and adding deionized water if needed.

After one year incubation, litter was retrieved, cleaned via gently brushing off adhering soils, dried at 65 °C to constant mass, and then weighed. Based on their differences in morphologies, textures and patterns of leaf veins, component litter was separated from mixtures and weighed. Litter mass loss, expressed as percentages of initial dry mass, was calculated for single-species litter, litter mixtures and their component species.

Calculating functional identity and functional diversity of litter mixtures

As a direct measure of functional identity, community-weighted mean (CWM) trait values of litter mixtures were calculated for each trait we measured (Mokany et al. 2008). This index was calculated according to the following equation:

$$CWM = \sum w_i \times x_i$$

where w_i and x_i are the initial mass proportion and chemical trait value of component species i in litter mixtures, respectively. To eliminate co-linearity among variables, a principal component analysis (PCA) was conducted for CWM values of eight traits across litter

Table 2 The established 32 litter mixtures that were selected along two independent gradients of species richness (SR) and functional dispersion (FDis), and their mean observed mass loss (OML) and litter mixing effect (LME)

| Litter mixtures	SR	FDis	CWM-1	CWM-2	FD-1	FD-2	OML (%)	LME (%)
Mm + Mc	2	0.66	1.15	−1.14	2.53	−2.68	30.84	0.51
Am+Ac	2	0.91	2.22	2.78	2.46	2.21	24.60	−8.97*
Mm + Ss	2	0.98	0.99	−2.01	2.65	−1.45	35.05	4.69
Cb + Mc	2	2.77	−1.50	−0.66	−0.52	−0.60	37.05	2.26
Sl + Am	2	2.80	−1.60	1.55	−0.59	−0.86	33.39	−4.27
Sl + Ac	2	2.84	−1.37	1.07	−0.60	−1.37	36.11	−3.73
Mc + Am+Ac	3	1.47	2.02	1.66	1.25	3.03	31.60	16.82*
Mm + Ss + Mc	3	1.62	1.20	−1.57	1.61	−1.27	33.96	8.32**
Cb + Mm + Ss	3	2.03	−0.08	−1.54	0.48	0.78	39.74	5.22*
Sl + Mm + Ac	3	2.53	−0.75	0.08	−0.62	−0.69	35.21	−3.34*
Sl + Mm + Am	3	2.69	−0.92	0.38	−0.67	−0.14	35.05	1.10
Sl + Mc + Am	3	2.86	−0.72	0.65	−0.74	−0.24	29.95	−7.23*
Mm + Ss + Mc + Ac	4	1.53	1.54	−0.54	0.61	0.05	30.31	−2.00
Mm + Mc + Am+Ac	4	1.63	1.64	0.86	0.58	1.44	26.64	−7.68**
Cb + Mm + Ss + Mc	4	1.94	0.30	−1.33	0.15	0.42	33.60	−4.27
Cb + Sl + Mc + Ac	4	2.72	−0.87	0.21	−0.68	−0.17	35.66	−3.91
Cb + Sl + Mc + Am	4	2.75	−0.99	0.44	−0.69	0.01	35.60	−0.55
Sl + Ss + Mc + Am	4	2.75	−0.31	−0.12	−0.69	0.04	31.00	−4.28**
Cb + Mm + Ss + Mc + Ac	5	2.04	0.68	−0.55	−0.06	0.17	34.91	2.65
Cb + Mm + Ss + Mc + Am	5	2.22	0.54	−0.38	−0.09	0.55	33.50	1.65
Cb + Sl + Mm + Ss + Mc	5	2.43	−0.73	−1.20	−0.35	0.17	35.04	−5.69*
Cb + Sl + Mm + Mc + Am	5	2.60	−0.69	−0.01	−0.62	0.15	33.93	−4.41**
Cb + Sl + Mm + Am+Ac	5	2.61	−0.61	0.65	−0.61	−0.15	33.25	−7.64**
Cb + Sl + Mc + Am+Ac	5	2.68	−0.48	0.82	−0.67	−0.04	36.89	6.70
Cb + Mm + Ss + Mc + Am+Ac	6	2.19	0.83	0.10	−0.10	0.42	33.91	4.64*
Sl + Mm + Ss + Mc + Am+Ac	6	2.37	0.22	0.04	−0.56	0.03	36.25	12.42**
Cb + Sl + Mm + Ss + Mc + Ac	6	2.47	−0.33	−0.58	−0.52	−0.10	34.64	−3.53**
Cb + Sl + Mm + Mc + Am+Ac	6	2.54	−0.29	0.39	−0.62	0.08	35.28	2.19
Cb + Sl + Mm + Ss + Mc + Am	6	2.57	−0.42	−0.43	−0.56	0.19	37.09	5.89*
Cb + Sl + Mm + Ss + Am+Ac	6	2.62	−0.35	0.13	−0.57	−0.06	36.66	3.41
Cb + Sl + Ss + Mc + Am+Ac	6	2.71	−0.23	0.27	−0.63	−0.01	35.19	2.71
Cb + Sl + Mm + Ss + Mc + Am+Ac	7	2.53	−0.10	−0.01	−0.57	0.08	34.56	0.88

CWM-1 and CWM-2, and FD-1 and FD-2 are the first two components of principal component analysis conducted on community-weighted mean trait and functional diversity values, respectively (Fig. 1). Asterisks denote the level of significance of Student *t*-tests to analyze whether litter mixing effects significantly differ from zero (*, $P < 0.05$; **, $P < 0.01$). Cb, *Cinnamomum burmannii*; Sl, *Sterculia lanceolata*; Mm, *Michelia macclurei*; Ss, *Schima superba*; Mc, *Machilus chinensis*; Am, *Acacia mangium*; Ac, *Acacia crassicarpa*

mixtures. Before conducting PCA, CWM trait values were standardized through the zero-mean approach. The first (CWM-1) and second (CWM-2) PCA components, separately accounting for 80.84% and 14.91% of the total variation, were used as independent composite variables to represent functional identity of litter mixtures in subsequent analyses (Fig. 1a). Scores of CWM-1 were positively related to C and OSF concentrations, and negatively related to P, Ca and ASF concentrations. Scores of CWM-2 increased with increasing N and AIF concentrations and decreasing Mn concentration (Fig. 1a).

