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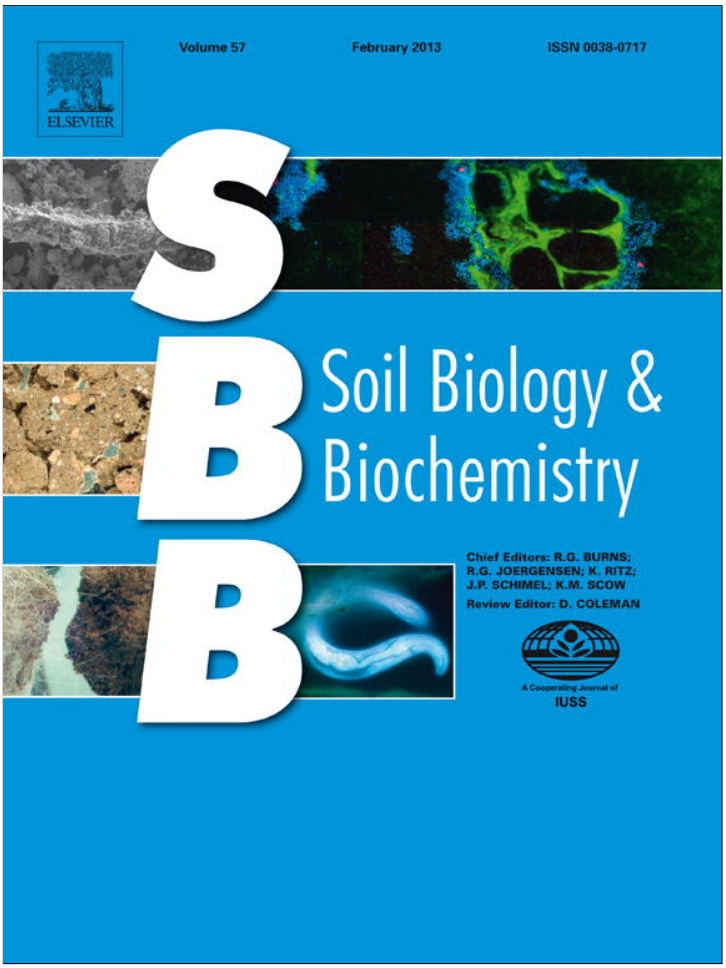

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Non-additive effect of species diversity and temperature sensitivity of mixed litter decomposition in the alpine meadow on Tibetan Plateau

Jichuang Duan [a,c], Shiping Wang [a,b,*], Zhenhua Zhang [b,d], Guangping Xu [e], Caiyun Luo [b], Xiaofeng Chang [b,d], Xiaoxue Zhu [b,d], Shujuan Cui [b,d], Xinquan Zhao [b], Wenying Wang [f], Mingyuan Du [g]

[a] Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China
[b] Key Laboratory of Adaptation and Evolution of Plateau Biota, Northwest Institute of Plateau Biology, Chinese Academy of Sciences, Xining 810008, China
[c] Binhai Research Institute in Tianjin, Tianjin 300457, China
[d] Biological Department, Graduate University of Chinese Academy of Sciences, Beijing 100049, China
[e] Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences, Guangxi 541006, China
[f] College of Life and Geography, Qinghai Normal University, Xining 810008, China
[g] National Institute for Agro-Environment Science, Tsukuba 305-8604, Japan

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ABSTRACT

Few studies of the effects of litter diversity on the temperature sensitivity of mixed litter mass loss (MLML) are available. We tested the hypothesis that high litter diversity would reduce the magnitude of effects of climate and environmental change on MLML with 0.5/1 mm litter bags and sampling once after 1 yr of decomposition, using 51 combinations of litter mixtures from 25 dominant species at 3200 and 3800 m elevations on the Tibetan Plateau. Generally, our study supported our hypothesis. High temperature (i.e. lower elevation) reduced the dependency of MLML and non-additive effects on species richness. Species composition significantly affected MLML and its Q_{10} (i.e. the ratio of litter mass loss rate at a temperature T_1 that is 10 °C lower than a temperature T_2) when species richness was less than 8. Shrubs significantly decreased the Q_{10} of MLML when the species richness of litter mixture was less than 4. These findings suggest that the influence of future warming on MLML may depend on the balance between the magnitude of the impacts of climate change on shrub invasion and loss of species diversity in alpine region.

