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Soil microarthropods support ecosystem productivity and soil C accrual: evidence from a litter decomposition study in the tallgrass prairie

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Abstract

Soil fauna have been found to accelerate litter decomposition rates across many ecosystems, but little is known about their impact on soil organic matter formation during decomposition and their influence on ecosystem carbon and nitrogen cycling during this process. In a three-year litterbag-free decomposition study, we suppressed microarthropod abundance by 38% and tracked the fate of ^{13}C- and ^{15}N-labeled litter into different soil organic matter fractions and the microbial community. Microarthropod suppression slowed litter mass loss and decreased litter carbon input into the soil and soil microbes during the first 18 months of decomposition. The microarthropod suppression did not alter the total amount of carbon and nitrogen incorporated in the soil after complete surface litter mass loss. However, lower early-stage microbial carbon uptake due to lower early-stage litter inputs to the soil, as well as a significant decrease in the C:N ratio of litter-derived organic matter inputs to the mineral soil fractions, made less nitrogen available for plant uptake in the microarthropod suppression treatment. Thus, the acceleration of early-stage, more labile litter inputs to the soil altered the timing and availability of carbon and nitrogen inputs to the soil. A simulation of these effects on the tallgrass prairie ecosystem using the DayCent model predicts lower net primary productivity and lower total soil C and N mineralization when soil microarthropods are less abundant. Our results highlight the importance of soil microarthropods for ecosystem functioning through their role in transforming decomposing litter organic matter into soil organic matter and the feedback of this process to ecosystem productivity and soil C sequestration.

Keywords: Biogeochemistry; litter decomposition; phospholipid fatty acids (PLFA); soil microarthropods; soil organic matter; stable isotopes

1. Introduction

With ever-increasing atmospheric CO_2 concentrations, understanding the mechanisms controlling how much carbon (C) is stored in the soil from accumulation of plant inputs and how much nitrogen (N) is released during litter decomposition remain some of the most pressing issues in terrestrial ecosystem science (Todd-Brown et al., 2014). Litter decomposition is one of the main processes contributing to the formation of soil organic matter (SOM). However, traditional litter decomposition studies only monitor litter mass loss and do not track the fate of decomposing litter C and N in the soil (Cotrufo et al., 2009). While much is known about how climate and litter chemistry affect plant litter decomposition rates (Couteaux et al., 1995; Gholz et al., 2000), recent studies have highlighted the need to explicitly acknowledge the role of decomposers, both microbes (Grandy and Neff, 2008; Wieder et al., 2013) and soil fauna (de Vries et al., 2013; Garcia-Palacios et al., 2013), to improve our understanding of ecosystem C and N dynamics. Soil fauna influence processes such as litter decomposition rates (Wall et al., 2008) and soil N cycling (Carrillo et al., 2011). However, the underlying mechanisms and their influence on soil organic matter formation and C sequestration during litter decomposition are not well known (Garcia-Palacios et al., 2013).

Soil fauna have significant impacts on litter decomposition rates in some ecosystems, which calls for their inclusion in decomposition models to better represent unexplained variation across regions (Wall et al., 2008; Garcia-Palacios et al., 2013). Microarthropods can accelerate litter decomposition by increasing litter surface to volume ratios, thus allowing microbes to better access litter by physically moving litter into the soil (Chamberlain et al., 2006). Additionally, microarthropods graze on microbial colonies and stimulate microbial activity while dispersing microbes and feces throughout the litter and into the soil (Petersen and Luxton, 1982;

82 Seastedt, 1984). Microbial transformation of fresh litter inputs in the soil is now thought to be the
83 main precursor to long-term stabilization of SOM on soil minerals (Grandy and Neff, 2008;
84 Miltner et al., 2009; Cotrufo et al., 2015). Therefore the role of soil microarthropods in either
85 directly increasing litter inputs to the soil or stimulating microbial litter decomposition could
86 have important implications for the contribution of decomposing litter to the formation of
87 persistent SOM and its C:N balance.

