

The effects of leaf litter evenness on decomposition depend on which plant functional group is dominant

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Abstract

Background and aims Climbing plants are increasing in dominance in the subtropical forests of South China and other areas around the world, altering patterns of plant dominance and evenness in community. We investigated how changes in species' identity and patterns of leaf litter evenness affected decomposition of litter mixtures.

Methods We used litter-bag method to study the influence of different relative abundance mixtures (75 % : 25 %; 50 % : 50 %; 25 % : 75 %) of plant litter from two functional groups (climbing plants and trees) on decomposition rates in a subtropical forest in Guangdong, China.

Results We found negative non-additive effects of mixing litter overall and species composition affected decomposition rates the most. In addition, when climbing plants were dominant, even mixtures decomposed slower significantly than uneven mixtures.

Evenness did not affect decomposition rates, however, when trees were dominant. The magnitude of antagonistic effects increased with increasing dominance of climbing plants but decreased with time, suggesting a strong negative feedback between litter proportion of climbing plant and decomposition rates at the initial stage.

Conclusion The evenness in leaf litter composition affects rates of decomposition, but these effects depend on which plant functional group is dominant. Thus, we should pay more attention to shifts in identity of dominant species and patterns of community evenness.

Keywords Litter decomposition · Species evenness · Relative abundance · Plant functional group · Climbing plants · Nonadditive effects

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Introduction

Human domination of ecosystems (Vitousek et al. 1997) has led to widespread changes in the species composition and shifts in dominant patterns of natural and managed ecosystems (Chapin 2003; Kardol et al. 2010). Over the past two decades, researchers have shown growing interest in understanding how various features of biodiversity affect ecosystem functioning (Cardinale et al. 2006; Loreau et al. 2002; Tilman 1999). Most early studies emphasized the roles of species richness for ecosystem functioning (Loreau et

al. 2002). However, species evenness, another component of biodiversity (Magurran 1988), received little attention although it also has important effects on ecosystem functioning (Hillebrand et al. 2008). For example, Wilsey and Potvin (2000) found that total biomass in an old field of Quebec increased linearly with increasing level of species evenness; Wilsey and Polley (2002) found that communities with low species evenness were less able to resist invaders and insect herbivores; Mattingly et al. (2007) reported that species evenness enhanced community productivity but provided no benefit to invasion resistance. Others, when evenness was not manipulated experimentally, found that productivity declined with increasing species evenness (Laird et al. 2003; Mulder et al. 2004). In microbial microcosms, Wittebolle et al. (2009) found that communities with higher initial evenness had higher levels of ecosystem function and functional stability.

Human activities and global change alter the relative abundance or biomass of species more frequently than the presence or absence of species (Chapin et al. 2000). There are numerous studies about changes in the relative abundance of plants among already coexisting plants due to global environmental change, for example: 1) In low-Arctic tundra and mid-latitude alpine regions, there is growing evidence of climate-driven increases in the abundance and extent of shrubs (e.g., Myneni et al. 1997; Tape et al. 2006), as well as decreases in the abundance of mosses and lichens (Walker et al. 2006) and bryophytes (Hobbie 1996). 2) In oligotrophic ecosystems, fast-growing clonal grasses are expanding (Valéry et al. 2009, and refs therein) because of increasing nutrient enrichment of the environment. 3) In tropical, subtropical and temperate forests, climbing plants are becoming dominant (Peng et al. 2009; Phillips et al. 2002; Wright et al. 2004).

Litter decomposition is a fundamental ecosystem process that greatly affects nutrient availability and carbon cycling (Swift et al. 1979). Changes in species relative abundance of leaf litter mixtures can affect ecosystem properties but these effects have not yet been well studied (Hillebrand et al. 2008). It is thus of interest to investigate how changes in species composition and relative abundance affect litter decomposition. The few studies that have tested the effects of leaf litter evenness on decomposition provide conflicting results. King et al. (2002) found no effect of litter evenness on decomposition in laboratory

microcosms. Swan et al. (2009) found that the interaction between litter evenness and richness significantly affect decomposition in a headwater stream. The highest decomposition rate occurred at the relative abundance found in the field. In contrast, Dickson and Wilsey (2009) found that richness and its interaction with evenness did not affect decomposition whereas greater species evenness increased decomposition. Ward et al. (2010) also found that higher levels of species evenness increased rates of decomposition while the identity of the dominant species also affected decomposition rates.

