RESEARCH ARTICLE

Large carnivore foraging contributes to heterogeneity in nutrient cycling

Michelle Peziol · L. Mark Elbroch ·
Lisa A. Shipley · R. Dave Evans ·
Daniel H. Thornton

Abstract

Context Carnivores influence the spatial heterogeneity of biogeochemical processes in ecological communities through predation and the deposition of animal carcasses, and these processes may lead to positive feedback loops that influence large-scale patterns of nutrient cycling.

Objectives We assessed whether ambush predator foraging impacted soil chemistry and plant forage quality, and then scaled these effects to the landscape to assess whether carnivores contribute to heterogeneity in resource distributions.

Methods We measured total nitrogen (N) and N stable isotope composition ($\delta^{15}N$) of soils and plants at 172 ungulate carcasses killed by mountain lions in the Yellowstone Ecosystem, USA. We measured kill rates and estimated the probability of a mountain lion foraging in any location to scale their carrion contributions to the landscape.

Results Carcasses altered total nitrogen N and $\delta^{15}N$ of soils and plants, and changes in $\delta^{15}N$ suggested that plants absorbed significant N from carcasses. On average, plant $\delta^{15}N$ at kill sites increased by 2.3 milles (‰), which is large compared to the 6.3 ‰ range of variation in local plants across xeric and mesic systems. We conservatively estimated that resident mountain lions in our study area annually contributed the carrion mass of a blue whale, or 44.1 kg of carrion and 1.4 kg of N per km². We also determined that mountain lion foraging was concentrated in just 4% of our study system.

Conclusions Ambush carnivore foraging may contribute to landscape-scale heterogeneity in nutrient distributions, and set the stage for positive feedback loops between carnivores and prey that drive biogeochemical processes.

M. Peziol · L. A. Shipley · D. H. Thornton
School of Environment, Washington State University, 642812, Pullman, WA 99164-2812, USA

M. Peziol · L. M. Elbroch (✉)
Panthera, 8 West 40Th Street, New York, NY 10018, USA
e-mail: melbroch@panthera.org

R. D. Evans
School of Biological Sciences and WSU Stable Isotope Core Facility, Washington State University, 644236, Pullman, WA 99164-4236, USA

Introduction

Carnivores impact the spatial heterogeneity of nutrients and biogeochemical processes via their indirect effects on prey, which influences where prey congregate, forage, and defecate, and directly, via predation

and the distribution of carcasses across landscapes (Schmitz et al. 2010; Monk and Schmitz 2022). Decomposing animal carcasses, in particular, initiate a series of chemical, biological and physical processes that contribute to ecosystem energy and nutrient cycling in aquatic and terrestrial systems (Barton and Bump 2019; Hilderbrand et al. 1999; Keenan et al. 2018). Although humans produce the most discarded animal remains, this refuse is concentrated in specific locations such as landfills, fisheries discards and along roads (Oro et al. 2013). Starvation, disease, and exposure to the elements also kill animals and provide carcasses in seasonal pulses across the year (DeVault et al. 2003; Wilson and Wolkovich 2011). In contrast, apex carnivores provision animal carcasses continuously over broad areas (Wilmers et al. 2003; Wikenros et al. 2013) and therefore have a unique spatio-temporal effect on the heterogeneity of biogeochemistry and ecosystem function (Bump et al. 2009a; Monk and Schmitz 2022). Carnivores also facilitate nutrient transfer across aquatic-terrestrial environments, by carrying carcasses from one system to the other (Hilderbrand et al. 1999).

Monk and Schmitz (2022) hypothesized that carnivores may contribute to large-scale nutrient heterogeneity by initiating feedback loops based on predation and subsequent nutrient subsidies to soils and plants that attracts future foraging by prey that begins the cycle all over again (Fig. 1). These patterns should be more easily detected when carnivores are ambush hunters and exhibit marked spatial homogeneity in hunting prey (i.e. they hunt in specific areas and not others) (e.g. solitary felids, Smith et al. 2020). The effects of carrion resources on ecosystems have, however, typically been studied piecemeal or have involved a small number of carcasses in a localized context. Some studies have revealed that decomposing carcasses modify soil temperature, soil moisture, and increase soil fertility through the addition of nutrients such as nitrogen (N), carbon and phosphorus (Bump et al. 2009a; Parmenter and MacMahon 2009). These changes to soils may last from 24 to

