

Ungulate Carcasses Perforate Ecological Filters and Create Biogeochemical Hotspots in Forest Herbaceous Layers Allowing Trees a Competitive Advantage

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ABSTRACT

Ecological filters and nutrient heterogeneity are important in the function of ecosystems. Herbaceous layers alter forest ecosystems by filtering tree species during early stages of tree reproduction and influencing nutrient cycling. Important aspects about how tree species successfully establish below and extend above this ecological filter are unanswered in forest ecology. We experimentally tested the effects of large ungulate carcasses on the filtering function of herbaceous layers. Even well-utilized carcasses created unexpected disturbances that reduced herbaceous cover, which effectively perforated the herbaceous layer filter that can differentially influence tree reproduction. Carcasses also created lasting biogeochemical “hotspots” in forest soils that may help maintain plant biodiver-

sity by creating resource heterogeneity and shifting competitive relationships. Because the spatial distribution of carcasses is influenced by predators, these data establish an unrecognized link between large carnivores, prey carcasses, and ecosystem processes. This link supports a novel understanding of disturbance by large herbivores in forest ecosystems by demonstrating an important interaction between predator–prey functional traits and tree seedling dynamics on either side of a major ecological filter.

Key words: disturbance; forest ecology; heterogeneity; patch dynamics; regeneration niche; resource pulses; spatial pattern; trophic cascades; forest biodiversity; ecological filter.

Received 23 February 2009; accepted 1 June 2009; published online 10 September 2009

Author Contributions: JKB conceived and designed study, performed research, analyzed data, wrote the paper; CRW conceived and designed study, and wrote the paper; JAV and ROP conceived and designed study; JMS and MDP performed research.

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INTRODUCTION

Despite its small stature, the herbaceous layer is proving to be of large importance to the structure and function of forest ecosystems (Gilliam 2007). Forest biodiversity, energy flow, nutrient cycling, and regeneration are significantly affected by the composition of herbaceous layers (Siccama and others 1970; Gilliam and Roberts 2003a; Whigham

2004) and herbaceous species outnumber tree species nearly 6:1 in most forests (Gilliam 2007). Although the herbaceous layer represents less than 1% of temperate forest biomass, it can contribute up to 20% of the foliar litter to the forest floor (Muller 2003). Herbaceous litter generally exhibits higher concentrations of limiting nutrients and can decompose twice as rapidly as tree litter (Muller 2003), thereby affecting energy flow and nutrient cycling to a degree that is disproportional to its relative biomass in forest ecosystems (Gilliam 2007).

Herbaceous layers are also an important link to overstory development because they significantly influence the early life history stages of tree reproduction. Tree seeds must first penetrate the herbaceous layer to reach the forest floor, germinate, and then grow above the herbaceous layer to potentially reach the overstory. Hence, the herbaceous layer can act as an ecological filter, selectively sifting tree seeds falling to the forest floor and mediating the microclimate for germinants and seedlings (George and Bazzaz 1999a, b; Coomes and others 2005; Gilliam 2007; Dearden and Wardle 2008). Under some conditions, persistent dominant herbaceous layers develop that are nearly impenetrable (Royo and Carson 2006). Large scale disturbances (for example, fire) permit tree species to “escape” this ecological filter but can also create heavy mortality among seedlings (Frelich 2002). Smaller scale, more frequent mechanisms that simultaneously reduce filtering effects by the herbaceous layer and positively influence early stages of tree reproduction remain unidentified. Here we show that even well-consumed large ungulate carcasses create unexpected disturbances that perforate dense herbaceous layers and provide nutrient pulses that increase tree germination and seedling growth on carcass sites relative to undisturbed sites.

Forest disturbance ecology has largely focused on large-scale, abiotic factors (for example, fire, floods, wind, ice, landslides) and less so on biotic factors (for example, herbivory, disease and insect outbreaks; Frelich 2002). The role of large ungulates in forest disturbance is characterized by cases of sustained over-browsing, which can reduce plant cover and diversity, alter biogeochemical cycling, and shift future overstory composition (Côte and others 2004). Recently, however, the nutrient rich and highly labile carcasses of large ungulates have been recognized as important disturbances in non-forested systems (Hobbs 2006; Carter and others 2007). Bison (*Bos bison*, L.), cattle (*B. Taurus*, L.), and white-tailed deer (*Odocoileus virginianus*,

Boddaert) carcasses can create strong, localized disturbances that deposit nutrients at intensities that exceed other natural processes, thus altering prairie species composition and biomass (Towne 2000). These grassland effects persisted 5 years postmortem, and in the low-resource environment of the Arctic tundra, the impact of a muskox (*Ovibos moschatus*, Zimmerman) carcass on surrounding vegetation was still dramatic after 10 years (Danell and others 2002). Although these studies emphasize that carcass-disturbances may have lasting effects in some systems, the effects of large ungulate carcasses in forest ecosystems remain unknown.

Large ungulate carcasses are typically very well-used, with soft tissue resources moving up a trophic level via consumption by predators and scavengers (Wilmers and others 2003) rather than entering decomposition pathways directly. For example, at deer carcass sites in the Upper Peninsula of Michigan, USA, little appears to remain except bone, hair, and rumen contents (first stomach chamber; Figure 1). Such appearances likely prevent one from recognizing that carcasses in forest ecosystems could also be important to soil nutrient heterogeneity, herbaceous layer coverage, and tree seedling establishment and growth. However, natural die-offs in large mammal populations, especially ungulates, are geographically widespread and declines of 70–90% are not uncommon (Young 1994). When die-offs occur, predator and scavenger populations are often satiated. Such instances of high carrion abundance, including seasonal road-kill and hunter gut piles, can lead to slow and incomplete carcass consumption, consumption of specific tissues only (for example, visceral organs), and intact carcasses that putrefy and decompose in situ. Under such conditions, carcasses would likely result in more intense nutrient pulses and disturbances because a higher percentage of the carcass biomass would enter soil communities. Therefore, if even well-used ungulate carcasses affect forest soil, floor, and tree seedlings in the herbaceous layer, then such effects would be conservative evidence that carcasses are linked to the spatial patterns of disturbance, nutrient heterogeneity, and shifting mosaics (sensu Bormann and Likens 1979) of tree regeneration in a novel way. Thus far no one has investigated such a link (but see Helfield and Naiman 2006 for similar links via salmon carcasses).

