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Earthworms, arthropods and plant litter decomposition in aspen (*Populus tremuloides*) and lodgepole pine (*Pinus contorta*) forests in Colorado, USA

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Summary

We compared the abundance and community composition of earthworms, soil macroarthropods, and litter microarthropods to test faunal effects on plant litter decomposition rates in two forests in the subalpine in Colorado, USA. Litterbags containing recently senesced litter of *Populus tremuloides* (aspen) and *Pinus contorta* (lodgepole pine) were placed in aspen and pine forests to monitor their decay rates and quantify litter microarthropod abundance. Earthworms and macroarthropods were collected by hand from the soil. Three species of earthworms were found in the aspen forest: *Octolasion cyaneum*, an anecic worm; *Dendrobaena octaedra*, an epigeic worm and *Aporrectodea trapezoides*, an endogeic worm. We found a higher density and fresh biomass of earthworms in the aspen (40 worms m^{-2} and 4.4 g m^{-2}) than in the pine forest (0.8 worms m^{-2} and 0.6 g m^{-2}). The lodgepole pine contained only earthworm species, *D. octaedra*. Macroarthropod density did not differ between the forests. Total density of microarthropods in the aspen and lodgepole pine forests was 6.40 and 5.24 individuals g^{-1} of dry litter, respectively and did not significantly differ between forests. The percent of mass remaining was different between litter species ($r^2 = 0.73$, $P < 0.01$). Aspen litter decayed significantly faster than pine regardless of location. The percent of mass remaining of aspen and lodgepole pine were significantly correlated with the density of earthworms in both forests ($P < 0.01$). In the pine forests, the percent mass remaining of aspen and lodgepole pine litter was also significantly correlated with the density of mites (Acarina) ($P = 0.03$), prostigmatid mites ($P = 0.02$) and the total abundance of litter fauna ($P = 0.02$). Our results suggest that introduced earthworms play an important role on litter decomposition in the aspen forest, and that litter decomposition in these subalpine sites might be influenced differentially by various groups of soil and litter fauna.

Key words: Decomposition, aspen, lodgepole pine, earthworms, microarthropods, subalpine forest

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Introduction

The decomposition of plant litter is central to many ecosystem functions such as soil formation and nutrient cycling (Seastedt 1984; Taylor et al. 1991). The rate of decay is influenced by the quality of the litter, the physical-chemical environment, and the biota (Swift et al. 1979). An excellent setting for studying the effects of soil invertebrates on decomposition is the subalpine forest, which has distinct vegetation types of differing substrate quality across constant climate and soil factors. In the Rocky Mountains of Colorado (USA), aspen (*Populus tremuloides* Michx.) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) are dominant tree species with contrasting nutrient content and secondary chemistry. Stump & Binkley (1992) described the quality of aspen leaves and lodgepole pine needles from various locations in the subalpine in Colorado. They found aspen leaves had higher N and lower lignin content than lodgepole pine needles. Differences in litter quality and chemistry may trigger changes in the abundance and community structure of earthworms (Zou & González 1996). In the Rocky Mountain region, litter quality effects on the biota community could be amplified in light of recent reports of earthworm invasions in the Canadian ranges. Invasions of European earthworms in Canada have been associated with dramatic changes in soil structure (Langmaid 1964), nutrient turnover, plant growth (Scheu & Parkinson 1994), and microarthropod abundance (MacLean & Parkinson 2000). González & Seastedt (2000, 2001) recognized the importance of litter microarthropod abundance and activities as regulating factors of litter decay rates in forests dominated by lodgepole pine in Colorado. However, little is known of the status of European worms and the effect different soil biota might have on litter decomposition in distinct vegetation of the subalpine in Colorado. In this study, we 1) quantified the abundance of earthworms, soil macroarthropods and litter microarthropods in aspen and lodgepole pine forests, and 2) examined the influence of fauna on the decay of aspen leaves and lodgepole pine needles in aspen and lodgepole pine forests and tested if the decomposer fauna exhibit different effects under diverse substrates. Four main questions were: 1) is the abundance of soil biota different between aspen and lodgepole pine forests? 2) is the decay of aspen and lodgepole litter related to the abundance of different groups of biota? 3) is there a differential effect of the soil biota on the decay of aspen and lodgepole pine litter within each forest? and 4) do European earthworms significantly affect the decay rates of aspen and lodgepole pine forests?