88 The use of dual ^{13}C- and ^{15}N-labeled leaf litter in decomposition studies is a powerful
89 method for identifying the amount, location and transformation of litter inputs to the soil (e.g.
90 (Bird et al., 2003; Fahey et al., 2011; Soong and Cotrufo, 2014) and soil food web (Ruf et al.,
91 2006; Pollierer et al., 2007), but to our knowledge has not been used to examine the role of soil
92 fauna in litter to soil C and N transformation processes *in situ*. Litter-derived ^{13}C and ^{15}N can be
93 traced into primary SOM fractions separated by density and size (Christensen, 2001) to examine
94 the relative stabilization, transformation and approximate mean residence time of fresh litter
95 inputs to the soil (Trumbore, 1993; von Lützow et al., 2008). Additionally, microbial
96 phospholipid fatty acid (PLFA) ^{13}C can be used to examine microbial community uptake of
97 decomposing litter C and microbial contribution to litter-derived C stabilization over time
98 (Moore-Kucera and Dick, 2008), while ^{15}N can be quantified in plant roots to trace the complete
99 recycling of N from litter decomposition to new plant productivity (Zeller et al., 2000). By
100 incubating ^{13}C- and ^{15}N-enriched *Andropogon gerardii* leaf litter on the soil surface for three
101 years in a tallgrass prairie in conjunction with a microarthropod suppression treatment using
102 naphthalene (Cotrufo et al., 2014), we were able to investigate the effects of soil microarthropods
103 on the litter decomposition process throughout its complete mass loss and on the fate of litter C
104 and N in the soil.

105 In this study, we investigate whether the acceleration of litter mass loss by
106 microarthropods alters C and N sequestration in SOM either directly or indirectly through their
107 influence on the microbial community. We hypothesize that soil microarthropods accelerate litter
108 mass loss by promoting fragmentation and the incorporation of litter fragments into the soil
109 (Luxton, 1972; Yang et al., 2012). Additionally, we hypothesize that soil microarthropods
110 stimulate microbial turnover through top-down predation and thus have trophic cascading effects
111 on the transformation of litter into SOM.
112
113 2. **Materials and Methods**
114 *2.1 Isotopically labeled litter production and analyses*
115 Uniformly 3.3804 atom % ^{13}C and 3.9917 atom % ^{15}N labeled *A. gerardii* Kaw was
116 grown in a ^{13}C and ^{15}N continuous labeling chamber as described in Soong et al. (2014). Upon
117 harvest after 22 weeks of growth in the chamber, the above-ground plant material was air-dried,
118 cut into 20 cm lengths and mixed. Three replicate sub-samples of the initial litter were analyzed
119 for water content by drying in an oven at 65 °C and for %C, %N, $\delta^{13}C$ and $\delta^{15}N$ on an elemental
120 analyzer connected to an isotope ratio mass spectrometer (EA-IRMS, Carlo Erba NA 1500
121 coupled to a VG Isochrom continuous flow IRMS, Isoprime inc.) and for % hemicellulose, %
122 cellulose and % acid un-hydrolysable residue (AUR) using the neutral detergent fiber (NDF) and
123 acid detergent fiber (ADF) methods (Van Soest et al., 1991). The litter was comprised of 44.3%
124 C, 1.47% N, 29% cellulose, 25% hemicellulose and 3.9% AUR.
125
126 *2.2 Experimental site and design*

The experiment was conducted at the Konza Prairie long-term ecological research station in Kansas, USA (39 °05'W, 96 °35'N; local site name R20B). This is a tallgrass prairie dominated by *A. gerardii*. The climate is temperate-continental with average annual precipitation of 835 mm and a mean annual temperature of 12.8 ºC. The soil is a silty clay Mollisol (8% sand, 46% silt, 46% clay) and the site is topographically situated on a foot slope position (Knapp et al., 1998). Four replicate soil cores were taken within the experimental area and divided into the 0-2, 2-5, 5-10 and 10-20 cm soil layers for determination of soil bulk density. We found no evidence of carbonates in these soils (measured using pressure transducer following acid addition).

The soil microarthropod suppression (MS) treatment began in June 2010. At that time we installed 80 20-cm diameter PVC collars to a depth of 5 cm. We removed the native litter layer from within the collars and applied 4 ml of glyphosate (Roundup®) to deter plant growth within the collars. In the laboratory we determined the native litter dry weight, which was on average 18.4 g per collar surface area. The soil MS treatment consisted of monthly additions to the soil surface of 477 g/m^2 of naphthalene to repel microarthropods. Naphthalene ($C_{10}H_8$) is a chemical additive used to suppress soil microarthropod abundances in field decomposition studies, which was shown to have no effect on soil nematodes and no overall effect on PLFA abundances although a small amount of naphthalene may be used by some bacterial groups at the site (Cotrufo et al., 2014).