Climbing plants are an important component of many forests around the world but have generally received little attention (Putz and Mooney 1991). Because climbing plants depend on others for physical support, they can allocate a greater amount of resources to the development of foliage (Putz and Mooney 1991), thus produce much higher leaf area per unit stem area than trees. Wright et al. (2004) found that the production and proportion of lianas' leaf litter increased between 1986 and 2002. In addition, the leaves of climbing plants have higher concentration of nitrogen (Kazda and Salzer 2000). As a consequence, we expect increases in the relative abundance of climbing plants will accelerate rates of leaf litter decomposition. However, we are not aware of studies of how increases in climbing plants have changed rates of decomposition.

In this study, in the context that climbing plant's dominance is increasing in Guangdong province, China (Peng et al. 2009), we used a factorial experiment to investigate how shifts in both the relative abundance of climbing plants in litter mixtures and the identity of the dominant plant functional group within these litter mixtures affect rates of decomposition. Given the importance of plant functional traits as drivers of decomposition (Cornwell et al. 2008), we predicted that: (1) litter from climbing plants will decompose faster than litter from trees; (2) mixing climbing plant litter with tree litter will hasten decomposition of tree leaf litter while slowing the decomposition of climbing plant leaf litter, and the mixture treatments will have an overall positive non-additive (synergistic) effects; (3) increasing the proportion of climbing plants will enhance decomposition of litter mixtures; (4) the effects of litter species evenness on decomposition rates will depend on which plant functional group dominates the litter mixtures.

Materials and methods

Study site

The study was conducted in the Dinghushan Biosphere Reserve (DHSBR, 23°10'N, 112°10'E), Guangdong Province, southern China. This is the first nature reserve in China and occupies an area of 1,133 hm² with elevation ranging from 10 to 1,000 m. The climate, is subtropical with monsoonal variation in rainfall (Kong et al. 1993). The mean annual rainfall is 1,927 mm with 75 % of the rain occurring between March and August (Huang and Fan 1982). Mean annual temperature is 21.0 °C with average temperatures ranging from 12.6 °C (January) to 28.0 °C (July) (Mo et al. 2006). We choose DHSBR as our study site in order to avoid man-made disturbance and litterbags loss since it is relatively inaccessible to rural population.

Litter collection

We collected leaf litter from six plant species (three climbing plants and three trees) of two plant functional groups (PFG) between July 2009 and August 2009 corresponding to the peak period of litter fall in DHSBR (Zhou et al. 2007). The litter came from different locations within an 80-km radius of DHSBR. Three climbing plant species (CP), *Merremia boissiana* (Mb), *Byttneria aspera* (Ba) and *Merremia umbellate* (Mu), were chosen because they have recently increased abruptly in abundance, killing many host trees and causing great ecological and economic damage in Guangdong Province (Peng et al. 2009). Three tree species (T), *Schima superba* (Ss), *Castanopsis chinensis* (Cc), *Castanopsis fissa* (Cf) are the most common tree species in DHSBR and thus contribute the most leaf litter to this ecosystem (Mo et al. 2006). They co-occur with these climbing plants in field. The leaf litter material consisted of freshly senesced leaf material from the soil surface or the plant itself depending on the species considered. All litter was air dried immediately after collection at room temperature and stored until further use. The litter of an individual species was mixed evenly before use.

Experimental design

We estimated rates of leaf litter decomposition using the “litter-bag” technique, a widely used method to

determine rates of litter mass loss over time. Each litter-bag was 20×25 cm, and made from polyvinyl mesh with 0.2×0.2 mm holes in one side and 2×2 mm in the other side. The larger upper mesh allowed mesofauna access to the litter while the finer bottom mesh prevented physical loss of small fragments. Each litter-bag was filled with a total of 4.0±0.1 g air-dried plant litter, weighted to the nearest milligram and sealed with rust-proof staples. These bags contained either a single species or one of 9 possible two-species mixtures (one from the PFG of CP and the other from the PFG of T) combination.

We applied three evenness treatments to each two-species mixture: 75 % CP+25 %T, 50 % CP+50 %T, 25 % CP+75%T (Table 1). Within these treatments, the first and the third had the same species composition and evenness level but different dominant species. We restrained ourselves to two-species and tree-climbing plant mixtures to focus on leaf litter species evenness effects rather than species richness effects. For every species and litter mixture, we prepared nine litter-bags (3 replicates×3 retrieval dates), leading to a total of 297 litter-bags: (6 monocultures+9 mixtures×3 evenness treatments)×3 replicates×3 retrieval dates.