Materials and Methods

Study site

This study was conducted in the subalpine life zone at the Niwot Ridge – Long Term Ecological Research (NWT-LTER) site. NWT-LTER is located 50 km west of Boulder, Colorado, at 40°03'N, 105° 36'W on the eastern slope of the Rocky Mountains. Four plots (1.2 × 0.8 m) dominated by *P. tremuloides* (aspen) and *P. contorta* var. *latifolia* (lodgepole pine) vegetation were randomly selected at an elevation of approximately 3000 m. The mean annual precipitation is about 692.0 mm and occurs mostly as snow during the winter and spring months. Annual totals of precipitation vary greatly from year to year. Annual mean temperature is 1.30 °C; in January it is –7.49 °C and in July it is 11.91 °C (Greenland 1989). Actual evapotranspiration is about 320 mm (González & Seastedt 2001). Soils in the subalpine are considered shallow and coarse textured (Johnson & Cline 1965). Peet (1981) and Stump & Binkley (1992) have respectively provided extensive descriptions of the vegetation, soils, and litter chemistry of these subalpine forests.

Experimental design

Recently senesced leaves of *P. tremuloides* and needles of *P. contorta* were collected from the forest floor during the fall of 1997. Measured amounts of ~ 3–5 g air-dried *P. tremuloides* leaves and *P. contorta* needles were placed separately in 14 × 14 cm fiberglass litterbags. Two mesh sizes were used on the top of the litterbags: 1.8 × 1.6 mm (small) and 3 × 4 mm (big). The bottom mesh of all litterbags was 1.8 × 1.6 mm. This mesh size prevents the loss of litter fragments from the litterbag and does not inhibit indirect effects of earthworm casts (González & Seastedt 2001). The big mesh size allowed easier access of micro- and macroarthropods. We placed a total of 320 litterbags in the field: 40 in each of the plots (2 forest types, 4 plots each). The 40 litterbags that were placed in each plot represent the two litter types (aspen and lodgepole pine) and two mesh sizes. An initial subsample of 64 litterbags (8 litterbags per site, 4 each of aspen and lodgepole pine, two mesh sizes) was collected and returned to the laboratory immediately after placement in the field. These bags were oven-dried at 60 °C to establish handling loss and dry mass relations (e.g., González & Seastedt 2001). From October 1997 to October 1999, litterbags were collected randomly from each of the aspen and pine plots during four collections (n = 2 bags per litter species and mesh per plot per date). A total of 64 litterbags were collected from the field per collecting date.

Faunal extractions

Litterbags (n = 4 per litter species per mesh per forest type and date) were placed in modified Tullgren extractors. A total of 32 litterbags were extracted per collecting date. This extraction technique (details found in González et al. 2001) removes mites and collembolans from the litterbags and also allows for a conservative estimate of other microarthropods (e.g., Protura, Psocoptera, Zoraptera, pseudoscorpions, diplopods, chilopods, etc.). Fauna were classified as Cryptostigmata, Mesostigmata, Prostigmata, Astigmata (suborders, Acarina), Collembola (springtails) and other microarthropods. Faunal densities were calculated per gram of dry litter at the time of sampling. Litterbags placed on the Tullgren extractor were oven-dried (60 °C) and reweighed to determine the remaining mass after faunal removal.

A total of 24 quadrants (0.1 m^2, 25 cm deep) were sampled for earthworms and arthropod macrofauna (e.g. millipedes, centipedes, beetles and others) in the aspen and pine forests (3 adjacent quadrants per plot). All soil fauna were hand-sorted from the soil and returned to the laboratory. Earthworms were allowed to empty their guts for one day, then rinsed with water, dried with paper towels and weighed. The worms were killed with 70 % EtOH, fixed with 10 % formaldehyde and stored in 5 % formaldehyde. Earthworms were identified to species, and classified into three categories defined by Bouché (1977): anecic worms, which burrow in soil and feed on surface litter, epigeic worms, which live and feed on the soil surface above mineral soil and endogeic worms, which inhabit mineral soil horizons and feed of soil enriched with organic matter. The arthropod macrofauna were identified to broad taxonomic groups (e.g. millipedes, centipedes, beetle and others) and stored in 70 % EtOH.