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1. Introduction

The relationship between biodiversity and ecosystem function has received a great deal of attention due to increasing global species decline (Loreau et al., 2002; Tilman et al., 2006; Meier and Bowman, 2008; Srivastava et al., 2009). Although effects (i.e. non-additive effects) of litter diversity (i.e. species richness and composition) on mixed litter mass loss (MLML) have been observed in terrestrial ecosystems (Wardle et al., 1997; Kaneko and Salamanca, 1999; Hector et al., 2000; Hättenschwiler et al., 2005; Srivastava et al., 2009) and in aquatic ecosystems (Gessner et al., 2004; LeRoy and Marks, 2006; Moore and Fairweather, 2006; Lecerf et al., 2007; Kominoski et al., 2007; Schindler and Gessner, 2009; Swan et al., 2009; Rosemond et al., 2010), no general relationship exists between litter species diversity and MLML, as both synergistic and antagonistic effects may result in an overall neutral trend (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Srivastava et al., 2009). The relative uncertainty of litter diversity effects on MLML may be due to differences in climate and environmental conditions, experimental design and choice of litter species (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; LeRoy and Marks, 2006; Srivastava et al., 2009; Rosemond et al., 2010). Therefore, a broad comparison among studies should be interpreted with great caution (Hättenschwiler et al., 2005). In particular, grassland ecosystems are critically underrepresented because few studies on the effects of litter mixture on decomposition have previously been reported for alpine ecosystems (Hector et al., 2000; Gartner and Cardon, 2004).

Global warming and associated environmental changes are predicted to affect most regions of the northern hemisphere and

* Corresponding author. Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100101, China. Tel.: +86 10 62849533; fax: +86 10 62849886.
E-mail address: wangsp@itpcas.ac.cn (S. Wang).

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will be peculiarly pronounced at high northern latitudes and high elevation during this century (ACIA, 2005; IPCC, 2007). Warming increased invasion of shrubs in the alpine region (Klein et al., 2007); and decomposition of shrub litters was lower which had higher temperature sensitivity of decomposition (Xu et al., 2010). In particular, litter decomposition rates may change owing to the shifts of species composition and lower litter quality induced by climate change (Cornelissen et al., 2007) which may alters microbial activity (Henry et al., 2005; Parton et al., 2007). Some results have been reported on the potential responses of single species litter decomposition to climate change (Murphy et al., 1998; Liski et al., 2003; Fierer et al., 2005; Cornelissen et al., 2007; Xu et al., 2010). However, recent results show that single species litter decomposition may not adequately represent natural ecosystems where litter from multiple species decomposes together (Gartner and Cardon, 2004; Hättenschwiler et al., 2005), because litter interactions may alter the response of decomposition rates extrapolated from single-species studies to climate change. Moreover, a lack of experiments with the same litter species richness under different climate conditions limits our understanding of the response of litter decomposition to future climate change. Therefore, evaluating the overall response of decomposition in mixed species litter to climate and environmental changes is critical to our understanding of litter decomposition and for modeling carbon and nutrient processes in terrestrial ecosystems under future climate change.

The objective of this study was to test the hypothesis that high litter diversity reduced the effect of warming on MLML. To meet this objective, the study involved 25 dominant litter species and 51 combinations of litter mixtures at five species richness levels at two elevations (i.e. 3200 and 3800 m a.s.l.) on the Tibetan Plateau. Our study addressed the following four hypotheses: 1) the dependencies of MLML and non-additive effects on litter species richness differ under different environmental conditions; 2) high litter species richness reduces the temperature sensitivity of MLML (i.e. Q_{10}, the ratio of litter mass loss rate at a temperature T_1 that is 10 °C lower than a temperature T_2); 3) non-additive effects of MLML vary with species composition and elevation; and 4) the effect of species composition, especially for shrubs, on the Q_{10} value decreases with increasing litter species richness.

2. Materials and methods

2.1. Experimental site

The experimental site is located at the Haibei Alpine Meadow Ecosystem Research Station (HBAMERS), a facility run by the Northwest Institute of Plateau Biology of the Chinese Academy of Sciences. HBAMERS is situated at latitude 37° 37′N, longitude 101° 12′E. The station lies in the northeast of the Tibetan Plateau in a large valley surrounded by the Qilian Mountains. The station experiences a typical plateau continental climate which is dominated by the southeast monsoon from May to September in summer and high pressure from Siberia in winter. Summers are short and cool, and winters are long and severely cold. Mean annual temperature is −2 °C, and mean annual precipitation is 500 mm, over 80% of which falls during the summer monsoon season. Mean elevation of the valley bottom is 3200 m.

