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Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses

Joseph K. Bump,[1] Rolf O. Peterson, and John A. Vucetich

School of Forest Resources and Environmental Science, 1400 Townsend Drive, Michigan Technological University, Houghton, Michigan 49931 USA

Abstract. Mechanistic links between top terrestrial predators and biogeochemical processes remain poorly understood. Here we demonstrate that large carnivores configure landscape heterogeneity through prey carcass distribution. A 50-year record composed of >3600 moose carcasses from Isle Royale National Park, Michigan, USA, showed that wolves modulate heterogeneity in soil nutrients, soil microbes, and plant quality by clustering prey carcasses over space. Despite being well utilized by predators, moose carcasses resulted in elevated soil macronutrients and microbial biomass, shifts in soil microbial composition, and elevated leaf nitrogen for at least 2–3 years at kill sites. Wolf-killed moose were deposited in some regions of the study landscape at up to 12× the rate of deposition in other regions. Carcass density also varied temporally, changing as much as 19-fold in some locations during the 50-year study period. This variation arises, in part, directly from variation in wolf hunting behavior. This study identifies a top terrestrial predator as a mechanism generating landscape heterogeneity, demonstrating reciprocal links between large carnivore behavior and ecosystem function.

Key words: animal–ecosystem links; carcass; carnivore; ecosystem function; heterogeneity; indirect effect; Isle Royale; moose; predator–prey; resource patch; spatial pattern; wolves.

Introduction

Theory and empirical examples indicate that when carnivores affect ecosystem processes and biodiversity it is generally thought that they do so primarily by their effects on the population dynamics and behavior of large herbivores (Estes 1995, Terborgh et al. 2001, Ives et al. 2005, Ray et al. 2005, Soulé et al. 2005). However, large, terrestrial carnivores might affect ecosystem function in an entirely different way by impacting landscape heterogeneity. If carnivores influence the distribution of carcasses that result from predation, they would also affect the spatiotemporal heterogeneity of soil and plant properties. To be true, carcasses produced via predation would have to be important to above- and belowground communities, and predation would have to occur in some locations at rates that are different than the rates for other causes of mortality (e.g., starvation, hunting). Data supporting such effects would provide empirical evidence for a mechanistic link between large carnivores and heterogeneity in terrestrial ecosystems. This would be important because it would identify a key mechanism that potentially explains a positive correlation between the presence of large, terrestrial carnivores and the maintenance of biodiversity (Ray et al. 2005). Here, we provide evidence that wolves configure soil and plant resource hotspots by directly influencing prey carcass distribution.

Soil heterogeneity is an important determinant of soil diversity (Tilman 1999, Ettema and Wardle 2002, Wardle 2002, Wardle et al. 2004, De Deyn and Van der Putten 2005), which causes patchiness of soil resources, influencing aboveground biodiversity and ecosystem function (Hutchings et al. 2000, Lovett et al. 2003). Biotic interactions affect the heterogeneity of soil resources frequently through plant–soil associations and invertebrate soil fauna (Wardle 2002, 2006). The effects of large herbivores on soil heterogeneity are typically characterized by indirect feedbacks between selective herbivory and leaf litter quality, and nutrient-rich patch generation through feces and urine deposition (Danell et al. 2006). Recently however, the nutrient-rich and highly labile carcasses of large ungulates have been recognized as being consequential in the generation of landscape heterogeneity (reviewed in Carter et al. 2007). In the absence of predators, bison (*Bos bison*), cattle (*B. taurus*), and deer (*Odocoileus virginianus*) carcasses can provide local nutrient pulses at intensities that exceed other natural processes, thus influencing plant composition and biomass (Towne 2000). However, the effects of predators and scavengers on carcass spatial distribution, temporal deposition, and the magnitude of nutrients released due to variable carcass consumption are unknown.

While carcasses produced by means other than predation (e.g., starvation, disease, vehicle collisions,

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[1] E-mail: jkbump@mtu.edu

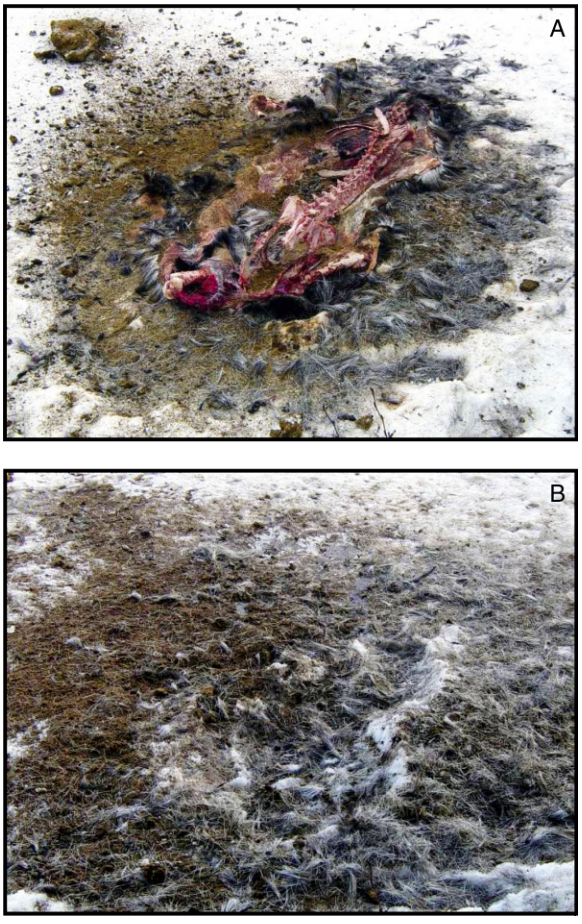

FIG. 1. Photographs of (A) wolf-killed moose in winter on Isle Royale National Park, Michigan, USA, and (B) the same carcass three days later. All that remains in photograph (B) is hair (gray) and rumen contents (dark green); the hide has been consumed, and bones have been scattered.