Data Analysis

All statistical analyses were performed using the software SPSS (SPSS 11.0 Win 98). Data were tested for homogeneity of variance by using the Levene's test of equality of error variance and skewness. Log-transformations were employed when the actual data did not meet the assumptions of normality. The significance level was set at $\propto = 0.05$.

Analyses of variance (using the general linear model procedure, GLM) was used to determine the significance of the four main factors (independent variables: forest site, litter species, mesh size, and days in the field) and their interaction on the percent of mass remaining (dependent variable). One-way ANOVAs were employed to determine whether differences existed in (1) percent of mass remaining between mesh sizes within each litter species and forest site, and (2) the density of the major groups of litter arthropods between litter species. A MANOVA (GLM) was used to evaluate the effects of forest site, litter species, mesh size and days in the field on the density of major groups of litter fauna. Student-Newman-Keuls (SNK) tests were used to compare the mean density of major groups of litter fauna among the different collecting dates. Differences in the density of soil faunal groups (earthworms and macroarthropods) between forest sites were determined by MANOVA. A simple linear correlation analysis (Pearson's Coefficient) was performed among the densities of the major groups of fauna and the mass loss of *P. tremuloides* and *P. contorta* in the aspen and lodgepole pine forests.

Results

There was a significant effect of forest site, litter species, mesh size and days in the field on the percent of mass remaining of *P. tremuloides* and *P. contorta* ($R^2 = 0.77$, $P \leq 0.05$ for all sources; Table 1). On average, litter decayed faster in the aspen forest than in the lodgepole pine forest. Aspen leaves decayed faster than pine needles in either forest site (Fig. 1). However, aspen leaves decayed faster in the aspen forest than in the lodgepole pine forest. After 2 yr, aspen litterbags had an average of 48 % mass remaining in the aspen forest as compared to an average of 56 % in the lodgepole pine forest (Fig. 1). The decay of pine needles did not differ between aspen and lodgepole pine forests.

Table 1. Results of four-way ANOVA for the effects of forest, litter species, mesh size, and days in the field on the percent of mass remaining

Source	df	F	P
Forest (F)	1	3.59	**0.05**
Litter (L)	1	484.78	**< 0.01**
Mesh (M)	1	4.75	**0.03**
Days in the field (D)	3	99.11	**< 0.01**
F × L	1	4.87	**0.03**
F × M	1	0.00	0.99
L × M	1	2.04	0.15
F × L × M	1	2.64	0.10
F × D	3	4.07	**< 0.01**
L × D	3	1.34	0.26
F × L × D	3	0.60	0.61
M × D	3	6.57	**< 0.01**
F × M × D	3	0.22	0.88
L × M × D	3	0.45	0.72
F × L × M × D	3	1.10	0.35
Error	254		