At 3200 m, the vegetation is dominated by *Kobresia humilis*, *Festuca ovina*, *Elymus nutans*, *Poa* spp., *Carex* spp., *Scripus distigmaticus*, *Gentiana straminea*, *Gentiana farreri*, *Leontop odiumnanum*, and *Potentilla nivea*. Litter samples of the 25 species based on the aboveground biomass of coloring leaves were collected randomly from this alpine meadow community grazed during winter by sheep in September 2008 at 3200 m, air-dried and stored indoors for 9 months until the beginning of the decomposition experiment. The chemical properties were shown in supplementary information Table 1. In briefly, there were 3 litter functional groups: 2 shrubs with a high lignin:N ratio (mean 10.9, ranging from 8.5 to 13.2), 3 graminoids with a medium lignin:N ratio (mean 6.1, ranging from 4.2 to 7.6) and 20 forbs with low lignin:N ratios (mean 2.6, ranging from 0.1 to 8.8, and only 4 out of 20 litter species had a lignin:N ratio of more than 4) (SI Table 1).

2.2. Experimental design

At the HBAMERS and about 3 km from HBAMERS, two 10 × 20 m plots were fenced in autumn 2005 and 2006 at 3200 and 3800 m above sea level along the southern side of the Qilian Mountains. The coverage of the vegetations at the two sites is more than 90%. Air-dried litter samples (4.0 g oven-dry mass at 65 °C) of single species and mixed litter samples of the community were placed in 4 × 6 cm litter bags with nylon cloth of 1 mm mesh for upper side and 0.5 mm mesh for bottom side. Species mixtures were assembled with the total mass of 4.0 g partitioned equally among mixed species, recording the exact mass of litter used. Because testing all combinations of species mixtures was impractical, species combinations were drawn at random for each of 5 species richness levels: 2, 4, 8, 16 and 25 species. Finally 19, 10, 11, and 10 combinations for the first four levels were adopted. Thus the experiment encompassed 76 treatments with 2 replicates, including 25 single-species litters decomposing in isolation, one 25-species mixture, and a total of 50 random species-mixtures comprising 2–16 species. There were 4 sites totally and two at each elevation used in the study. Litter bags were randomly distributed within each location at spacings of 20–30 cm apart on 20 June 2009. Litter samples with bag were cleaned quickly with tap water to remove dust of bag surface, dried at 65 °C for 48 h, and weighed on 21 June 2010.

2.3. Data calculation

Chemical traits in litter were determined in 4 sub-samples. Ash-free dry mass (AFDM) was determined after combustion of subsamples at 550 °C for 4 h. Four unexposed samples of each litter species were used to determine the initial dry mass and AFDM in the same way. The initial carbon and nitrogen (N) content of the 25 litter species was determined as per the methods described in AOAC (1984). Litter chemistry was measured by sequentially digesting material into fractions that correspond with soluble cell contents, cellulose, hemicellulose, lignin and acid insoluble ash

Table 1
ANOVA of effects of species composition at each species richness level and elevation on mass loss and non-additive effects of mixed litter mass loss.

Species richness	Model	Mass loss			Non-additive effect		
		df	*F*	*P*	df	*F*	*P*
1	Elevation (*E*)	1	211.822	<0.001	/	/	/
	Composition (*C*)	24	26.552	<0.001	/	/	/
	E × *C*	24	1.607	0.078	/	/	/
2	Elevation (*E*)	1	172.265	<0.001	1	1.137	0.293
	Composition (*C*)	18	19.184	<0.001	18	5.307	<0.001
	E × *C*	18	1.109	0.381	18	1.296	0.245
4	Elevation (*E*)	1	59.740	<0.001	1	0.199	0.660
	Composition (*C*)	9	3.165	0.015	9	3.439	0.010
	E × *C*	9	1.147	0.378	9	0.722	0.684
8	Elevation (*E*)	1	41.684	<0.001	1	4.323	0.049
	Composition (*C*)	10	4.914	<0.001	10	6.038	<0.001
	E × *C*	10	0.721	0.927	10	0.646	0.760
16	Elevation (*E*)	1	30.891	<0.001	1	3.932	0.061
	Composition (*C*)	9	1.863	0.118	9	2.336	0.055
	E × *C*	9	1.279	0.307	9	1.411	0.248

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(Van Soest, 1963; Ryan et al., 1990) on a forage fiber analyzer (ANKOM 200, Macedon, New York, USA). All nutrient concentrations were calculated on the basis of AFDM. Decomposition was determined as percentage litter *AFDM* mass loss over the duration of the experiment.