Fig. 1 Conceptual model summarizing the 5 stages of a mountain lion (*Puma concolor*) foraging and N redistributions in natural systems: 1) Forage selection, where ungulates select patches of nitrogen-rich forage, 2) Predation, and carcass deposition at preferred hunting locations, 3) Initial Carcass Decay, when carnivores feed, scavengers begin visiting the carcass, and decomposition begins, 4) Active and Advanced Decay, when the transfer of carcass fluids into the soil peaks, increasing total soil N., and 5) Skeletal Decay, when plants growing at kill sites are enriched with N from the ungulate carcass. Black arrows represent our research components, and the yellow arrow represents evidence-based speculation on the final part in the positive feedback loop, which begins the cycle all over again
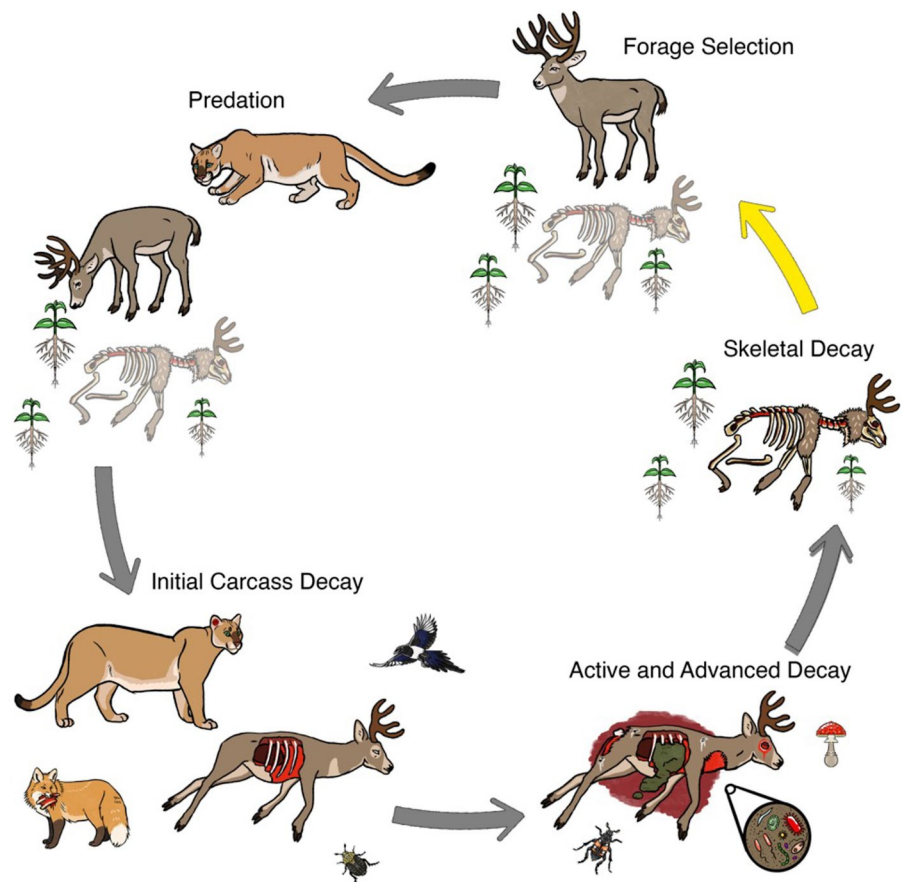
84 months after carcass deposition (Melis et al. 2007; Parmenter and MacMahon 2009). Other research on carcasses has shown that changes in soil chemistry, including electrical conductivity, gaseous emissions and adjustments to pH (Benninger et al. 2008; Keenan et al. 2018), lead to changes in plant chemistry and nutrient content that may affect plant growth and reproduction (Towne 2000; Yang 2004; Melis et al. 2007). Changes in plant chemistry, in turn, influence herbivore foraging behaviors, as ungulates select for nitrogen-rich forage (Wilmshurst and Fryxell 1995; Danell et al. 2002). Carcasses also alter the distribution and diversity of invertebrate and microbial communities (Schimel and Bennett 2004; Barry et al. 2019, Risch et al. 2020), structure vertebrate scavenger communities (Sebastián-González et al. 2020) and affect energy flow in ecosystems through the distribution of resources via scavenger pathways (DeVault et al. 2003; Wilson and Wolkovich 2011). Bump et al. (2009a) provided among the most continuous narratives to date, linking wolf (*Canis lupus*) predation of 17 moose (*Alces alces*) carcasses to nutrient deposition in soils that resulted in changes in foliar nutrient content.

