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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Interactive responses of grass litter decomposition to warming, nitrogen addition and detritivore access in a temperate old field

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Abstract Plant litter decomposition has been studied extensively in the context of both climate warming and increased atmospheric N deposition. However, much of this research is based on microbial responses, despite the potential for detritivores to contribute substantially to litter breakdown. We measured litter mass-loss responses to the combined effects of warming, N addition and detritivore access in a grass-dominated old field. We concurrently assessed the roles of litter treatment origin vs. microenvironment (direct warming and N-addition effects) to elucidate the mechanisms through which these factors affect decomposition. After 6 weeks, mass loss increased in N-addition plots, and it increased with detritivore access in the absence of warming. After 1 year, warming, N addition, and detritivore access all increased litter mass loss, although the effects of N addition and warming were non-additive in the detritivore-access plots. For the litter-origin experiment, mass loss after 6 weeks increased in litter from N-addition plots and warmed plots, but unlike the overall decomposition response, the N-addition effect was enhanced by detritivore access. Conversely, for the microenvironment experiment, detritivore access only increased mass loss in unfertilized plots. After 1 year, detritivore access increased mass loss in the litter-origin and microenvironment experiments, but there were no warming or N-addition effects. Overall, our results provide support for a substantial role of detritivores in promoting litter mass loss in our system. Moreover, they reveal important interactions between litter origin, microclimate and detritivores in determining decomposition responses to global change.

Keywords Climate warming · Detritivory · Litter origin · Nitrogen deposition · Old field

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Introduction

Responses of soil processes remain a major uncertainty in attempts to predict ecosystem responses to global change (Pendall et al. 2008). Changes to the dynamics of plant litter decomposition are an important component of these responses (Singh and Gupta 1977; Vitousek 1982), with the turnover of plant litter contributing to C flux between terrestrial and atmospheric pools (Chapin et al. 2002). Litter decomposition is also the dominant source of nutrients in many terrestrial ecosystems, and it thus influences primary productivity, because plant C turnover and nutrient mobilization {e.g. N mineralization) are closely linked (McGill and Cole 1981). In addition, litter can modify soil microclimate (Beatty and Sholes 1988; Deutsch et al. 2010), and interfere with the establishment of newly germinated plants (Bosy and Reader 1995).

Overall, litter mass loss is correlated with climate, tissue chemistry and soil biology (Swift et al. 1979; Seastedt 1984; Aerts 1997), all of which can be influenced by drivers of global change, such as climate warming and N deposition (Knorr et al. 2005; Aerts 2006; Blankinship et al. 2011). Warming effects on decomposition can occur directly through changes to microbial activity and extracellular enzyme activity (Wan et al. 2007; Brzostek et al. 2012), and indirectly as a result of soil drying (Allison and Treseder 2008) or via changes to plant tissue quality (An

et al. 2005). Likewise, N addition can directly alter microbial activity (Carreiro et al. 2000), or may influence litter chemistry, altering its subsequent decomposition (Henry et al. 2005).

In addition to the influence of bacteria and fungi on organic matter decomposition (Pritchard 2011), soil detritivores also contribute substantially to litter breakdown (Swift et al. 1979; Wolters 2000; Wall et al. 2008; García-Palacios et al. 2013). Soil fauna can respond to warming and N addition (Blankinship et al. 2011; Gan et al. 2013; Holmstrup et al. 2012), but the magnitude and direction of these responses can differ considerably from those of microbes. For example, in response to N addition, specific groups of soil fauna can be particularly sensitive to NH_4^+ toxicity (Wei et al. 2012) or salt desiccation (Lohm et al. 1977). Furthermore, the combined effects of factors such as warming and fertilization on soil organisms can vary substantially from their individual effects (Sjursen et al. 2005). Evidence from microcosm experiments suggests that decomposition responses to global change treatments, such as warming and increased CO_2 concentration, can be influenced strongly by detritivore effects (Coûteaux et al. 1991; Rouifed et al. 2010). Nevertheless, many studies examining global change effects on decomposition often exclude soil fauna, and macrofauna in particular, which could not only result in an underestimate of litter turnover, but the effects of the latter could interact with the global change factors (see Wall et al. 2008).

The time scale of responses may further complicate the relationship between abiotic and biotic controls over decomposition. For example, positive responses of C turnover to warming can occur shortly after litter incubation (Xu et al. 2012b), yet changes in C pools, microbial biomass and C use efficiency can negate the effect of warming over longer time scales (Bradford et al. 2008; Allison et al. 2010). Likewise, despite short-term positive effects of N addition on the decomposition of newly senesced litter, the turnover of recalcitrant material that accumulates as decay progresses can be slowed by N addition (Fog 1988), possibly as a result of inhibition of ligninolytic enzyme activity (Carreiro et al. 2000). The role of soil fauna in litter processing can vary by season (Wu et al. 2009) or stage of decay (Tian et al. 1998; Xin et al. 2012), and owing to evidence of low functional redundancy (Ayres et al. 2009a), these observations may reflect temporal shifts in detritivore community composition (Levings and Windsor 1996; Zhu et al. 2010). The consequences of this temporal variation may be further exacerbated by interspecific variation in detritivore sensitivity to factors such as warming and drought (Kardol et al. 2011).

The objective of this study was to examine the effects of warming, N addition and detritivore access on litter mass loss, both after 6 weeks and 1 year, in a temperate old field. In particular, we were interested in identifying interactions between the global change treatments and detritivore access, because these interactions would indicate that global change factors can affect litter decomposition indirectly by affecting detritivore activity. Furthermore, these interactions would suggest there are biases in global change decomposition experiments employing mesh litter bags, where detritivore access to litter is restricted. In addition to returning litter collected from the global change experiment to the respective treatment plots, we performed two alternative transplant experiments to further explore the mechanisms explaining mass-loss responses in the global change experiment; we transplanted litter collected from the treatment plots into a common, untreated environment (i.e. to isolate the effects of litter treatment origin), and also transplanted untreated litter from the field into the treatment plots (i.e. to isolate the direct effects of warming and N addition on mass loss).