On 1 November 2009, we lay the litter-bags flat on top of soil at a random orientation and held these in

Table 1 Litter mixture treatment summary

| Mixture species | CP-dominant (Uneven) | Even | T-dominant (Uneven) |
|-----------------|----------------------|-------|---------------------|
| Mb Ss | 75:25 | 50:50 | 25:75 |
| Mb Cf | 75:25 | 50:50 | 25:75 |
| Mb Cc | 75:25 | 50:50 | 25:75 |
| Ba Ss | 75:25 | 50:50 | 25:75 |
| Ba Cf | 75:25 | 50:50 | 25:75 |
| Ba Cc | 75:25 | 50:50 | 25:75 |
| Mu Ss | 75:25 | 50:50 | 25:75 |
| Mu Cf | 75:25 | 50:50 | 25:75 |
| Mu Cc | 75:25 | 50:50 | 25:75 |

Species abbreviations are as follows: CP, climbing plants: (Mb, *Merremia boissiana*; Ba, *Byttneria aspera*; Mu, *Merremia umbellate*), T, trees: (Ss, *Schima superba*; Cf, *Castanopsis fissa*; Cc, *Castanopsis chinensis*). The order of the relative proportion of each species under “Uneven” reflects the order of species listed in the “Mixture species” column

place using bamboo pins. We placed these into three replicate plots ~50 m apart. Each plot contained three complete (all treatments) sets of litterbags, one for each of the three retrieval times. Before installing these, we remoistened the litterbags with distilled water to minimize the negative effects of air-drying on litter decomposition (Taylor 1998). We strung together litter bags to be harvested at a particular date using nylon chord. This facilitated retrieving the litterbags at different dates while minimized disturbance to the remaining litterbags.

We retrieved the litterbags after 60, 120 and 240 days. After opening each bag, we cleaned any remaining litter from adhering soil particles and organic matter using tweezers and brush. Litter in mixtures was sorted by species. Given the strong morphological and structural differences among the climbing plants and trees, litter species identification was relatively easy even after 240 days. We then oven-dried the litter for at least 72 h at 70 °C and weighed the separated samples to determine the remaining leaf dry mass.

Litter analysis

To estimate specific leaf area (SLA, in cm²/g), we collected 15 fresh leaves from each species, weighed them individually, and used a leaf area meter (Li-3100A, Li-Cor, USA) to measure leaf area. Immediately before the field experiment, we oven-dried subsamples of litter from each species at 70 °C for 72 h to determine the ratio of air-to oven-dry leaf mass. The dried leaves were ground into fine powder using a micro-plant mill to measure leaf nitrogen (N) using an azotometer (Kjeltec 2300, Foss, Sweden) and leaf carbon (C) (TOC-V_{cph}, SHIMADZU, JAPAN). Ash content was measured by burning 2 g leaf litter powder samples in a 550 °C muffle furnace (Vulcan A-550, Vulcan, UK) for 6 h and weighing the remaining mass, then dividing the ash mass by the sample mass.

Data analysis

We estimated the litter mass remaining within each litterbag sampled at each date as the percentage of the initial litter dry weight by species. The expected remaining mass of litter mixtures was estimated based on the remaining mass in the single-species litterbags

of the component species decomposing in the same plot. This was calculated as follows (Hoorens et al. 2010):

$$\begin{aligned} \text{Expected mass remaining} = & (M_1 / (M_1 + M_2)) \times R_1 \\ & + (M_2 / (M_1 + M_2)) \times R_2 \end{aligned}$$

Where *R* refers to the remaining mass of a species in the single species litterbag and *M* refers to the estimated initial litter oven-dry weight of a species in the mixture. The relative mixture effect was calculated as the ratio [(Expected - observed) / expected] × 100 mass remaining for each mixture (Wardle et al. 1997). A ratio different from zero indicates a non-additive effect of mixing litters on decomposition. More precisely, positive ratios reflect synergistic mixture effects while negative ratios reflect antagonistic mixture effects.

To investigate which initial leaf litter parameters correlated with decomposition rates of single species litters in our study, we performed a simple regression of the mean mass remaining in the single-species litters at the end of the study on their mean initial parameters.

For each sampling date (i.e., at 60, 120 and 240 days), we used analysis of variance (ANOVA) to examine: 1) differences in remaining mass among the six species; 2) differences in remaining mass between the two functional groups (T vs CP); 3) differences in mass remaining among the three mixture treatments (pooled single species, even mixtures, and uneven mixtures); 4) differences among pooled single species, even mixtures, CP-dominant uneven mixtures and T-dominant uneven mixtures; 5) effects of neighbor PFG's identity on decomposition of the target PFG within mixtures among different evenness treatments.

We used Student's *t*-tests to test whether non-additive (antagonistic and synergistic effects) litter mixture effects were significantly different from zero. In addition, at each time, we use ANOVA to compare the differences of litter mixture effects among the CP-dominant mixtures, even mixtures and T-dominant mixtures.

