

White-tailed deer (*Odocoileus virginianus*) fecal pellet decomposition is accelerated by the invasive earthworm *Lumbricus terrestris*

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Abstract Exotic European earthworms have expanded into worm-free forests of the United States. Concurrently, populations of the white-tailed deer, *Odocoileus virginianus*, have also increased. During winter, deer use hemlock stands for cover while browsing elsewhere, creating a net organic matter flux into these stands. Deer fecal pellets can provide annual inputs of 48.1 kg C, 1.4 kg N, and 1.3 kg Ca per hectare. We tested the hypothesis that these pellets were readily consumed by invading earthworms. The litter-feeding anecic earthworm *Lumbricus terrestris* redistributed fecal pellets and accelerated mass and nutrient loss rates. These losses are likely due to the combination of enhanced fragmentation and decomposition as earthworms drag pellets into their burrows for consumption. This nutrient subsidy may be an important source of high quality “litter” input to hemlock stands, which may in turn facilitate the invasion of these stands by earthworms under high deer densities.

Keywords Calcium · C:N ratio · European nightcrawler (*Lumbricus terrestris*) · Fecal pellets · White-tailed deer (*Odocoileus virginianus*)

Introduction

The role of invasive European earthworm communities in forests of North America has recently been recognized as an important change agent in these ecosystems (Bohlen et al. 2004a). Native earthworms extirpated from the northcentral and northeastern United States and much of Canada during the advance of the Laurentian ice sheet have been slow to recolonize following retreat (James 1999). Meanwhile European Lumbricid species have spread, facilitated by human activities (James and Hendrix 2004). Earthworms have been described as ‘ecosystem engineers’ because of their ability to modify not only their own environment, but that of many other organisms as well (Jones et al. 1994). Earthworm introduction into forested settings can result in large declines in soil carbon and nitrogen stocks (Alban and Berry 1994; Bohlen et al. 2004b; Hale et al. 2005b), altered soil morphology including the complete elimination of organic horizons (Alban and Berry 1994; Hale et al. 2005a), and a suite of other changes (Hendrix and Bohlen 2002).

Lumbricus terrestris, commonly known as the nightcrawler, is an invasive earthworm that has a large impact on forest soils. This species has long been known to feed discriminately on litter and miscellaneous organic debris, dragging material from the forest floor into deep vertical burrows (Darwin 1881; Reynolds 1977). Although most material is consumed within the burrow, some intact and fragmented detritus

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is mixed with earthworm castings at the burrow entrance (Shipitalo and Protz 1988). These debris piles are known as middens, and are readily distinguishable from the surrounding forest floor (Fig. 1a). Middens are believed to serve multiple purposes: (1) provide physical protection from surface predation by blocking or plugging the burrow entrance (Darwin 1881; Edwards and Lofty 1977), (2) allow unpalatable or excessively large litter and organic debris to partially decompose in these ‘biological hotspots’ before consumption (Cooke and Luxton 1980; Subler and Kirsch 1998; Brown et al. 2000; Migge-Kleian et al. 2006) and (3) serve as a palatable food cache. In areas of high populations, *L. terrestris* midden density (and therefore population) can reach approximately 30–80 per m² in forest settings (Bohlen et al. 2004c). In such high densities, the forest floor has been stripped



Fig. 1 *Lumbricus terrestris* midden in a *Acer saccharum* dominated stand, composed predominantly of leaf litter (a), compared to a *Lumbricus terrestris* midden from a *Tsuga canadensis* dominated stand, composed of mixed deciduous litter and *Odocoileus virginianus* fecal pellets (b)

clear of accessible organic material, with the only non-woody detritus present in individual middens.

Eastern hemlock dominated stands are a favored winter yarding habitat of white-tailed deer (*O. virginianus*) in the Upper Midwest (Verme 1973, Euler and Thurston 1980). Snow interception by the upper canopy reduces snowpack depth, wind velocity, and minimizes thermal heat loss (Ozoga and Gysel 1972), as well as permitting escape from predation and energy conservation (Messier and Barrette 1985). Given the range of known population densities (MDNR 2006), fecal pellet contribution per deer (Rogers 1987), and C and N content of fecal pellets, we calculate the annual nutrient contribution from fecal pellets at 5.9 to 48.1 kg C/ha, 0.1 to 1.4 kg N/ha, and 0.13 to 1.3 kg Ca/ha. This is a general estimate for stands across the Upper Great Lakes region, and can vary spatially as a function of yarding area as a percentage of landscape, time spent in yards, and quality/input of exogenous forage.