Given that FDis can be calculated for litter mixtures with as few as two species, this index was chosen as the multi-trait index to assess FD effects on litter mixture decomposition (Laliberté and Legendre 2010). Calculations of FDis were performed in R using the FD package (Laliberté et al. 2014). Before these calculations, all trait values were
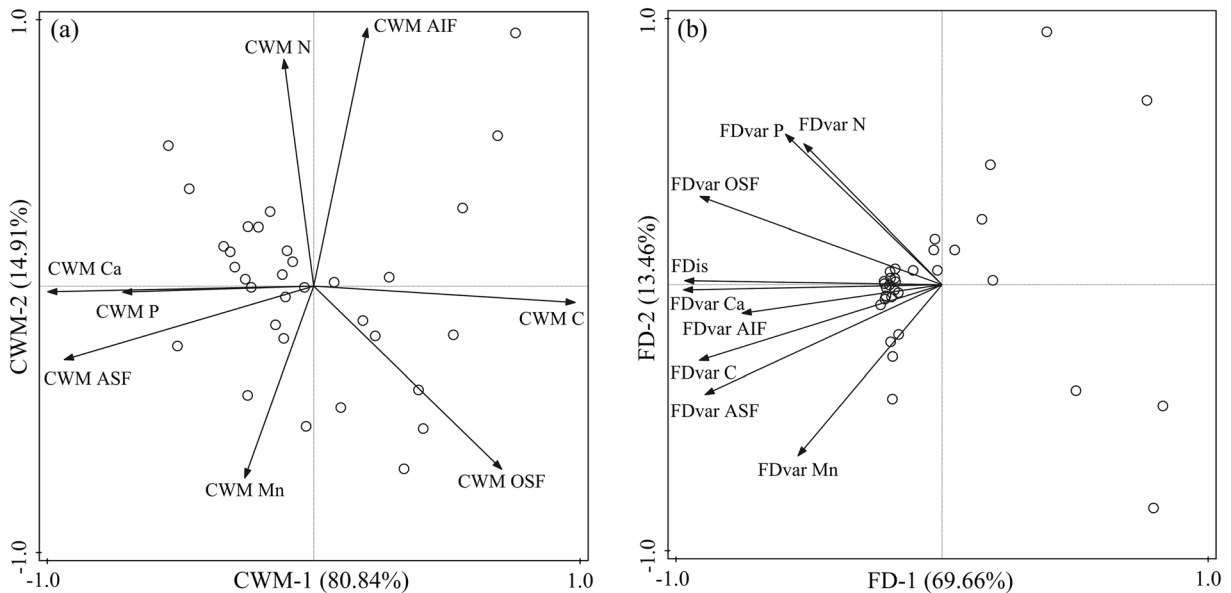
Fig. 1 Principal component analyses (PCA) of community-weighted mean (CWM) values of eight traits (a) and functional diversity (FD) values (b). In panel (a), the first (CWM-1) and second (CWM-2) principal components were used to represent functional identity of litter mixtures. In panel (b), PCA was conducted on functional divergence (FDvar) of each single trait and a multi-trait

FD index of functional dispersion (FDis), where the first (FD-1) and second (FD-2) principal components were used to represent functional diversity of litter mixtures. Percentages of variations explained by the first two principal components are given in parentheses. Open circles represent litter mixture treatments. OSF, organic soluble fraction; ASF, acid soluble fraction; AIF, acid insoluble fraction

standardized by the zero-mean approach. Apart from FDis measured from multiple traits, we also measured another FD index based on single trait which may provide other information about functional properties of litter mixtures (Butterfield and Suding 2013). Functional divergence for each single trait (FDvar) was calculated according to the following equations proposed by Mason et al. (2003):

$$FDvar = \frac{2}{\pi} \arctan(5V), \quad V = \sum w_i (\ln x_i - \overline{\ln x})^2 \quad \text{and}$$

$$\overline{\ln x} = \sum w_i \times \ln x_i$$

where x_i is the chemical trait value of component species i and w_i is the initial mass proportion of component species i in litter mixtures. Likewise, PCA was conducted for FDvar values of eight traits and the multi-trait index of FDis following the same procedure as in CWM trait values. The first (FD-1) and second (FD-2) PCA components, separately explaining 69.66% and 13.46% of the total variation, were applied as independent composite variables representing functional diversity in subsequent analyses (Fig. 1b). Scores of FD-1 were negatively related to FDvar P, FDvar OSF, FDvar Ca, FDvar AIF, FDvar C, FDvar ASF and FDis. Scores of FD-2 were positively related to FDvar N and negatively related to FDvar Mn (Fig. 1b).

Statistical analysis

One-way ANOVA was performed to analyze species-specific effects on mass loss of single-species decomposition (four replicates per species with a total sample size of 28). Post hoc mean comparisons were evaluated by Tukey's multiple comparisons. Pearson correlations were used to analyze pairwise relationships between single-species decomposition and litter chemical traits.

For litter mixtures, their expected mass loss was calculated as the sum of mass loss of each component species decomposing alone weighted by its initial mass proportion in mixtures. According to Wardle et al. (1997), litter mixing effect was calculated by the following equation:

$$\text{Litter mixing effect} = \frac{\text{observed} - \text{expected}}{\text{expected}} \times 100\%$$

where 'observed' and 'expected' are the observed and expected mass loss of a litter mixture, respectively. Student t-tests were used to assess whether there was non-additive effect for each litter mixture (four replicates per litter mixture). If litter mixing effect did not significantly differ from zero, it indicates additive effects. Significantly positive and negative deviations from zero indicate synergistic and antagonistic non-additive effects, respectively.

We first used a mixed linear model to test the effect of species richness on observed mass loss and mixing effect of litter mixtures. The first model was fitted with species richness as a fixed factor and litter mixture treatment as a random factor accounting for the differences in litter mixture treatments within each level of species richness. Furthermore, to test the effects of functional identity and functional diversity on observed mass loss and mixing effect of litter mixtures, a second mixed linear model was applied. In the second model, CWM-1, CWM-2, FD-1 and FD-2 were included as fixed factors, with species richness and litter mixture treatment (nested in species richness) as random factors.