The litter decomposition experiment began on September 29, 2010, when 18.4 g dry-mass equivalent of ^{13}C ($\delta^{13}C$= 2113‰) and ^{15}N ($\delta^{15}N$= 10,309‰) labeled air-dried *A. gerardii* leaf litter was added to the PVC collars, and lasted for three years. Coarse plastic netting was used to cover the collars to prevent loss of the labeled litter or input of external litter. Five destructive soil and litter harvests occurred on May 1, 2011 (7 months), October 8, 2011 (12

150 months), April 13, 2012 (18 months), September 29, 2012 (24 months) and September 25, 2013
151 (36 months).
152 The experiment consisted of a split-split-plot fully randomized complete block design
153 with 4 replicate blocks. Within each replicate block, 5 whole plots (4 m^2) were randomly
154 assigned to one of the five sampling dates. Each whole plot was split in half by naphthalene
155 treatment (split-plots) so that in one half three subplots were treated with naphthalene (MS)
156 while three subplots were not (Control). Each subplot consisted of two PVC collars, one with the
157 labeled *A. gerardii* litter addition and one that was left as bare soil for use in the isotope mixing
158 model as described below. For each PVC collar, soil was sampled at different depths (split-split
159 plots). The experiment is thus treated as a split-split plot on a randomized complete block design,
160 with sampling times assigned to whole plots, naphthalene treatment assigned to subplots and
161 depth segment assigned to sub-subplots.
162
163 *2.3 Litter and soil sampling*
164 At each harvest date, we collected soil and litter samples from each collar. First, the litter
165 was collected and stored in plastic bags. Then an intact soil core (6 cm diameter) was collected to
166 5 cm depth for microarthropod extraction and quantification. We excavated the remaining soil
167 within the collar by incremental depths (0-2, 2-5, 5-10 and 10-20 cm) and the soil from each
168 layer was stored separately in plastic bags at 4°C until they were processed within two weeks of
169 collection. During the October 8, 2011, September 29, 2012 and September 25, 2013 sampling
170 we additionally collected roots from *A. gerardii* plants growing immediately outside collars.
171
172 *2.4 Microarthropod extraction and quantification*

We extracted microarthropods from the 0-5 cm intact cores using Tullgren funnels (48 h dark followed by 48 h low, 48 h medium and 48 h full light/heat intensity) (Crossley and Blair, 1991). Microarthropods were enumerated and sorted by groups into separate microcentrifuge tubes (0.5 mL) by handpicking individuals under a dissecting microscope (Olympus SZX10, 30X magnification). The following groups were distinguished: oribatid mites (Acari: Oribatida), predatory mites (Acari: Mesostigmata and predatory Prostigmata) and springtails (Collembola). All microarthropods (maximum 100) for each group were then transferred to a pre-weighed tin capsule (8x5 mm, Elemental Microanalysis BN/170056) containing 120 μL of deionized water. The tin capsules containing the microarthropod groups were dried for 3 days, weighed for final sample weights and analyzed for %C, %N, ^{13}C and ^{15}N using a CE-1110 EA coupled via Conflo II interface to an IRMS (ThermoFinnigan Delta Plus). Gravimetric soil moisture was calculated by oven-drying 50 g of fresh soil at 105 °C for 48 h. Soil microarthropod numbers were subsequently converted to individuals per kg dry soil.

2.5 Bulk soil and litter analyses

At each harvest, the remaining litter was picked clean of any non-*A. gerardii* leaves, roots and soil, then weighed at field moisture. A subsample of the litter was oven-dried at 65 ºC for analysis of gravimetric water content and another subsample was combusted at 660 °C in a muffle oven to determine ash content for the determination of ash-corrected litter dry mass. The bulk soil was sieved to 2 mm and a subsample was analyzed for gravimetric water content by mass loss after drying at 105 ºC. The root samples were rinsed of all residual soil and oven-dried at 65 ºC. All oven-dry litter, soil and root samples were then pulverized and analyzed for %C, %N, $\delta^{13}C$ and $\delta^{15}N$ on an EA-IRMS.

196

197 *2.6 Soil organic matter fractionation*

198 To separate the uncomplexed SOM and the primary organo-mineral complexes
199 (Christensen, 1992), we employed a physical SOM fractionation scheme as described in Soong
200 and Cotrufo (2015). Briefly, after dispersion, soil from the 0-2 and 2-5 cm soil layers from both
201 the bare-soil and labeled-litter collars was fractionated by density into a light fraction (LF <1.85
202 g cm^{-3}) and a heavy fraction. The latter was separated by size into sand-sized (>53 μm), silt-sized
203 (>2 μm) and clay-sized (<2 μm) fractions. All fractions were oven-dried at 105 ºC prior to
204 weighing and analysis of %C, %N, $\delta^{13}C$ and $\delta^{15}N$ on an EA-IRMS (see Appendix S1,
205 Supplementary Table 1 for more information on the SOM fraction distribution).