We included time as a fixed factor as we chose the timing for each retrieval period (Dickson and Wilsey 2009). The factor "species composition" included 9 numbers representing the identity of the 9 mixtures. The residuals were checked to satisfy the assumptions

of ANOVA, data were log-transformed when necessary. Levels of significance are indicated as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

Results

Decomposition in monospecific litters

The quantity of litter remaining in the bags after 240 days of decomposition ranged from 25.09 ± 2.06 % (mean \pm SD for all means in results) (Mb) to 74.77 ± 3.62 % (Cc) (Fig. 1). The two climbing plants Mb and Ba decayed significantly faster than the other climber (Mu) and the three tree species ($P < 0.01$, Fig. 1). Ba's mass remaining at day 60 was significantly lower than the other five species ($P < 0.05$). Comparing all trees to the climbing plants across the three collection dates demonstrates that tree leaf litter decays more slowly (Fig. 2). Trees always had more mass remaining than climbing plants. By day 240, climbing plants had 42.30 ± 6.69 % mass remaining versus 71.27 ± 1.98 % for trees.

Ash content correlated significantly with % litter mass loss (240 days, $r = 0.83$, $P = 0.04$, $n = 6$). SLA correlated marginally significantly with % litter mass loss (240 days, $r = 0.78$, $P = 0.07$, $n = 6$). Thus, species containing greater concentrations of ash and having larger SLA were faster to decompose. Neither the concentrations of N in the leaf litter nor the C:N values

had any discernible effect on decomposition rate ($P > 0.40$ in both cases).

Decomposition in mixtures: the role of species evenness

Mass loss from the mixed litter bags averaged 42.43 ± 1.54 % and ranged from 16.38 % to 79.18 % over the 240 days of the experiment. Ignoring the identities of dominant species, species evenness *per se* as a main effect had no significant effect on decomposition rates (Table 3). Yet the species composition of the litter mixtures strongly affected rates of decomposition independently of the effects of time and the other variables ($P < 0.001$, Table 3, Fig. 3). Litter mass decreased fastest in the mixture of Cf and Mb and decreased slowest in the mixture of Cc and Mu (Fig. 3).

Including the identities of dominant species and their relative abundances (RA) in analyses of decomposition rate allowed both RA and species composition and the interactions between RA and time to be significant ($P < 0.001$, Table 4). Overall rates of decomposition tended to be fastest in litter mixtures dominated by climbing plants, intermediate in even mixtures, and slowest in T-dominant uneven mixtures (Fig. 4). There were significant differences in decomposition between litter mixtures dominated by climber vs. tree species by day 120 and 240 (Fig. 4).

Fig. 1 Mass remaining (mean \pm SE) over 240 days incubation of six species. Differences among litters were tested by one-way ANOVA followed by Tukey post-hoc test, different letters denote significant differences (At each date, the first three bars are climbing plants, the other three bars are trees)

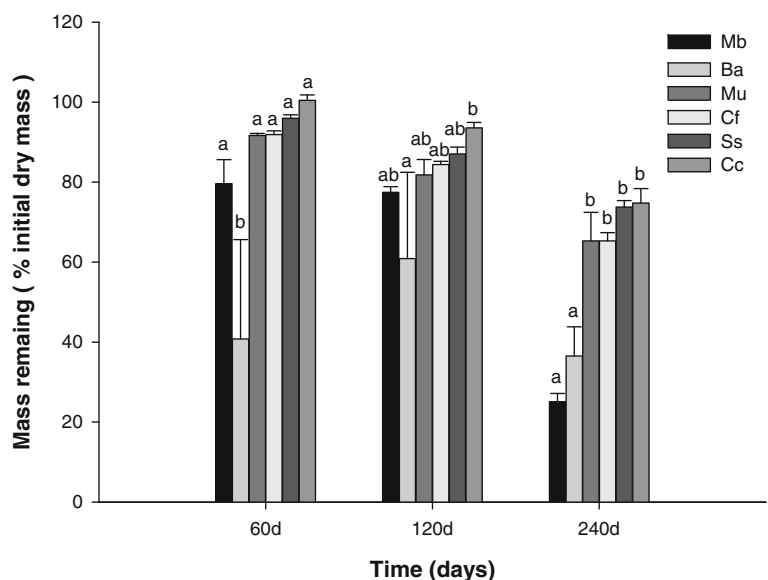
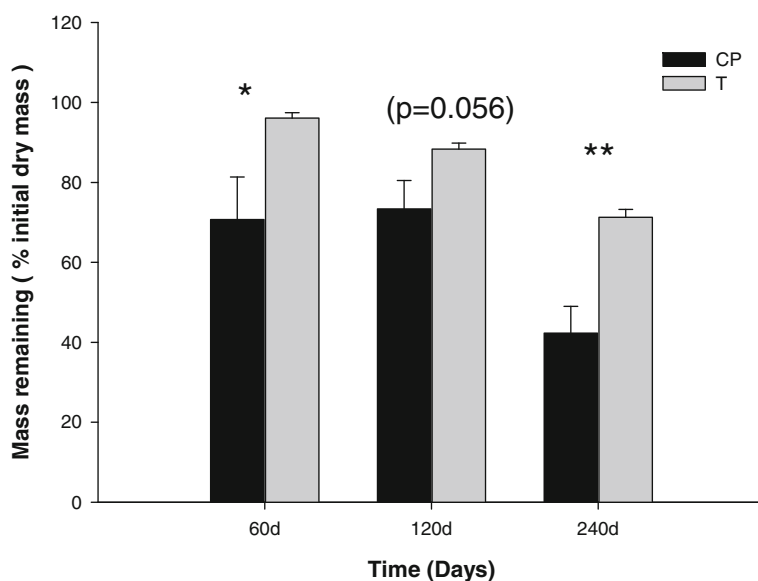