hunter-deposited remains) may remain intact long enough to putrefy and decompose largely in place, carcasses from predation are typically very well utilized, moving up a trophic level via consumption by predators and scavengers (Wilmers et al. 2003). For example, at sites where wolves (*Canis lupus*) have killed moose (*Alces alces*) in Isle Royale National Park, Michigan, USA, little appears to remain except bone, hair, and rumen contents (first stomach chamber; Fig. 1). Such appearances likely prevent one from recognizing that carcasses produced via predation could also be as important to soil and plant heterogeneity as are carcasses produced in other ways. Moreover, large predators partly determine the spatiotemporal distribution of carcasses on the landscape, which can result in distinct kill-site clustering and carrion availability patterns (Wilmers et al. 2003, Wilmers and Getz 2004). Do carcasses produced via predation result in biogeochemical hotspots, and if so, do top predators influence the hotspot spatiotemporal distribution? Observing that carcasses produced via predation are distributed in distinct patterns and subsequently affect soil resources, would be evidence that carnivores are linked to heterogeneity in a novel way. Thus far, no data support such a link.

We show how wolves affect soil and plant heterogeneity by influencing prey carcass distribution. Differences in forest soil macronutrient availability, microbial biomass and composition, and plant leaf nitrogen were compared at wolf-killed moose carcass and paired control sites for ~3.5 years postmortem at Isle Royale National Park, USA. We used data from 3654 carcass locations recorded since 1958 to determine how total moose carcass density and the ratio of wolf-killed : starvation-killed carcasses changed over time and space.

METHODS

Carcass locations

Moose carcass locations from 1958 to 2006 ($N = 3654$) were determined in winter during aerial surveys, with subsequent ground inspection and necropsy, and in spring and summer through extensive, island-wide hiking (Peterson 1977, Vucetich and Peterson 2004). Wolf-killed moose are distinguished readily from other mortality causes. Kills were classified as wolf-caused when wolves were observed making the kill, or evidence supported wolves as the cause (e.g. wolves feeding on fresh carcass, presence of chase tracks, signs of struggle). Kills were classified as starvation-caused when intact, undisturbed, emaciated carcasses were found, or evidence supported starvation as the cause (i.e., articulated skeletons amid prodigious maggot casings, indicating carcasses were predominantly consumed by invertebrates).

Soil nutrient and isotope analysis

In late May–early June of 2004 soils were sampled at 17 wolf-killed moose carcass sites selected randomly, of which 12 died in the winter of 2003–2004 and 5 died during the winter of 2002–2003. Each site was subsequently sampled in spring of 2005 and 2006, thereby providing a postmortem chronology spanning ~3.5 years. At the time of sample collection, predators and scavengers had removed most of the soft tissue; small amounts of connective tissue remained on bones. Hair and rumen contents are not consumed by vertebrate scavengers and were present at all sites. Bone scatter was highly variable. Because a rumen and hair mat indicate where each moose fell, was initially consumed, and lost the majority of body fluid, sampling within this zone was the most consistent approach to determining biogeochemical changes at carcass sites.

Two soil cores (4 cm diameter × 10 cm depth) were sampled beneath the rumen remains at each carcass center (hereafter "carcass"; Fig. 1) and two cores (hereafter "control") were sampled 6 m out from the center in opposite directions, perpendicular to the slope gradient. Soil core holes were not filled. The distance between carcass and control cores was determined based

on the spread of hair and rumen remaining at carcass sites; ~6 m spacing ensured that hair mats, rumen, or other carcass remains did not enter control cores. Paired samples were found within the same forest canopy type. This paired sampling design minimized site and climate effects on carcass vs. control comparisons. Core carcass area was estimated as the area of an ellipse with major and minor axis measured from the spread of hair and rumen at kill sites.

We measured nitrogen (N), phosphorus (P), and potassium (K) levels at paired sites (carcass and control) because these macronutrients are generally limiting to primary productivity in boreal and temperate systems (Danell et al. 2006). Soils were dried, and inorganic N (i.e., NH_4^+ and NO_3^-) was extracted with 1 N KCl (0.0134 mol/L KCl) and analyzed calorimetrically. A Bray P1 extractant was used to determine soil available P, and a Mehlich 3 extractant was used to determine exchangeable K levels (Brown 1998). Analyses of nutrient concentrations were conducted at the Michigan State University Soil and Plant Nutrient Laboratory, East Lansing, Michigan, USA. For each postmortem sampling period, i.e., 4, 16, 28, and 40 months, 11, 7, 8, and 5 carcass sites were randomly selected for stable N isotope ($\delta^{15}N$) concentration analysis. Sample size decreased with time post-mortality because the exact location of previously sampled carcass sites could not always be found with high confidence in all cases; National Park permitting did not allow permanent site marking and GPS locations only had 5-m accuracy. Soils for $\delta^{15}N$ analysis were homogenized for each postmortem sampling period ($N = 31$) in a bearing shaker mill and analysis was performed on a Costech elemental combustion system 4010 (Costech Analytical Technologies, Valencia, California, USA) connected to a Thermo Finnigan ConfloIII interface (Thermo Fisher Scientific, Waltham, Massachusetts, USA) and Delta-plus continuous flow-stable isotope ratio mass spectrometer (Thermo Fisher Scientific) at Michigan Technological University's Ecosystem Science Center, Houghton, Michigan, USA. Certified standards were run at the beginning and end of the analysis to check for calibration stability. Stable-isotope values are reported in standard δ notation, and are reported on the atmospheric air scale for $\delta^{15}N$ (Fry 2006). An internal standard was run every 10 samples. Precision based on repeated measures of internal standards was $\pm 0.5‰$ for $\delta^{15}N$.