To identify species-specific response to mixing, relative individual performance (RIP) of the seven species was calculated as follows (Barantal et al. 2011):

$$RIP = \frac{mixture - alone}{alone} \times 100\%$$

where 'mixture' and 'alone' represent mean mass loss of a species decomposing in mixtures and alone, respectively. Student t-tests were used to assess whether RIP of each species was significantly different from zero, with the number of litter mixtures for which the analyzed species was present as sample size. These analyses produced seven separate t-values (i.e. the seven studied species) and then the Bonferroni correction was applied with a significance level of 0.007 (Cabin and Mitchell 2000). Significantly positive and negative differences between RIP and zero indicate that species decompose markedly faster and slower in mixtures than alone, respectively. Relationship between mean RIP of each species and its mean mass loss when decomposing alone was analyzed by a regression analysis with the sample size being seven. Furthermore, a mixed linear model was conducted to analyze whether the RIP of a component species was affected by its functional identity, functional identity of its neighbors (i.e. other species decomposing in the same litter mixture), and trait differences between this component species and its neighbors. In this model, FIT-1, FIT-2, FIN-1, FIN-2, TD-1 and TD-2 were included as fixed factors, with species richness and litter mixture treatment (nested in species richness) as random factors. Functional identity of a component species was represented by FIT-1 and FIT-2, which were the first two components of PCA conducted on the eight chemical traits of the seven species (Fig. S1a). Functional identity of neighbors was represented by FIN-1 and FIN-2, which were the first two

components of PCA conducted on the eight chemical traits (only one neighboring species for two-species mixtures) or CWM values of eight chemical traits (more than one neighboring species for three- to seven-species mixtures) of neighbors (Fig. S1b). Trait differences (TD) between the component species and its neighbors for each single trait were calculated as:

$$TD = \sum(w_i \times TD_i)$$

where w_i is the initial mass proportion of a neighboring species i in all neighbors, and TD_i is the difference in trait values between the component species and the neighboring species i (i.e. $TD_i = Trait_{component} - Trait_i$). TD values are zero when the component species has the same trait value as its neighbors, and are negative or positive when the component species has separately lower or higher trait values than its neighbors. TD-1 and TD-2, the first two components of PCA conducted on TD values of eight traits, were applied as independent composite variables to represent trait differences between the component species and its neighbors (Fig. S1c). Before conducting these three PCA analyses, trait values and TD values were standardized through the zero-mean approach.

In contrast to selecting litter mixtures along the gradient of FDis for two- to five-species mixtures, all possible six- and seven-species mixtures were included in our experiment. To analyze whether this unbalanced experimental design could affect our results, a sensitivity analysis was conducted. In this analysis, six-species mixtures were selected according to the selection criteria for the two- to five-species mixtures and the seven-species mixture was excluded to form a balanced experiment design, which led to a total of 30 litter mixtures. After that, linear mixed models were used to analyze the effects of species richness, functional diversity and functional identity on observed mass loss and mixing effect of litter mixtures as mentioned above. Given that similar results were obtained from these two scenarios (Fig. S2), only the results obtained from 32 litter mixtures were reported.

For these mixed linear models, model selection was based on the second-order Akaike information criterion (AIC_c) values, where the best model was the one with the lowest AIC_c value (Burnham and Anderson 2002). When model selection generated several models with their AIC_c values being less than two units compared with the best model (i.e. $\Delta AIC_c < 2$), model averaging

was conducted to determine which factors were statistically significant. This was done because models with $\Delta AIC_c < 2$ were not considered meaningfully different (Grueber et al. 2011).

Analyses of one-way ANOVA, *t*-test and Pearson correlation were conducted with SPSS 16.0 (SPSS Inc., Chicago, USA). Mixed linear model and model averaging were carried out using the nlme package (Pinheiro et al. 2017) and the MuMIn package (Bartoń 2016) in R, respectively. Significant level of these analyses was set at $\alpha = 0.05$.

Results

Initial chemical traits and their relationships with single-species decomposition

Chemical traits of leaf litter varied widely among the studied tree species (Table 1). For instance, initial ASF concentration showed ca. 2-fold variation among the seven tree species, ranging from 26.92% for *A. mangium* to 54.02% for *S. lanceolata*. There was *ca.* 8-fold variation in initial Ca concentration ranging from 4.32 mg·g^{-1} for *A. mangium* to 33.10 mg·g^{-1} for *S. lanceolata*. Initial C concentration was highest in *M. chinensis* (51.08%) and lowest in *S. lanceolata* (42.49%; Table 1). For single-species decomposition, mass loss of leaf litter varied significantly among tree species after one year incubation, ranging from 24.39% ± 1.13% for *A. mangium* to 46.34% ± 0.91% for *C. burmannii* (mean ± SE, $n = 4$; Fig. 2a). Pearson correlation revealed that mass loss of single-species decomposition was significantly positively related to initial ASF ($r = 0.95$, $P < 0.01$) and Ca ($r = 0.85$, $P = 0.02$) concentrations, and negatively related to initial C concentration ($r = -0.86$, $P = 0.01$; Fig. 2b).

Drivers of litter mixture decomposition and litter mixing effects

Observed mass loss of litter mixtures varied widely among treatments, ranging from 24.60% ± 0.77% to 39.74% ± 0.49% (mean ± SE, $n = 4$; Table 2). Mixed linear models showed that observed mass loss of litter mixtures was mainly determined by functional identity (Table 3). Specifically, CWM-1 had significantly negative effects on observed mass loss ($Z = 2.90$, $P < 0.01$),

indicating that mass loss increased with increasing P, Ca and ASF concentrations and decreasing C and OSF concentrations (Fig. S3a). Furthermore, observed mass loss was negatively related to CWM-2 ($Z = 3.43$, $P < 0.01$), indicating faster decomposition rates with higher Mn concentration, but lower N and AIF concentrations (Fig. S3b). Species richness and functional diversity had no significant effects on observed mass loss of litter mixtures (Fig. 3a, Table 3).