Our study focusing on mountain lions (*Puma concolor*) examined several components of Monk and Schmidtz's (2022) hypothesis about the positive feedback loop linking predation with future foraging by prey. Mountain lions are a widely-distributed, stalk-and-ambush carnivore in the Americas well-suited to these questions. They 1) often kill prey larger than themselves, 2) tend to conceal their food or feed under cover, and 3) do not disarticulate carcasses as they feed (Elbroch et al. 2017). Mountain lions also experience high levels of kleptoparasitism and appear to disproportionately contribute carrion resources to ecosystems (Allen et al. 2015; Elbroch et al. 2017). Therefore, mountain lions are more likely to create localized hotspots than other large carnivores like gray wolves that dismember carcasses and distribute nutrients more widely.

Here, we report on 172 ungulates killed by mountain lions, where we tracked N soil chemistry and plant forage quality (Fig. 2). We also used kill site characteristics to map the probability of mountain lion hunting in order to determine whether they exhibited spatial homogeneity in their foraging patterns, and distributed carcasses in select areas more than others. Then we estimated mountain lion kill rates, which in combination with our mapping the relative probability of mountain lion hunting across the landscape allowed us to scale up what we learned at individual kill sites to estimate the potential heterogeneity of mountain lions on N cycling at the landscape-scale (Barton et al. 2019). We focused on N because it is a key limiting resource in many terrestrial ecosystems and its cycling affects both the quantity and nutritional quality of plants, which can in turn, affect herbivore fitness (Augustine et al. 2003). We also focused on $\delta^{15}N$, as this can be used to estimate the source of N enrichment in soils and plants (Robinson 2001; Yang 2004).

We tested six hypotheses in our research: 1) soils at mountain lion kill sites exhibit elevated total N and $\delta^{15}N$ as the carcass degrades over time; 2) mountain lion kill sites that occur in summer exhibit higher soil N than kill sites made in winter, because snow cover and a lack of decomposers prevents carcass-derived nutrients from entering the soil; 3) larger carcasses exhibit higher soil N and $\delta^{15}N$ than smaller carcasses; 4) plants growing at kill sites exhibit higher total N and $\delta^{15}N$ than control plants, mediated through uptake of N deposited into the soil from carcasses; 5) plants supplemented with N from ungulate carcasses grow faster and exhibit reduced cell wall components, such as cellulose and lignin; plants supplemented with N from carcasses have higher levels of digestible energy (DE, kJ/g); 6) mountain lions disproportionately kill prey in a small portion of the study area, where carcasses and their impacts on biogeochemistry accumulate over time.

Materials and methods

Study area

Our study area comprised 2,314 km^2 of the southern Greater Yellowstone Ecosystem (GYE) (Fig. 2) an area characterized by short, dry summers and high-snowfall winters (Elbroch et al. 2017). Elevations ranged from 1,800 m in the valleys to > 3,600 m in the mountains; low habitats were characterized by grasslands and big sagebrush (*Artemisia tridentata*), and higher ones by aspen (*Populus tremuloides*) and coniferous forests. Apex carnivores included mountain lions, American black bears (*Ursus americanus*), grizzly bears (*U. arctos horribilis*), and gray wolves.