206

207 *2.7 PLFA extractions and ^{13}C-PLFA measurements*

208 A subsample of the 2 mm-sieved bulk soil from the 0-2 and 2-5 cm depth layers collected
209 from the bare-soil and enriched-litter collars was picked clean of all visible roots, frozen (-20ºC)
210 and lyophilized for 48 h prior to phospholipid fatty acid (PLFA) extraction. We extracted PLFAs
211 on these samples using conventional methods (Bligh and Dyer, 1959; Denef et al., 2007) as
212 described in detail by Gomez et al. (2014).

213 The biomarker PLFAs analyzed within this dataset included: 18:1ω9c and 18:2ω6,9c
214 (indicative of saprophytic fungi), 16:1ω5 (indicative of arbuscular mycorrhizal fungi; AMF),
215 i15:0, a15:0, i16:0, i17:0 and a17:0 (indicative of Gram-positive bacteria), cy17:0, cy19:0,
216 16:1ω7c and 18:1ω7c (indicative of Gram-negative bacteria), 14:0, 15:0 and 18:0 (non-specific
217 bacterial markers) and 10Me PLFAs (indicative of Actinobacteria) (Kroppenstedt, 1985; Olsson
218 et al., 1995; Zelles, 1997). ^{13}C values were corrected using working standards (12:0 and 19:0)

calibrated on an EA-IRMS. Fatty acid methyl esters (FAME) concentrations and ^{13}C signatures were measured by capillary gas chromatography-combustion-isotope ratio mass spectrometry (GC-c-IRMS) (Trace GC Ultra, GC Isolink and DeltaV IRMS, Thermo Scientific). Details on the instrument parameters can be found in Gomez et al. (2014). PLFAs were identified and quantified using an external 37 FAME and bacterial acid methyl ester (BAME) mix (Sigma Aldrich, St Louis, MO, USA). To identify those fatty acids not available in commercial standard mixes, several samples were analyzed by GC-MS (Shimadzu QP-2010SE) and spectral matching using the NIST 2011 mass spectral library (Shimadzu). To obtain $\delta^{13}C$ values of the PLFAs, measured $\delta^{13}C$ FAME values were corrected individually for the addition of the methyl group during transesterification by simple mass balance (Denef et al., 2007). The abundance of individual PLFAs was calculated in absolute C amounts (PLFA-C, ng g^{-1} soil) based on the PLFA-C concentrations in the liquid extracts and used as a proxy for microbial biomass.

2.8 Root analysis

Twelve, 24 and 36 months after the start of the study, we collected roots of *A. gerardii* grasses growing immediately outside all of the litter-treated collars as well non-labeled background *A. gerardii* roots from immediately outside of the four replicate block area (to avoid any potential isotope contamination). Roots were oven-dried (65 °C), pulverized and analyzed for $\delta^{15}N$ on an EA-IRMS to determine any MS treatment effect on N uptake of the decomposing litter by nearby plants.

2.9 DayCent simulation of microarthropod suppression

We parameterized the ecosystem model DayCent (Parton et al., 1998) based on conditions at our site, including a standard tallgrass prairie land management practice of burning every four years, as a base run of the control treatment in our experiment. In order to simulate the observed effects of microarthropods on the biogeochemistry of the system, we ran the same model with a 20% reduced surface litter decay rate and reduced C:N ratio of surface-active and slow SOM pools by 30%, approximately corresponding to the measured reductions of our MS treatment on litter and soil C and N processing (see following results). The simulation of the control and MS treatments began in year 1900 and were applied through year 2100, with daily mean temperature and precipitation data informing the model from 1984 through 2013 (climhy.lternet.edu; Konza Prairie dataset).

2.10 Data analysis

We tested the effect of the MS treatment on microarthropod abundances, $\delta^{13}C$ and $\delta^{15}N$ of the microarthropods, litter mass remaining, C and N remaining at each sampling time point, PLFAs and root $\delta^{15}N$ from the litter-added plots using a general linear mixed model. Microbial community analyses of fungi:bacteria ratio were calculated by summing the PLFA-C from all of the biomarkers from each group from the litter-added plots and analyzed using the same general linear mixed model. The model included MS treatment and time of sampling as fixed effects and block and block × sampling time as random effects.

The litter contribution to the soil, soil physical fractions and PLFA-C was assessed for the litter-added plots as compared to the bare soil plots within each subplot. The isotopic mixing model was applied as follows:

$$f_{litter} = \frac{\delta_S - \delta_B}{\delta_{litter} - \delta_B}$$

263 where f_{litter} is the litter-derived C (or N) fraction of bulk soil, SOM or PLFA sample, δ_S and δ_B is
264 the $\delta^{13}C$ (or $\delta^{15}N$) of the specific bulk soil, SOM or PLFA sample from the litter-treatment collar
265 (δ_S) and the bare soil (δ_B), and δ_{litter} is the $\delta^{13}C$ (or $\delta^{15}N$) of the initial litter. The amount of litter-
266 derived C and N in these pools were obtained by multiplying the f_{litter} values to corresponding C
267 (or N) pool sizes. Litter-derived C and N pools in the SOM fractions and litter-derived PLFA-C
268 pools were calculated for the 0-5 cm soil depth summing the respective 0-2 and 2-5 cm pool
269 sizes.