In this study, we experimentally examined the effect of white-tailed deer carcasses (*Odocoileus virginianus*) on herbaceous layers and soils in a northern hardwood forest in the Upper Peninsula of Michigan, USA. Differences in soil macronutri-

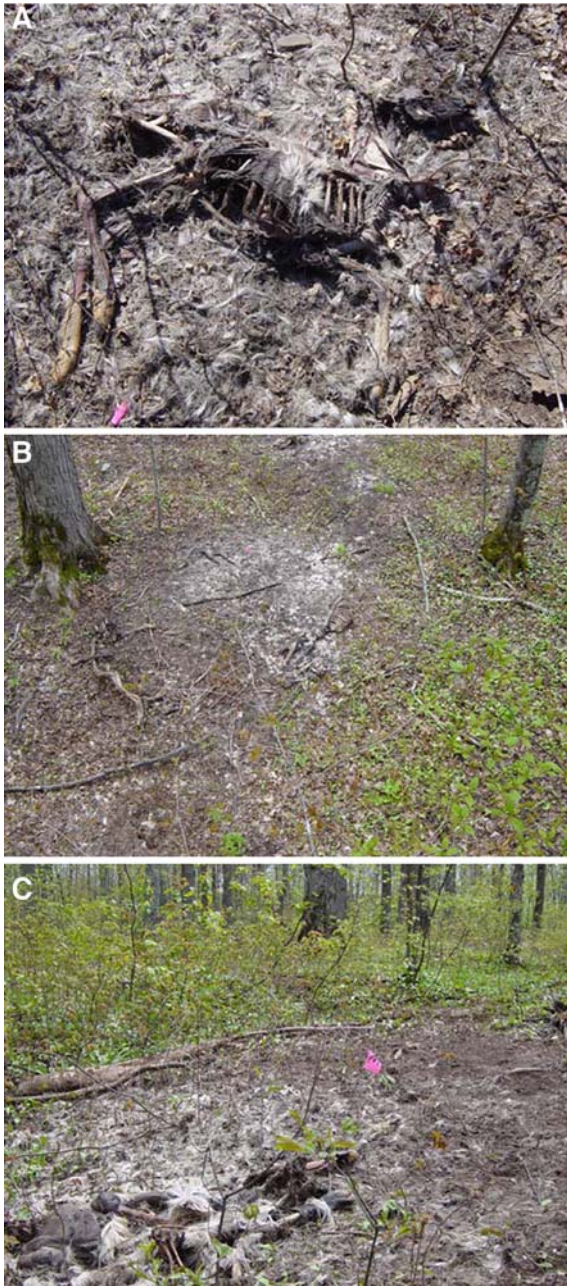


Figure 1. Photograph of a one-week-old, scavenged white-tailed deer carcass (A). Photographs of a deer carcass site in spring (B) and early summer (C).

ent availability, ground-layer litter depth, bare soil, and spring and summer herbaceous layer species composition, were compared at deer carcass and paired control sites for 2 years postmortem. We also compared tree seedling germination, leaf tissue nitrogen, and growth between carcass and control sites to understand if carcass disturbances are linked to seedling germination and growth, which are critical early life stages that ultimately influence forest succession, composition, and structure

(Frelich 2002; Gilliam 2007). Because predators and scavengers were not excluded from experimental plots, we expected carcasses to be well-used, with near complete consumption of soft tissues, as is most often the case in our study system (Figure 1). Therefore, we predicted no difference in the soil and herbaceous layer response to carcass and control treatments.

MATERIALS AND METHODS

Field Site and Carcass Experiment

To examine the effect of deer carcasses on herbaceous layers, we placed 40 experimental plots in a northern hardwood forest at the Ford Center Research Forest near Alberta, MI, USA: Sect. 18, T49 N-R33 W Baraga County, MI. Soils in this area were dominated by Allouez sandy loams and canopy layers were dominated by sugar maple (*Acer saccharum*, L.). This site was well-suited for examining carcass–herbaceous layer dynamics because trout lily (*Erythronium americanum*, L.) and spinulose shield fern (*Dryopteris spinulosa*, Jacquin) were the most abundant herbaceous species in the spring and summer, respectively. Percent cover over many areas of the experimental site reached approximately $95\% \text{ m}^{-2}$ for trout lily and approximately $75\% \text{ m}^{-2}$ for spinulose shield fern, suggesting that these herbaceous species are prevalent enough to act as ecological filters influencing energy and nutrient cycling (that is, vernal dam hypothesis; Muller and Bormann 1979) and the density, species composition, growth, survival, and spatial distribution of the seedling bank below the canopy (that is, fern layers as ecological filters; George and Bazzaz 1999a, b). Windthrow has been the primary mode of disturbance since heavy logging in the late 1800s and early 1900s. To minimize potential differences in available light reaching the herbaceous stratum, plots were located under a homogenous canopy, containing no large gaps, and with continuous cover during the experiment.