Perhaps equally as important, deer fecal pellets might have higher concentrations of N and calcium (Ca) than hemlock litter. Tree species with higher litter calcium have been found to be strongly associated with increased earthworm biomass (Reich et al. 2005). Eastern hemlock litter is low in nutritional value, making it unpalatable to *L. terrestris*. In contrast, deer fecal pellets in yarding areas are primarily derived from exogenous food sources, representing a net input of material from outside the stand. Thus it is possible that if *L. terrestris* readily use these deer pellets, then deer could facilitate earthworm invasion into hemlock stands. Although we are not aware of any literature on deer pellet use, feces of domesticated cattle and pigs are known to be readily consumed by *L. terrestris* in controlled studies (Fostgate and Babb 1972; Roepstorff et al. 2002), and the anecic earthworm *Martiodrilus carimaguensis* has been observed to consume macroinvertebrate fecal pellets (Mariani et al. 2001). Our repeated observation of pellets in middens (Fig. 1b) led us to believe that *L. terrestris* might readily consume deer pellets in natural forest settings.

Furthermore, research has suggested that deer browsing is not the critical factor preventing hemlock regeneration, and that other disturbances and ecosystem processes may be at play (Mladenoff and Stearns 1993). It is worth considering the role of soil disturbance by *L. terrestris* as another factor in

regional hemlock decline. As populations of both *L. terrestris* and white-tailed deer have increased in recent years, novel biogeochemical feedbacks between hemlock, deer and earthworms might be playing an increasingly important role in forest nutrient and stand dynamics. As a first step in exploring the interaction of deer, earthworms and eastern hemlock, we tested the hypothesis that earthworms consume and accelerate the decomposition of deer pellets in hemlock-dominated stands.

Methods

This study was conducted at the Huron Mountain Club (HMC) in Marquette County, MI USA (lat. 46°21'51" long. -81°21'46"). The HMC is a private 8,000 ha preserve, consisting of one of the largest intact old growth hemlock dominated northern hardwood forests remaining in the Great Lakes region. For this study, we used *T. canadensis* dominated plots from a larger experimental matrix (Lilleskov EA and Karberg NJ, In Preparation). Plots were surveyed for intensity of earthworm colonization by physical forest floor attributes, midden counts and biomass surveys. The experimental design consisted of eight plots across two stand locations (Howe Lake and Second Pine Lake): two plots at each location containing no detectable *L. terrestris* colonization (0 middens/m²), and two at each location containing detectable colonization (7–20 middens/m²).

Each 20 m² plot was surveyed shortly after snowmelt (5/1/06) for *O. virginianus* fecal pellets. A pile was defined as all pellets within a 75 cm radius of the main concentration consisting of uniform size, shape, and color. When differences were observed in the physical appearance within the 75 cm radius, the piles were counted separately. The total number of piles was tallied, and ½ of the piles were sampled, pooled by plot, and retained for analysis. Pellets were dried at 55°C and weighed, yielding an average mass of 25.5 ± 2.8 g (SE) per pile. For each plot, pellets were pooled and six separate subsamples were then weighed to 25.5 ± 0.5 g (SE). The first was retained for an initial analysis, while the remaining five were returned to their respective plots at random coordinates, and marked with flagging. Pellet quality effects were controlled by pairing two piles within in each plot with fecal pellets obtained from one common

plot. No differences were observed in decomposition characteristics between the native and common pellets. At intervals pellets were collected within the 75 cm radius of the flag, oven dried at 55°C, weighed, ground, and analyzed for C:N on a Fisons elemental analyzer, and for other elements (Ca, Mg, Na, etc.) through ICP analysis at the Cornell University Nutrient Analysis Laboratory. Regression Analysis was performed using the Regression Wizard function in SigmaPlot version 8.02., and the unpaired *T*-test was performed using SPSS 13.0 for Windows.