270 We tested the effect of the MS treatment, sampling time and soil depth on the amount of
271 litter-derived C and N incorporation (and C:N ratios) into the bulk soil, SOM fractions and
272 PLFAs using a general linear mixed model including MS treatment, time of sampling, soil depth
273 and all interactions as fixed effects and replicate block, block × sampling time and block ×
274 sampling time × MS treatment as random effects with standard variance components. We
275 analyzed differences in the DayCent simulations of the control and MS scenarios over the years
276 1900-2100 using a paired t-test. Significance of all pairwise differences was determined using
277 the Tukey-Kramer method for multiple comparisons. We checked for normality of the data and
278 homogeneity of variances of the residuals and applied a log-transformation when necessary. We
279 analyzed all general linear mixed models using SAS® software version 9.3. In all cases, we used
280 type III tests of fixed effects.
281

282 **3. Results**

283 *3.1 Microarthropod suppression*

284 The abundance of total microarthropods, including oribatid mites, predatory mites and
285 collembolans, was reduced from an average of 642 individuals kg^{-1} dry soil (20,445 individuals

286 m^{-2}) in the control to 395 individuals kg^{-1} dry soil (12,580 individuals m^{-2}) in the MS treatment
287 ($F_{1,67}$=8.40; p=0.0051) in the top 0-5 cm of the bare soil and litter-added plots. The reduction of
288 oribatid mites (the most abundant group) was the main driver of this effect. The abundance of
289 oribatid mites was reduced by 50% ($F_{1,65}$=10.16, p<0.001) in the MS treatment across all time
290 harvests, while predatory mites were reduced by 34% ($F_{1,65}$=0.70, p=0.4055), and collembolans
291 were not affected at all (1% reduced, $F_{1,65}$=1.36, p=0.2475). By averaging the $\delta^{13}C$ and $\delta^{15}N$
292 values of all three microarthropod groups within each sample, we found that over the course of
293 our experiment the microarthropods in the MS treatment were significantly less enriched in both
294 ^{13}C ($F_{1,12}$=30.23; p=0.0001) and ^{15}N ($F_{1,12}$=16.74, p=0.0015) as compared to the control (see
295 Appendix S1; Supporting Information).
296
297 *3.2 Microarthropod suppression effect on litter mass loss*
298 After 36 months of decomposition in the field, the labeled *A. gerardii* litter had lost 98%
299 of its initial mass (Fig. 1a). Sampling time ($F_{4,30}$=110.80; p<0.0001) and MS treatment
300 ($F_{1,30}$=5.88, p=0.0215) had significant effects on the amount of litter mass remaining during the
301 experiment. At 12 and 18 months the control treatment had significantly less mass remaining
302 than the MS treatment. However, there was no difference in the mass remaining after 7, 24 or 36
303 months of incubation in the field (Fig. 1a).
304 By applying the isotope-mixing model to the litter ^{13}C and ^{15}N content we could examine
305 the amount of endogenous and exogenous, e.g. coming from the environment (Zeller et al., 2000;
306 Frey et al., 2003), C and N in the litter over time. We found no significant differences in
307 exogenous C (Fig. 1b) and N (Fig. 1c) incorporated into the litter between the MS treatment and
308 control and the ratio of endogenous C:N remaining in the litter was only different at the 12

month harvest (t=3.46; p=0.0005). Exogenous N was an important source of N during decomposition, accounting for approximately 30% of the litter N content from 6-24 months.

3.3 Microarthropod suppression effect on litter inputs belowground

Litter-derived C and N were recovered down to 20 cm in the soil, with the majority recovered in the top 5 cm (Fig. 2). As litter decomposition progressed over time, the total amount of litter-derived C in the soil increased (Fig. 2). After 98% mass loss at 36 months, we recovered 19% and 18% of the initial litter C in the soil down to 20 cm in the control and MS treatment, respectively, with no statistically significant difference between treatments ($F_{1,6}$=0.12; p=0.7417). However, over all five harvests and four depths, there was a small but significant MS treatment effect of decreasing litter-derived C in the soil ($F_{1,105}$=5.48; p=0.0174). There was no effect of MS treatment on litter-derived N incorporation into the soil ($F_{1,90}$=0.02; p=0.8950) and 55-59% of the initial litter N was incorporated into the soil at the end of the study. This resulted in 15% higher C:N ratios in the control than the MS bulk soils across all five harvests ($F_{1,105}$=5.47; p=0.0212).