Fig. 2 Study area location in the southern Greater Yellowstone Ecosystem, Teton County, Wyoming, USA (inset), including landownership/management boundaries indicated by shades of green. Yellow icons represent mountain lion (*Puma concolor*) kill sites sampled for soil total N and plant forage quality from 2014–2018
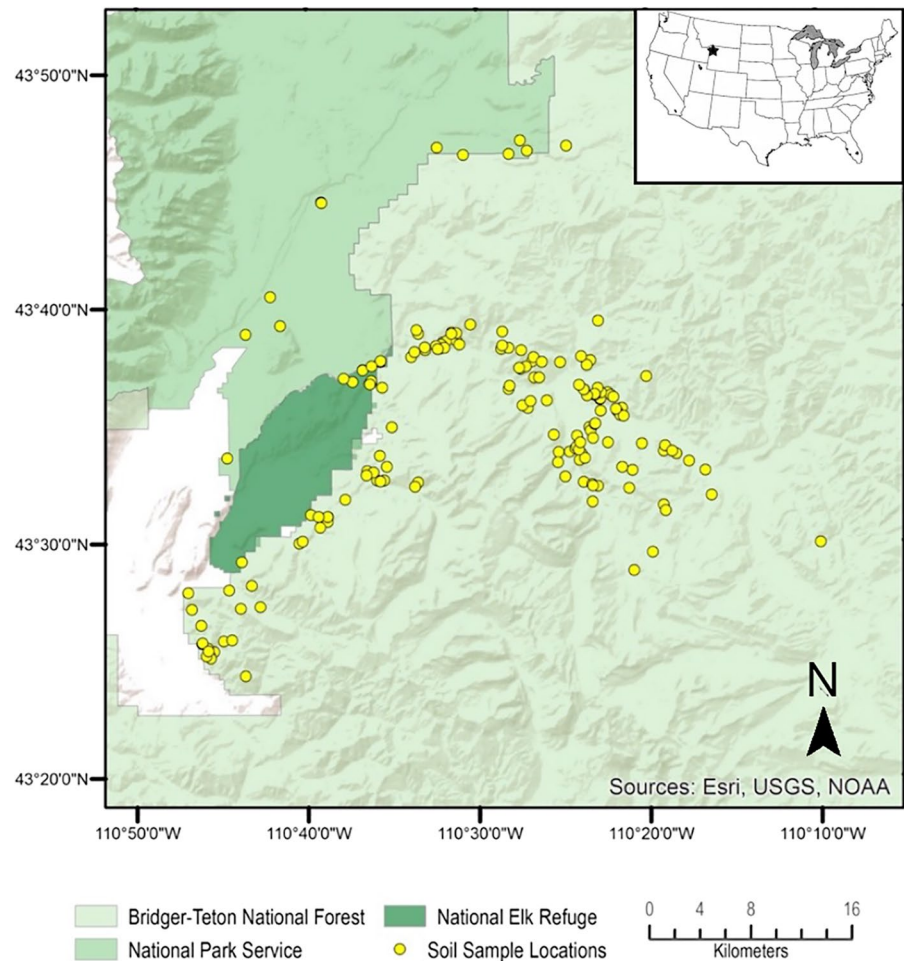
Ungulate prey included elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and North American pronghorn (*Antilocapra americana*).

Locating kill sites and identifying prey remains

Following guidelines approved by Institutional Animal Care and Use Committees (Jackson IACUC 027-10EGDBS-060210; National Park Service IACUC Protocol IMR_GRTE_Elbroch_Cougar_2013-2017), we captured and fit 50 mountain lions with Global Positioning System (GPS) collars that acquired location data at 2-h intervals. We defined GPS clusters as spatially aggregated location data (within 150 m of each other) spanning

at minimum 4 h and a maximum of 2 weeks (see Elbroch et al. 2017). Researchers investigated clusters quickly (generally within a week of the animal leaving the sight, and with a maximum delay of 30 days), visiting each GPS point in a cluster and conducting a circular search of an area with radius 30 m. When prey were found, we identified prey remains from hair, skin, rumen, and bone fragments, and we assessed the state of prey remains (e.g., bite marks, the lay of the carcass, which parts were fed upon) to determine if the mountain lion had killed or scavenged the prey. Then we estimated age and sex-specific mass of ungulate carcasses based on values derived from literature sources (Pojar and Bowden 2004; Elbroch et al. 2014). We initiated soil sampling if the prey was an ungulate at least 1-year in age.