We calculated the rate of mass loss as the difference between the mass of litter initially present in the litterbag and the mass of the remaining litter on a given harvest date divided by the amount of litter initially present. Observed (O) and expected (E) mass loss of litter mixture were expressed as a fraction of initial litter mass. Expected mass loss was defined as the mean mass loss of the component litter species decomposing in isolation weighted by their relative initial mass in the mixture (Gartner and Cardon, 2004; Lecerf et al., 2007). Deviation between the observed (O) and expected (E) mass loss in litter mixtures was calculated as difference $O - E$. Values not different from zero indicate additivity, whereas positive and negative values suggest synergistic and antagonistic effects on decomposition, respectively. Instead of calculating relative deviations (i.e. $(O - E)/E \times 100\%$ (Wardle et al., 1997; Loreau, 1998)), E was used as a covariate in statistical analysis, which provides a formal test for the influence of E on $O - E$ (Lecerf et al., 2007).

2.4. Soil temperature and soil moisture along the elevation gradient

At the center of each plot weather stations (Onset Computer Corporation, Japan) were used to monitor soil temperature and soil moisture at 5 cm soil depth. The sensors were connected to a CR1000 datalogger (Campbell Scientific, Logan, Utah, U.S.A), and soil temperature and soil moisture were measured every 1 min, and then 30-min averages were stored. These results were reported by Xu et al. (2010). In briefly, the annual average soil temperature were 3.3 and 0.1 °C, and soil moistures were 18.6 and 8.1% at 5 cm at 3200 and 3800 m, respectively (Xu et al., 2010).

2.5. Temperature sensitivity (Q_{10})

Temperature is the main factor that affects litter decomposition in the alpine region (Luo et al., 2010). Therefore, based on the litter mass losses at different elevations, the temperature sensitivity of litter mass loss (Q_{10}) was calculated using the difference between the mean annual soil temperatures (T) at 5 cm soil depth between the two elevations (Howard and Howard, 1993; Kirshbaum, 1995) at each level of litter species richness:

$$Q_{10} = \left(\frac{R_2}{R_1}\right)^{\frac{10}{T_2 - T_1}}$$

where R_1 and R_2 indicate mean litter mass loss at T_1 (i.e. 3800 m) and T_2 (i.e. 3200 m) temperature levels, respectively.

2.6. Statistical analyses

Two-way analysis of variance (ANOVA) (SPSS 13.0, SPSS Inc. Chicago, Illinois, USA) was used to assess the significance of the impacts of elevation and litter species richness and/or functional group (i.e. graminoids, forbs and shrubs), and their interactions on observed litter mass loss. Paired t tests were used to assess whether observed and expected mass loss in individual mixed species litter bags differed at each of the two study elevations. Hierarchical ANCOVA was used to test whether the difference $O - E$ depended on elevation, litter species richness, species composition for each species richness, and the interaction between elevation and species richness. Using Type III sums of squares, expected litter mass loss (E) as a covariate was introduced in the ANCOVA on the difference $O - E$ in order not to interfere with correlated factors, such as species composition of litter mixtures (Kaneko and Salamanca, 1999). One-way ANOVA was used to assess the significance of the impact of litter species composition or functional group on the Q_{10} value. Regression analyses were carried out separately at both elevations using nonlinear curve fitting between litter mass loss, or $O - E$, or Q_{10} and litter species richness. All significances are reported at 0.05 level in the text.

3. Results

3.1. Response of mixed litter decomposition to species richness

Generally, the mean annual decomposition rates for all species richness were about 34.8 and 27.6% at 3200 and 3800 m, respectively (Fig. 1A). However, litter species richness ($F_{5,\ 296} = 4.807$, $p < 0.001$) and elevation ($F_{1,\ 296} = 51.555$, $p < 0.001$) significantly affected litter mass loss, whereas there was no interaction between them ($F_{5,\ 296} = 0.316$, $p = 0.903$). Litter mass loss increased with increasing litter species richness at both elevations, but the dependency of litter mass loss on litter species richness (i.e. slope of the regression equation) was higher at 3800 m than at 3200 m (Fig. 1A). The mean litter mass loss with absolute single species and mixed litters increased by 28% at 3200 m compared with that at 3800 m, whereas the mean relative difference of litter mass loss between 3200 and 3800 m decreased with increasing litter species richness (Fig. 1B), being 44.0, 41.5, 39.9, 29.7, 28.9 and 13.5% at species richness levels of 1, 2, 4, 8, 16 and 25, respectively.

The non-additive effects of the MLML were significantly affected by litter species richness ($F_{4,\ 193} = 7.173$, $p < 0.001$), but not by elevation ($F_{1,\ 193} = 1.167$, $p = 0.281$) and their interaction ($F_{4,\ 193} = 0.354$, $p = 0.841$). The magnitude of non-additive effects of MLML increased with increasing litter species richness, while the dependency of non-additive effects of MLML was greater at 3800 m than at 3200 m (Fig. 1C). Generally, both synergistic and antagonistic effects of litter mixing on mass loss were found at 3200 and 3800 m, and antagonistic effects were dominant for species richness 2 and 4 at 3800 m (Fig. 1C). Species richness nearly significantly affected the mean temperature sensitivity of MLML (i.e. Q_{10} value) ($F_{5,\ 153} = 1.947$, $p = 0.090$), and the mean Q_{10} value decreased with increasing litter species richness (Fig. 1D).