Soil microbial analysis

For each postmortem sampling period (i.e., 4, 16, 28, and 40 months), five carcass sites ($N = 20$) were selected randomly for microbial analysis. In spring of 2005 and 2006, four subsample soil cores (4 cm diameter × 5 cm depth) were extracted from carcass and control plots at kill-site locations. Soil cores were immediately pooled for each period, homogenized through manual mixing with removal of rocks and large roots, and frozen within ~2 h for phospholipid fatty acid (PLFA) analysis at Microbial Insights, Rockford, Tennessee, USA (2005 samples) and the Balser Soil Microbial Laboratory at the University of Wisconsin, Madison, Wisconsin, USA (2006 samples). Duplicate samples were sent to each laboratory to correct for extraction differences between labs. PLFA analysis evaluates the specificity of phospholipid membrane structure in functional and taxonomic groups of microbes (Bossio et al. 1998), which provides a quantitative measurement of total microbial biomass and bacterial and functional groups, thereby permitting a description of microbial community composition.

Moose carcass isotope analysis

The total N and $\delta^{15}N$ concentrations in hair, bones, and rumen contents that were collected from the remains at 6 carcass sites (4 months postmortem) in winter 2005 were measured on a mass spectrometer as for soils.

Aster leaf tissue analysis

In early June 2006, leaf tissue of large-leaf aster (*Aster macrophyllus*) was sampled at 36 carcass sites, including all sites sampled for soils analysis. We selected large-leaf aster because this species is native throughout much of the eastern and central range of moose in North America, is important as one of the first forage species consumed by moose in spring, is consumed throughout summer (Murie 1934), and is a near-ubiquitous understory species on Isle Royale. Sampled plants were located as close as possible to carcass and control soil core holes; usually within 10 cm and always within 100 cm. For each site, carcass and control leaves of equal size were clipped at their base from one actively growing plant, dried at 18°C to a constant mass, double-rinsed with distilled water to remove any surface debris, dried again, and then individually homogenized in a bearing shaker mill. Measurement of total carbon, total N, and $\delta^{15}N$ concentrations was performed on a mass spectrometer as for soils.

Statistical analyses for soil and leaf samples

Soil sample (macronutrients, $\delta^{15}N$, PLFA) and leaf tissue (N, $\delta^{15}N$) data were analyzed using mixed-model repeated-measures analysis of variance (ANOVA) to test the expectation of positive carcass effects on soil macronutrient and $\delta^{15}N$ concentrations; total microbial biomass, bacterial and fungal PLFAs, fungal-to-bacteria ratios; leaf N and $\delta^{15}N$ concentrations, respectively. We expected carcasses to have a negative effect on leaf carbon-to-nitrogen ratios. Planned contrasts were done at each sampling time to evaluate the magnitude of the carcass effect at 4, 16, 28, and 40 months postmortem. Brown-Forsythe and O'Brian tests were used to confirm assumptions of circularity (i.e., the variance of the difference of observations between any pair of times is the same).

Moose carcass distribution analysis

Rates of moose mortality are expected to shift on decadal or longer time scales in direct response to habitat changes such as forest fires and predator dynamics such as variable pack number and changes in pack social structure (Peterson 1977), and indirectly from disease dynamics and climate change (Wilmers et al. 2006). Temporal change in mortality patterns was investigated by dividing the carcass database into two 24-year periods: 1958–1982 and 1983–2006. We chose the two largest, equal-length time periods possible because we did not know if carcass patterns changed temporally. Such a comparison had the greatest power to demonstrate temporal differences in carcass distribution. This was done for the entire carcass data set and the investigation of the ratio of wolf-killed : starvation-killed carcasses.

The influence of wolves on moose carcass distribution was analyzed using a map algebra approach (Wang and Pullar 2005) in a geographic information system (ArcGIS; ESRI 2008). This is the most parsimonious method available given the long-term point location data set. First, two carcass density maps were created: one for wolf-killed moose and one for starvation-killed moose. Of the moose carcass locations recorded from 1958 to 2006 ($N = 3654$), mortality was known with high confidence to be caused by wolves for 939 individuals, and by starvation for 577 individuals. To ensure higher confidence in mapping results, carcasses classified as probable wolf or probable starvation mortality were not included in the distribution analyses. The number of carcasses per square kilometer was calculated for each carcass location by mortality type. The 1-km^2 scale is representative of the scale of moose–wolf predation events (Peterson 1977): Moose that stand their ground when wolves approach are generally not killed; all observed encounters on Isle Royale that ended in a kill occurred after the prey initially ran from wolves and chases are not commonly long; wolves most often give up chases within 1–2 km. Second, the density map created for wolf-killed moose was divided by the density map created for starvation-killed moose ($\text{mortality}_{\text{wolf}}/\text{mortality}_{\text{starv}}$), yielding a map surface illustrating the relative likelihood of wolf-killed moose to starvation-killed moose across the landscape. Values >1 indicate areas where carcass distribution is more influenced by wolves, and values <1 indicate where carcass distribution is more influenced by moose (values of 1 indicate equal influence). The ratio maps permit an explicit assessment of how the influence of wolves on the spatial distribution of moose carcasses changed over time because if wolves have no influence on carcass distribution, then we expect the ratio of wolf-killed : starvation-killed carcasses to be equal across the landscape.

High- and low-density carcass clustering was analyzed using global and local indicators of spatial association (i.e., Getis-Ord general G and local Getis-Ord Gi*; Getis and Ord 1992, Fortin and Dale 2006). The Getis-Ord general statistic summarizes spatial autocorrelation for the entire island, while the local Getis-Ord Gi* statistic assesses autocorrelation within a "neighborhood" of locations within an investigator-determined radius (1 km in this study). Hence, the Getis-Ord general G statistic tests the hypothesis that there is no spatial clustering over the entire island, and the Getis-Ord Gi* statistic identifies areas of density relatedness and significant clustering at the 1-km scale, i.e., "hot- and cold-spots" (Getis and Ord 1992, Fortin and Dale 2006). Each test produces Z scores, which, if less than -1.96 or greater than 1.96 (i.e., one standard deviation), are considered significant at alpha $= 0.05$. The higher (or lower) the Z score, the stronger the intensity of the clustering. A Z score near zero indicates no apparent clustering within the study area. A positive Z score indicates clustering of high values, while a negative Z scores indicates clustering of low values. We used Euclidian distance and inverse-distance-squared methods in the clustering analysis.