Across litter mixtures, litter mixing effects ranged from −8.97% ± 2.51% to 16.82% ± 3.81% (mean ± SE, $n = 4$; Table 2). Six out of 32 litter mixtures showed significantly higher observed mass loss than expected mass loss, and nine out of 32 litter mixtures had significantly lower observed mass loss than expected mass loss (Table 2). Furthermore, no significant differences were found between mean observed and expected mass loss in these 32 litter mixtures ($t_{31} = 0.31$, $P = 0.76$). Mixed linear models showed that variations in litter mixing effects cannot be explained by species richness (Fig. 3b). In addition, functional identity and functional diversity also had no significant effects on litter mixing effects (Table 3).

Relative individual performance in litter mixtures

To identify species-specific response to litter mixing, component species were separated from mixtures to calculate their relative individual performance (RIP). Mean RIP ranged from −7.86% to 10.26% and varied widely among the studied seven tree species (Fig. 4a). Specifically, mass loss of *M. macclurei* (mean RIP ± SE = 5.68% ± 1.93%, $t_{20} = 3.08$, $P < 0.01$) and *A. mangium* (mean RIP ± SE = 10.26% ± 4.45%, $t_{18} = 2.43$, $P = 0.03$) was significantly higher when decomposed in mixtures than alone. Compared with decomposing alone, the presence of other species significantly reduced the mass loss of *C. burmannii* (mean RIP ± SE = −2.90% ± 0.38%, $t_{16} = -2.23$, $P = 0.04$) and *S. lanceolata* (mean RIP ± SE = −7.86% ± 1.57%, $t_{19} = -5.27$, $P < 0.01$). No significant differences in mass loss of other three species were found between decomposing in mixtures and alone (Fig. 4a). After Bonferroni correction, only RIP of *S. lanceolata* differed significantly from zero. Regression analysis revealed that there was negative linear relationship between RIP of our studied seven tree species and mass loss of these species

Fig. 2 Leaf litter mass loss (mean ± SE, $n = 4$) of seven tree species decomposing alone (a) and their relationships with initial litter chemical traits (b). In panel (**a**), lowercase letters indicate significant differences among tree species in leaf litter mass loss from a one-way ANOVA with Tukey's multiple comparison tests at $P < 0.05$. In panel (**b**), relationships between mass loss and initial chemical traits were analyzed by Pearson correlation with open and gray bars representing non-significant and significant results, respectively. OSF, organic soluble fraction; ASF, acid soluble fraction; AIF, acid insoluble fraction
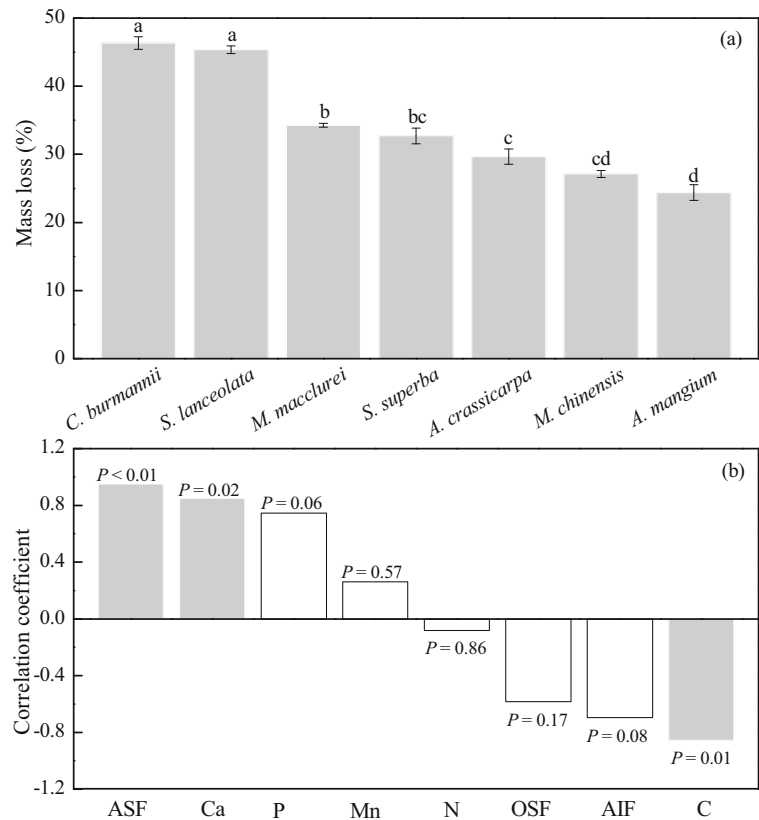
decomposing alone ($P = 0.02$; Fig. 4b). Mixed linear models showed that RIP of a given species was influenced by its functional identity and trait differences between this species and its neighbors

Table 3 Results of mixed linear models to analyze the effects of functional identity and functional diversity on observed mass loss and mixing effect of litter mixtures

Response variable	Predictor	Estimate	Z-value	P-value
Observed mass loss	CWM-1	−0.58	2.90	< 0.01
	CWM-2	−0.47	3.43	< 0.01
	FD-1	−0.06	0.23	0.82
	FD-2	0.21	1.28	0.20
Litter mixing effect	CWM-1	0.26	0.86	0.39
	CWM-2	−0.22	1.27	0.20
	FD-1	−0.07	0.21	0.83
	FD-2	0.10	0.47	0.64

Functional identity and functional diversity of litter mixtures are separately quantified by CWM-1 and CWM-2, and FD-1 and FD-2, which are the first two components of principal component analyses conducted on community-weighted mean trait and functional diversity values, respectively (Fig. 1, Table 2)

(Table 4). Specifically, RIP was negatively related to FIT-1, indicating that a given species had larger RIP when it had higher C and OSF concentrations, and lower P, Ca and ASF concentrations (Fig. S4a). A given species had larger RIP when it had higher TD-1 scores than its neighbors (i.e. other species decomposing in the same litter mixture), corresponding to higher C, OSF and AIF concentrations, and lower P, Ca, ASF concentrations (Fig. S4b).