3.2. Response of litter decomposition to species composition

We analyzed the role of species composition on MLML for each species richness level. The effect was significant in four out of the five species richness levels but not for species richness 16 (Table 1). There were no significant interactions between species composition and elevation for all litter species richness levels (Table 1).

Species composition significantly influenced the non-additive effects of MLML for each species richness level except for 16 species richness, but the effect of elevation was only found when species richness was 8 (Table 1). There were no interactions between species composition and elevation on the non-additive effects of MLML (Table 1). When species richness was less than 8, there were significant effects of species composition on the relative difference of MLML between elevations and mean Q_{10} values, but these effects of species composition disappeared when species richness was 8 or 16 (Table 2).

3.3. Effect of shrubs on mixed litter decomposition

The mean litter decomposition rate was lower for the shrub functional group than for graminoids and forbs functional groups

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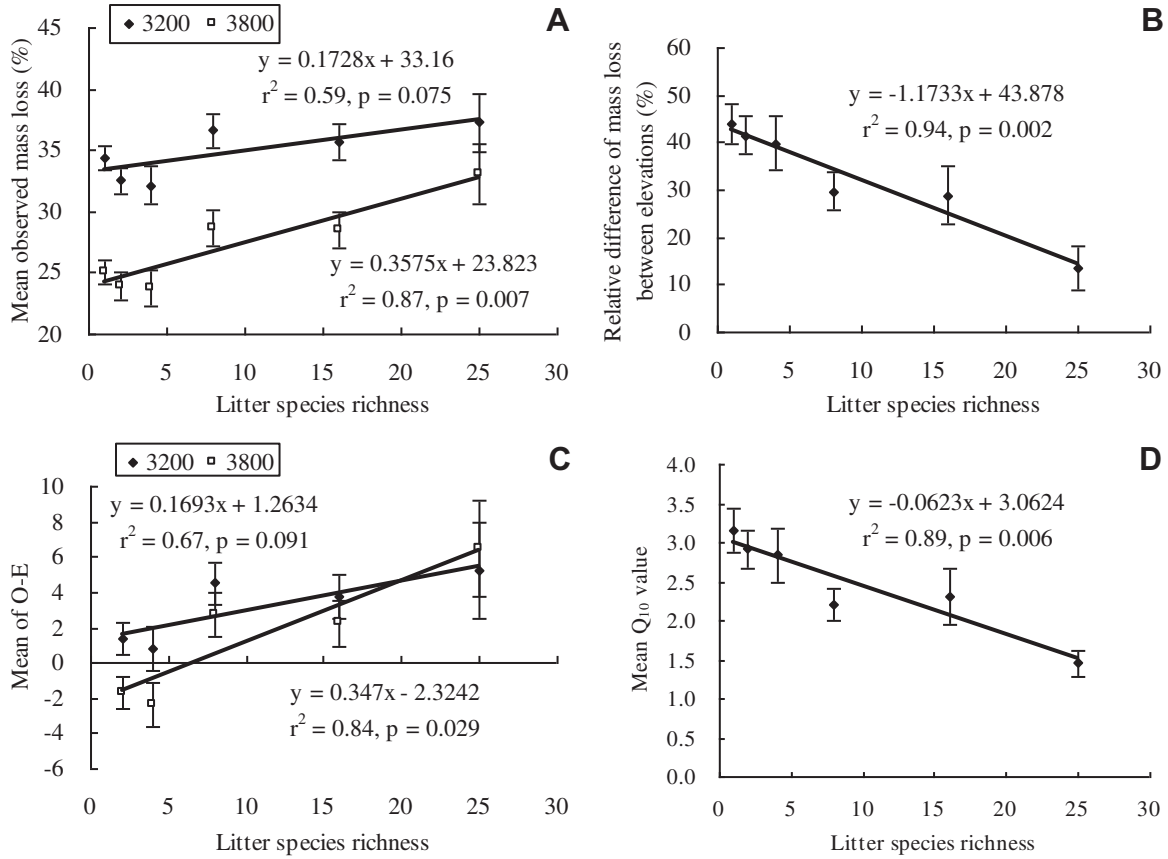

Fig. 1. The effects of litter species richness on mean observed mass loss (A), relative difference of mass loss between elevations (B), non-additive effect (C) and temperature sensitivity of mixed litter mass loss (Q_{10}) (D). Bars in Figures are standard errors.