A two-factor, randomized block design was used to test for effects of carcasses and deer herbivory on soil and plant response to treatments over three growing seasons. Deer herbivory was added as a factor because herbivory by locally abundant deer may mask carcass disturbance effects. The experimental design consisted of four treatments (unmanipulated, herbivory-control, carcass-disturbance, and carcass-disturbance with herbivory-control) with 10 replicates per treatment. Plots in the carcass-disturbance and carcass-disturbance with herbivory control treatments received an

intact, road-killed deer carcass that was previously frozen. Carcasses were placed laterally on the ground surface, centered in plots, in late April 2005. The timing of carcass placement reflects the natural system in which prey kill-rates typically increase throughout winter, most large die-offs occur in late winter, and winter-kill carcasses often remain intact due to snow cover and satiated scavengers (Langenau 1996; Doepker and others 1996; Huntzinger 2006).

Deer carcasses were approximately the same size (mean \pm 1SD = 56 ± 9 kg, $N = 40$). Daily observations and surveys of wildlife signs were subsequently conducted until soft tissues were more than 95% consumed. Plots in the unmanipulated and herbivory-control treatments received no deer carcasses. In each herbivory-control and carcass-disturbance with herbivory control plot we placed cylindrical, open-top cages (1.5 m \times 2 m diameter) constructed of 15.24 cm square, wire mesh staked with 1 m metal bars at two opposing points. Cages were erected after carcasses were consumed. Each treatment plot in a block was within a 25 m radius, and all blocks were within 1 km of each other.

Soil Macronutrients

We measured nitrogen (N), phosphorus (P), and potassium (K) levels because these macronutrients are generally limiting to primary productivity in temperate systems (Frellich 2002). Soils were collected before treatment in mid April 2005, and after treatment in early September 2005 and 2006. At each sampling time, four soil cores (4 cm diameter \times 10 cm depth) were collected within 1 m of the center of each plot, well within the area disturbed by the carcass given that the core area encompassing carcass remains and disturbed by predator and scavenger activity averaged 6.25 m² ($N = 40$). Cores were then pooled, homogenized, weighed, and dried to a constant weight at 105°C. Due to financial limitations, a random sub-sample of soils from five blocks was analyzed for inorganic nitrogen [that is, nitrate (NO₃⁻) and ammonium (NH₄⁺)], magnesium (Mg), calcium (Ca), K, and P following standard procedures (Brown 1998). Inorganic N was extracted with 1 N KCl and analyzed calorimetrically, a Mehlich 3 extractant was used to determine exchangeable Mg, Ca, and K levels, and a Bray P1 extractant was used to determine soil available P. Although recent work has demonstrated the importance of organic nitrogen uptake in some ecosystems (Lipson and Näshholm 2001), and other methods exist for

indexing available N (Binkley and Matson 1983), these assays are appropriate methods for assessing gross nutrient pools available to plants and microbial communities in northern, temperate forest soils (Brown 1998). Analysis of nutrient concentrations was conducted blind by Michigan State University Soil and Plant Nutrient Lab. Macronutrient data were analyzed using one-way mixed-model (carcass and herbivory exclusion treatments) repeated measures analysis of variance (ANOVA) and a priori planned contrasts to test the hypothesis of positive carcass effects on macronutrient concentrations. Brown-Forsythe and O'Brian tests were used to confirm assumptions of circularity (that is, the variance of the *difference* of observations between sampling times is the same for each plot; Gotelli and Ellison 2004).

Herbaceous Layer Composition and Forest Floor Cover

In May and August of 2005 and 2006 herbaceous layer composition (aerial percent cover m⁻¹, including bare ground) was measured for all species less than 50 cm tall on all plots. To reduce observer bias, a single observer performed ocular estimates. To ensure positive identification, plots were later revisited to identify unknown species in flower. Species importance values (IV = [relative percent cover + frequency]/2), were used to assess differences in the relative dominance of herbaceous species between treatments. Individual importance values were calculated for each species present on at least 50% of sample plots and remaining species were pooled into a single category. Percent cover and importance value data were analyzed using matched-pairs analysis to test the hypothesis of no difference between treatment plots within each year. Alpha level ($\alpha = 0.006$) was Bonferroni adjusted to account for multiple comparisons. Normal probability plots and Levene tests were used to confirm assumptions of normality and homoscedasticity, respectively.

Tree Seedling Tissue Quality, Germination, and Growth

We measured foliar nitrogen, which strongly regulates photosynthetic potential (Messaoud and Houle 2006), in sugar maple seedlings (<50 cm tall), the dominant seedling and overstory species present. To assess whether maple seedlings likely assimilated nitrogen sources affected by carcasses, we measured stable nitrogen isotope ($\delta^{15}\text{N}$) values of foliage for treatments with and without carcasses

(Fry 2006). Leaves from sugar maple seedlings were collected during early June 2005–2007 from each treatment for measurement of total carbon (C), total N (dry mass) and stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) concentrations. Leaves of equal size were clipped at their base from actively growing plants, double rinsed with distilled water to remove debris, dried at 17°C to a constant weight, and then individually homogenized in a bearing shaker mill. Analysis was performed blind on a Costech Elemental Combustion System 4010 connected to a Thermo Finnigan ConFloIII Interface and Deltaplus Continuous Flow-Stable Isotope Ratio Mass Spectrometer at Michigan Technological University's Ecosystem Science Center. IAEA, USGS, and NIST certified isotopic standards were run at the beginning of each analysis. One certified standard was also run at the end of the analysis to check for calibration stability. Stable isotope values are reported in standard δ notation, and are reported on the VPDB scale for $\delta^{13}\text{C}$ and on the atmospheric air scale for $\delta^{15}\text{N}$. An internal standard was run every 10 samples. Precision based on repeated measures of internal standards was $\pm 0.25\%$ for $\delta^{13}\text{C}$ and 0.5% for $\delta^{15}\text{N}$.