Discussion

To assess the relative effects of functional identity, functional diversity and species richness on litter mixture decomposition and litter mixing effects, 32 different mixtures of leaf litter from seven subtropical tree species were created by manipulating two independent gradients of species richness and functional diversity. Litter mixture decomposition was significantly influenced by functional identity but not by functional diversity or species richness. Litter mixing effects ranged from
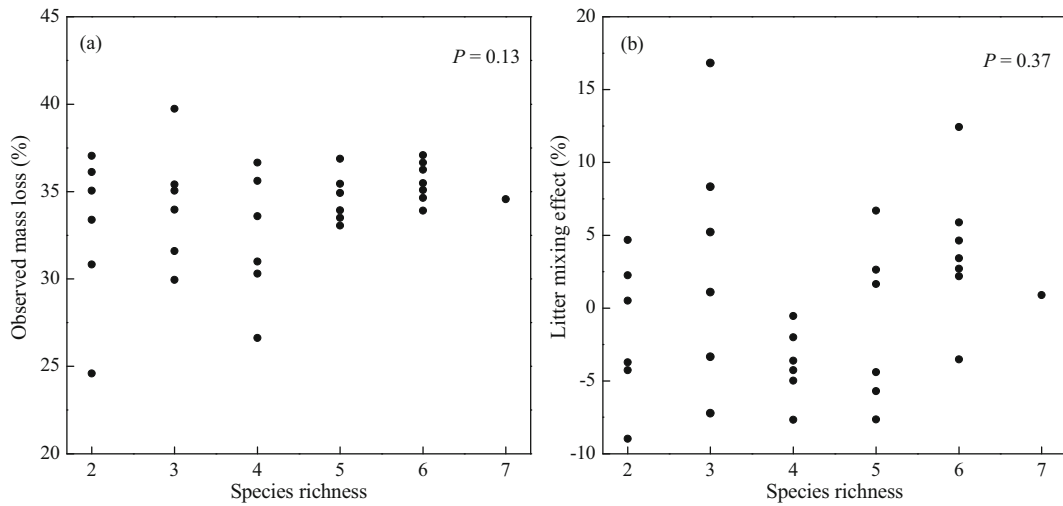
Fig. 3 Observed mass loss (**a**) and litter mixing effect (**b**) of the 32 litter mixtures as a function of species richness. *P* values are obtained from mixed linear models with species richness as a fixed factor and litter mixture treatment as a random factor. Each point represents the mean value of one litter mixture treatment ($n = 4$)

−8.97% to 16.82%, which did not significantly relate to functional diversity or species richness (Table 3, Fig. 3b). Furthermore, mass loss of the two fast-decomposing species was inhibited and that of two out of the five slow-decomposing species was promoted by the presence of other species (Fig. 4).

Fig. 4 Relative individual performances of seven species across all litter mixture treatments (a) and their relationships with the mass loss of these species decomposing alone (b). In panel (**a**), error bars represent 95% confidence intervals (CIs). When 95% CIs do not overlap with $y = 0$, there are significant differences in mass loss for species decomposing in mixtures and alone. *n*, sample size being the number of litter mixtures for which the analyzed species was present. In panel (**b**), vertical and horizontal error bars represent standard errors of relative individual performances of seven species and their mass loss decomposed alone, respectively
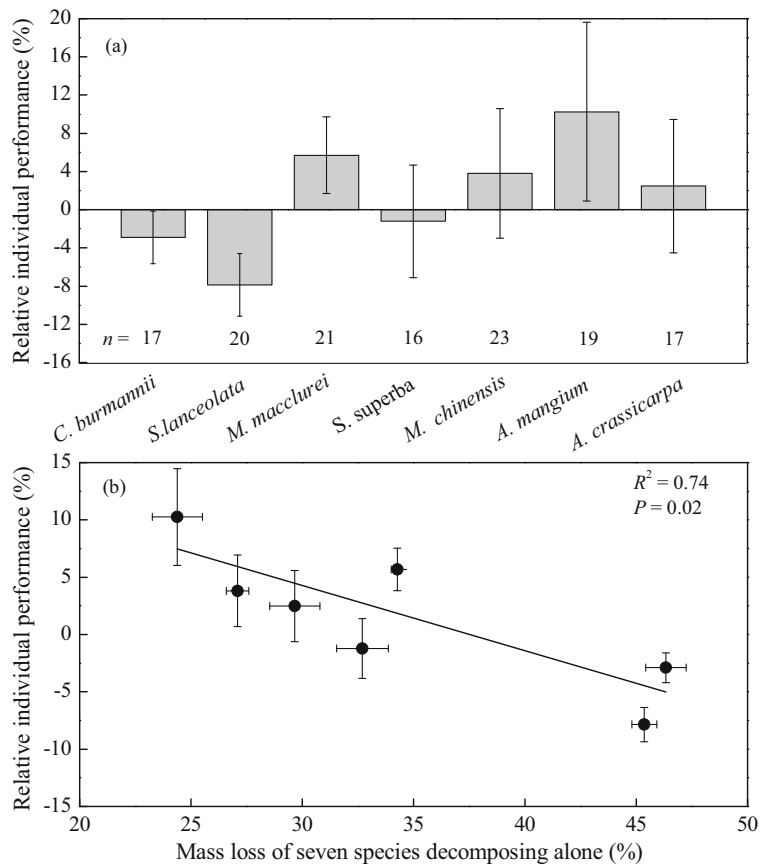
Table 4 Results of mixed linear models to analyze the effects of functional identity of a given component species, functional identity of its neighbors, and trait differences between this component species and its neighbors on relative individual performance of the component species

Predictor	Estimate	Z-value	P-value
FIT-1	−0.31	6.28	< 0.01
FIT-2	0.08	1.83	0.07
FIN-1	−0.05	0.86	0.39
FIN-2	0.05	0.88	0.38
TD-1	0.41	6.19	< 0.01
TD-2	0.08	1.47	0.14

Functional identity of the component species and its neighbors are separately quantified by FIT1 and FIT2, and FIN-1 and FIN-2, which are the first two components of principal component analyses conducted on chemical trait values of the seven species (Fig. S1a) and community-weighted mean trait values of neighbors (Fig. S1b), respectively. Trait differences are quantified by TD-1 and TD-2, which are the first two components of a principal component analysis conducted on difference values of the eight traits between the component species and its neighbors (Fig. S1c)