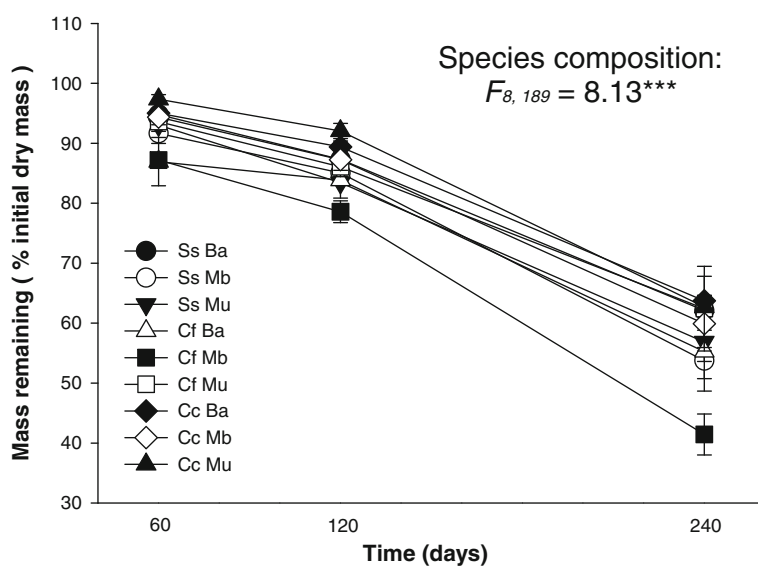
Fig. 2 Mass remaining (mean±SE) of the two PFGs over 240 days. Differences among PFGs (CP, climbing plants; T, trees) were tested by one-way ANOVA



Mixed tree and climbing plant litter decomposition: antagonist or synergetic effects?

We found a significant antagonistic effect between tree and climbing plant litter with negative mean relative mixture effects at day 60 (mean=-20.87 %, $t=-3.51$, $df=80$, $P<0.001$) and 120 (mean=-9.76 %, $t=-3.25$, $df=80$, $P=0.002$). However, the overall relative mixture effect by day 240 did not differ significantly from 0 (mean=-4.65 %, $t=-1.42$, $df=80$, $P=0.160$). Thus, antagonistic effects declined with time, even there was synergistic effect by day 240 (although not statistical significant).

Fig. 3 The effects of litter species composition on average litter mass remaining (mean±SE) of the nine mixture treatment across time

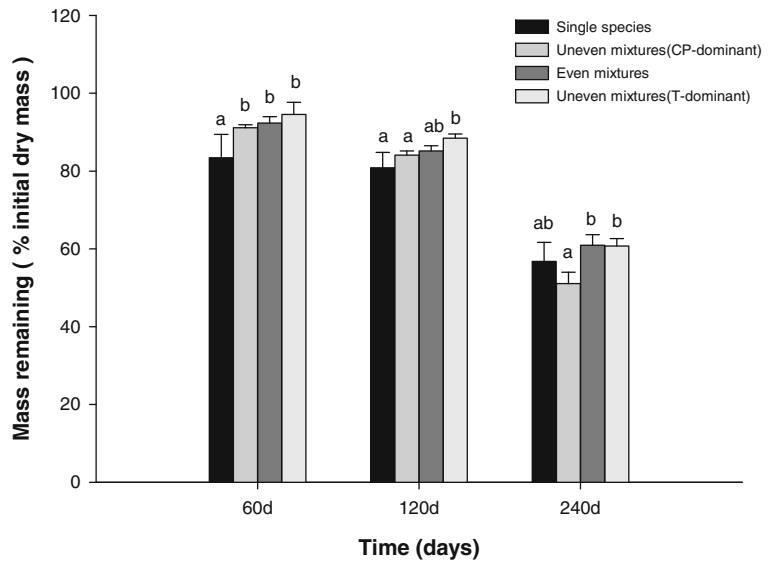


The relative mixture effect also varied among the different relative abundance treatments ($F_{2,162}=6.019$, $P=0.003$) with greater antagonistic effects in mixtures dominated by climbing plants (Fig. 5).