Sugar maple seed mast was high in 2006, hence seedling germination and summer survival was measured in 2007. A single observer conducted double-counts of germinants in a 0.25 m^2 area centered on each treatment plot in late May and mid-August. Germinant density for each sampling time was averaged for each treatment and is expressed per m^2 . After leaf-fall in 2007, available maple seedlings (height < 50 cm, diameter range = 3.5–7.8 mm) from each plot (that is, within 0.5 m of the center) were collected for growth analysis. Seedlings were air dried and stems were then cut 3 cm above the root collar. Terminal stem surfaces were sanded to reveal cellular structure and help identify false and light rings. Annual ring widths were measured to the nearest 0.01 mm using a binocular microscope and sliding-stage micrometer. Widths were measured along two perpendicular ring series for each seedling. This procedure was done twice, blind to treatment, and ring-widths were then averaged for each sample.

Tissue quality, stable isotope, and germination data were analyzed using statistical methods described for soil macronutrients. Ring width data were analyzed using a paired *t*-test to test the hypothesis of zero difference between mean ring widths for 2 years pre- and post-treatment. Normal probability plots and Levene tests were used to confirm assumptions of normality and homoscedasticity, respectively.

RESULTS

Direct observation and field signs (scat and tracks) indicated that predators (gray wolves, *Canis lupus*, L.; coyotes, *Canis latrans*, L.) and vertebrate scavengers (for example, red fox, *Vulpes vulpes*, L.; ravens, *Corvus corax*, L.; bald eagles, *Haliaeetus leucocephalus*, L.) visited carcass plots, removing more than 95% of the soft tissue within 3 weeks of carcass additions. The core area (convex polygon) encompassing carcass remains and disturbed by predator and scavenger activity averaged 6.25 m^2 ($N = 40$). Deer herbivory did not affect the response of any soil, ground, or herbaceous layer attribute to treatments (herbivory effect with ANOVA and matched-pairs analyses always resulted in nonsignificance; $P > 0.54$). Consequently, results presented here are from single factor analyses with pooled results. Results for unmanipulated and herbivory-control treatments were pooled into one treatment (hereafter control) and results for carcass-disturbance and carcass-disturbance with herbivory exclusion treatments pooled into one treatment (hereafter carcass).

Prior to treatment no difference in macronutrients (P, K, Mg, Ca, NO_3^- , NH_4^+) existed between treatment plots (Figure 2). At 3 and 15 months after treatment, soils at carcass sites had 80 and 60% more phosphorus, respectively, ($F_{1,56} = 11.6$, $P = 0.001$), 52 and 33% more potassium ($F_{1,56} = 5.7$, $P < 0.020$), 895 and 208% more nitrate ($F_{1,56} = 5.8$, $P < 0.019$), and 298 and 137% more ammonium ($F_{1,56} = 18.1$, $P < 0.022$) relative to adjacent control sites (Figure 2A, B, E, F). Differences between carcass sites and control sites exhibited a temporal pattern of initial increase and subsequent decrease (Figure 2).

Dominant spring and summer herbaceous species responded negatively to the carcass additions for two growing seasons after treatment ($P = 0.0002$ to < 0.0001 ; Table 1). The decrease in percent cover (20–22%) and importance value (9.5–24%) of dominant herbaceous species on carcass sites relative to control sites was highest the first growing season after treatment (Figure 3). With the exception of fern importance values, these effects persisted during the second growing season after treatment (Figure 3). No difference was found between treatments for all other summer herbaceous species (Table 1). Coverage of the dominant tree seedling decreased with moderate significance ($P = 0.008$) the first growing season after treatment (Table 1). Spring litter depth decreased ($F_{3,156} = 28.8$, $P < 0.001$) and percent bare ground increased ($F_{3,156} = 19.7$, $P < 0.003$) on

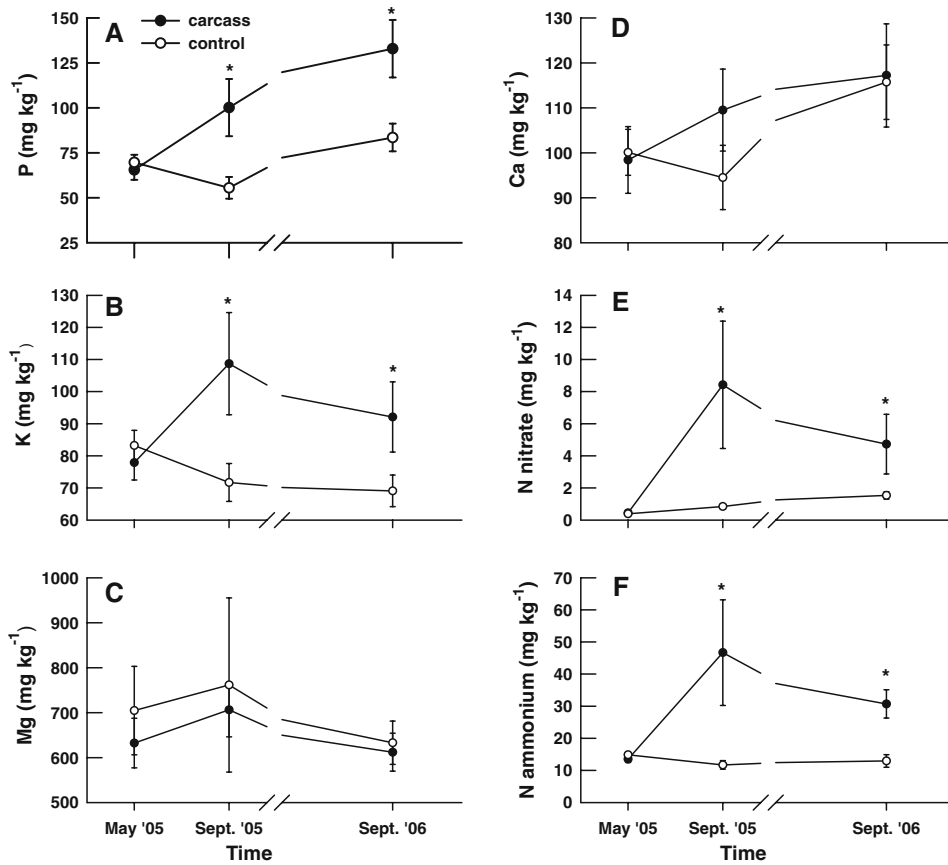


Figure 2. Indices of nutrient availability in soils from white-tailed deer carcass sites (solid circles) and paired control sites (open circles) before carcass treatment (May 2005) and at the end of two growing seasons after treatment (Sept. 2005, Sept. 2006). **A** Phosphorus, **B** potassium, **C** magnesium, **D** calcium, **E** nitrate, and **F** ammonium. Asterisks (*) indicate significant ($P < 0.05$) differences for planned contrasts between carcass and control sites at each postmortem sampling time. Error bars show mean \pm SE (some are too small to be seen). Note break in x-axis and the different y-axis scales.