Materials and methods

Study site

The experiment was conducted at an old field site in London, ON, Canada (43°1′46″N, 81°12′52″W) between October 2010 and October 2011. The site is a former agricultural field that has not been plowed or mowed in over 25 years. Dominant vegetation at the site includes two grass species, Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.), with the forb Canada thistle (*Cirsium arvense* L.) and legume bird's-foot trefoil (*Lotus corniculatus* L.) present in patches. The mean annual temperature for the site is 7.5 °C (8.1 °C over the experimental period), with a low monthly mean of −6.3 °C (January) and a high monthly mean of 20.5 °C (July), and mean annual precipitation of 981 mm (1,100 mm over the experimental period), with a low monthly total of 61 mm (February) and a high monthly total of 97 mm (December) (Canadian Climate Normals 1971–2000, Environment Canada, National Climate Data and Information Archive). The soil is classified as silt loam glacial till (Hagerty and Kingston 2011), with pH 7.6 and is composed of approximately 50 % sand, 41 % silt, and 9 % clay (Bell et al. 2010).

Warming and N-addition experiment

Warming and N-addition treatments were applied to 1-m^2 circular plots set up in a factorial block design, including two levels of warming (ambient and heated) crossed with two N treatments (control and N fertilized). All four treatment combinations were replicated across ten different blocks for a total of 40 plots; see Turner and Henry (2009)

for full details of the experiment. Increased temperature of approximately 2–3 °C at the soil surface was achieved using 150-W ceramic infrared heaters (Zoo-Med Laboratories, San Luis Obispo, CA) which mimic solar heating without the production of photosynthetically active radiation (Shen and Harte 2000). The plots were warmed continuously since the initiation of the experiment in late 2006. Soil temperature and moisture data were collected hourly using 107-BAM-L temperature probes at 2-cm depth and CS-616 time domain reflectometers at 0- to 15-cm depth, respectively (Campbell Scientific). N treatments began in early 2007 and were added annually in two forms: a 20 kg N ha^{-1} pulse of aqueous NH_4NO_3 added at snow melt in early spring, and 40 kg N ha^{-1} of slow-release NH_4NO_3 pellets added in early summer. Application rate was based on estimates of increased N deposition expected for this area by 2050 (Galloway et al. 2004). Previous observations from this experiment indicate that this site is N limited, with N-fertilized and non-fertilized plots differing in aboveground productivity (1,150 vs. 900 g m^{-2}), foliar N concentration (1.65 vs. 1.45 %), and soil N content (18.2 vs. 13.2 g kg^{-1}; Turner and Henry 2009; Hutchison and Henry 2010). Likewise, aboveground productivity has increased by as much as 20 % in response to heating in some years (Hutchison and Henry 2010).

Sample collection and litter bag design

In early September 2010, senesced grass tissue was collected from the global change treatment plots, as well as from similar areas in the same field outside of the plots. Only standing dead material was collected in order to avoid including loose surface litter from previous years' growth. The litter was air dried for 3 days at room temperature. A sub-set of control samples were dried at 65 °C for 3 days in order to estimate initial sample dry weights prior to placement in the field. Litter subsamples prepared for the decomposition experiment were pooled, with a consistent 3:1:1 ratio of *B. inermis* stems to *B. inermis* leaves to *P. pratensis* tillers (approximately 500 mg air-dried mass, total) in order to standardize litter content among subsamples. Two different types of litter containment techniques were employed in order to manipulate detritivore access to the material. A detritivore-restriction treatment was achieved using standard nylon mesh litter bags (10 × 5 cm bag size, 100-µm mesh size, hereafter referred to as 'mesh' samples), which allowed for the exclusion of both meso- and macro-soil fauna. In order to allow free access to litter by detritivores, a second set of samples was constructed without the use of mesh by securing both ends of each litter sample using spring-loaded paper clamps (hereafter referred to as 'open' samples). The method of using bags with larger mesh sizes in order to allow detritivore access was not appropriate for our purposes because individual grass pieces were thin, and larger holes would have resulted in the loss of material, whereas the open samples kept the ends of each litter segment clamped in place. Litter pieces used for open samples were approximately 9 cm in length, similar to the length of pieces used in the mesh bags.

The accuracy of litter bag decomposition results can be biased by artifacts arising from changes to litter microclimate (Suffling and Smith 1974; Kampichler and Bruckner 2009; Bokhorst and Wardle 2013), and in our study there was a risk that such artifacts could be confounded with differences in detritivore access between open and mesh-enclosed samples. As a control to identify potential differences in the direct effects of the mesh bags vs. clamps on litter decomposition, the mass loss of mesh vs. open samples in the absence of soil fauna (through the use of plastic exclosures) was compared in the field, both over 6 weeks ($n = 5$) and over 1 year ($n = 5$). These controls were based on an approach suggested by Bradford et al. (2002) for testing for the effects of different mesh sizes on mass loss in the absence of soil fauna. There was a lack of a difference in mass loss between open and mesh sample controls after both 6 weeks [$P = 0.289$; open = 24.46 % (±0.02 %); bag = 27.29 (±0.02 %)] and 1 year [$P = 0.667$; open = 55.11 % (±0.03 %); bag = 57.29 % (±0.03 %)], which suggests that the differences we observed between open and mesh-enclosed samples in the main experiment were caused primarily by detritivore access. However, in the case of the open samples, affixing the material at the ends resulted in approximately 5 % of the material being obstructed by the clamp contact points and hence restricted from detritivore access. Likewise, because microfauna have a body size <100 µm (Swift et al. 1979), this size class would not have been restricted from the mesh-enclosed samples. Therefore, the detritivore-access effects we observed were likely a conservative estimate of actual soil faunal effects. Lastly, although litter fragmentation could have potentially caused an overestimate of litter turnover in the open samples, upon retrieval these samples were intact (i.e. the litter bundles spanned the length of the opening between clamps), suggesting that mass loss due to breakage was minimal.