An examination of the SOM fractions in the 0-2 and 2-5 cm depths revealed a significant overall effect of the MS treatment of reducing litter-C incorporation into the LF ($F_{1,45}$ =10.58; p= 0.0022), sand-sized ($F_{1,60}$ =11.63; p =0.0012), silt-sized ($F_{1,45}$=26.05; p<0.0001) and clay-sized fractions ($F_{1,60}$=14.66; p=0.0003; Fig. 3, 0-2 and 2-5 cm depths summed). The MS treatment had a significant interaction with time and was not significant at the final soil harvest (p>0.05) for litter-derived C in the SOM fractions (Fig. 3). There was no consistent effect of the MS treatment on litter N inputs to any of the measured SOM fractions (Fig. 3). Consequently, C:N ratios were significantly higher in the control LF ($F_{1,45}$=6.36; p=0.0153), sand-sized ($F_{1,60}$ =7.79; p=0.0070),

332 silt-sized ($F_{1,60}$ =146.32; p=<0.0001) and clay-sized ($F_{1,75}$=86.17; p<0.0001) SOM fractions than
333 the MS fractions. It remained 25% higher in the silt- and clay-sized fractions even at the final
334 harvest ($F_{1,12}$=62.72 (clay) and $F_{1,12}$ =106.89 (silt); p<0.0001 (both); Fig. 4, 0-2 and 2-5 cm
335 depths summed).

336 The roots of *A. gerardii* grasses growing immediately outside of the litter-treated collars
337 showed a measurable uptake of litter-derived N compared to the background. At the 12-month
338 harvest, δ^{15}N enrichment of the roots adjacent to the control plots was significantly higher
339 (average 49‰ δ^{15}N, standard error= 13) than the MS plots (average 26‰ δ^{15}N, standard error=
340 8; $F_{1,20.9}$=4.44; p=0.0474). At the 24 and 36 month harvests the two treatments did not differ and
341 δ^{15}N enrichment reached 81‰ (standard error= 19) at the 36-month harvest.

342

343 *3.4 Microarthropod effect on microbial community and litter-derived C incorporation*

344 There was no effect of MS treatment on the overall abundance of PLFAs in the litter-
345 added plots ($F_{1,45}$=0.27; p=0.6087). However, the MS-treated plots had a lower amount of litter-
346 C incorporation into all of the PLFAs than the control plots, which was statistically significant
347 throughout the experiment ($F_{1,45}$=28.42; p<0.0001; Fig. 5a). Microbial incorporation of litter C
348 into PLFAs decreased with depth from the 0-2 cm soil layer to the 2-5 cm soil layer ($F_{1,45}$
349 =28.42; p<0.0001). All of the microbial groups identified had incorporated litter-derived C
350 throughout the 36-month incubation, with decreasing amounts over time (Fig. 5a, Appendix S2).
351 By the 36-month harvest, overall PLFA litter-derived C incorporation was low and the amount of
352 litter-derived C in the PLFAs remained stable between the 24 and 36-month harvests (Fig. 5a).

353 The total abundance of fungal PLFA-C to bacterial PLFA-C (ratio=0.19) was not affected
354 by the MS treatment. However, the MS treatment did have a slightly greater amount of litter-

355 derived C in the fungal PLFAs relative to the bacterial PLFAs (0.200 for MS and 0.178 for
356 control; $F_{1,60}$ =5.90; p=0.0182).
357 We calculated the relative litter-derived C incorporation into microbial PLFAs by
358 dividing the amount of litter-derived C found in the PLFAs by the total amount found in the bulk
359 soil of the same layer at each sampling time (Fig. 5b). PLFA relative litter-derived C
360 incorporation in the 0-2 cm soil depth was lower than the 2-5 cm depth ($F_{1,45}$ =43.97; p<0.0001),
361 and decreased over time ($F_{4,15}$=76.79; p<0.0001). The MS treatment did not differ significantly
362 from the control treatment in relative microbial litter-derived C incorporation ($F_{1,45}$=1.21;
363 p=0.2774).
364
365 *3.5 Ecosystem response to microarthropod suppression in DayCent*
366 DayCent simulation of the role of microarthropods in increasing initial litter mass loss
367 rates (Fig. 1) and increasing the C:N ratio of litter inputs to the surface soil active and slow SOM
368 pools (Fig. 4) resulted in marked shifts in ecosystem C and N availability when projected over
369 time (Fig. 6). Major inter-annual fluctuations are mainly driven by a four-year burn cycle and
370 climatic events, but significant shifts of 12% reduced NPP (t_{400}=4.91, p<0.0001), both above-
371 and belowground, 21% reduced total N mineralization (t_{400}=6.48, p<0.0001), 11% reduced total
372 soil C after 200 years (t_{400}=169.60, p<0.0001) and reduced C in the active (t_{400}=3.38, p<0.0008)
373 and slow surface (t_{400}=3.09, p<0.0021) SOM pools, but no difference in surface litter mass
374 (t_{400}=-0.18, p=0.8579) due to the MS treatment are projected (Fig. 6).
375
376 **4. Discussion**