Results and discussion

Summary mass and C, N, and Ca data are displayed according to the presence/absence of *L. terrestris* by sampling dates in Table 1. The percentage of original mass and nutrients remaining were negatively correlated to midden density (Fig. 2), which can be used as a surrogate for active population density (Lee Frelich pers. comm.). After 165 days 98% of the original mass was lost under the highest midden density, compared to a 20% mass loss in uninhabited plots. These trends for earthworm-induced increases in mass loss are similar to those reported for deciduous leaf litter in other regional forest types (Hale et al. 2005b; Suarez et al. 2006).

Earthworm effects on pellet chemistry were element-specific. Pellet C concentrations did not differ as a function of *L. terrestris* presence, and were stable throughout the study. Pellet N concentrations were lower in the presence of *L. terrestris* throughout the entire study, including at *t* = 0; this difference tended to become more pronounced with time. The dynamics of the major cations (Na, Mg, K, and Mn) were all very similar, so only Ca will be discussed here and displayed in Table 1. Calcium concentrations were similar among initial and final collection dates, and presence and absence of *L. terrestris*.

C:N ratios of pellets tended to be greater in the presence of *L. terrestris* (~39), compared to in its absence (~35–36). Initial differences in C:N ratios may have been caused by fungal colonization of pellets prior to collection. These differences in C:N were characterized by the increasing fecal pellet N concentration in the absence of *L. terrestris*, in contrast with stable pellet N concentrations in its

Table 1 Summary decomposition and nutrient data (standard error) for *Odocoileus virginianus* fecal pellet decomposition by absence and presence of *Lumbricus terrestris*

Collection date	Initial	7/8/06	8/5/06	8/17/06	9/20/06	10/20/06
Mass loss (%)						
Absent	n/a ^a	18.2 (3.7)	16.2 (4.9)	22.2 (6.4)	14.0 (4.0)	20.0 (4.0)
Present	n/a ^a	56.0 (8.4)	46.4 (10.0)	43.5 (2.9)	52.0 (7.0)	68.0 (14.0)
C conc. (g/g)						
Absent	0.50 (0.002)	0.51 (0.001)	0.51 (0.002)	0.50 (0.01)	0.51 (0.002)	0.52 (0.004)
Present	0.50 (0.004)	0.51 (0.01)	0.50 (0.002)	0.50 (0.004)	0.46 (0.04)	0.51 (0.002)
N conc. (mg/g)						
Absent	13.7 (0.39)	14.5 (0.32)	14.4 (0.29)	13.8 (0.64)	14.5 (0.34)	15.0 (0.17)
Present	13.0 (0.34)	12.2 (0.46)	12.9 (0.27)	12.4 (0.34)	13.0 (0.41)	12.9 (0.43)
C:N ratio						
Absent	36.4 (1.2)	35.2 (1.0)	35.2 (0.9)	36.3 (2.0)	34.8 (0.8)	34.6 (0.3)
Present	38.9 (1.4)	41.4 (1.7)	39.0 (1.0)	39.8 (1.2)	38.6 (1.9)	39.5 (1.7)
Ca conc. (mg/g)						
Absent	13.1 (0.36)	nd ^b	nd ^b	nd ^b	nd ^b	13.0 (0.48)
Present	12.4 (0.83)	nd ^b	nd ^b	nd ^b	nd ^b	11.9 (0.77)

Initial date is 5/1/06

^a n/a = Not applicable

^b nd = Not determined

presence (Table 1). Pellets collected from plots in the absence of *L. terrestris* accumulated significantly more N than pellets from *L. terrestris* inhabited plots (Fig. 3). The N accumulation was not affected by earthworm abundance, suggesting that there was a threshold effect controlled by earthworm presence/absence. Fungal activity can lead to increases in N content of decomposing material as hyphae import N during early decomposition (Frey et al. 2000). Fungal abundance is typically reduced in worm-colonized soils (Brown and Doube 2004) and movement of pellets by earthworms would disrupt hyphal linkages, reducing N import. Previous studies have reported increases in the C:N ratio of residual litter in worm-colonized plots. The higher C:N ratio has been interpreted as either earthworm facilitation of litter N release or preferential removal of litter with higher N concentrations (Hale et al. 2005a), but reduced fungal import of N into litter could also contribute to these patterns.