Litter mass-loss experiments

Litter samples (both mesh and open) removed from the experimental plots were subsequently returned to their corresponding treatment plots (e.g. litter from N-addition plots was returned to the N-addition plots; $n = 10$ each for both mesh and open samples for each treatment combination and sampling period; Fig. 1). In order to clarify the mechanisms (i.e. litter origin vs. environmental conditions) underlying the treatment effects on litter mass loss, in addition to the aforementioned non-transplanted 'integrated response'

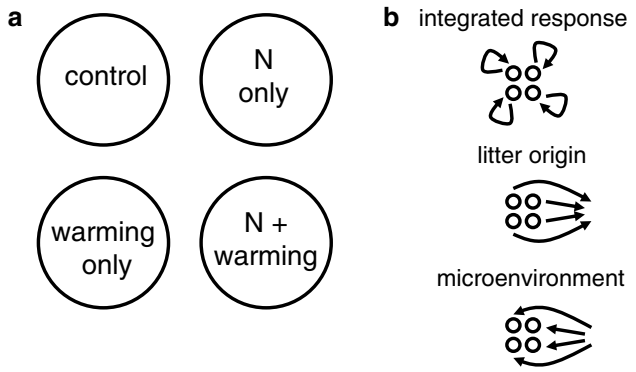

Fig. 1 Schematic diagram (not to scale) of **a** the four treatment combinations in the warming and N-addition experiment and **b** the transfer of both open and mesh-enclosed samples (each *arrow*) between the warming and N-addition plots (*circles*) and the untreated field (*area outside the circles*) for the integrated response, litter-origin and microenvironment experiments. There were 40 plots in total ($n = 10$ each for both mesh and open samples for each treatment combination, sampling period and transplant experiment)

samples, litter transplants were used for two alternative experiments: a litter-origin experiment, which involved the transplantation of litter from global change treatment plots into a common garden in the field, and a microenvironment experiment, which involved the transplantation of control litter from the surrounding field into the global change plots ($n = 10$ each for both mesh and open samples for each treatment combination, sampling period and transplant experiment; Fig. 1). The common garden was a 4 × 1.5-m patch placed in amongst the experimental blocks at the field site. It featured an intact plant community and litter layer, and thus the environmental conditions experienced by the transplanted litter would have been consistent with those of the control plots in the warming and N-addition experiment. All litter samples were placed in direct contact with the soil surface and then covered using the loose litter that had been displaced to insert them. Litter samples were placed in the field on 16 October 2010 and were subsequently recovered at two different time periods; one following 6 weeks and another after 1 year. A total of ten replicate litter samples (one per block) was used for each treatment combination for each of the two sampling dates, resulting in 480 total litter samples for the entire study. Following each collection period, litter samples were oven-dried at 65 °C for 3 days and then weighed. Final dry weights were compared with the water mass-corrected initial air dry weights in order to determine % mass loss.

Data analyses

For each of the six combinations of the two sampling dates and the three transplant configurations, we used three-way fixed-effects ANOVAs to test for the effects on mass loss of the fixed factors (N addition, warming, and detritivore access) as well as their interaction terms, with plot identity, nested in warming and N addition, added as a random factor to account for the placement of the mesh and open samples in the same plots. We used % mass loss as the dependent variable which was calculated as 1-(final dry mass/initial dry mass). All mass-loss data were normalized by square root transformation prior to analysis. For soil temperature and moisture we used two-way fixed-effects ANOVAs to test for the effects of warming and N addition, followed by Tukey's tests to determine significantly different treatment combinations. Our analyses were conducted using the Fit model platform in JMP 4.0 (SAS Institute, Cary, NC).

Results

Integrated response experiment

For the litter samples collected from and returned to the plots of the warming and N-addition experiment, after 6 weeks of decomposition, mass loss varied on average from 13 to 23 % (Fig. 2a). There was 4 % greater mass loss in N-fertilized plots than in control plots ($P = 0.002$; Table 1; Fig. 2a; all percent treatment effects are reported as absolute changes in % mass loss). Additionally, there was a significant interaction between warming and detritivore access ($P = 0.002$; Table 1), with open samples experiencing 5 % greater mass loss than mesh samples in ambient temperature plots, but not in heated plots (Fig. 2a). Open samples in ambient temperature plots experienced 5 % higher mass loss than open samples in heated plots, but this did not occur for the mesh samples (Fig. 2a). After 1 year, mass loss varied on average from 47 to 75 % (Fig. 2b). There were significant increases in mass loss of 4, 16, and 20 % with warming, N addition and detritivore access, respectively ($P = 0.016$, $P = 0.003$ and $P < 0.001$; Table 1; Fig. 2b), although these main effects were not completely additive; there was a significant three-way interaction ($P = 0.045$; Table 1), whereby warming and N addition individually increased litter mass loss in the presence of detritivores, but their combined application had no additional effect (Fig. 2b).

Litter-origin experiment

For the samples collected from the warming and N addition plots that decomposed in the common garden, after 6 weeks there was a significant interaction between N addition and detritivore access ($P = 0.019$; Table 1), with