Soil and plant sampling

We sampled 172 ungulate prey killed by mountain lions from November 2014 through October 2018, as determined by opportunity and arriving in time to initiate early sampling. We collected soil samples, 2.5 cm in diameter × 8 to 10 cm deep, beneath rumen remains, and a corresponding control sample taken approximately 6 m away from the rumen at the start of the study to represent pre-carcass deposition. The control was considered time 0 in our analyses. Rebar was placed through rumen contents to identify sampling locations over time and each carcass site was sampled at 3, 6, 9, 12, 18, 24, 30 and 36 months post deposition. However, not all carcasses were sampled at every interval due to permit restrictions limiting access to portions of the study area in winter; this resulted in the following missed samples: 10% of 3-month samples, 8% of 6-month samples, 30% of 9-month samples, 34% of 12-month samples, 23% of 18-month samples, 62% of 24-month samples, 62% of 30-month samples, and 79% of 36-month samples. We dried soil samples at 35 °C for 24 h and stored them at room temperature until further processing.

During the 2017 and 2018 summer soil sampling period, we sampled 65 kill site locations. We collected herbaceous plant species found growing at the rumen center and a paired control plant of the same species growing as close as possible to the location of the soil sample control. We only selected control plants with similar overstory characteristics, to mitigate differences due to sunlight exposure. We sampled plants once from each kill site, and samples varied in their collection date from 18, 24, 30 or 36 months post deposition. We dried samples at 35 °C for 48 h and stored them at room temperature until further processing.

We oven dried soil and vegetation samples, sifted out large debris with a 2 mm mesh sieve, and then ground samples with a ball-mill until particles were <250 um in size. We performed isotopic analysis at the Washington State University Stable Isotope Core Facility. Samples were analyzed for total N (%) and δ^{15}N (‰) using an Elemental Combustion System 4010 elemental analyzer (Costech Analytical, Valencia, CA, USA) coupled to a Delta Plus XP continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen) (Brenna et al.

1997; Qi et al. 2003). The isotope ratio was calculated as:

$$\delta = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1000, \text{‰}$$

where $R = {}^{15}$N/^{14}N. The primary standard for N is N_2 in air, and the internal precision reported here was 0.07 ‰ standard deviation (SD) for δ^{15}N. Acetanilide, corn, and keratin were used to develop a two-point normalization regression for the N analysis.

To determine the fiber content and digestible energy (DE) content of plant samples, we used sequential detergent analysis consisting of neutral detergent fiber (NDF), acid detergent fiber, acid detergent lignin (ADL), and acid insoluble ash (Goering and Van Soest 1970, with sodium sulfite, Ankom Fiber Analyzer 200/220®, Ankom Technology, Fairport NY, USA). We determined gross energy (GE, kJ/g) content using a bomb calorimeter (C5000, IKA Works, Inc., Wilmington, NC, USA) in the Wildlife Habitat Lab at Washington State University. We estimated the dry matter digestibility (DMD) (%) using a recent modification (Cook et al. 2022) of the summative equations of Robbins et al. (1987), developed and tested with elk and black-tailed deer (Hanley et al. 1992). We calculated DE content (kJ/g) for all samples from GE content × DMD (Robbins et al. 1995). Total N (%) values were converted to crude protein by a standard N conversion factor of 6.25, which controls for the non-protein N (Robbins 2012). All nutritional measurements were reported on a dry matter basis.

Soil and plant analyses

We tested four a priori models using a linear mixed model (GLMM) with a normal distribution and identity link and the library *lem4* in RStudio version 1.1.456 to explain total N and δ^{15}N levels in soil samples: 1) a null model without covariates, 2) a model that only included time from carcass deposition (measured in months), 3) a model that included an interaction between time and season, and 4) a model that included an interaction between time and carcass mass. We also included a random intercept for each separate kill site, to account for the correlations of repeated observations at each kill site and other confounding variables associated with specific locations.