Single-species decomposition and its relationships with initial chemical traits

Our results showed wide variations among the studied seven tree species in leaf litter decomposition rates which were positively correlated with initial Ca and ASF concentrations and negatively with initial C concentration (Fig. 2). This result is inconsistent with the commonly held views that N and lignin are the key factors regulating litter decomposition (Aerts 1997; Cornwell et al. 2008). Another study conducted in our study site also found that initial N concentration was not an important factor influencing leaf litter decomposition (Li et al. 2001). The lack of a significant correlation between N concentration and litter decomposition may be due to high N deposition in our study site with the wet deposition being *ca*. 43 kg N·ha^{-1}·yr.$^{-1}$ (Huang et al. 2015) and the accumulation of N through long-term biological N$_2$ fixation in tropical forests (Hedin et al. 2009). Indeed, despite having high N concentration, leaf litter of the two N-fixing *Acacia* trees was found to have the slowest decomposition rates, possibly due to the lowest ASF concentration of these two species (Table 1, Fig. 2). In line with our result, previous studies also showed that ASF concentration (cellulose, hemi-cellulose and starch) rather than AIF concentration (lignin, tannin and cutin) was significantly related to mass loss of leaf litter, indicating energy starvation for

decomposers (Allison and Vitousek 2004; Hättenschwiler et al. 2011; Hobbie 1996). This significant effect of ASF may be because its low concentration prevents AIF degraders from obtaining enough energy required for AIF decomposition, given the priming effects of labile C on decomposition of recalcitrant C (Hättenschwiler et al. 2011; Hobbie 1996). Furthermore, leaching of soluble compounds, being independent of decomposer activity, is also an important determinant of litter decomposition for early-stage decomposition (Soong et al. 2014). Therefore, leaching of soluble compounds may contribute significantly to mass loss and then explain variations in decomposition rates among the studied tree species in our short-term incubation study, especially when litter was chopped into the same size, which can increase surface area favorable for leaching (Soong et al. 2014).

Apart from C quality, Ca concentration was found to be another significant factor influencing leaf litter decomposition (Fig. 2), which was consistent with previous studies (Berg et al. 2017; Hobbie et al. 2006). This could be because Ca is an essential constituent of fungal cell walls and has positive effects on proliferation of white-rot fungi, which can produce ligninolytic enzymes (Aponte et al. 2012). Furthermore, Ca concentration is positively related to abundance of soil fauna, which has important contributions to litter decomposition (Hobbie et al. 2006). Therefore, Ca has been found to play important roles in lignin decomposition and positively relate to litter decomposition rates (Aponte et al. 2012; Berg et al. 2017). In our study site, the high N deposition as mentioned above could lead to coupled leaching of nitrate and Ca (Perakis et al. 2006), which can restrain growth of decomposers through preventing them from obtaining enough soil Ca.

Drivers of litter mixture decomposition and litter mixing effects

Our results showed that functional identity but not functional diversity or species richness significantly influenced litter mixture decomposition (Table 3). The possible explanation for the non-significant effect of species richness is that functional trait of litter rather than its taxonomic identity affects decomposition (Frainer et al. 2015; Scherer-Lorenzen 2008; Tardif and Shipley 2015). The non-significant effect of functional diversity is surprising, given that agreement is growing that functional identity and functional diversity are two

complementary indices in explaining litter mixture decomposition (Finerty et al. 2016; García-Palacios et al. 2017). In line with our finding, some studies also found that functional diversity had no significant effects on litter mixture decomposition (Barantal et al. 2011; Frainer et al. 2015; Tardif and Shipley 2015). These results may indicate that the explanatory power of functional diversity is much smaller relative to that of functional identity in explaining variations in litter mixture decomposition. Indeed, previous studies have also shown that functional identity is more important than functional diversity in explaining other ecosystem processes, such as primary productivity (Tobner et al. 2016) and soil nitrification rates (Laughlin 2011). However, our results should be interpreted with caution, given that effects of functional diversity on litter mixture decomposition have been found to be influenced by incubation time (Lecerf et al. 2011), indices representing litter decomposition (García-Palacios et al. 2017) and the presence or absence of soil fauna (Barantal et al. 2014). Furthermore, it should be noted that our study just focused on litter diversity but not the overall plant diversity effects on decomposition. In addition to the direct litter mixture-driven diversity effects on decomposition, plant diversity could also affect decomposition indirectly through changing microenvironmental conditions (Barantal et al. 2011; Hector et al. 2000; Joly et al. 2017). For example, Joly et al. (2017) showed that decomposition of cellulose paper and wood sticks was influenced by plant diversity, which could modify decomposition environment mainly through functional identity and diversity of litterfall. Therefore, much more work is needed to fully understand plant diversity effects on litter decomposition in our studied ecosystem, considering that the simple index (i.e. mass loss) was used to represent litter decomposition and the indirect effect of plant diversity on decomposition was neglected in this short-term laboratory incubation study.

Although the main driver of litter mixture decomposition is the mean decomposability of its component litter, differences between observed and expected decomposition rates of litter mixtures have been frequently reported (i.e. litter mixing effect; Hättenschwiler et al. 2005). Indeed, our study exhibited six and nine out of 32 litter mixtures separately showing synergistic and antagonistic non-additive effects with the litter mixing effects ranging from −8.97% to 16.82% (Table 2). A modeling study conducted by Finzi and Canham (1998) has shown that mixing effects, although not large

themselves, may have significant ecological functions. Differences among component litter species in chemical traits have been expected to be the prerequisite of litter mixing effects (Gessner et al. 2010; Hättenschwiler et al. 2005). In contrast with this expectation, our results showed that functional diversity was not significant in explaining variations in litter mixing effects among litter mixtures (Table 3). This non-significant result may be because some important plant traits suggested to be useful in explaining litter mixing effects were neglected in the present study, notably some compounds of secondary metabolites (e.g. condensed tannins) and physical traits related to water-holding capacity (Hättenschwiler et al. 2011; Makkonen et al. 2013). For example, Makkonen et al. (2013) found that dissimilarity in traits of water-holding capacity among component litter species significantly related to litter mixing effects. Therefore, much more litter traits should be considered to fully understand the relationship between functional diversity and litter mixing effects for future studies, given that this relationship is far from generalizable with positive (Meier and Bowman 2008), neutral (Barantal et al. 2011) or even negative results (Tardif and Shipley 2015) having been reported.