Table 1. Mean (\pm SE) Percent Cover of Herbaceous Layer Species

Species	Treatment			Paired analysis*	
	Year	Carcass	Control	t-ratio	P-value
<i>Percent cover</i>					
<i>Erythronium americanum</i> ¹ (Trout lily)	2005	4.3 \pm 0.5	26.5 \pm 3.8	-5.90	<0.0001
	2006	0.5 \pm 2.0	14.0 \pm 2.6	-5.15	<0.0001
<i>Dryopteris spinulosa</i> ² (Spinulose shield fern)	2005	8.2 \pm 1.8	28.6 \pm 3.8	-6.07	<0.0001
	2006	3.4 \pm 0.9	8.4 \pm 1.5	-3.22	0.002
<i>Acer saccharum</i> ³ (Sugar maple)	2005	9.4 \pm 0.9	14.7 \pm 1.6	-2.76	0.008
	2006	17.5 \pm 2.6	21.7 \pm 3.0	-1.20	0.238
All other species ⁴	2005	9.1 \pm 1.4	13.4 \pm 2.3	-4.25	0.049
	2006	17.3 \pm 2.6	17.6 \pm 3.3	-0.09	0.927

¹Dominant spring herb.

²Dominant summer herb.

³Dominant tree seedling.

⁴Includes summer herb species only.

*Comparisons of the difference between matched pairs of treatment plots (N = 40 for each test; Bonferroni adjusted $\alpha = 0.006$).

carcass sites compared to control sites, which, combined with the nutrient pulse (Figure 2), may have contributed to increased maple seedling germination on carcass sites (Figure 4, $F_{1,77} = 50.0$, $P < 0.001$).

Foliar nitrogen levels were 101 and 24% higher in plants growing on carcass sites compared to

control sites ($F_{1,57} = 34.3$, $P < 0.0001$) for the first two growing seasons after treatment (Figure 5A), indicating higher photosynthetic potential for plants on carcass sites. The mean foliar carbon-to-nitrogen ratio decreased 50% over the first growing season (Figure 5C, $F_{1,57} = 57$, $P < 0.0001$), indicating higher aggregate leaf tissue quality at carcass

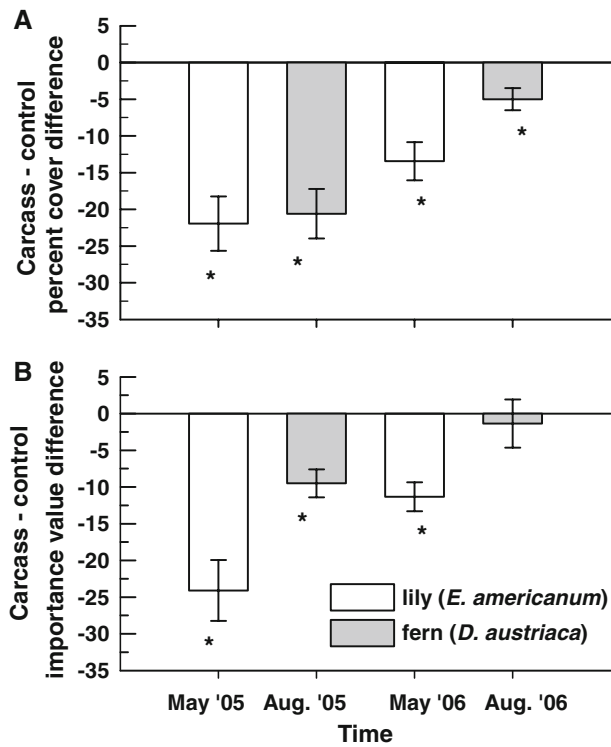


Figure 3. Comparison of mean white-tailed deer carcass-control differences in percent cover (A) and importance value (B) for dominant spring (lily) and summer (fern) herbaceous species. Reference line is at 0, indicating no difference between treatments. Error bars show mean \pm SE. Note break in x-axis scales. Asterisks (*) indicate a mean difference significantly below 0 ($P < 0.05$).

sites. Maple foliage from carcass sites had elevated $\delta^{15}\text{N}$ compared to control sites during all three growing seasons after treatment, but lagged in response relative to carcass effects on soil N increase (Figure 5B, $F_{1,57} = 38.1$, $P < 0.0001$). Tree ring width of maple seedlings 2 years before treatment did not differ between carcass and control plots (t -ratio = 1.39, $df = 37$, $P = 0.17$), but for 2 years after treatment seedlings on carcass plots exhibited increased ring widths compared to control plots after treatment (t -ratio = 6.46, $df = 37$, $P < 0.0001$, Figure 6). The mean difference in ring width for this comparison was 1.6 mm between carcass and control plots.