Our models assumed that the initial values of total N and δ^{15}N were those in samples collected at the

control sites at time 0, and then subsequent measurements of total N and δ^{15}N at carcass sites represented concentrations through time (i.e., the first measurement under the carcass was at 3 months). We applied a natural log transformation to both total N and δ^{15}N, as preliminary residual plots from fitted models indicated non-constant variance across the range of fitted values. We used Akaike Information Criterion (AIC$_c$), adjusted for small sample size to rank model performance. We used Tukey's post hoc test on our best-fitting model to further examine how mean values of total N and δ^{15}N differed between months.

Because our top model determined via model selection only included time from carcass deposition (months), we ran two additional, posthoc single covariate GLMM analyses to draw inference with regards to our hypotheses 2 and 3. For these analyses, we included the random intercept for each separate kill site described above, and one additional covariate, carcass weight or season, to determine whether these variables also impacted soil N and δ^{15}N.

For an initial comparison of plant forage quality, we used paired *t*-tests to explore the prediction that plants growing at kill sites would have higher total N, δ^{15}N, gross energy (GE) and DE content, and lower cell wall (NDF), cellulose, and acid detergent lignin (ADL) content. When we received a significant result for any paired t-test, we followed up with a GLM analysis with a normal distribution and identity link to determine which of three factors (time since the kill was made, weight of carcass, season: summer vs. winter) explained the difference between paired samples (kill site and control).

Scaling carcass effects

We conducted a Resource Selection Function (RSF) analysis in a use-availability design (Manly et al. 2007) to map the probability of a mountain lion killing prey in any given location across our study area. To define our study area, we calculated a 95% kernel density estimation with a 1 km buffer bounding 128,032 mountain lion GPS locations from 50 individual mountain lions from 2001 through 2016. We used confirmed mountain lion kill sites ($n = 1,853$) as our used resource, for which we generated 5 times as many non-overlapping random locations ($n = 9,265$) within our study site to represent unused but available environmental conditions.

For each kill site and random location, we calculated the following relevant covariates for mountain lion kill site resource selection (Cristescu et al. 2019, Elbroch et al. 2014, Lendrum et al. 2014): topography (elevation, aspect, and slope), land cover (tree canopy cover, vegetation type), and distance metrics (distance to roads, distance to streams and distance to forest edge). We obtained elevation data (elevation; continuous, meter) from 2013 United States Geological Survey (USGS) 10- and 30-m Digital Elevation Models (https://catalog.data.gov). We derived inclination (slope; continuous, degrees) and aspect (sine [aspect(E-W); continuous, radians] and cosine [aspect(N-S); continuous, radians] transformed) from the ASTER Global Digital Elevation Map layer using the Spatial Analyst surface tools in ArcGIS 10.4.1 (ESRI, Redlands, CA, USA). Rather than using aspect directly, we converted it into a continuous representation of south-ness scaled from –1 (north) to 1 (south) using—cos $((aspect \times \pi)/180)$. We obtained tree canopy data (continuous, percentage) from National Land Cover Database (NLCD) 2016 USFS tree canopy cover (https://mrlc.gov). We acquired vegetation layers including vegetation type from NLCD 2016 (https://mrlc.gov). To reduce model parameters, we broadly reclassed vegetation types into seven distinct habitat classes: conifer and mixed forests (mixed forest), herb/grass (grassland), wetlands (riparian), shrub (shrub-steppe), deciduous forest (deciduous forest), water, snow/ice, and rock/bare (other), developed/urban, pasture/hay and crops (developed).

To estimate forest edge, we converted all forested lands from the Gap Analysis Program into a polygon layer in ArcGIS 10.1 (ESRI, Redlands, CA, USA), and then created a distance to forest edge layer from the perimeter of each forested section following methods of Elbroch et al. (2014). For distance to roads, we obtained a road layer for our study area from USGS National Transportation Dataset's road segment layers (https://catalog.data.gov) and combined primary (highways) and secondary roads (local roads including unpaved roads and 4WD roads) into one layer in ArcGIS 10.4.1 (ESRI, Redlands, CA, USA). We then used the Euclidean distance function to calculate distance to roads. We generated a distance to streams layer from USGS's high-resolution (1:24,000 scale) National Hydrography Dataset (https://USGS.gov) and extracted rivers and perennial streams into one layer in ArcGIS 10.4.1(ESRI, Redlands, CA, USA).