Relative individual performance in litter mixtures

Apart from the perspective of functional diversity, separating component litter from mixtures to assess species-specific responses to litter mixing is suggested to be another important way to identify the mechanisms underlying litter mixing effects, which is usually neglected by previous studies (Gartner and Cardon 2004; Hättenschwiler et al. 2005). In the present study, the short-term incubation allowed us to accurately separate component litter from litter mixtures. Results showed that RIP of a given component species was influenced by its functional identity and trait differences between this component species and its neighbors (Table 4). Indeed, mass loss of the two fast-decomposing species (i.e. *C. burmannii* and *S. lanceolata*) was significantly decreased when decomposing in mixtures compared with decomposing in isolation (Fig. 4a), which was in line with previous studies (Barantal et al. 2011; Lin et al. 2013). The rationale behind this phenomenon may be that the presence of slow-decomposing litter characterized by high AIF concentrations inhibits decomposition of fast-decomposing litter (Gessner et al. 2010). This is because AIF, such as lignin and tannins, not only forms

complex with extracellular enzymes, but also possibly influences structural and enzymatic proteins within hyphae, thus restricting microbial growth and activity (Gessner et al. 2010; Hättenschwiler et al. 2005).

In contrast with the two fast-decomposing species, mass loss of two of the five slow-decomposing species (i.e. *A. mangium* and *M. macclurei*) was higher in the presence of other species than decomposing alone (Fig. 4a). Two potential effects, i.e. priming effect and dilution effect, have been proposed to explain the positive response of slow-decomposing litter to mixing (Barantal et al. 2011; Gessner et al. 2010). The priming effect suggests that fast-decomposing litter with high labile C concentrations will increase growth and activity of decomposers, and then promote decomposition of slow-decomposing litter (Gessner et al. 2010). The dilution effect proposes that the high concentrations of secondary metabolites of slow-decomposing litter could be diluted when mixed with fast-decomposing litter, and then increase decomposer biomass per unit mixed-litter mass (Barantal et al. 2011). Owing to the opposite patterns of fast-decomposing and slow-decomposing litter responding to mixing, our results showed that the relative individual performance of component litter negatively related to their mass loss of single species decomposing alone (Fig. 4b). This result may explain why litter mixing effect was negligible when considering 32 litter mixture treatments as a whole, although large litter mixing effects were found in some treatments owing to the presence of particular species. Therefore, our results suggest that assessing species-specific responses to mixing could be a useful way to fully understand interspecific interactions among component litter species and litter mixing effects.

Conclusions

A novel experimental design was conducted to orthogonally separate the effects of functional identity, functional diversity and species richness on litter mixture decomposition and litter mixing effects. Our results showed that functional identity was the only significant factor explaining variations in mass loss among litter mixtures. Through analyzing differences between observed and expected mass loss of litter mixtures, six and nine out of 32 litter mixtures separately exhibited synergistic and antagonistic non-additive effects with the litter mixing effects ranging from −8.97% to 16.82%, which cannot be explained by functional diversity or species richness. Across the 32 litter mixtures, these synergistic and antagonistic non-additive effects were almost cancelled with each other. Additionally, mechanisms underlying litter mixing effects were also explored via analyzing species-specific responses to mixing. Results showed that the two fast-decomposing species and two out of the five slow-decomposing species had significantly negative and positive responses to litter mixing, respectively. These results highlight that assessing species-specific responses to mixing is useful in exploring mechanisms underlying interactions among component litter species within mixtures.

References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439–449

Allison SD, Vitousek PM (2004) Extracellular enzyme activities and carbon chemistry as drivers of tropical plant litter decomposition. Biotropica 36:285–296

Aponte C, García LV, Marañón T (2012) Tree species effect on litter decomposition and nutrient release in Mediterranean oak forests changes over time. Ecosystems 15:1204–1218

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

Barantal S, Roy J, Fromin N, Schimann H, Hättenschwiler S (2011) Long-term presence of tree species but not chemical diversity affect litter mixture effects on decomposition in a neotropical rainforest. Oecologia 167:241–252

Barantal S, Schimann H, Fromin N, Hättenschwiler S (2014) C, N and P fertilization in an Amazonian rainforest supports stoichiometric dissimilarity as a driver of litter diversity effects on decomposition. Proc R Soc B 281:20141682

Bartoń K (2016) MuMIn: Multi-model inference. R package version 1(15):6 https://cran.r-project.org/web/packages/MuMIn/index.html

Berg B, Johansson MB, Liu CJ, Faituri M, Sanborn P, Vesterdal L, Ni XY, Hansen K, Ukonmaanaho L (2017) Calcium in

decomposing foliar litter – a synthesis for boreal and temperate coniferous forests. For Ecol Manag 403:137–144

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer-Verlag, New York, USA

Butterfield BJ, Suding KN (2013) Single-trait functional indices outperform multi-trait indices in linking environmental gradients and ecosystem services in a complex landscape. J Ecol 101:9–17

Cabin RJ, Mitchell RJ (2000) To Bonferroni or not to Bonferroni: when and how are the questions. Bull Ecol Soc Am 79:246–248

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. Am J Bot 98:572–592

Ceballos G, Ehrlich PR, Barnosky AD, García A, Pringle RM, Palmer TM (2015) Accelerated modern human-induced species losses: entering the sixth mass extinction. Sci Adv 1: e1400253

Cornwell WK, Cornelissen JHC, Dorrepaal E, Eviner VY, Godoy O et al (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol Lett 11:1065–1071

Finerty GE, de Bello F, Bílá K, Berg MP, Dias ATC, Pezzatti GB, Moretti M (2016) Exotic or not, leaf trait dissimilarity modulates the effect of dominant species on mixed litter decomposition. J Ecol 104:1400–1409

Finzi AC, Canham CD (1998) Non-additive effects of litter mixtures on net N mineralization in a southern New England forest. For Ecol Manag 105:129–136