(Fig. 2A), whereas the mean Q_{10} value of litter decomposition was greater for the shrub functional group compared with forbs and graminoids functional groups (Fig. 2B). The effect of shrubs on the non-additive effects of MLML was inconsistent for 2-species mixed litters (Fig. 2C) and 4-species mixed litters (Fig. 2D), and both synergistic and antagonistic effects were found at 3200 and 3800 m. The mean Q_{10} values were significantly lower for mixed litter with shrub than for litter of the shrub alone, and the effect of shrubs on the mean Q_{10} values of MLML was relatively stable when the species richness of the mixed litter with shrub was more than 4 (Fig. 2B).

4. Discussion

4.1. Effect of species richness

Inconsistent results have been obtained with respect to the effects of litter species richness on mixed litter mass loss (Wardle et al., 1997; Hector et al., 2000; Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Lecerf et al., 2007; Kominoski et al., 2007; Schindler and Gessner, 2009; Gessner et al., 2010). Many experiments reported to date only have included a range of species richness from two to four which strongly limits a thorough assessment of species richness effects and a more general description of litter mass loss as a function of litter species richness (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Kominoski et al., 2007; Gessner et al., 2010). To our knowledge, this is the first study that involved 25 dominant litter species with different physical structures and chemical compositions in the alpine meadow (SI Table 1), and our results show that non-additive effects were different at lower species richness levels from those at higher species richness levels at the same elevation (Fig. 1C). In our study both synergistic and antagonistic effects of litter mixing on decomposition were found at 3200 and 3800 m (Fig. 1C). Generally, synergistic effects were greater than antagonistic effects (i.e. about 45–55% vs. 27–31%) at 3200 and 3800 m. Therefore, climate and environmental change do not affect the direction of non-additive effects in the alpine region. Non-additive mixing effects are likely a consequence of complex interactions between litter species mediated by abiotic factors and litter consumers (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Gessner et al., 2010). This result may be attributed to two reasons. The first reason is that mixing litter of different chemical and physical properties alters the resource qualities and physical habitat complexity within leaf packs, resulting in changes in decomposition rates and decomposer abundance and activity (Hector et al., 2000; Kominoski et al., 2007, 2009; Sanpera Calbet et al., 2009). Thus, different litter mixtures led to great differences in chemical components (i.e. lignin and N) and

Table 2
ANOVA of the effects of species composition at each species richness level on relative difference between elevations and the temperature sensitivity (Q_{10} value) of litter mass loss.

Species richness	Relative difference of litter decomposition between elevations			Q_{10}		
	df	*F*	*P*	df	*F*	*P*
1	24	8.430	<0.001	24	13.250	<0.001
2	18	4.151	<0.001	18	5.060	<0.001
4	9	4.296	0.016	9	3.064	0.048
8	10	2.118	0.117	10	1.884	0.157
16	9	1.121	0.427	9	0.926	0.541