Decomposition in monoculture vs. mixed litter of the same species

By separating litter remnants by species, we were able to test how leaf decomposition was affected by species, the identity of other species in the mixture, and the relative abundance (evenness) of species within the mixture. The differences of mass remaining of

Fig. 4 Differences of mass remaining (mean±SE) among single species, even mixtures, CP-dominant uneven mixtures and T-dominant uneven mixtures over 240 days



the same species between monoculture litter and in mixture ranged from -27.48 % to +12.57 % by day 240. Trees had strongly antagonistic effects on two of the three climbing plants (Mb and Ba). Climbing plants had synergistic effects on the decomposition of litter from all the three trees but these were not significant.

The identity of target species had a significant influence on individual performance of that species in mixtures ($F_{5, 324}=47.42, P<0.001$), while the identity of neighbor species in the mixtures had a marginally significant effect on individual performance of the target species ($F_{4, 324}=2.37, P=0.052$). The identity of

target species explained 33.86 % of the variance, about 25 times higher than the identity of neighbor species did (data not shown).

Between the functional groups, we found that rates of decomposition in climber leaves declined when mixed with leaves from the trees (Fig. 6). In contrast, climber leaves had little influence on rates of decomposition in the tree species in the day 60 and 120 samples (Fig. 6). By day 240, however, climber leaves significantly accelerated the decomposition of tree leaves when they were mixed uneven, tree species still hampered CP's decomposition, but not significantly (Fig. 6).

Fig. 5 The relative mixture effect on mass remaining (mean±SE) over time. Differences of the relative mixture effect among different evenness levels were tested by ANOVA followed by Tukey post-hoc test. We used t-test to check whether the relative mixture effect was significantly different from zero, which was indicated by * or *p*-value

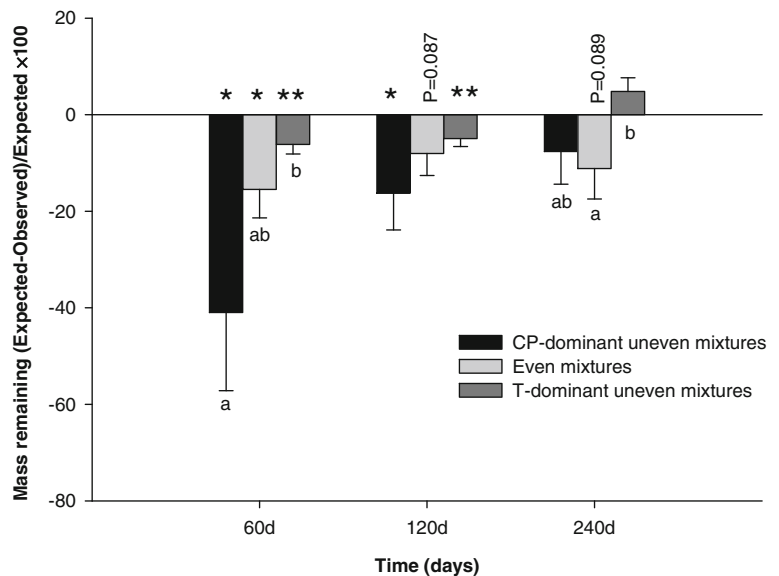
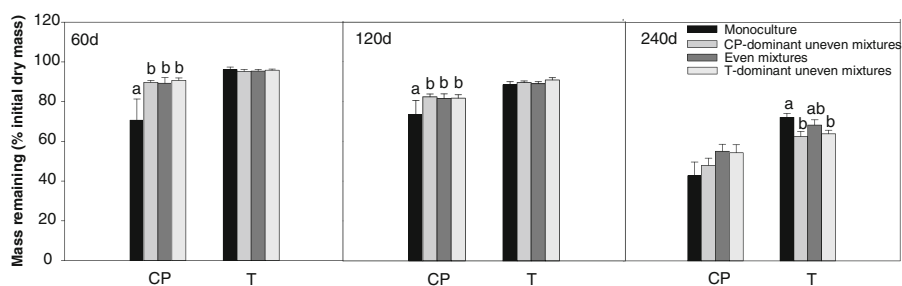


Fig. 6 Mass remaining of climbing plants and tree litter in mixtures over time (mean±SE)



Discussion

As expected, leaves from at least two of the three climbing plants decomposed faster than leaves from the three tree species (Fig. 1). However, in contrast to our expectations, the presence of litter from climbing plants did not increase rates of decomposition of the tree leaves in mixtures while tree litter slowed rates of climber litter decomposition. This resulted in overall negative non-additive effects in mixtures, although higher proportions of climbing plant litter in mixtures did increase overall decomposition rates of mixtures as we predicted. Our results demonstrated that species evenness within leaf litter mixtures can significantly affect rates of litter decomposition, but that these effects depend on which plant functional group dominated the litter bag. Our findings demonstrate that shifts in the identity and relative abundance of the dominant species and functional group can change short-term rates of decomposition.