Results are presented with island-scale maps that depict carcass density in the first time period (1958–1982) and relative change in the second time period (1983–2006) for all carcass locations and the ratio of wolf-killed : starvation-killed moose. Four examples of ratio maps of wolf-killed : starvation-killed moose are also presented per hectare at various scales because carcass sites create noteworthy biological activity across the island at a 1-ha scale. Carcass sites are nutrient and energy focal points, receiving exuvia and puparia materials from dead insects, feathers from avian scavengers, and fecal and urine deposition from scavengers, grazers, and predators. Consequently, a single moose carcass is ecologically important on the scale of at least 1 ha, even though the intense macronutrient effects are likely restricted to the core area encompassing carcass remains at kill sites.

Results

Soils at carcass sites had 100–600% more inorganic nitrogen (NH_4^+ and NO_3^-; $F_{1,51} = 20.1$, $P < 0.0001$), phosphorus ($F_{1,49} = 18.1$, $P < 0.0001$), and potassium ($F_{1,46} = 10.1$, $P = 0.0027$) relative to surrounding control sites for several growing seasons (Fig. 2). Differences between carcass sites and control sites exhibited a temporal pattern of initial increase and subsequent decrease (Fig. 2). This pattern may reflect either a lagged soil response to decomposing carcass remains or (and) positive macronutrient feedbacks at carcass sites. Positive feedbacks would occur because carcass sites receive nutrients and energy from exuviae and puparia materials from dead invertebrates, and fecal and urine deposition from scavengers, grazers, predators, and scent-marking vertebrates (Towne 2000, Carter et al. 2007). Such activity means that, although these intense macronutrient effects are likely restricted to the core area encompassing carcass remains at kill sites (which is, on average, 9 m^2 for wolf-killed moose on Isle Royale), a

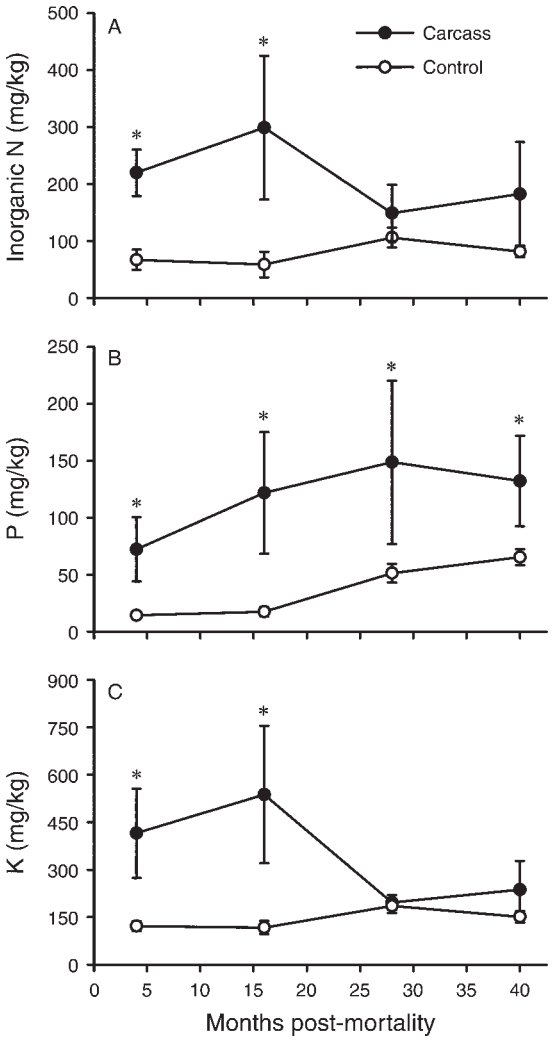

FIG. 2. Indices of macronutrient availability: (A) inorganic nitrogen (nitrate + ammonium), (B) phosphorus, and (C) potassium, in soils from wolf-killed moose carcass sites (solid circles) and paired control sites (open circles) at 4, 16, 28, and 40 months postmortem. Asterisks (*) indicate significant ($P < 0.05$) differences for planned contrasts between carcass and control sites at each postmortem sampling time. Error bars show mean ± SE (some are too small to be seen). Note the different y-axis scales.

single carcass could be ecologically important at larger scales.

Carcass sites had, on average, a 38% higher total abundance of bacterial and fungal phospholipids fatty acids (PLFAs) vs. control sites ($F_{1,27} = 11.9$, $P = 0.0018$). Bacterial PLFAs were 30–50% more abundant at carcass compared to control sites and appeared to track the macronutrient availability patterns postmortem (Fig. 3A). Fungal PLFAs were 81% more abundant at carcass compared to control sites at the latest postmortem sampling (Fig. 3B). The fungal-to-bacterial ratio increased significantly from 0.15 to 0.66 ($F_{3,14} = 6.1$, $P = 0.0071$; Fig. 2) in the carcass plots compared to control plots with time.

We found that foliar-nitrogen levels were 47%, 29%, and 25% higher in plants growing on carcass sites compared to control sites ($F_{1,39} = 22.6$, $P < 0.0001$) at 4-, 16-, and 28-months postmortem, respectively (Fig. 4A). Mean foliar carbon-to-nitrogen ratio decreased 25% over the first three growing seasons ($F_{1,39} = 13.6$, $P = 0.0007$), indicating higher aggregate forage quality at carcass sites. Aster foliage and soils from carcass sites had elevated $\delta^{15}N$ compared to control sites at least half the time, but lagged in response compared to the foliar nitrogen response ($F_{1,46} = 5.5$, $P = 0.023$; Fig. 4C, $F_{1,45} = 15.5$, $P = 0.0003$; Fig. 4B). This pattern may reflect slower decomposition of some isotopically heavy, recalcitrant carcass remains (e.g., bone or hair). Moose remains (i.e., bone, hair, rumen) show enriched $\delta^{15}N$ relative to their plant diet ($\delta^{15}N_{prey} = 1.12‰ \pm 0.19‰$ [mean ± SE], $N = 18$).