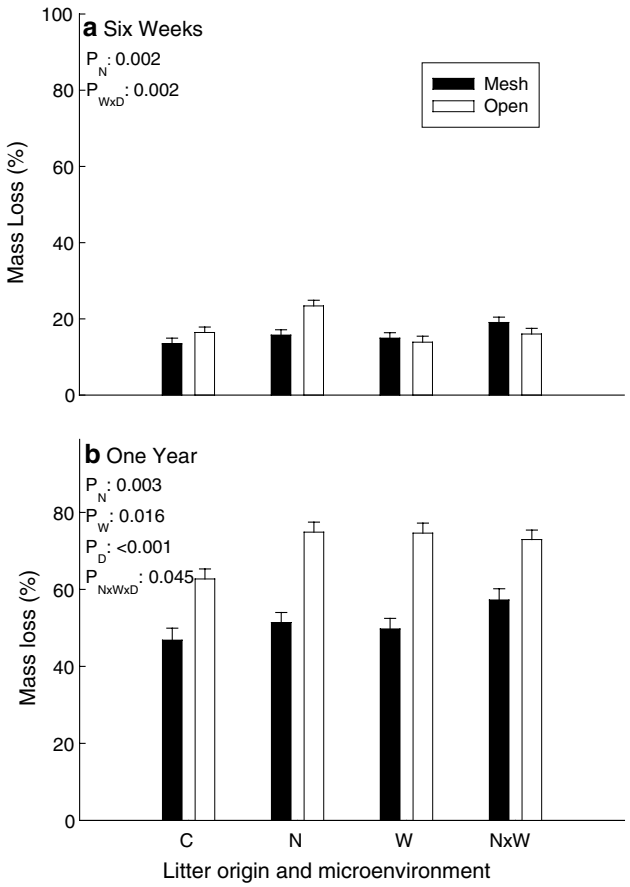

Fig. 2 Interactive effects of N addition (*N*), warming (*W*), and detritivore (*D*) access on litter mass loss (%) in the integrated response experiment after **a** 6 weeks and **b** 1 year. *Bars* represent mean ± SE, with significant three-way ANOVA results presented in the *upper-left corners*

material obtained from N-fertilized plots experiencing 10 % greater mass loss than material from non-fertilized plots when samples were open to detritivores, but not when detritivores were restricted (Fig. 3a). There was also increased mass loss of 4 % in litter from warmed plots and increased mass loss of 5 % in litter from N-addition plots ($P = 0.039$ and $P = 0.014$, respectively; Table 1; Fig. 3a). After 1 year, detritivore access increased mass loss by 6 % ($P = 0.015$; Table 1; Fig. 3b), but none of the other treatment effects were significant.

Microenvironment experiment

For the untreated litter samples decomposed in the plots of the warming and N-addition experiment, after 6 weeks there was a significant interaction between N addition and detritivore access ($P = 0.014$; Table 1), with the mass loss of open samples double that of mesh samples in non-fertilized plots, but not in N-fertilized plots (Fig. 4a). Heated plots experienced a significant increase in soil temperature and a significant decrease in soil moisture over this time (Table 2), and aboveground plant biomass had increased significantly by 44 % in response to N addition the prior summer (Henry et al. 2014). After 1 year, detritivore access increased mass loss by 21 % ($P < 0.001$; Table 1; Fig. 4b), but there were no other significant treatment effects. There was no significant effect of heating on mean soil temperature over 1 year (Table 2) because with increased melting of snow cover, the heated plots were exposed to cold air temperatures and were often colder than the ambient plots over winter. However, soil temperature was significantly

Table 1 Summary of ANOVA *P*-values for the effects of the warming (*W*), N-addition (*N*) and detritivore-access (*D*) treatments on litter mass loss after 6 weeks and 1 year

	6 Weeks			1 Year		
	Integrated[a]	Litter origin[b]	Microenvironment[c]	Integrated[a]	Litter origin[b]	Microenvironment[c]
$W_{(1,36)}$	0.297	0.039	0.534	0.016	0.412	0.882
$N_{(1,36)}$	0.002	0.014	0.601	0.003	0.352	0.986
$D_{(1,36)}$	0.254	0.716	<0.001	<0.001	0.015	<0.001
$W \times N_{(1,36)}$	0.280	0.936	0.473	0.165	0.850	0.088
$W \times D_{(1,36)}$	0.002	0.995	0.770	0.999	0.822	0.352
$N \times D_{(1,36)}$	0.819	0.019	0.014	0.711	0.253	0.794
$W \times N \times D_{(1,36)}$	0.128	0.353	0.953	0.045	0.427	0.969

df in parentheses

[a] Integrated samples were both collected from and decomposed in the treatments plots

[b] Litter-origin samples were collected in the plots but decomposed in a common garden

[c] Microenvironment samples were untreated litter decomposed in the treatment plots

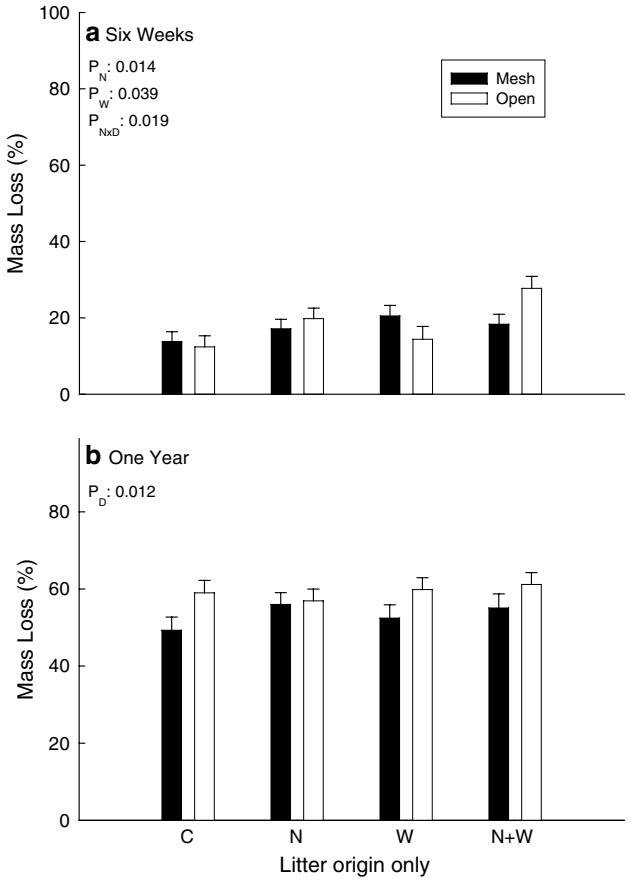

Fig. 3 Interactive effects of N, W, and D on litter mass loss (%) in the litter-origin experiment after **a** 6 weeks and **b** 1 year. *Bars* represent mean ± SE, with significant three-way ANOVA results presented in the *upper-left corners*. For abbreviations, see Fig. 2