We found overall antagonistic effects in litter mixtures of species differing in physical and chemical leaf traits (Table 2) in our study. Others also reported antagonistic interactions in rates of decomposition within leaf litter mixtures (Reviewed by Gartner and Cardon 2004). Mixtures of different species could provide complementary sets of resources to detritivores and microbial communities, enhancing rates of

overall decomposition (Kaneko and Salamanca 1999). Alternatively, inhibitory compounds from one species could depress overall decomposer community activity (Blair et al. 1990; McArthur et al. 1994; Nilsson et al. 1999). Overall effects on the decomposition of litter mixtures will thus depend on the balance of these stimulatory and inhibitory effects. Potential mechanisms for these interactions include nutrient transformation among litter species (Schimel and Hattenschwiler 2007) and changes in the composition or behavior of decomposer communities of microbes and detritivores (Gessner et al. 2010; Hattenschwiler and Bretscher 2001; Hattenschwiler and Gasser 2005; Swan and Palmer 2006).

Separated litter from individual species within mixtures can help us to assess species-specific responses and neighbor effects and to uncover the mechanisms underlying decomposition patterns in mixtures, but few previous litter mixture experiments have done this (Prescott et al 2000; Hoorens et al 2009). Despite only using two-species mixtures in this study, the design of this experiment allowed us to separate the effects of the target species from those of co-occurring litter species on litter decomposition in mixtures. As like Hoorens et al. (2009) and Barantal et al. (2011), we found that the identity of target species had the strongest influence on the decomposition of individual species in mixtures. Nevertheless, we found tree litter

Table 2 Leaf litter structural and biochemical characteristics (mean±SD) of six species. For N, C:N, Ash, $n=4$, for SLA, $n=15$

| Species | N(%) | C:N | ASH(%) | SLA(cm ² /g) |
|------------------------------|------------|-------------|-------------|-------------------------|
| Climbing Plant (CP) | | | | |
| <i>Byttneria aspera</i> | 1.21(0.08) | 22.83(1.98) | 11.08(0.41) | 179(39) |
| <i>Merremia boissiana</i> | 1.08(0.07) | 26.83(2.41) | 11.62(0.25) | 312(52) |
| <i>Merremia umbellate</i> | 1.65(0.04) | 18.46(0.3) | 6.13(0.11) | 237(35) |
| Tree (T) | | | | |
| <i>Castanopsis fissa</i> | 1.01(0.05) | 33.25(1.75) | 5.34(1.27) | 91(21) |
| <i>Schima superba</i> | 0.96(0.09) | 33.86(3.13) | 8.96(1.70) | 97(24) |
| <i>Castanopsis chinensis</i> | 1.06(0.05) | 29.85(1.63) | 5.00(0.32) | 93(22) |

Table 3 Results of ANOVA to test the effects of time, species evenness (even and uneven, see Table 1), and species composition on the observed mass remaining of litter mixtures

| Source | <i>df</i> | SS | <i>r</i> ² | MS | <i>F</i> | <i>P</i> |
|-------------------------|-----------|--------|-----------------------|---------|----------|----------|
| Time | 2 | 56,149 | 72.53 | 28074.6 | 403.67 | < 0.001 |
| Evenness level (E) | 1 | 71 | 0.09 | 71.2 | 1.02 | 0.31 |
| Species composition (C) | 8 | 4,523 | 5.84 | 565.4 | 8.13 | < 0.001 |
| Time×E | 2 | 411 | 0.53 | 205.3 | 2.95 | 0.055 |
| Time×C | 16 | 991 | 1.28 | 62 | 0.89 | 0.581 |
| E×C | 8 | 748 | 0.97 | 93.5 | 1.34 | 0.224 |
| Time×E×C | 16 | 1,379 | 1.78 | 86.2 | 1.24 | 0.241 |
| Residuals | 189 | 13,145 | 16.98 | 69.5 | | |

slowed decomposition of climber leaves while climber litter hardly affected tree litter decomposition, resulting in overall antagonistic effects in mixtures. In contrast, Hoorens et al. (2009) found that the identity and characteristics of neighbor species hardly affected litter decomposition. McArthur et al. (1994) also found that rates of decay of slowly decomposing species were rarely boosted in mixtures but that such species could inhibit the decay of normally fast decomposing species.