Carcass density changed as much as 19-fold for various areas of the island between the two time periods (Fig. 5A, B). In some areas, wolf-killed moose were 12 times more common than starvation-killed moose (Fig. 5C). The distribution of wolf-killed moose showed a striking degree of clustering at the island-scale, with <0.1% likelihood that the clustering of wolf-killed

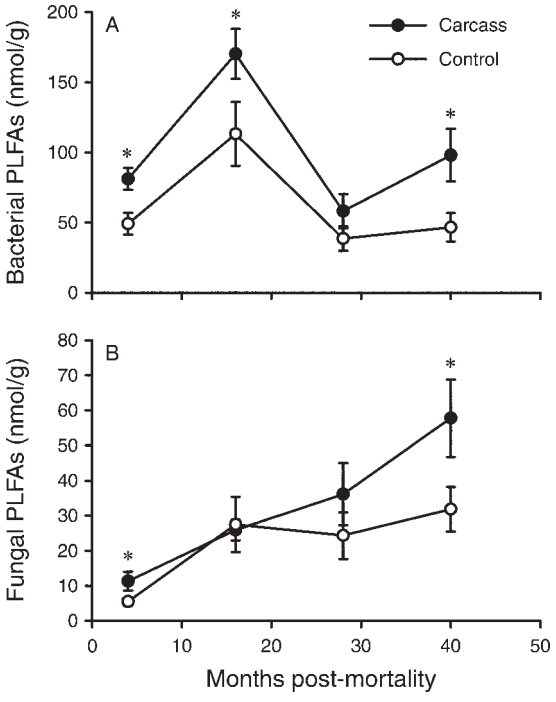

FIG. 3. (A) Soil bacterial and (B) fungal phospholipids fatty acids (PLFAs) from wolf-killed moose carcass sites (solid circles) and paired control sites (open circles) at 4, 16, 28, and 40 months postmortem. Asterisks (*) indicate significant ($P < 0.05$) differences for planned contrasts between carcass and control sites at each postmortem sampling time. Error bars show mean ± SE (some are too small to be seen). Note the different y-axis scales.

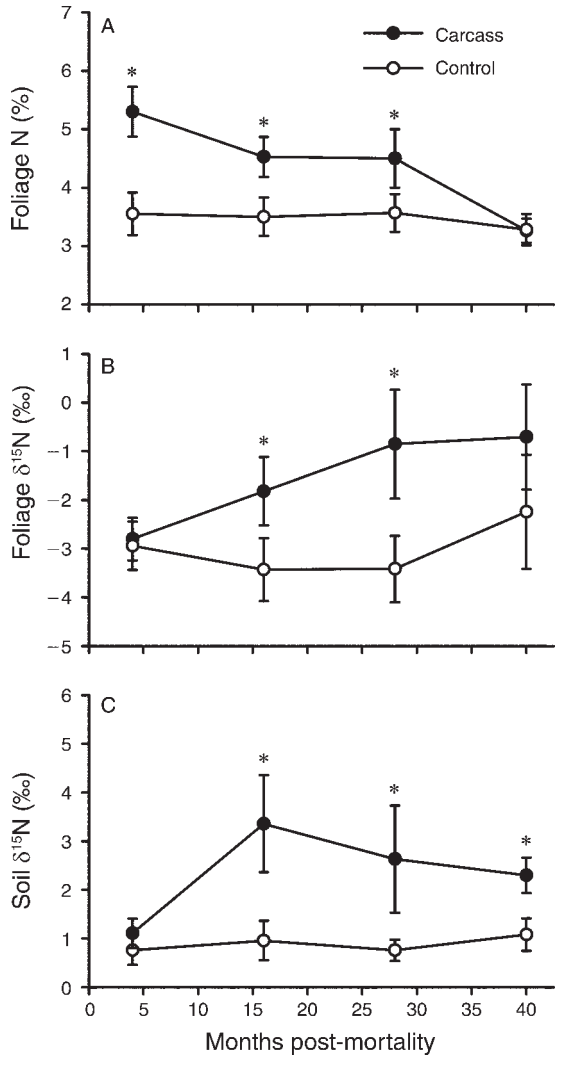

FIG. 4. (A) Foliage nitrogen content, (B) foliage $\delta^{15}N$, and (C) soil $\delta^{15}N$ from wolf-killed moose carcass sites (solid circles) and paired control sites (open circles) at 4, 16, 28, and 40 months postmortem. Asterisks (*) indicate significant ($P < 0.05$) differences for planned contrasts between carcass and control sites at each postmortem sampling time. Error bars show mean ± SE. Note the different *y*-axis scales.

moose carcass sites resulted from random chance (Getis-Ord Gi Z score = 4.13 standard deviations; Fig. 5C, D). The ratio of a wolf-killed moose compared to a starvation-killed moose occurring in some areas declined as much as 9-fold and increased in other areas by up to fivefold between time periods (Fig. 5D). At a 1-km^2 scale, wolf-killed carcass "hot spots" were up to seven times more tightly clustered than "cold spots" of low carcass density (local Getis-Ord Gi* Z scores ranged from −4.02 to 27.6 standard deviations). Wolves preferentially travel along shorelines (Peterson 1977), which results in high-density predation zones in close proximity to water, such as a river drainage, an isthmus, a harbor, and a peninsula (Fig. 5E–H, respectively). Changes in wolf pack number and subsequent territory shifts may explain the absence of the high wolf-killed : starvation-killed region along a river drainage illustrated in Fig. 5E during the second 24-year period of the study (Peterson 1977).