Over the course of the study, *L. terrestris* presence accelerated the total loss of C, N, and Ca from deer fecal pellets, and losses were positively correlated with *L. terrestris* population density (Fig. 2). This trend was driven predominantly by the mass loss of

material, and aided by an increase in the N concentration of fecal pellets only in the absence of *L. terrestris* (Fig. 3). This study found a 158% cumulative increase in C loss from fecal pellets in the presence of *L. terrestris*, a 290% increase in N loss, and a 218% increase in Ca loss. The increase in decomposition by *L. terrestris* can be explained by a combination of factors. Pellet diameters prohibit intact pellets from entering burrows; actual disappearance of material occurs after pellets are fragmented. Fragmentation can be facilitated through direct feeding, whereby *L. terrestris* strips smaller pieces away with its mouthparts (Edwards and Bohlen 1996). Physical disruption of pellet stability may occur while it is relocated by an individual worm, hastening its decomposition. Earthworm mucous, deposited during contact, is an important C and N source for microbial activity (Lavelle et al. 1989; Curry et al. 1995) that can inoculate litter with an energy source that facilitates microbial growth and decomposition. Further fecal pellet decomposition may also be facilitated by their locations as part of the midden, a 'biological hotspot' characterized by increased labile organic matter and microbial activity (refs. as cited in introduction).

Fig. 2 Percentage of original mass (a), carbon (b), nitrogen (c), and calcium (d) remaining from *Odocoileus virginianus* fecal pellets by the active *Lumbricus terrestris* population (measured with midden density as a surrogate)

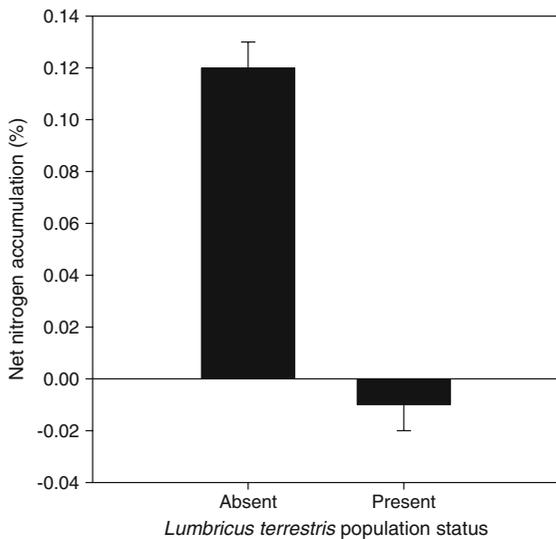
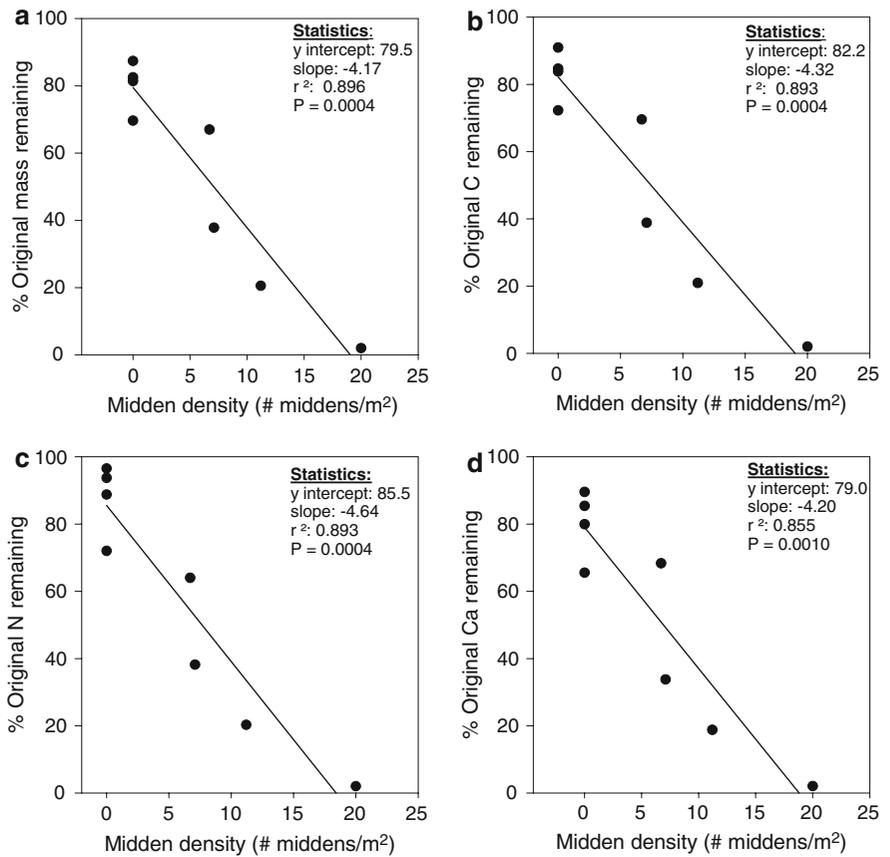