Note: n = 286; $R^2 = 0.77$

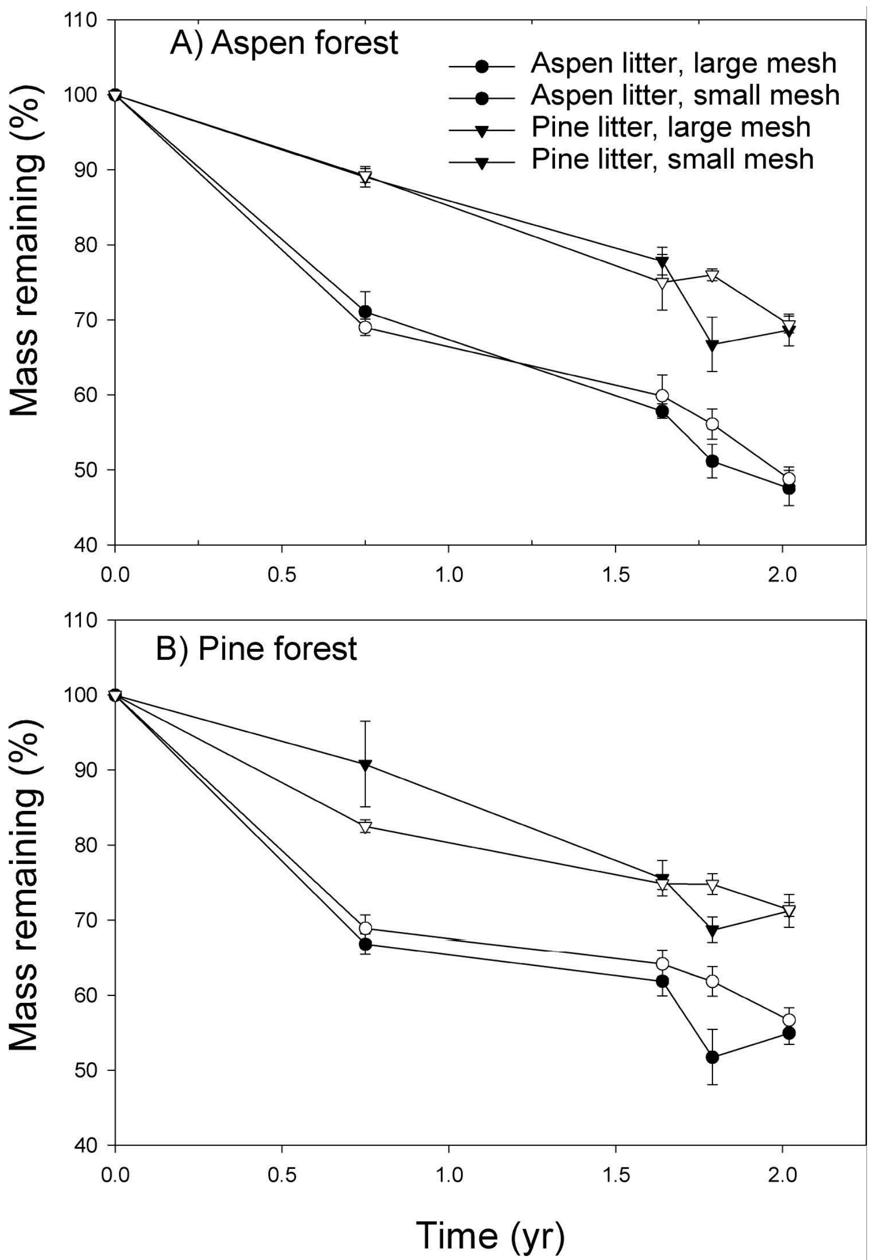

Fig. 1. Percent of mass remaining of *P. tremuloides* (aspen) leaves and P. contorta (lodgepole pine) needles in litterbags of 1.8 × 1.6 mm (small) and 3 × 4 mm (big) mesh in a) aspen and b) lodgepole pine forests

There was no significant effect of forest site and mesh size on the density of major groups of litter microarthropods (Table 2). There was a significant effect of litter species and days in the field on the density of major groups of litter microarthropods (Table 2). The densities of total acari, mesostigmatid mites, prostigmatid mites and total microarthropods were higher in aspen leaves than in lodgepole pine needles (Table 3). The densities of total acari, mesostigmatid mites and total litter microarthropod were the lowest at the beginning, highest by the middle and then declined by the end of the experiment. The density of collembolans, oribatid (Cryptostigmata) mites, and other litter microarthropods did not vary along the experiment (SNK; $\alpha = 0.05$).

Three earthworm species were found in the aspen and lodgepole pine forests: *Octolasion cyaneum*, an anecic worm; *Dendrobaena octaedra*, an epigeic worm; and *Aporrectodea trapezoides*, an endogeic worm. The aspen forest had all three species while the pine forest contained only the epigeic species (Table 4). In the aspen, epigeic worms had the highest density, followed by anecic worms; endogeic worms had the lowest density. The total fresh biomass of earthworms was 4.4 (± 1.9 SE) g m^{-2} in the aspen vs. 0.6 (± 0.5 SE) g m^{-2} in the lodgepole pine forest. The density of

Table 2. Effects of forest, litter species, mesh size and days in the field on the densities (numbers per g dry litter) of total Acarina, Cryptostigmata, Mesostigmata, Prostigmata, Astigmata, Collembola, other and total litter fauna in *P. tremuloides* and *P. contorta* litterbags. Statistical values are based on a four-way MANOVA ($n = 64$) using a Pillai's Trace test

Source	df	F	P	Power
Forest (F)	1	1.32	0.28	0.47
Litter (L)	1	4.37	**<0.01**	0.97
Mesh (M)	1	0.28	0.97	0.12
Days in the field (D)	3	6.69	**<0.01**	1.00
F × L	1	1.14	0.37	0.41
F × M	1	0.54	0.81	0.20
L × M	1	0.54	0.81	0.20
F × L × M	1	1.52	0.20	0.54
F × D	3	1.45	0.11	0.91
L × D	3	1.69	**0.04**	0.95
F × L × D	3	0.66	0.87	0.49
M × D	3	1.16	0.30	0.81
F × M × D	3	0.65	0.89	0.48
L × M × D	3	1.11	0.35	0.78
F × L × M × D	3	1.09	0.37	0.77