Discussion

Carcasses directly affect belowground biogeochemical processes that are important ecological drivers of aboveground community structure and functioning (Wardle et al. 2004). Nutrient inputs like those in Fig. 2 typically cause rapid microbial growth in soil communities, which then mobilize organic detritus into plant-available forms (Wardle 2002). Soil microbial communities can influence ecosystem functions such as plant biodiversity and productivity (Ettema and Wardle 2002, Wardle 2002, Wardle et al. 2004, De Deyn and Van der Putten 2005). Fungal scavengers may have increased over time by preying upon what had been an earlier abundance of bacteria, which could explain the shift in microbial community composition (Yang 2004; Fig. 3). Increased microbial abundance at carcass sites (Fig. 3) could improve resource availability for plants within the carcass footprint. The increased $\delta^{15}N$ in soils and foliage at carcass sites suggests that a carcass-derived nitrogen source leads to higher available nitrogen in soils, resulting in increased plant nitrogen assimilation (Fig. 4). These results indicate that the belowground effects of carcass-derived nutrients can be used in plant growth for three growing seasons postmortem, which may influence aboveground trophic interactions. For example, large herbivores are attracted to patches of nitrogen-rich forage (Danell et al. 2006). Hence, carcass sites become foraging sites (Towne 2000), and the probability of repeated foraging within and around carcass sites initiates a positive feedback of recurrent nutrient supplementation from feces and urine deposition.

The long-term changes in island-wide carcass density (Fig. 5A, B) are attributable, in part, to shifts in moose habitat selection arising from shifts in forest composition following extensive forest fires in 1936 and subsequent forest succession. Fire patterns and differential regeneration of balsam fir *Abies balsamea* (L.), an ecologically important winter-browse species, correlate with the typical island-wide spatial pattern in moose density. Currently, the highest moose densities (~5.4 individuals/km^2) are at the east end, with low densities at mid-island in major 1936 burn areas (~0.8 individuals/km^2), and moderate densities (~1.8–3.4 individuals/km^2) at the west end (Vucetich and Peterson 2004). The largest burn area was in the middle one-third of the island (Peterson 1977), which is where temporal changes in carcass density are most pronounced (Fig. 5A, B). The two 24-year periods also coincide with before and after a predator disease outbreak and crash of the wolf population from 1980 to 1982 (Peterson et al. 1998). Hence, to the extent that predator disease modulates