DISCUSSION

Large ungulate carcasses effectively perforated the herbaceous layer filter that can differentially influence seed predation, germination, and seedling growth and survival (sensu George and Bazazz 1999a, b, 2003). Contrary to our expectation, even

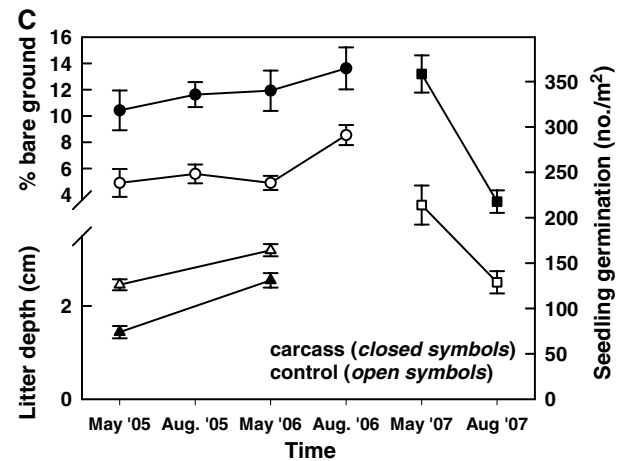
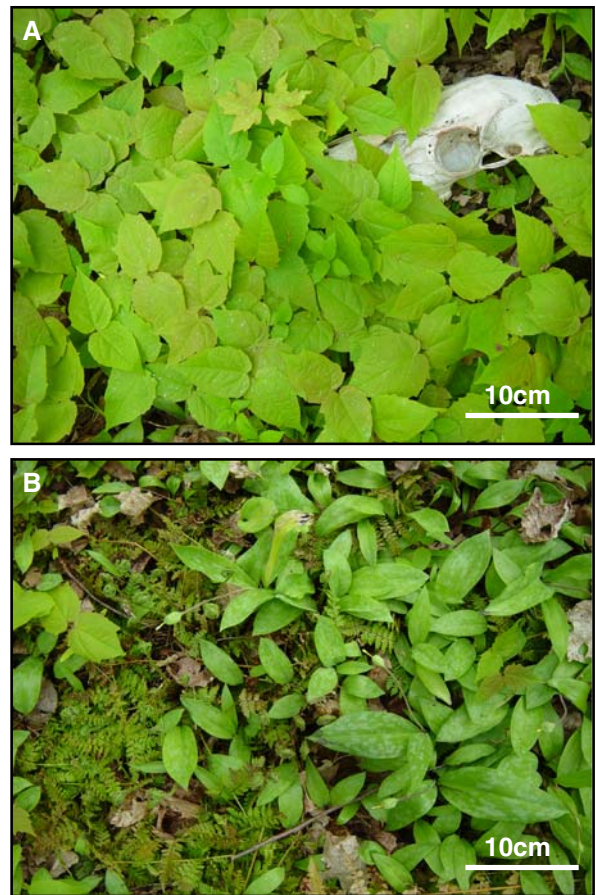


Figure 4. Contrasting white-tailed deer carcass (A) and control (B) sites in spring after heavy sugar maple mast in previous fall season. Mean litter depth (triangles), bare soil (circles), and sugar maple seedling germination (squares) on deer carcass and control sites (C). Significant ($P < 0.05$) differences exist between carcass and control treatments at each sampling time.

well-utilized large herbivore carcasses created disturbances that reduced the cover of dominant herbaceous layer species in spring and summer

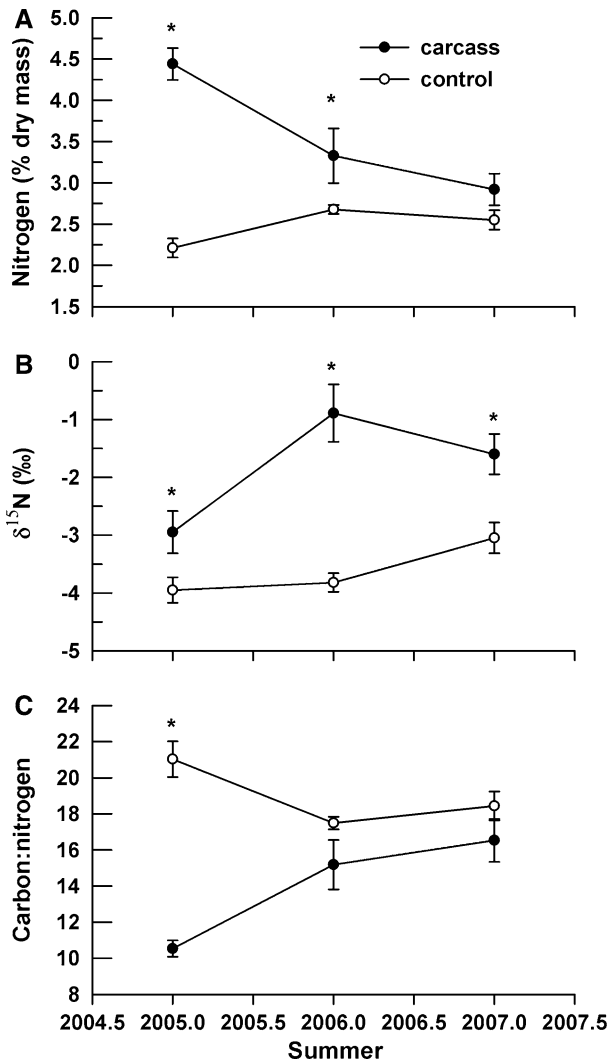


Figure 5. Foliar nitrogen content (A), $\delta^{15}\text{N}$ (B), and carbon:nitrogen ratio (C) from white-tailed deer carcass (solid circles) and paired control sites (open circles) in sugar maple leaves for three growing seasons after treatment. Asterisks (*) indicate significant ($P < 0.05$) differences for planned contrasts between carcass and control sites at each sampling time. Error bars show mean \pm SE. Note different y-axis scales.