Table 3. Mean (± standard error, $n = 32$) and relative density (numbers per g of dry litter) of microarthropods in *P. tremuloides* and *P. contorta* litterbags. Asterisks (*) within a faunal group represent significant difference of density between litter species (Tests of Between-Subjects Effects of MANOVA, ∝ = 0.05)

	Aspen Leaves		**Pine Needles**	
Taxonomic unit	Density	%	Density	%
Acarina‡	**7.30 ± 1.18***	89.2	**3.18 ± 0.44**	57.0
Mesostigmata	**2.13 ± 0.64***	26.0	**0.72 ± 0.17**	12.9
Prostigmata	**2.16 ± 0.32***	26.4	**1.06 ± 0.20**	19.0
Astigmata	1.30 ± 0.35	15.9	0.75 ± 0.17	13.5
Cryptostigmata	0.05 ± 0.04	0.6	0.05 ± 0.04	0.9
Collembola	0.62 ± 0.28	7.6	2.27 ± 1.29	40.7
Others	0.26 ± 0.12	3.2	0.12 ± 0.07	2.3
Total‡	**8.18 ± 1.31***		**5.57 ± 1.36**	

Note: Statistics performed on log +1 transformed data
‡ Includes unknowns and immatures

Table 4. Mean (± standard error) and relative density (numbers per square meter) of earthworms and macroarthropods in the soil in forests dominated by *P. tremuloides* and *P. contorta*. P-values represent the significance of the difference in density of a faunal group between forests (MANOVA, ∝ = 0.05)

	Aspen Forest		**Pine Forest**		**MANOVA**	
Taxonomic unit	Density	%	Density	%	*P*-value	Power
Oligochaeta†	44.44 ± 17.88	52.6	0.77 ± 0.77	3.5	**<0.01**	0.81
Octolasion cyaneum	5.56 ± 2.94	6.6	0	0	**0.03**	0.59
Dendrobaena octaedra	17.78 ± 9.39	21.1	0.77 ± 0.77	3.5	**0.04**	0.55
Aporrectodea trapezoides	1.11 ± 1.11	1.3	0	0	0.24	0.21
Macroarthropods	40.00 ± 11.18	47.4	21.54 ± 5.17	96.5	0.11	0.35

† Includes unknown immatures

Table 5. Pearson correlation coefficients (*r*) (and, two-tailed probality values) for the percent of mass remaining of *P. tremuloides* and *P. contorta* and mean abundance of a) microarthropods (number per g dry litter) collected from the litterbags, and soil fauna (numbers per square meter) in aspen and lodgepole pine forests (n = 4)

Variable	**Aspen Forest**	**Pine Forest**
a) Microarthropods in litterbags		
Acarina †	−0.92 (0.08)	**−0.97 (0.03)**
Mesostigmata	−0.94 (0.06)	−0.51 (0.49)
Prostigmata	−0.78 (0.22)	**−0.98 (0.02)**
Astigmata	−0.42 (0.58)	−0.88 (0.12)
Cryptostigmata	−0.43 (0.56)	−0.01 (0.99)
Collembola	0.98 (0.02)	−0.49 (0.51)
Others	−0.44 (0.56)	−0.71 (0.29)
Total	0.21 (0.80)	**−0.98 (0.02)**
b) Soil fauna		
Oligochaeta †	**−0.99 (<0.01)**	**−0.98 (0.02)**
O. cyaneum	**−0.99 (<0.01)**	**−0.98 (0.02)**
D. octaedra	**−0.99 (<0.01)**	**−0.98 (0.02)**
A. trapezoides	**−0.99 (<0.01)**	**−0.98 (0.02)**
Macroarthropods	**−0.99 (<0.01)**	**−0.98 (0.02)**

† Includes unknown immatures

macroarthropods was 40 individuals m^{-2} in the aspen forest and 21.5 m^{-2} in the lodgepole pine forests (Table 4). The density of macroarthropods was not significantly different between the forests ($P = 0.11$, $R^2 = 0.12$). The correlation analysis (Table 5) showed that the percent of mass remaining of *P. tremuloides* and *P. contorta* was significantly and negatively related to the density of earthworms and soil macroarthropods in both forests. However, only in the lodgepole pine forest, the percent of mass remaining of *P. tremuloides* and *P. contorta* was significantly and negatively related to the density of prostigmatid mites and total microarthropods.