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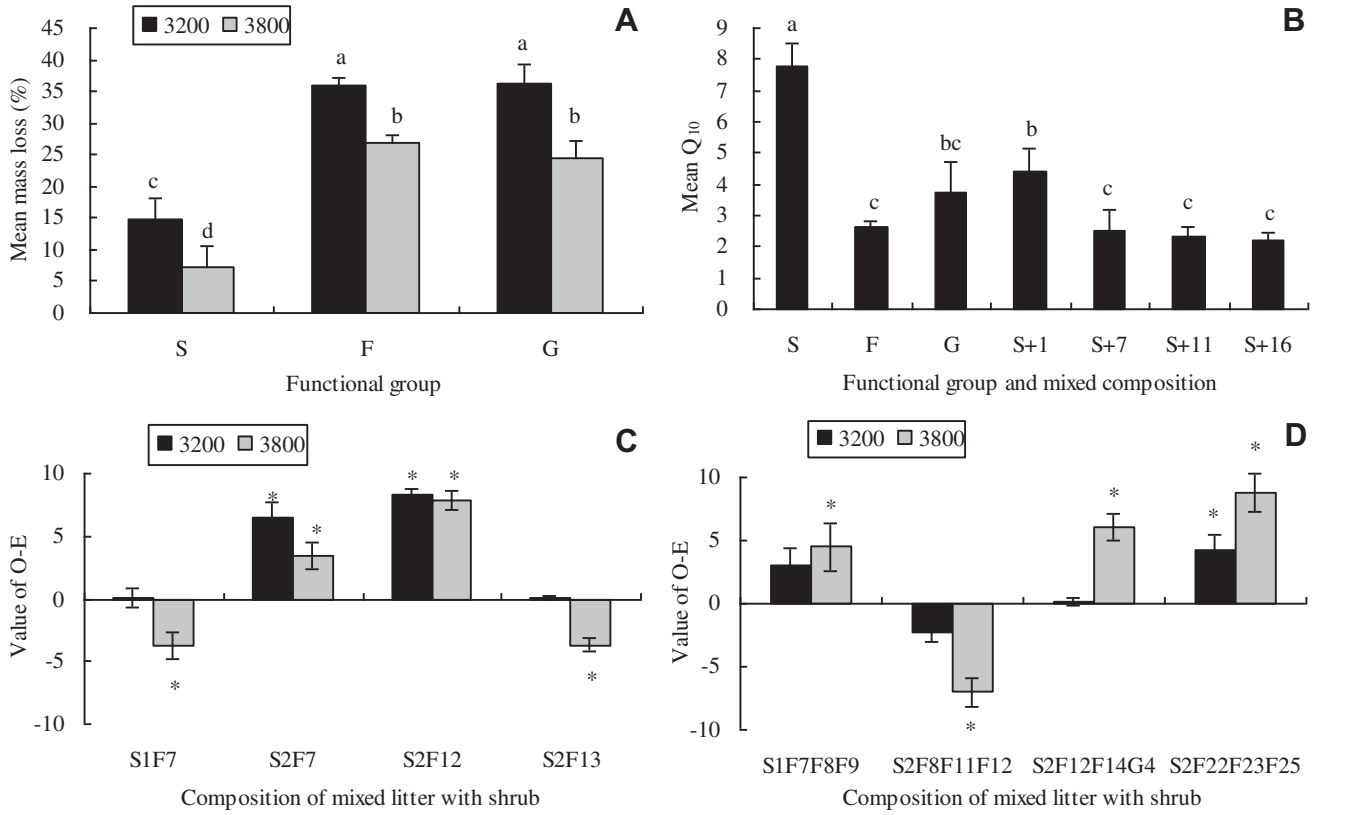

Fig. 2. The effects of functional group and their mixtures on litter mass loss (A), temperature sensitivity of mixed litter mass loss (Q_{10}) (B) and non-additive effects (C and D) and S: shrub; F: forbs; G: graminoids. In B, S + 1, S + 7, S + 11 and S + 16 means one shrub mixed with 1, 7, 11 and 16 other species of either forbs or graminoids, respectively. The number followed by a letter in C and D is the order of species shown in SI Table 1. Bars are standard errors in the Figures. Different letters among life forms in A and B and asterisk between observed and expected values in C and D indicate significant differences at 0.05 level.

their ratios which controlled litter decomposition rates (Melillo et al., 1982; Murphy et al., 1998). The second reason is that one of the mechanisms behind the litter mixture effects on decomposition involves active microbial nutrient transfer and passive transfer via leaching with water flow from one litter type to another (Tiunov, 2009; Gessner et al., 2010). Based on stoichiometric theory (Frost et al., 2005), the transfer of nutrients and carbon compounds from one litter type to another by either passive or active means could increase or decrease microbial exploitation of litter species with low concentrations of the transferred leaf constituents, leading to either accelerated or decelerated decomposition (Hättenschwiler et al., 2005; Gessner et al., 2010). In our study, active microbial nutrient transfer may override passive transfer from one litter type to another via leaching water flows due to lower temperatures and aridity at 3800 m compared with 3200 m (Xu et al., 2010). Thus, slowly released nutrients may be kept for a longer time inside the remaining litter which may result in a greater dependency of the non-additive effect on litter species richness. In contrast, at 3200 m due to higher temperature and rainfall (Xu et al., 2010), quickly released nutrients will be leached soon via rainfall before microorganisms use them, which may cause less dependency of the non-additive effect on litter species richness compared with 3800 m.

Many studies show that warming increases litter mass loss (Murphy et al., 1998; Fierer et al., 2005; Cornelissen et al., 2007; Xu et al., 2010; Luo et al., 2010). These effects are likely to be most manifest in cold biomes (high-latitude and high-elevation sites) because predicted warming is greatest, and decomposition is strongly temperature limited in these regions (Aerts, 2006). Most existing studies have been conducted using single-species litter, whereas some studies hypothesize (Gartner and Cardon, 2004; Hättenschwiler et al., 2005) that it is hard to predict the response of litter decomposition to climate change in real natural ecosystems where many litter species are mixed if predictions are based on litter decomposition studies with single-species litter. Our study is the first to indicate that high species richness reduces the increasing magnitude of MLML induced by environmental change (Fig. 1B). For example, although high species richness increased MLML at both elevations, its response to increasing species richness was almost 2 times as large at 3800 m compared to 3200 m (Fig. 1A). Similar to previous reports that higher species richness results in greater stability of primary production (Tilman et al., 2006), we found that greater species richness causes a lower temperature sensitivity of MLML (Fig. 1D), implying that high species richness may increase the stability of MLML under future warming conditions.