(Table 1; Figure 3). Carcass disturbance also resulted in significant pulses of growth-limiting nutrients for at least two growing seasons post-mortem (Figure 2). These effects resulted in higher germination, foliar N, and growth for tree seedlings at carcass sites compared to control sites (Figures 4, 5, 6). These data support a novel understanding of disturbance by large herbivores in forest ecosystems. This is important because mechanisms that structure nutrient, light, and space availability are critical to seedling development, and thereby future forest composition because such mechanisms

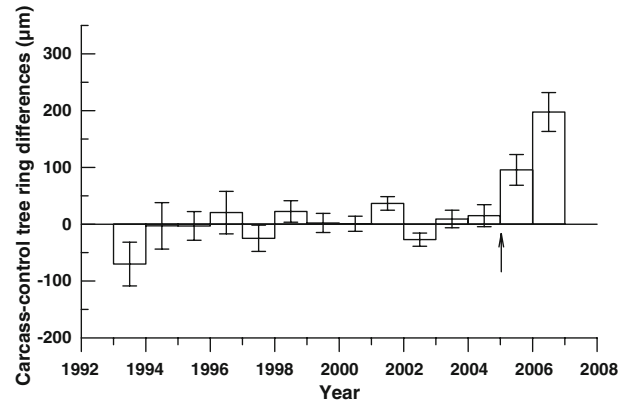


Figure 6. Mean white-tailed deer carcass-control differences in tree ring width for sugar maple seedlings growing on carcass and paired control sites. Reference line is at 0, indicating no difference between treatments. Error bars show mean \pm SE. Arrow indicates start (2005) of experimental treatment.

influence the trajectory, rate, and spatial patterns of regeneration (Grubb 1977; Frelich 2002).

The growth rate of tree seedlings is often correlated with light availability (George and Bazazz 2003; Delagrange and others 2004; Gilliam 2007). Other experimental work has demonstrated that when dominant fern cover, similar to that present in this study, in deciduous forests is decreased, light levels below the fern layer increase, resulting in higher seedling germination, growth, and survival of specific species (George and Bazazz 1999a, b). Maple seedling germination patterns, in particular, are positively correlated with photosynthetic photon flux density (Messaoud and Houle 2006). Higher light levels, although not measured here, likely occurred at carcass disturbed sites because the cover of dominant species decreased (Table 1). Increases in light availability due to carcass disturbance almost certainly contributed to the strong growth response of maple seedlings on carcass sites (Figure 6). Maple seedling cover decreased on carcass sites the first season following treatment (Table 1). This change suggests that a reduction in competition for light and nutrients among maple seedling conspecifics may also contribute to the seedling foliar N and growth response (Figures 5, 6). Increased foliar N for carcass site seedlings would enhance photosynthetic rates compared to control site seedlings at any given light level because foliar N is strongly related to carbon fixation (Elvir and others 2005). The total disturbance effect of large ungulate carcasses, therefore, appears to be at least three-fold. Carcasses provide nutrient pulses, likely increase light availability, and alter competitive relationships in forest herbaceous layers.

In addition to perforating the physical filter created by herbaceous foliage, large herbivore carcasses create biogeochemical “hotspots” (Figures 1, 2) in forest ecosystems that may help maintain tree and herbaceous species biodiversity by creating resource heterogeneity. Resource heterogeneity is a mechanism that likely provides unique regeneration niches for trees and maintains coexistence in competing plant species (Grubb 1977; Pacala and Tilam 1994; George and Bazazz 1999a, b; Chesson 2000; Catovsky and others 2002). For example, spatial heterogeneity in microenvironments led to large differences in growth and survival of dominant tree species in southern Appalachian forests (Beckage and Clark 2003). In a tallgrass prairie system, the pulse of resources released from bison carcasses resulted in differences in species composition between disturbed and undisturbed patches that persisted at least 5 years postmortem, thereby contributing to grassland heterogeneity (Towne 2000). The decrease in the importance of dominant spring and summer herbaceous species suggest that carcass-derived resources in forests may shift competitive relationships among species with different resource, light, and space use efficiencies, thereby affecting subsequent germination, survival, growth, and reproduction. Hence, this work identifies the need to study the long-term effects of large carcasses on plant species coexistence, dominance, biodiversity, and spatial distribution in forest ecosystems.

Importantly, the disturbance observed at carcass sites occurs at a spatial scale and frequency similar to other factors (for example, pit and tip-up mounds created by wind throw, nurse logs) that promote the maintenance of species diversity in temperate forest communities (Harmon and Franklin 1989; Beaty 2003; Christie and Armesto 2003). For example, over a 25-year period in an unmanaged hardwood forest in Michigan, the mean rate of wind throw was 13 trees $\text{km}^{-2} \text{y}^{-1}$ (Brewer and Merritt 1978). Recent deer densities in our study region are approximately 12 km^{-2} and the mean life expectancy is 2–3 years (Doepker and others 1996; Halls 1984). Therefore, annual mortality is approximately 4–6 deer $\text{km}^{-2} \text{y}^{-1}$ (that is, the reciprocal of life expectancy multiplied by deer density). Hence, carcass disturbance can occur at a rate equal to 30–46% of the wind throw disturbance rate and on the scale of pit and tip-up mounds. Many hardwood forests are managed, which likely increases the importance of carcass disturbances because wind throw is less common (Schulte and others 2007) and deer densities are typically higher in managed forests compared to unmanaged forests (Alverson and others 1988).

When natural die-offs in large ungulate populations occur, carcass distribution can exhibit strong spatial patterns. For example, deer in northern hardwood forests typically congregate in cedar (*Thuja occidentalis* L.) and hemlock [*Tsuga canadensis* (L.) Carr.] stands during the winter (that is, deer-yards; Halls 1984). Such aggregations can create areas of high carcass density when die-offs occur. Declines of about 20–30% in Michigan’s Upper Peninsula deer population (~100,000–200,000 individuals) have been documented during the winters of 1955/56, 1978/79, 1985/86, 1993/94, and 1995/96 (Langenau 1996; Doepker and others 1996). In such years, we would expect the deer carcass effects demonstrated here (Table 1; Figures 2, 3, 4, 5, 6) to be highly aggregated on the landscape. In mild Upper Peninsula winters approximately 35,000 deer die due to starvation, about 70,000 in moderate winters (Michigan Department of Natural Resources 2008). The potential long-term consequences of repeated carcass deposition on soils and herbaceous layers in areas of high mortality, such as deer-yards, remain unexamined, yet our results suggest that repeated carcass deposition would likely have significant effects on herbaceous layer dynamics.