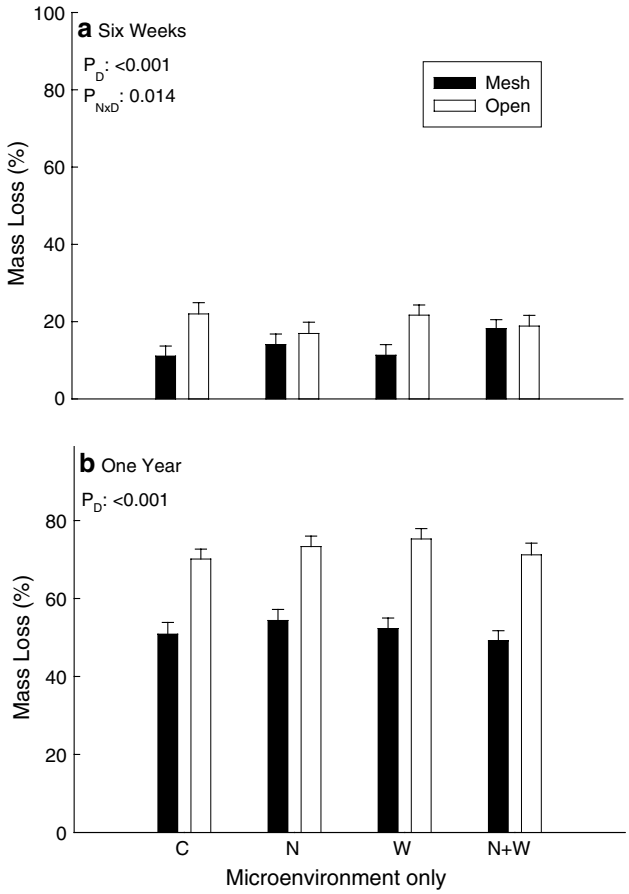

Fig. 4 Interactive effects of N, W, and D on litter mass loss (%) in the microenvironment experiment after **a** 6 weeks and **b** 1 year. *Bars* represent mean ± SE, with significant three-way ANOVA results presented in the *upper-left corners*. For abbreviations, see Fig. 2

Table 2 Summary of W and N effects on mean (±SE) soil temperature (2-cm depth) and moisture (0–15 cm) measurements recorded after 6 weeks and 1 year of litter incubation

	Soil temperature (°C)		Soil moisture (vol/vol)	
	6 weeks	1 year	6 weeks	1 year
Control	6.5 (±0.1)a	10.0 (±0.1)	0.305 (±0.007)a	0.316 (±0.006)a
W	7.5 (±0.2)b	10.3 (±0.2)	0.286 (±0.005)b	0.301 (±0.005)b
N	6.9 (±0.1)a,b	10.1 (±0.1)	0.304 (±0.004)a	0.316 (±0.005)a
W × N	7.1 (±0.2)b	10.3 (±0.1)	0.284 (±0.007)b	0.298 (±0.006)b

Significant differences within a sampling period are denoted by *different letter combinations* for each soil variable (Tukey's honest significant difference tests). For abbreviations, see Table 1

higher in the warmed plots than in the ambient plots by 0.7 °C on average following snow melt through to the end of the experiment. Aboveground plant biomass increased significantly by 14 % in response to N addition and decreased significantly by 26 % in response to warming over the summer of the decomposition experiment (Henry et al. 2014).

Discussion

Overall, our results indicated a substantial role of detritivores in promoting litter mass loss in our system, and they revealed important interactions between litter origin, microclimate and detritivores in determining decomposition responses to warming and N addition. After 6 weeks,

open litter samples experienced greater mass loss than mesh samples in ambient temperature plots, but not in heated plots, suggesting that detritivores played an important role in litter turnover in the ambient temperature plots, but their activities were reduced by warming. Warming and associated decreases in soil moisture can impose climatic stress on the detritivore community (Pritchard 2011), decreasing soil faunal abundance, biomass, and diversity (Briones et al. 1997; Blankinship et al. 2011; Xu et al. 2012a). Although we were unable to separate the direct effects of increased temperature from those of possible desiccation stress, a direct negative warming effect was unlikely, given that there was a relatively small temperature difference between warmed and ambient temperature plots (<1 °C; Table 2), and such a small temperature increase might instead be expected to increase metabolic function and consumer activity in invertebrates (Dangles et al. 2013), thus increasing the effect of detritivore access, rather than decreasing it. As for soil moisture, it is often a key regulator of litter processing by detritivores in grass-dominated systems (O'Lear and Blair 1999; Wall et al. 2008), and meta-analysis results reveal that precipitation has a significant influence on the activity of faunal detritivores at a global scale (García-Palacios et al. 2013). In our study, soil moisture from 0- to 15-cm depth was approximately 7 % lower in warmed plots than in ambient temperature plots during the first 6 weeks of decomposition (Table 2). More extreme differences would have been present at the soil surface, enhancing desiccation stress for the detritivores. Nevertheless, the warming effects observed for the integrated response samples after 6 weeks were not also observed for the microenvironment samples, and the latter would have been expected to exhibit the same response if desiccation alone was responsible for the warming effect. Warming can also influence plant tissue quality (Peñuelas et al. 2008), but there was not a significant interaction between warming and detritivore access for the litter-origin samples. Therefore, in comparing the results of the transplant experiments as a whole, the treatment responses of the integrated response samples were not simply an additive function of the responses of the microenvironment and litter-origin samples. This result suggests that simple mechanistic explanations of litter responses in global change experiments based on plant quality and microclimate may be inadequate, and there may be important synergies between the latter two factors in terms of defining the integrated response of litter mass loss.

After 1 year of litter decomposition, the significant interaction between detritivore access and warming was no longer present. Acclimation or recovery by the detritivore community may explain such transient effects of warming or moisture limitation on C turnover (Balser et al. 2006; Holmstrup et al. 2012). Alternatively, warming effects on C dynamics can vary seasonally (Templer and Reinmann 2011), and the lack of an interaction between warming and detritivore access may have reflected an absence of water stress over the spring and summer during the decomposition period (precipitation over this time was ~20 % above normal). Regardless of the mechanism, mass loss from the open samples after 1 year was 20 % greater than from the mesh samples, whereas the interaction between warming and detritivore access after 6 weeks only accounted for a difference of 2 %, and this disparity in effect sizes also may explain why no residual effects of the 6-week response could be detected after 1 year.