4.2. Effect of species composition

Many studies show that the number of litter species is much less important in controlling litter mass loss than the taxonomic composition of litter mixture (Wardle et al., 1997; Kominoski et al., 2007; Schindler and Gessner, 2009; Swan et al., 2009). The functional trait approach represents a promising framework to explain patterns of non-additive litter mixing effects across species mixtures (Epps et al., 2007; Meier and Bowman, 2008; Hoorens et al., 2010). It is expected that non-additive litter mixing effects will be stronger in litter mixtures consisting of species with dissimilar physical and chemical traits than in litter mixtures made of functionally equivalent species (Schindler and Gessner, 2009).

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However, some studies suggested that the presence of a recalcitrant litter species inhibits microbial activity and subsequent decomposition of a fast decomposing species (Kominoski et al., 2007). We only found synergistic effects in 2 out of 4 2-species mixed litters using litter from a shrub (i.e. *Dasiphora fruticosa* or *Hippophae tibetica*) and a forb at 3200 m, whereas both synergistic and antagonistic effects were observed at 3800 m site (Fig. 2C). When mixed species richness with shrub increased to 4, significant synergistic effects were found in 1 and 3 combinations out of 4 mixed litters at 3200 and 3800 m, respectively (Fig. 2D). These results indicate that the effects of litter mixture on litter mass loss are interactions between litter composition and climate and environmental conditions (Table 1), which is consistent with previous reports (Lecerf et al., 2007). Moreover, the incorporation of shrubs with high recalcitrant components involved synergistic and antagonistic effects depending on the traits of the mixed litter species, and the role of shrubs decreased with increasing species richness (Fig. 2). Similar results were observed for 4 kinds of litter mixtures containing grasses (i.e. *Carex scabrirostris*, *Kobresia tibetica* and *Elymus nutans*) mixed with forbs at species richness 2 at both 3200 and 3800 m. There were 2 and 3 synergistic effects, and 5 and 6 antagonistic effects for 11 kinds of forbs–forbs mixtures with species richness 2 at 3200 and 3800 m. Therefore, species-specific responses to litter mixture may actually be more common than anticipated but have remained largely undetected because species were not separately analyzed (Hättenschwiler et al., 2005). Our study confirmed that the effects of litter composition on mass loss varies with climate change, and that its role decreases with increasing species richness, because we found that the effect of species composition on mass loss was significant (i.e. sampling effect (Hector et al., 2002)) when species richness was less than 8 (Table 1), whereas the effect of shrubs on MLML decreased with increasing species richness (Fig. 2B). Previous studies may amplify the effect of species composition on MLML (Wardle et al., 1997; Kominoski et al., 2007; Schindler and Gessner, 2009; Swan et al., 2009) because they report results of mixtures of less than 8 species.

Previous studies reported that warming decreased species richness by about 30% and proportion of grasses in the community, but increased shrubs and/or forbs in alpine (Klein et al., 2004, 2007) and tundra regions (Post et al., 2008). However, species losses and extinctions are predicted to be nonrandom (Huston et al., 2000). If we can predict which species are expected to be lost given specific environmental changes, knowing how those species interact with other species to influence ecosystem function is of paramount importance (Gartner and Cardon, 2004; Hättenschwiler et al., 2005), because the temperature sensitivity of litter mass loss is different for different species or functional groups (Gartner and Cardon, 2004; Hättenschwiler et al., 2005; Cornelissen et al., 2007). Therefore, the net effect of future warming on MLML in alpine regions will depend on the balance of the following positive and negative feedbacks: (1) warming increases MLML (Xu et al., 2010; Luo et al., 2010; Fig. 1A in the study); and (2) decreasing species richness especially under shrub invasion induced by warming in alpine meadows (Klein et al., 2004, 2007) may decrease MLML, but may also cause a higher temperature sensitivity of MLML. These contrary effects may compensate each other which will keep MLML relatively stable in alpine regions under future warming conditions.

4.3. Conclusions

In summary, high species richness significantly increased litter mass loss and its non-additive effects, but warming decreased the dependencies of MLML and its non-additive effects on litter species richness. The effects of species composition on litter mass loss and its temperature sensitivity were significant when species richness was less than 8. Generally, environmental change did not change the direction and magnitude of non-additive effects. This study is critical to understanding MLML and to modeling carbon and nutrient processes in terrestrial ecosystems under future climate change.

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Appendix A. Supporting information

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2012.08.009.

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