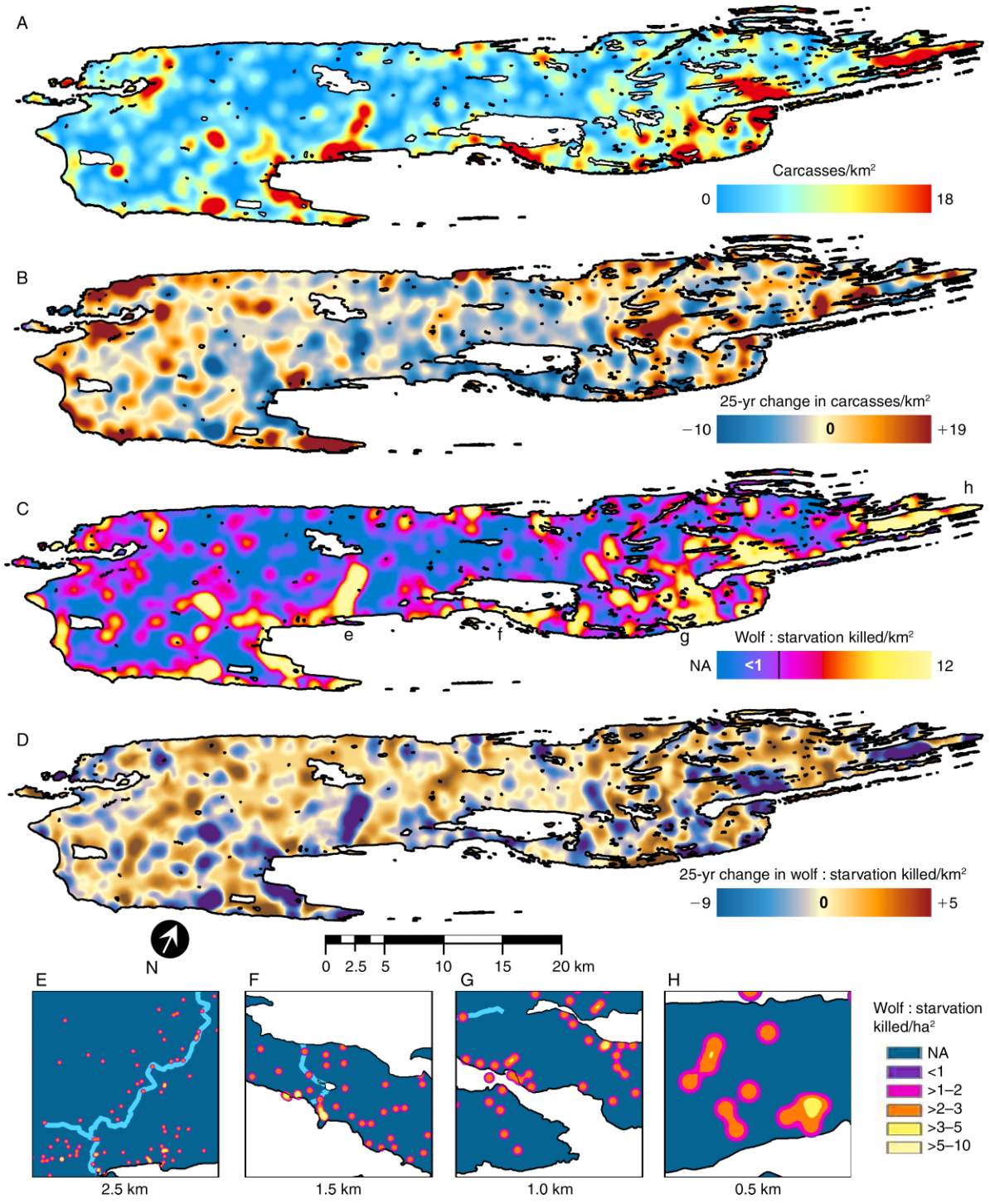

FIG. 5. Distribution maps of moose carcasses in Isle Royale National Park, USA. (A) Carcass density from 1958 to 1982. (B) Change in carcass density in 1983–2006 compared to 1958–1982. (C) Ratio of wolf : starvation killed moose density 1958–1982. Values >1 indicate areas where wolf-killed moose are more numerous, and values <1 indicate areas where starvation-killed moose are more numerous (values of 1 indicate equal occurrence). NA indicates regions in which both wolf- and starvation-killed moose were not coincident. Land areas adjacent to lowercase letters e–h correspond to panels (E)–(H). (D) Change in wolf : starvation killed moose density between 1983–2006 compared to 1958–1982. (E–H) Areas of high wolf : starvation killed moose are a river drainage, an isthmus, a harbor, and a peninsula, respectively. Note increasing scales from panel (E) to panel (H) and that ratio density is expressed per hectare. NA is defined as in panel (C).

top-down control of the moose population (Wilmers et al. 2006), disease also indirectly influences carcass patterns.

The varying spatial structure of wolf-killed : starvation-killed moose carcasses (Fig. 5C–H) indicates that wolves, through their predatory behavior, directly influence carcass location on a smaller scale (i.e., hectares to kilometers). This influence is evidence of a mechanistic link between a large carnivore's predatory behavior and heterogeneity in soil nutrients, microbial communities, and producer tissue quality (Figs. 2–4). These results indicate an important way by which large terrestrial predators that feed on large ungulates can influence spatiotemporal dynamics of ecosystem processes, including the landscape mosaic of nutrient cycling, species interactions, and, potentially, biodiversity. Even highly consumed carcasses that are produced in winter cause substantial resource "hot spots" in southern boreal forest and soils, with effects on belowground communities and aboveground producers (Figs. 2–5). These predator-mediated effects occur on the scale of other important factors in forest ecosystems (e.g., tip-up mounds, lightening strikes, nurse trees, seeps, mineral licks, wallows, ant hills). At the landscape scale, long-term carcass deposition patterns could influence forest dynamics by shifting competitive relationships among tree seedlings through changes in the nutrient concentrations in their growth environment, thereby affecting subsequent growth, survival, and reproduction (Coomes and Grubb 2000, Wardle 2002, Beckage and Clark 2003). The slower growth rates and longer life spans of trees relative to moose (~1–2 orders of magnitude) increase the chance that an individual tree will benefit from a carcass "hotspot" in its lifetime. The cumulative landscape effects of repeated carcass deposition in areas of high kill density remain unexamined.

The results we observed in a forest ecosystem are likely to occur elsewhere where large carnivore-ungulate relationships are intact. For example, we have observed similar above- and belowground biogeochemical effects at elk carcass sites in Yellowstone National Park, USA (J. K. Bump, *unpublished data*), where wolves are known to influence elk carcass distribution (i.e., flat grasslands close to streams and roads were found to be favorable to wolf hunting success; Kauffman et al. 2007). In the low-resource environment of the Arctic tundra, the impact of a muskox (*Ovibos moschatus*) carcass on surrounding vegetation was still dramatic after 10 years (Danell et al. 2002), which emphasizes that carcass effects may last longer in some systems. Similar dynamics likely occur in South American, African, and Asian systems with intact large carnivore–ungulate prey relationships (Danell et al. 2006).

Nearly all wild ungulates are hunted by humans, which results in carcass distribution patterns significantly different than those created by wild carnivores. Hunter-kills arrive in abundant pulses that coincide with hunting seasons and are highly correlated with access along roads, resulting in less spatial dispersion in kill sites than wild predator-kills at the landscape scale (Wilmers et al. 2003, Wilmers and Getz 2004). In contrast, wild predators hunt continuously and across a broader range. While spatiotemporal differences exist between human-hunter and wild-predator kill sites, our results suggest that the remains that are nearly always left at hunter-kills (gut piles with rumen contents) may result in similar biogeochemical effects. Similarly, die off of domestic ungulates has the potential to create similar carcass effects; however, domestic carcasses are frequently removed, and government agencies in the USA forbid leaving domestic carcasses on public rangelands where they may attract large carnivores and scavengers (Freilich et al. 2003). These anthropogenic particulars emphasize the importance of understanding large-animal carcass dynamics in the context of natural resource management.

When large terrestrial carnivores affect ecosystem processes and biodiversity, it is typically believed that the mechanism involves strong species interactions (e.g., trophic cascades; Estes 1995, Terborgh et al. 2001, Ives et al. 2005, Ray et al. 2005, Soulé et al. 2005). These interactions critically depend on a carnivore population's ability to suppress local prey populations, thereby releasing the next lower trophic level from predation or herbivory. The effects that we demonstrate do not require that predators suppress the abundance of their prey. Consequently, we contend that this study demonstrates a new mechanism whereby carnivores affect ecosystem function by creating ecosystem heterogeneity at multiple scales, thereby increasing our understanding of the role of large carnivores in terrestrial ecosystems. Other examples of top-down effects along biogeochemical pathways are emerging (Frank 2008, Holtgrieve et al. 2009). This study also contributes to an emerging awareness about how carcasses of vastly different sizes, from whales to salmon to cicadas, may have significant and lasting effects in diverse ecological systems (Towne 2000, Smith and Barco 2003, Yang 2004, Helfield and Naimen 2006, Carter et al. 2007). The connections we discovered are strong, yet unexpected, because carnivores and soil heterogeneity are seemingly unrelated. Such connections are relevant to policy makers involved in predator management globally and they capture public attention which creates values that powerfully motivate conservation (Jepson and Canney 2003).