During our three-year decomposition study, microarthropod abundance was reduced by 38% in the MS treatment. Our experiment confirms previous findings that the acceleration of litter mass loss by microarthropods is limited to the early stages of decomposition (Smith and Bradford, 2003; Garcia-Palacios et al., 2013).

Although we found the MS treatment to only affect the first 18 months of litter decomposition, this early phase may be the most critical to mineral-associated SOM formation and litter-derived N recycling (Cotrufo et al., 2015). The immediate contribution and persistence of litter-derived C and N in the silt and clay fractions during the initial winter period, prior to major contributions to the LF, indicates that leaching of dissolved organic matter (DOM) is a likely mechanism for the contribution of litter-derived OM to the mineral soil fractions (Kalbitz et al., 2005; Cotrufo et al., 2015; Soong et al., 2015). During the 12 to 18-month mid-phase of the experiment, we saw an influx of litter fragments in the LF, along with a prominent effect of the MS treatment on decreasing litter-derived C inputs to all of the SOM fractions and reducing the C:N ratio of litter-derived OM in the SOM fractions. It was during these early and mid-phases of decomposition that microbial PLFA incorporation of litter-derived C as well as relative microbial incorporation of the litter-derived C were both highest. This could be due to increasing proportional lignin content of the litter over time (Berg, 2000), which is associated with a lower substrate use efficiency (Lekkerkerk et al., 1990). The reduced C:N ratio of the litter-derived OM in the SOM fractions in the MS treatment (Fig. 4) indicated enhanced microbial transformation of the original litter material and N immobilization (Paul, 2014). Since microbial uptake and transformation of litter inputs are thought to be precursors to stabilized SOM formation (Wickland et al., 2007; Grandy and Neff, 2008), the role of microarthropods in increasing litter OM inputs to the soil during the early high substrate use efficiency period of litter decomposition

400 may be important to the formation of mineral-associated SOM during decomposition. At the
401 final 36-month soil harvest, we saw an influx of litter-derived LF to the soil for both the MS and
402 control treatment. However, there was no MS treatment effect on this final stage of litter inputs
403 to the soil when microbial substrate use efficiency was at its lowest. Our litterbag-free incubation
404 method allowed us to capture this final physical input of litter fragments to the soil, which is
405 often inhibited by litterbag studies (Cotrufo et al., 2010).
406 Microarthropods and other soil fauna play an important role in litter decomposition rates
407 globally (Wall et al., 2008; Garcia-Palacios et al., 2013) and may be critical drivers of soil C and
408 N cycling (de Vries et al., 2013), but the mechanisms underlying these patterns are not clear. Our
409 MS treatment decreased the amount of ^{13}C incorporation in microbial PLFAs without changing
410 the proportion of litter-derived C in the soil taken up by the microbes, indicating that the
411 microarthropods increased litter inputs to the soil but did not stimulate more rapid microbial
412 uptake of litter-derived C. The decline in PLFA incorporation of ^{13}C over time also suggests the
413 importance of microbial litter-derived C incorporation during the earlier stages of decomposition.
414 Furthermore, it was only during the earlier stages of decomposition, when litter quality was high,
415 that we saw an MS effect on litter-derived N uptake by surrounding *A. gerardii* growing roots. In
416 frequently disturbed ecosystems such as the tallgrass prairie, which is frequently burned (Collins
417 and Wallace, 1990), these early-stage impacts of microarthropods on C and N uptake by soil
418 microbes and plants could have a great impact on ecosystem productivity.
419 One of the most apparent and lasting effects of the MS treatment was on lowering the
420 C:N ratio of litter-derived OM inputs to the silt and clay fractions of the soil. Fungi generally
421 have a higher C:N ratio than bacteria (Paul, 2014). However, we did not see a shift in the
422 fungi:bacteria ratio to indicate that this change in C:N ratio was caused by a top-down impact of