Frainer A, Moretti MS, Xu WJ, Gessner MO (2015) No evidence for leaf-trait dissimilarity effects on litter decomposition, fungal decomposers, and nutrient dynamics. Ecology 96: 550–561

García-Palacios P, Shaw EA, Wall DH, Hättenschwiler S (2017) Contrasting mass-ratio vs. niche complementarity effects on litter C and N loss during decomposition along a regional climatic gradient. J Ecol 105:968–978

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

Gessner MO, Swan CM, Dang CK, McKie BG, Bardgett RD, Wall DH, Hättenschwiler S (2010) Diversity meets decomposition. Trends Ecol Evol 25:372–380

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24:699–711

Handa IT, Aerts R, Berendse F, Berg MP, Bruder A, Butenschoen O, Chauvet E, Gessner MO, Jabiol J, Makkonen M, McKie BG, Malmqvist B, Peeters ETHM, Scheu S, Schmid B, van Ruijven J, Vos VCA, Hättenschwiler S (2014) Consequences of biodiversity loss for litter decomposition across biomes. Nature 509:218–221

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

Hättenschwiler S, Coq S, Barantal S, Handa IT (2011) Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. New Phytol 189:950–965

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

Hedin LO, Brookshire ENJ, Menge DNL, Barron AR (2009) The nitrogen paradox in tropical forest ecosystems. Annu Rev Ecol Evol Syst 40:613–635

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol Monogr 66: 503–522

Hobbie SE, Reich PB, Oleksyn J, Ogdahl M, Zytkowiak R, Hale C, Karoleski P (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87: 2288–2297

Huang J, Zhang W, Zhu XM, Gilliam FS, Chen H, Lu XK, Mo JM (2015) Urbanization in China changes the composition and main sources of wet inorganic nitrogen deposition. Environ Sci Pollut Res 22:6526–6534

Joly FX, Milcu A, Scherer-Lorenzen M, Jean LK, Bussotti F, Dawud SM, Müller S, Pollastrini M, Raulund-Rasmussen K, Vesterdal L, Hättenschwiler S (2017) Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. New Phytol 214:1281–1293

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305

Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1:0–12 https://cran.r-project.org/web/packages/FD/index.html

Laughlin DC (2011) Nitrification is linked to dominant leaf traits rather than functional diversity. J Ecol 99:1091–1099

Lecerf A, Marie G, Kominoski JS, LeRoy CJ, Bernadet C, Swan CM (2011) Incubation time, functional litter diversity, and habitat characteristics predict litter-mixing effects on decomposition. Ecology 92:160–169

Li ZA, Peng SL, Rae DJ, Zhou GY (2001) Litter decomposition and nitrogen mineralization of soils in subtropical plantation forests of southern China, with special attention to comparisons between legumes and non-legumes. Plant Soil 229:105–116

Liang JJ, Crowther TW, Picard N, Wiser S, Zhou M, et al (2016) Positive biodiversity-productivity relationship predominant in global forests. Science 354: aaf8957

Lin GG, Mao R, Zhao L, Zeng DH (2013) Litter decomposition of a pine plantation is affected by species evenness and soil nitrogen availability. Plant Soil 373:649–657

Makkonen M, Berg MP, van Logtestijn RSP, van Hal JR, Aerts R (2013) Do physical plant litter traits explain non-additivity in litter mixtures? A test of the improved microenvironmental conditions theory. Oikos 122:987–997

Mao B, Mao R, Hu YL, Huang Y, Zeng DH (2016) Decomposition of Mongolian pine litter in the presence of understory species in semi-arid Northeast China. J For Res 27:329–337

Mason NWH, MacGillivray K, Steel JB, Wilson JB (2003) An index of functional diversity. J Veg Sci 14:571–578

Meier C, Bowman WD (2008) Links between plant litter chemistry, species diversity, and below-ground ecosystem function. Proc Natl Acad Sci U S A 2008:19780–19785

Mokany K, Ash J, Roxburgh S (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. J Ecol 96:884–893

Perakis SS, Maguire DA, Bullen TD, Cromack K, Waring RH, Boyle JR (2006) Coupled nitrogen and calcium cycles in forests of the Oregon coast range. Ecosystems 9:63–74

Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp S, Willigen BV (2017) Nlme: linear and nonlinear mixed effects models. R package version 3:1–131 https://cran.r-project.org/web/packages/nlme/index.html

Ryan MG, Melillo JM, Ricca A (1990) A comparison of methods for determining proximate carbon fractions of forest litter. Can J For Res 20:166–171

Scherer-Lorenzen M (2008) Functional diversity affects decomposition processes in experimental grasslands. Funct Ecol 22:547–555

Soliveres S, van der Plas F, Manning P, Prati D, Gossner M et al (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459

Soong JL, Calderón FJ, Betzen J, Cotrufo MF (2014) Quantification and FTIR characterization of dissolved organic carbon and total dissolved nitrogen leached from litter: a comparison of methods across litter types. Plant Soil 385:125–137

Tardif A, Shipley B (2013) Using the biomass-ratio and idiosyncratic hypotheses to predict mixed-species litter decomposition. Ann Bot 111:135–141

Tardif A, Shipley B (2015) The relationship between functional dispersion of mixed-species leaf litter mixtures and species' interactions during decomposition. Oikos 124:1050–1057

Tobner CM, Paquette A, Reich PB, Gravel D, Messier C (2014) Advancing biodiversity–ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. Oecologia 174:609–621

Tobner CM, Paquette A, Gravel D, Reich PB, Williams LJ, Messier C (2016) Functional identity is the main driver of diversity effects in young tree communities. Ecol Lett 19:638–647

Trogisch S, He JS, Hector A, Scherer-Lorenzen (2016) Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. Plant Soil 400:337–350

Wardle DA, Bonner KI, Nicholson KS (1997) Biodiversity and plant litter: experimental evidence which does not support the view that enhanced species richness improves ecosystem function. Oikos 79:247–258

Zhang W, Zhu XM, Liu L, Fu SL, Chen H, Huang J, Lu XK, Liu ZF, Mo JM (2012) Large difference of inhibitive effect of nitrogen deposition on soil methane oxidation between plantations with N-fixing tree species and non-N-fixing tree species. J Geophys Res 117:G00N