Fig. 3 Total nitrogen accumulation in *Odocoileus virginianus* fecal pellets in the presence and absence of *Lumbricus terrestris* (unpaired T -test, $P = 0.0060$)

Since browse other than fallen hemlock branches is virtually absent in the hemlock stands of our study area, *O. virginianus* feed mostly in adjacent areas. Therefore, much of fecal pellet input represents a net import of C, N, and Ca for the *L. terrestris* community and the stand. Understanding the timing and fate of these nutrient inputs will be important for determining the carbon, nutrient and regeneration dynamics of hemlock-dominated forests as populations of both deer and earthworms increase in relative abundance and range overlap.

Although deer and worm impacts in and around hemlock stands at our sites are considerable, other sites will have even greater impacts of both deer and earthworms. At our sites *O. virginianus* density is less than 65 individuals per 1,000 ha and *L. terrestris* density peaks at ~20 adult individuals per m^2 , whereas reported densities in the region exceed 200 per 1,000 ha and 80 per m^2 , respectively (Michigan Department of Natural Resources 2006, Bohlen et al. 2004c). We

calculated an average annual fecal pellet input of 8.3 kg C/ha (range = 3.6–18.3), 0.22 kg N/ha (range = 0.1–0.47), and 0.21 kg Ca/ha (range = 0.1–0.49) in hemlock stands at our study site, although pellet inputs exceeding 36.3 kg C/ha, 1.07 kg N/ha, and 1.0 kg Ca/ha have been found in other hemlock dominated stands in the region (Jill Witt and Chris Webster, pers. comm.). In these high population stands, deer fecal pellet input represents substantial nutrient input, and is equivalent to the influx from 3 to 27% of deciduous tree litter inputs in our study plots. As deciduous litter inputs can be even lower in patches dominated more strongly by hemlock (e.g., Ferrari 1999), deer pellet inputs are likely to be an ecologically significant food source at sites with high hemlock and deer populations.

Pellet inputs are likely to be a highly significant part of the nutrient subsidy to earthworms in hemlock stands because of the low leaf turnover rates and low litter quality in hemlock, combined with high deer population use of yards. Deer use of yards is a function of snowpack depth and air temperature, (Ozoga and Gysel 1972) deer population density, and hemlock stand size and area as a proportion of the landscape (Weber et al. 1983). Deep snowpack, high deer density, and a low proportion of suitable yard area in the landscape will lead to high deer population density in yards, driving deer pellet inputs into these stands to very high levels. We hypothesize that under conditions of high deer density in yards, deer pellet inputs will facilitate earthworm invasion into hemlock stands and subsequent alteration of soil properties, with unknown but potentially large consequences for hemlock stand dynamics. Earthworm effects could be either positive (e.g., by removing deciduous leaf litter) or negative (e.g., by burying or consuming seeds, altering surface soil nutrient availability, or changing surface soil physical conditions). Future efforts should determine the impact of earthworms and earthworm-deer interactions on hemlock stand biological and biogeochemical dynamics.

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