The overall positive effect of warming on litter mass loss we observed after 1 year was consistent with the general trend of increased decomposition with increased temperature in the absence of drought (Aerts 2006; Butenschoen et al. 2011). In addition to the possible recovery by the detritivore community noted above, the observation that the warming effect increased over 1 year may also be attributed to shifts in litter quality, because the temperature sensitivity of organic matter decomposition can increase over time in response to declining C quality (Conant et al. 2008). Although warming over winter can increase the frequency and intensity of freeze–thaw cycles at the soil surface (by reducing snow cover), which can disrupt the physical structure of litter and ultimately accelerate decomposition (Taylor and Parkinson 1988; Melick and Seppelt 2004), in the year we conducted our decomposition study, soil freeze–thaw cycles did not occur. However, standing litter in grass-dominated fields would likely be exposed to freeze–thaw cycles over winter, and such effects are not accounted for in decomposition experiments, such as the present study, where litter bags are placed on the soil surface.

Our observation that samples in N-addition plots experienced greater mass loss than samples in non-fertilized plots was consistent with other studies of the effects of N addition on litter turnover in grass-dominated systems (Hunt et al. 1988). However, both the direction and magnitude of N effects on litter decomposition often depend on site-specific factors (Hobbie 2005), with the trend of positive responses in systems exposed to low levels of background N deposition (<5 kg N ha^{-1} $year^{-1}$; Knorr et al. 2005). This value is similar to the N deposition rate of 6 kg N ha^{-1} $year^{-1}$ recorded for the region of our study (total inorganic N deposition, National Atmospheric Deposition Program 2006). For the litter-origin and microenvironment experiments there were interactions between detritivore access and N addition after 6 weeks. With respect to litter origin, N-fertilized plants often exhibit high N content in their senesced tissues (Johnson 1992; Henry et al. 2005), and N-rich material is often targeted by soil fauna (Tian et al. 1993; Bastow 2011; Wickings and Grandy 2013), which is consistent with our results from the integrated and

litter-origin experiments. N addition also increased mass loss to some extent in the mesh-enclosed samples, which is consistent with the stimulation of microbial decomposition by N addition (Coûteaux et al. 1995; Aerts 1997). However, for the control litter transplanted into N-addition plots in the microenvironment experiment detritivore-access effects were reduced, suggesting that the added mineral N had a direct negative effect on detritivores. These opposing effects of litter origin and microenvironment on detritivore-access effects may explain why no interactions between N addition and detritivore access occurred for the integrated response experiment.

The positive effect of N addition on litter turnover observed after 6 weeks remained present after 1 year. Contrary to this observation, at later stages of decomposition, N fertilization can impede the decay of the lignin-dense, recalcitrant fraction of plant litter (Fog 1988) as a result of decreases in microbial ligninolytic enzyme activity (Carreiro et al. 2000). However, lignin content does not always predict long-term N fertilization effects on litter decomposition, particularly in temperate grasslands (Hobbie 2008), possibly because the lignin content of grasses such as *P. pratensis* is relatively low (Holman et al. 2007).

In addition to their main effects, the combination of 1 year of warming, N, and detritivore manipulation resulted in a significant three-way interaction. Warming and N addition individually increased litter mass loss in the presence of detritivores, but their combined application had no additional effect. The value at which mass loss plateaued for all treatments (~75 %) may have represented a threshold above which the soil fauna could no longer increase litter decay. This suggestion is consistent with previous observations of temporal variation in the influence of soil fauna on litter mass loss [i.e. the contribution of soil fauna to litter turnover can become limited by decreased plant quality at later stages of decay (Slade and Riutta 2012)]. A similar plateau was also observed after 1 year in the microenvironment experiment, where despite significant increases in litter decomposition in the presence of detritivores, mass-loss values did not exceed 80 %.

Following 1 year of decomposition there were significant increases in mass loss with detritivore access, but the effect size for the litter-origin samples was less than a third of that of the other samples, possibly as a result of low detritivore densities in the area of the field where the common garden plots were established. Alternatively, differences in detritivore-access effects between the integrated and litter-origin samples may reflect the principles of the home field advantage hypothesis, whereby litter processing is maximized when both plant material and faunal detritivores originate from the same environmental matrix (Ayres et al. 2009b). However, the relative abundances of the dominant plant species were consistent throughout the field site, and in the absence of data regarding soil faunal composition and density, explanations regarding this result remain speculative.

Conclusion

Much of the current knowledge regarding the influence of environmental change on plant decomposition relies on evidence from mesh litter bag studies. However, soil fauna may also exert a significant influence over litter decay (García-Palacios et al. 2013). Therefore, further quantification of detritivore responses is critical to the understanding of the interactive effects between biotic and abiotic controls on litter turnover (Butenschoen et al. 2011; A'Bear et al. 2012). The interactions between global change and detritivore-access treatments we observed after 6 weeks highlight important differences between soil faunal and microbial responses that may ultimately influence the dynamics of litter turnover under future environmental conditions. Nevertheless, our data suggest that acclimation of the detritivore community to the negative effects of warming and N addition may occur over time. Contrary to our expectation, substantial differences between treatment responses in our integrated response experiment and those of the litter-origin and microenvironment experiments suggest that simple mechanistic explanations of litter responses in global change experiments (i.e. litter origin, plot microclimate) are inadequate. Moreover, at the later stages of decomposition this synergistic relationship was further modulated by the presence of detritivores, which suggests that the omission of detritivore effects in global change decomposition studies may underestimate the magnitude of mass loss substantially.