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Literature Cited

Beckage, B., and J. S. Clark. 2003. Seedling survival and growth of three southern Appalachian forest tree species: the role of spatial heterogeneity. Ecology 84:1849–1861.

Bossio, D. A., K. M. Scow, N. Gunapala, and K. J. Graham. 1998. Determinants of soil microbial communities: effects of agricultural management, season, and soil type on phospholipid fatty acid profiles. Microbial Ecology 36:1–12.

Brown, J. R. 1998. Recommended chemical soil test procedures for the North Central Region. Research Publication no. 221. Missouri Agricultural Experimental Station, Columbia, Missouri, USA.

Carter, D. O., D. Yellowlees, and M. Tibbett. 2007. Cadaver decomposition in terrestrial ecosystems. Naturwissenschaften 94:2–24.

Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70: 171–207.

Danell, K., R. Bergström, P. Duncan, and J. Pastor. 2006. Large herbivore ecology, ecosystem dynamics, and conservation. Cambridge University Press, Cambridge, UK.

Danell, K., D. Berteaux, and K. A. Brathen. 2002. Effect of muskox carcasses on nitrogen concentration in tundra vegetation. Arctic 55:389–392.

De Deyn, G. B., and W. H. Van der Putten. 2005. Linking above- and belowground biodiversity. Trends in Ecology and Evolution 20:625–633.

ESRI. 2008. ArcGIS. Version 9.3. ESRI, Redlands, California, USA.

Estes, J. A. 1995. Top-level carnivores and ecosystem effects: questions and approaches. Pages 151–158 *in* C. G. Jones and J. H. Lawton, Linking species and ecosystems. Chapman and Hall, New York, New York, USA.

Ettema, C. H., and D. A. Wardle. 2002. Spatial soil ecology. Trends in Ecology and Evolution 17:177–183.

Fortin, M., and M. R. T. Dale. 2006. Spatial analysis: a guide for ecologists. Cambridge University Press, Cambridge, UK.

Frank, D. A. 2008. Evidence for top predator control of a grazing ecosystem. Oikos 117:1718–1724.

Freilich, J. E., J. M. Emlen, J. J. Duda, D. C. Freeman, and P. J. Cafaro. 2003. Ecological effects of ranching: a six-point critique. BioScience 53:759–765.

Fry, B. 2006. Stable isotopes in ecology. Springer-Verlag, New York, New York, USA.

Getis, A., and J. K. Ord. 1992. The analysis of spatial association by use of distance statistics. Geographical Analysis 24:189–206.

Helfield, J. M., and R. J. Naiman. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. Ecosystems 9: 167–180.

Holtgrieve, G. W., D. E. Schindler, and P. K. Jewett. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. Ecological Research 1:1–11.

Hutchings, M. J., E. A. John, and A. J. A. Stewart. 2000. The ecological consequences of environmental heterogeneity. Cambridge University Press, Cambridge, UK.

Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator–prey interactions, and biodiversity and ecosystem functioning. Ecology Letters 8: 102–116.

Jepson, P., and S. Canney. 2003. Values-led conservation. Global Ecology and Biogeography 12:271–274.

Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. Ecology Letters 10:690–700.

Lovett, G. M., C. G. Jones, M. G. Turner, and K. C. Weathers. 2003. Ecosystem function in heterogeneous landscapes. Springer-Verlag, New York, New York, USA.

Murie, A. 1934. The moose of Isle Royale. University of Michigan Press, Ann Arbor, Michigan, USA.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. Scientific Monograph Series 11. U.S. National Park Service, Washington, D.C., USA.

Peterson, R. O., N. J. Thomas, J. M. Thurber, J. A. Vucetich, and T. A. Waite. 1998. Population limitation and the wolves of Isle Royale. Journal of Mammalogy 79:828–841.

Ray, J. C., K. H. Redford, R. S. Steneck, and J. Berger. 2005. Large carnivores and the conservation of biodiversity. Island Press, London, UK.

Smith, C. R., and A. R. Baco. 2003. Ecology of whale falls at the deep-sea floor. Oceanography and Marine Biology 41: 311–354.

Soulé, M. E., J. A. Estes, B. Miller, and D. L. Honnold. 2005. Strongly interacting species: conservation policy, management, and ethics. BioScience 55:168–176.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert, and L. Balbas. 2001. Ecological meltdown in predator free forest fragments. Science 294:1924–1926.

Tilman, D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. Ecology 80: 1455–1474.

Towne, E. G. 2000. Prairie vegetation and soil nutrient responses to ungulate carcasses. Oecologia 122:232–239.

Vucetich, J. A., and R. O. Peterson. 2004. Grey wolves—Isle Royale. Pages 281–292 *in* D. W. Macdonald and C. Sillero-Zubiri. The biology and conservation of wild canids. Oxford University Press, London, UK.

Wang, X. Y., and D. Pullar. 2005. Describing dynamic modeling for landscapes with vector map algebra in GIS. Computational Geosciences 31:956–967.

Wardle, D. A. 2002. Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton, New Jersey, USA.

Wardle, D. A. 2006. The influence of biotic interactions on soil biodiversity. Ecology Letters 9:870–886.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

Wilmers, C. C., and W. M. Getz. 2004. Simulating the effects of wolf–elk population dynamics on resource flow to scavengers in Yellowstone National Park. Ecological Modelling 177: 193–208.

Wilmers, C. C., E. S. Post, R. O. Peterson, and J. A. Vucetich. 2006. Disease mediated switch from top-down to bottom-up control exacerbates climatic effects on moose population dynamics. Ecology Letters 9:383–389.

Wilmers, C. C., D. R. Stahler, R. L. Crabtree, D. W. Smith, and M. G. Wayne. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecology Letters 6:996–1003.

Yang, L. H. 2004. Periodical cicadas as resource pulses in North American forests. Science 26:1565–1567.