The soil response to carcasses (Figure 2) may include the effects of positive macronutrient feedbacks at carcass sites. Positive feedbacks occur because carcass sites are nutrient and energy focal points, receiving exuviae and puparia materials from dead invertebrates, and fecal and urine deposition from scavengers, large herbivores, and predators (Carter and others 2007). For example, bird droppings whitewashed course woody debris and leaf litter at carcass sites. Such activity means that although the intense N, P, and K effects are likely restricted to the core area encompassing carcass remains at kill sites, a single carcass could be ecologically important at larger scales (that is, ha-km) by influencing the landscape mosaic of herbaceous layer and forest overstory links (Gilliam and Roberts 2003b).

The lagged response in foliage $\delta^{15}\text{N}$ on carcass sites (Figure 5B) may reflect slower decomposition of some isotopically heavy, recalcitrant carcass remains (for example, bone or hair). The bones and hair of large herbivores show enriched $\delta^{15}\text{N}$ relative to their plant diet due to preferential retention of heavier isotopes in consumers (Fry 2006). The increased $\delta^{15}\text{N}$ in foliage at carcass sites suggests that a carcass-derived N source leads to higher available N in soils, resulting in increased plant N assimilation (Figure 5), which may influence aboveground trophic interactions. For example,

herbivores are attracted to patches of nitrogen-rich forage (Danell and others 2006). Hence carcass sites become foraging sites (Towne 2000; Danell and others 2006), and the probability of repeated foraging within and around carcass sites initiates a positive feedback of recurrent nutrient supplementation from frass, feces, and urine deposition. Deer herbivory was not a significant factor in plant response to carcass disturbance, perhaps because of predator and scavenger activity at carcass sites. Increased invertebrate herbivory of plants growing on carcass sites remains unexamined.

These results also indicate an important way by which the predators of large herbivores can influence the landscape mosaic of nutrient cycling and species interactions. If carnivores affect the distribution of carcasses that result from predation, they would also affect the spatiotemporal heterogeneity of soil and plant properties. Recent research in southern boreal forests and grasslands in North America indicates that the carcasses of moose (*Alces alces*, L.) and elk (*Cervus canadensis*, Erxleben) produced via wolf predation are important to above and belowground communities (Bump unpublished manuscript). Predation by wolves also occurs in some locations at rates that are different than the rates for other causes of mortality such as starvation and hunting (Wilmers and others 2003; Kauffman and others 2007). For example, wolves preferentially travel along shorelines in Isle Royale National Park (Peterson 1977), which results in moose kills being significantly clustered near water (Peterson 1977; Bump unpublished manuscript). Similarly, landscape analysis of wolf-killed elk in Yellowstone National Park shows that flat grasslands near streams and roads are favorable to wolf hunting success (Kauffman and others 2007). In northern hardwood forests, wolves preferentially kill deer within pack territories, avoiding areas of territory overlap, presumably to minimize the chance of lethal interactions with wolves from other packs (Mech 1977). Hence, across three distinct systems, wolf hunting behavior affects the landscape distribution of carcasses. These wolf-carcass-landscape links demonstrate how the functional traits of species in large mammal predator-prey systems are linked to ecosystem processes, such as resource heterogeneity, through carcass distribution.

Humans also hunt nearly all wild ungulates, which results in spatial and temporal carcass distributions patterns that are different than those created by wild carnivores. Carcasses and gut piles left by hunters arrive in super abundant pulses and with less dispersion than wild predator-kills (for

example, Wilmers and others 2003). Through hunting, wounding loss, and vehicle collisions humans killed about 2.5–4 times more deer than wolves in Michigan's Upper Peninsula (~61,000 human caused versus ~15,000–25,000 by wolves, Michigan Department of Natural Resources 2008). Large ungulate mortality due to vehicle collisions is widespread and exhibits distinct spatial patterns (Romin and Bissonette 1996). These differences in kill timing and distribution emphasize that the important ecological effects of large animal carcasses can be significantly affected by human behavior as well as the hunting behavior of wild predators.

This study contributes to a growing recognition that carcasses of vastly different sizes, from whales to salmon to cicadas, have significant and lasting effects in diverse ecological systems (Towne 2000; Smith and Baco 2003; Yang 2004; Helfield and Naiman 2006; Carter and others 2007). The effect of deer carcasses on forest herbaceous layers demonstrated here expands this awareness significantly because large herbivores are nearly ubiquitous in temperate and boreal forests (Danell and others 2006). Large herbivore carcasses, therefore, can be understood as biotic disturbance mechanisms with important ecological effects across multiple biomes.

ACKNOWLEDGEMENTS

Special thanks to Dave Stimac, Caitlin Bump, Sam Gardner, Brett Huntzinger, Peter Hurley, Amy Schrank, Brian Henry, and Jim Schmierer. Research was supported by a Biosphere Atmosphere Research & Training fellowship (NSF IGERT grant 9972803) and an NSF (DEB-0424562) grant to R.O.P. and J.A.V. The research described in this paper has also been funded in part by the United States Environmental Protection Agency (EPA) under the Greater Research Opportunities (GRO) Graduate or Undergraduate Program (EPA GRO grant F5F71445 to J.K.B.) EPA has not officially endorsed this publication and the views expressed herein may not reflect the views of the EPA. Experiments complied with current USA law.

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