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References

A'Bear AD, Boddy L, Jones TH (2012) Impacts of elevated temperature on the growth and functioning of decomposer fungi are influenced by grazing collembola. Glob Change Biol 18:1823–1832

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

Aerts R (2006) The freezer defrosting: global warming and litter decomposition rates in cold biomes. J Ecol 94:713–724

Allison SD, Treseder KK (2008) Warming and drying suppress microbial activity and carbon cycling in boreal forest soils. Glob Change Biol 14:2898–2909

Allison SD, Wallenstein MD, Bradford MA (2010) Soil-carbon response to warming dependent on microbial physiology. Nat Geosci 3:336–340

An Y, Wan S, Zhou X, Subedar AA, Wallace LL, Luo Y (2005) Plant nitrogen concentration, use efficiency, and contents in a tallgrass prairie ecosystem under experimental warming. Glob Change Biol 11:1733–1744

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

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

Balser TC, McMahon KD, Bart D, Bronson D, Coyle DR, Craig N, Flores-Mangual ML, Forshay K, Jones SE, Kent AE, Shade AL (2006) Bridging the gap between micro- and macro-scale perspectives on the role of microbial communities in global change ecology. Plant Soil 289:59–70

Bastow JL (2011) Resource quality in a soil food web. Biol Fertil Soil 48:501–510

Beatty SW, Sholes ODV (1988) Leaf litter effect on plant-species composition of deciduous forest treefall traps. Can J For Res 18:553–559

Bell TH, Klironomos JN, Henry HAL (2010) Seasonal responses of extracellular enzyme activity and microbial biomass to warming and nitrogen addition. Soil Sci Soc Am J 74:820–828

Blankinship JC, Niklaus PA, Hungate BA (2011) A meta-analysis of responses of soil biota to global change. Oecologia 165:553–565

Bokhorst S, Wardle D (2013) Microclimate within litter bags of different mesh size: implications for the "arthropod effect" on litter decomposition. Soil Biol Biogeochem 58:147–152

Bosy JL, Reader RJ (1995) Mechanisms underlying the suppression of forb seedling emergence by grass (*Poa pratensis*) litter. Funct Ecol 9:635–639

Bradford M, Tordoff G, Eggers T, Jones T, Newington J (2002) Microbiota, fauna, and mesh size interactions in litter decomposition. Oikos 99:317–323

Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecol Lett 11:1316–1327

Briones MJI, Ineson P, Piearce TG (1997) Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. Appl Soil Ecol 6:117–134

Brzostek ER, Blair JM, Dukes JS, Frey SD, Hobbie SE, Melillo JM, Mitchell RJ, Pendall E, Reich PB, Shaver GR, Stefanski A, Tjoelker MG, Finzi AC (2012) The effect of experimental warming and precipitation change on proteolytic enzyme activity: positive feedbacks to nitrogen availability are not universal. Glob Change Biol 18:2617–2625

Butenschoen O, Scheu S, Eisenhauer N (2011) Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. Soil Biol Biochem 43:1902–1907

Carreiro MM, Sinsabaugh RL, Repert DA, Parkhurst DF (2000) Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81:2359–2365

Chapin FI, Matson P, Mooney H (2002) Principles of terrestrial ecosystem ecology. Springer, New York

Conant RT, Drijber RA, Haddix ML, Parton WJ, Paul EA, Plante AF, Six J, Steinweg JM (2008) Sensitivity of organic matter decomposition to warming varies with its quality. Glob Change Biol 14:868–877

Coûteaux MM, Mousseau M, Celerier ML, Bottner P (1991) Increased atmospheric CO2 and litter quality—decomposition of sweet chestnut leaf litter with animal food webs of different complexities. Oikos 61:54–64

Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. Trends Ecol Evol 10:63–66

Dangles O, Herrera M, Mazoyer C, Silvain J-F (2013) Temperature-dependent shifts in herbivore performance and interactions drive nonlinear changes in crop damages. Glob Change Biol 19:1056–1063

Deutsch ES, Bork EW, Willms WD (2010) Soil moisture and plant growth responses to litter and defoliation impacts in Parkland grasslands. Agric Ecosyst Environ 135:1–9

Fog K (1988) The effect of added nitrogen on the rate of decomposition of organic matter. Biol Rev 63:433–462

Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, Vorosmarty CJ (2004) Nitrogen cycles: past, present, and future. Biogeochemistry 70:153–226

Gan HJ, Zak DR, Hunter MD (2013) Chronic nitrogen deposition alters the structure and function of detrital food webs in a northern hardwood ecosystem. Ecol Appl 23:1311–1321

García-Palacios P, Maestre FT, Kattge J, Wall DH (2013) Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecol Lett 16:1045–1053

Hagerty TP, Kingston MS (2011) The soils of Middlesex County. Ontario Ministry of Agriculture and Food, Guelph

Henry HAL, Cleland EE, Field CB, Vitousek PM (2005) Interactive effects of elevated CO_2, N deposition and climate change on plant litter quality in a California annual grassland. Oecologia 142:465–473

Henry HAL, Hutchison JS, Kim M, McWhirter BD (2014) Context matters for warming: interannual variation in grass biomass responses to sevenyears of warming and N addition. Ecosystems (in press)

Hobbie SE (2005) Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. Ecosystems 8:644–656

Hobbie SE (2008) Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. Ecology 89:2633–2644

Holman JD, Hunt C, Thill D (2007) Structural composition, growth stage, and cultivar effects on Kentucky bluegrass forage yield and nutrient composition. Agronomy 99:195–202

Holmstrup M, Sørensen JG, Maraldo K, Schmidt IK, Mason S, Tietema A, Smith AR, Emmett B, Schmelz RM, Bataillon T, Beier C, Ehlers BK (2012) Increased frequency of drought reduces species richness of enchytraeid communities in both wet and dry heathland soils. Soil Biol Biochem 53:43–49

Hunt HW, Ingham ER, Coleman DC, Elliott ET, Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69:1009–1016

Hutchison JS, Henry HAL (2010) Additive effects of warming and increased nitrogen deposition in a temperate old field: plant productivity and the importance of winter. Ecosystems 13:661–672

Johnson DW (1992) Nitrogen retention in forest soils. J Environ Qual 21:1–12

Kampichler C, Bruckner A (2009) The role of microarthropods in terrestrial decomposition: a meta-analysis of 40 years of litterbag studies. Biol Rev 84:375–389

Kardol P, Reynolds WN, Norby RJ, Classen AT (2011) Climate change effects on soil microarthropod abundance and community structure. Appl Soil Ecol 47:37–44