Discussion

The main goal of this study was to quantify the abundance of different groups of the soil fauna in aspen and lodgepole pine forests and to determine whether they relate to the decay of litter from those forests. We used litterbags of two mesh sizes separately containing aspen leaves and lodgepole pine needles to determine if soil fauna of different groups contribute differentially to the decay of litter of contrasting quality. We found that: (1) the percent of mass remaining of aspen and lodgepole pine litter was different between the aspen and lodgepole pine forests, litter species and size of the mesh, (2) the abundance of major groups of litter microarthropods and soil macroarthropods did not differ between forests, (3) litter microarthropods were not affected by the mesh size of the litterbags, (4) the abundance and community composition of earthworms was higher in aspen than in lodgepole pine forests, and (5) the abundance of macroarthropods and earthworms was negatively related to the percent of mass remaining in both forests but in the lodgepole pine was also negatively related to groups of litter microarthropods.

Several studies have successfully correlated litter decay rates to substrate quality indices in different ecosystems (e.g., Aber et al. 1990; Melillo et al. 1982; Taylor et al. 1991). In the Rocky Mountain region, Stump and Binkley (1992) found that the ratio of lignin:N in lodgepole pine needles was higher than in the aspen leaves, and that it strongly related to their decay rates. This study confirmed that substrate quality is a major determinant of decomposition in aspen and lodgepole pine forests as the decay of the aspen leaves was higher than the lodgepole pine in spite of location. However, we expected lodgepole pine needles to decay faster in the aspen than in the lodgepole pine forests as the abundance and community composition of earthworms was significantly higher in the later. The decay of lodgepole pine needles did not differ significantly between forests. These results point to the strength of substrate quality effects on the decay of lodgepole pine needles which can override the effects of the more diverse soil fauna community in the aspen as compared to the lodgepole pine forests. Although we do not imply a cause and effect relation by means of correlations, the importance of soil fauna on decomposition in the lodgepole pine forest was evident as the percent of mass remaining of both litter species was significantly and negatively related to the abundance of soil macrofauna and litter microarthropods.

González & Seastedt (2001) reported increases of 12–50 % in litter breakdown rates due to the effects of litter microarthropods in a lodgepole pine forest in Colorado. In this study, the percent of mass remaining of aspen and lodgepole pine litter was significantly affected by mesh size. The abundance of litter microarthropods was neither different between the forests nor affected by mesh size. The small mesh size (1.8×1.6 mm) did not inhibit the activities of litter microarthropods but excluded macroarthropod effects on decay. However, the abundance of soil macroarthropods was not different between the forests. Thus, the abundance and community composition of earthworms largely control decay rates in aspen forests. This study shows that both litter microarthropod and macrofauna are important determinants of decay in the lodgepole pine forest. It has been shown that litter microarthropods have large effects on the microbial activities in the lodgepole pine forest in the subalpine (González et al. 2001). Therefore, a potential soil fauna – microbial interaction might explain the decay rate of the recalcitrant lodgepole pine needles.

Invasions of European earthworms in the Canadian ranges of the Rocky Mountains have been reported. Dymond et al. (1997) found high densities of *Dendrobaena octaedra* in aspen and pine forests (3218 and 627 worms m^{-2}, respectively) in Alberta. They also found another epigeic species, *Dendrodilus rubidus* in the aspen forests. To our knowledge, this study is the first record of European worms in the Rocky Mountains of Colorado. We report a much lower density of *D. octaedra* and a more diverse assemblage of earthworms in the aspen forest of this study than that found by Dymond et al. (1997).

We conclude there is a significantly higher abundance and community structure of European earthworms in the aspen than in the lodgepole pine forests in Colorado. We confirmed substrate quality to be a major determinant of decomposition of aspen and lodgepole pine litter. However, our results suggest that introduced earthworms play an important role on litter decomposition in the aspen forest, and that litter decomposition in these subalpine sites might be influenced differentially by various groups of soil and litter fauna.

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