This study began at November, a dry season at our study site. Given that microbial activities and leaching are weak during the dry season (Cornejo et al. 1994), rates of litter decomposition may depend more on the level of activities of soil animals. Though we did not analyze microbial or invertebrates abundance, we observed that leaves from climbing plant were heavily fed upon by detritivores in monoculture but not in litter mixtures. This might have resulted from that detritivores in our study site preferentially feeding on climbing plant litter but avoiding tree litter in mixtures

since tropical trees are generally rich in secondary leaf compounds (Hallam and Read 2006). Consequently, when mixtures contain tree litters, detritivores will not feed on climbing plant litter. This would explain the significant antagonistic effects in litter mixtures in our study.

Our study showed that the negative non-additive effects of litter mixtures decreased over time (Fig. 5). This is probably because, at the end of the study during wet season, leaching and decomposition of inhibitory compounds in tree litter decreased the magnitude of curbs of microbial activities in climbing plant litter. Wardle et al. (1997) reported that non-additive effects changed over time and both positive and negative effects of mixing occurred for the same combination of species depending upon the time of harvest; they explained that these effects are due to the complex nature of the decomposition processes being further complicated by the various interactions occurring between the various components of the litter mixtures. De Marco et al. (2011) found that there were

Table 4 Results of ANOVA to test the effects of time, abundance levels of CP (25 %: T-dominate, 50 %: even, 75 %: CP-dominant, see Table 1), and species composition on the observed mass remaining of two-species litter mixtures

| Source | <i>df</i> | SS | <i>r</i> ² | MS | <i>F</i> | <i>P</i> |
|-------------------------|-----------|--------|-----------------------|---------|----------|----------|
| Time | 2 | 56,149 | 72.53 | 28074.6 | 454.66 | < 0.001 |
| Relative Abundance (RA) | 2 | 1,438 | 1.86 | 718.8 | 11.64 | < 0.001 |
| Species composition (C) | 8 | 4,523 | 5.84 | 565.4 | 9.16 | < 0.001 |
| Time×RA | 4 | 713 | 0.92 | 178.3 | 2.89 | 0.024 |
| Time×C | 16 | 991 | 1.28 | 62 | 1.00 | 0.456 |
| RA×C | 16 | 1,390 | 1.80 | 86.9 | 1.41 | 0.144 |
| Time×RA×C | 32 | 2,210 | 2.85 | 69.1 | 1.12 | 0.318 |
| Residuals | 162 | 10,003 | 12.92 | 61.7 | | |

antagonistic effects both in *Cistus* and *Quercus* mixtures in the early phase of decomposition; the magnitude of these effects increased with time in *Cistus* mixtures but decreased in *Quercus* mixtures.

Few other studies have explicitly investigated the role of litter species evenness on litter mixture decomposition. Our study clearly demonstrated that species evenness can have significant effects on litter decomposition, but the effects depend on the identity of the dominant plant functional group (Tables 3, 4; Fig. 4). When we only considered even and uneven (pooled CP-dominant uneven and T-dominant uneven together) mixtures, species evenness had no significant effects on decomposition rates ($P=0.31$, Table 3). This may be because the positive and negative effects among PFGs balance each other (Hoorens et al. 2010). As a result, we could not detect significant roles when we chose species evenness *per se* as a main factor in our analysis. If we took the identity of PFGs into account, we observed a negative relationship between species evenness and decomposition rates when climbing plants were dominant but a neutral relationship when trees were dominant. The relationship between species evenness and decomposition rates depended on which PFG is dominant in mixture.

Other studies that investigated the relationships between species evenness and decomposition rates have not had consistent conclusions. Dickson and Wilsey (2009) and Ward et al. (2010) observed positive relationships between species evenness and decomposition rates. However, King et al. (2002) reported that changes in litter evenness had no effect on mass loss or leachate N concentration in mixtures; while Swan et al. (2009) found that greatest mass loss occurred when natural field values of evenness were reflected in mixtures rather than in even mixtures. Here, in a subtropical forest ecosystem, the relationships between litter evenness and decomposition rates depended on the identity of the dominant species and PFGs. This may explain the lack of a consistent relationship between leaf litter evenness and decomposition rate.

It should be emphasized that our study was only 240 days long, so our findings relate to the early stages of decomposition only and therefore cannot predict long term decomposition rates. However, our study clearly demonstrated that changes in relative abundance of species and shifts in identity of dominant plant functional groups can have significant influences on rates of litter decomposition. This could have substantial implications

for situations when the evenness of already co-existing species and the identity of dominant species might be changed in the context of global change. Determining how changes in species evenness and identity of dominant species influence ecological processes such as litter decomposition warrants further exploration.

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