Knorr M, Frey SD, Curtis PS (2005) Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86:3252–3257

Levings SC, Windsor DM (1996) Seasonal and annual variation in litter arthropod populations. In: Leigh EG Jr, Rand AS, Windsor DM (eds) The ecology of a tropical forest: seasonal rhythms and

long-term changes. Smithsonian Institutional Press, Washington, DC, pp 355–387
Lohm U, Lundkvist H, Persson T, Wiren A (1977) Effects of nitrogen fertilization on the abundance of enchytraeids and microarthropods in Scots pine forests. Stud For Suec 140:1–23
McGill WB, Cole CV (1981) Comparative aspects of cycling of organic C, N, S and P through soil organic matter. Geoderma 26:267–286
Melick DR, Seppelt RD (2004) Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated free-thaw cycles. Antarct Sci 4:399–404
O'Lear H, Blair J (1999) Responses of soil microarthropods to changes in soil water availability in tallgrass prairie. Biol Fertil Soil 29:207–217
Pendall E, Rustad L, Schimel J (2008) Towards a predictive understanding of belowground process responses to climate change: have we moved any closer? Funct Ecol 22:937–940
Peñuelas J, Sardans J, Ogaya R, Estiarte M (2008) Nutrient stoichiometric relations and biogeochemical niche in coexisting plant species: effect of simulated climate change. Pol J Ecol 56:613–622
Pritchard SG (2011) Soil organisms and global climate change. Plant Pathol 60:82–99
Rouifed S, Handa IT, David J-F, Hättenschwiler S (2010) The importance of biotic factors in predicting global change effects on decomposition of temperate forest leaf litter. Oecologia 163:247–256
Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Annu Rev Entomol 29:25–46
Shen KP, Harte J (2000) Ecosystem climate manipulations. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods in ecosystem science. Springer, New York, pp 353–369
Singh JS, Gupta SR (1977) Plant decomposition and soil respiration in terrestrial ecosystems. Bot Rev 43:449–528
Sjursen H, Michelsen A, Jonasson S (2005) Effects of long-term soil warming and fertilisation on microarthropod abundances in three sub-arctic ecosystems. Appl Soil Ecol 30:148–161
Slade E, Riutta T (2012) Interacting effects of leaf litter species and macrofauna on decomposition in different litter environments. Basic Appl Ecol 13:423–431
Suffling R, Smith DW (1974) Litter decomposition studies using mesh bags: spillage inaccuracies and the effects of repeated artificial drying. Can J Bot 52:2157–2163
Swift MJ, Heal OW, Anderson JM (1979) Decomposition in Terrestrial Ecosystems. University of California Press, Berkeley
Taylor BR, Parkinson D (1988) Does repeated freezing and thawing accelerate decay of leaf litter? Soil Biology Biogeochem 20:657–665
Templer PH, Reinmann AB (2011) Multi-factor global change experiments: what have we learned about terrestrial carbon storage and exchange? New Phytol 192:797–800
Tian G, Brussaard L, Kang BT (1993) Biological effects of plant residues with contrasting chemical compositions under humd tropical conditions: effects on soil fauna. Soil Biol Biochem 25:731–737
Tian G, Adejuyigbe CO, Adeoye GO, Kang BT (1998) Role of soil microarthropods in leaf decomposition and N release under various land-use practices in the humid tropics. Pedobiologia 42:33–42
Turner MM, Henry HAL (2009) Interactive effects of warming and increased nitrogen deposition on 15-N tracer retention in a temperate old field: seasonal trends. Glob Change Biol 15:2885–2893
Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. Am Nat 119:553–572
Wall DH, Bradford MA, St. John MG, Trofymow JA, Behan-Pelletier V, Bignell DE, Dangerfield JM, Parton WJ, Rusek J, Voigt W, Wolters V, Gardel HZ, Ayuke FO, Bashford R, Beljakova OI, Bohlen PJ, Brauman A, Flemming S, Henschel JR, Johnson DL, Jones TH, Kovarova M, Kranabetter JM, Kutny L, Lin K-C, Maryati M, Masse D, Pokarzhevskii A, Rahman H, Sabar MG, Salamon J-A, Swift MJ, Varela A, Vasconcelos HL, White D, Zou X (2008) Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. Glob Change Biol 14:2661–2677
Wan S, Norby RJ, Ledford J, Weltzin JF (2007) Responses of soil respiration to elevated CO_2, air warming, and changing soil water availability in a model old-field grassland. Glob Change Biol 13:2411–2424
Wei CZ, Zheng HF, Li Q, Lu XT, Yu Q, Zhang HY, Chen QS, He NP, Kardol P, Liang WJ, Han XG (2012) Nitrogen addition regulates soil nematode community composition through ammonium suppression. PLoS ONE 7:e43384
Wickings K, Grandy AS (2013) Management intensity interacts with litter chemistry and climate to drive temporal patterns in arthropod communities during decomposition. Pedobiologia 56:105–112
Wolters V (2000) Invertebrate control of soil organic matter stability. Biol Fertil Soils 31:1–19
Wu H, Lu X, Jiang M, Bao X (2009) Impacts of soil fauna on litter decomposition at different succession stages of wetland in Sanjiang Plain, China. Chin Geog Sci 19:258–264
Xin W, Yin X, Song B (2012) Contributions of soil fauna to litter decomposition in Songnen sandy lands in Northeastern China. J Arid Environ 77:90–95
Xu G-L, Kuster TM, Günthardt-Goerg MS, Dobbertin M, Li M-H (2012a) Seasonal exposure to drought and air warming affects soil collembola and mites. PLoS ONE 7:e43102
Xu ZF, Pu XZ, Yin HJ, Zhao CZ, Liu Q, Wu FZ (2012b) Warming effects on the early decomposition of three litter types, Eastern Tibetan Plateau, China. Eur J Soil Sci 63:360–367
Zhu X, Gao B, Yuan S, Hu Y (2010) Community structure and seasonal variation of soil arthropods in the forest-steppe ecotone of the mountainous region in Northern Hebei, China. J Mt Sci 7:187–196