423 microarthropods on a shifting microbial community. Instead it appears that the microarthropods
424 themselves may have a direct role in inducing N mineralization, as previously reported (Carrillo
425 et al., 2011).
426 A simple manipulation of the structural litter inputs to the soil and the C:N ratios of the
427 surface SOM active and slow pools in DayCent allowed us to examine the ecosystem-scale
428 impacts of a long-term microarthropod reduction. Although DayCent does not include
429 representations of soil biota, it has been shown to represent the biogeochemistry of the tallgrass
430 prairie ecosystem in Kansas well (Lu et al., 2001). Our manipulation of the litter and soil pools in
431 DayCent demonstrates how the biogeochemical impacts of microarthropods that we observed
432 could be integrated into existing ecosystem models to quantify their effects on ecosystem
433 processes. The simulation represents the results that we found when we reduced microarthropod
434 abundances by 38% in the top 0-5 cm of the soil, so it may underestimate the role of
435 microarthropods on the ecosystem. However, these modeling results suggest that the increased
436 early-stage litter decomposition C inputs to the soil and higher C:N ratio of litter-derived SOM
437 associated with greater microarthropod abundances have important long-term implications for
438 ecosystem processes.
439 *4.1 Conclusions*
440 The use of naphthalene in a three-year, litterbag-free study of ^{13}C- and ^{15}N-labeled leaf
441 litter decomposition allowed us to quantify the effects of microarthropod suppression on the fate
442 of litter-derived C and N in the soil over time. An equal fraction (18-19%) of litter-derived C
443 remained in the soil after complete surface litter mass loss under control and 38% reduced
444 microarthropod abundances. We observed an initial effect of the MS treatment on litter mass
445 loss, incorporation of litter-derived C into SOM and soil microbes, and litter-derived N into plant

roots. Although none of these treatment effects persisted until the end of the study, they may have disproportionally large effects in frequently disturbed ecosystems such as the tallgrass prairie where the litter layer is burned off every two to four years (Collins and Wallace, 1990). The major persistent effect of the MS treatment was a reduced C:N ratio of litter-derived SOM formation. A simulation of this impact using DayCent revealed how the effect of a reduction in microarthropod abundances could have cascading impacts on plant N availability, soil C storage and net primary productivity. These results demonstrate that soil fauna, such as microarthropods, play key roles in the functioning of ecosystems and deserve explicit consideration in both empirical studies and models of soil biogeochemical processes.

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Fig. 1. Litter mass remaining (a) during three years of decomposition in the field for the control (black symbols) and microarthropod-suppression (MS, white symbols) treatments of the ^{13}C- and ^{15}N-labeled *A. gerardii* litter. Carbon (b) and Nitrogen (c) endogenous mass losses (circles) and exogenous mass gains (triangles). Endogenous values are based on the ^{13}C and ^{15}N lost from the original litter, and exogenous values are calculated based on initial litter ^{13}C and ^{15}N dilution from exogenous soil inputs. Values are averages, with bars as standard error (n=4).

Fig. 2. Average litter-derived C recovered in the soil for the control (open) and microarthropod-suppression (MS, cross-hatched) treatment. Error bars are standard error (n=4).

Fig. 3. Litter-derived C (circles) and N (triangles) in 0-5 cm a) light fraction, b) sand-sized, c) silt-sized, and d) clay-sized soil organic matter fractions for the control (black symbols) and microarthropod-suppression (MS; white symbols) treatments. Scales are different between panels to highlight treatment effects. Values are averages, with error bars as standard error (n=4).

Fig. 4. Litter-derived C to N ratios in the a) light fraction, b) sand-sized, c) silt-sized, and d) clay-sized soil organic matter fractions in the 0-5 cm soil depth for the control (black symbols) and microarthropod-suppression (MS; white symbols) treatments. Values are averages, with error bars as standard error (n=4).

Fig. 5. a) PLFA incorporation of litter-derived C for the control (dark bars) and microarthropod-suppression (MS; white bars) treatment for the 0-2 cm depth (open bars) and 2-5 cm depth (cross-hatched bars). b) Relative microbial incorporation of litter-derived C calculated as the ratio of ng of litter-derived PLFA C per ng^{-1} of litter-derived C in the soil for the control (black) and MS (white) in the 0-2 cm depth (circles) and 2-5cm depth (triangles). Values are averages, with error bars as standard error (n=4).

Fig. 6. DayCent simulations of the impacts of a 38% microarthropod suppression on decreasing early-stage litter mass loss rates by 20% and decreasing the C:N ratio of the active and slow surface soil organic matter pools by 30% on a) net primary productivity, b) surface structural litter mass, c) total nitrogen mineralization and d) soil organic matter total carbon. The control scenario is simulated by the black line and the microarthropod-suppression scenario is simulated by the grey line. In both simulations, burning occurs every four years.

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