To evaluate the influence of habitat variables on kill site selection, we used generalized linear mixed models (GLMM) with a logit link function and binomial distribution, using the library *lem4* in RStudio version 1.1.456. Individual mountain lions were included as a random intercept to account for variation among individuals in areas selected for kills. We evaluated 16 a priori candidate models (Supporting Materials, Table S1) using AICc (Burnham and Anderson, 2002) adjusted for small sample size, ΔAICc, and Akaike weights (w_l).

We tested for predictive performance of the top model, given our data, using area under the curve (AUC) (Hanley and McNeil 1982; Boyce et al. 2002) and then conducted model validation using *k*-fold cross-validation (Boyce et al. 2002). In each cross-validation, the estimated probabilities were binned into 10 equal bins and correlated with the observed proportion of kills within the evaluation set. Next, we calculated Spearman rank correlation between the model suitability scores and bin classes. We then used the top model to map relative probabilities of kills across our study area.

We quantified mountain lion kill rates (predation events/week) for all ungulate prey across seasons for nine animals intensively tracked from 2012–2016 (Table S5), following Knopff et al. (2010). Then we used the densities of independent, resident mountain lions for our study area reported in Elbroch et al. (2018), to scale average mountain lion kill rates to total predation rates. Following Barton et al. (2019), we estimated total mountain lion contributions of carcass biomass by multiplying the average mass of an ungulate carcass in our study (157 kg) by the total predation rate of mountain lions.

Results

Soils

We collected 1,007 soil samples from 172 kill sites. Mass of ungulate carcasses ranged from 28 to 385 kg depending on species, sex and age. Soil samples were collected from 125 elk carcasses with a mean mass of 191.4 ± 80.1 kg (SD), 29 mule deer carcasses (mean $= 67.0 \pm 16.6$ kg), 11 bighorn sheep carcasses (mean $= 58.0 \pm 32.0$ kg), 4 white-tailed deer carcasses (mean $= 70.8 \pm 30.0$ kg), and 3 pronghorn carcasses

(mean $= 48.3 \pm 2.4$ kg). The mean difference between peak soil N and Time 0 was 0.48%, and for soil δ^{15}N, 2.31 parts per mille (‰) (Fig. 3).

We identified one top model that best explained patterns for both total N and δ^{15}N (Supporting Materials, Table S2); this model only included time after carcass deposition. There was little evidence of model selection uncertainty for our model set, with the top model garnering 98% of the weight of evidence for total N and 99% for δ^{15}N. Peak total N (%) values for soil occurred 12 months after carcass deposition (Fig. 3A). Tukey post-hoc multiple comparison tests revealed that mean total N values were significantly greater for all months except month 36 when compared to the reference month 0 (Supporting Materials, Table S3). No other monthly comparisons were significantly different from each other. Peak δ^{15}N (‰) in soils occurred at 3 months after carcass deposition (Fig. 3B). Tukey post-hoc multiple comparison tests revealed that there was significantly greater mean δ^{15}N for months 3, 6 and 18 when compared to the reference month 0 (Supporting Materials, Table S3).

We found that season did affect soil N in our single covariate test ($F_{1, 1004} = 9.13$, $P < 0.91$, $\beta = 0.09 \pm 0.03$ SE reference summer), but that carcass weight did not ($F_{1, 1004} = 0.69$, $P < 0.41$). We did not find any effect of season in our single covariate test on δ^{15}N ($F_{1, 1004} = 0.01$, $P = 0.91$), but we did for carcass weight on δ^{15}N ($F_{1, 1004} = 19.31$, $P < 0.01$, $\beta = 0.0006 \pm 0.0001$ SE).

Plants

We sampled 65 kill sites at 18, 24, 30 and 36 months post deposition for a total of 130 plant samples. Total N concentration (mean difference $= 0.54$; paired *t*-test, $t_{64} = 4.94$, $P < 0.001$) and δ^{15}N (mean difference $= 2.3$; paired *t*-test, $t_{64} = 4.38$, $P < 0.001$) of plants growing at kill sites were significantly higher than control plants. Differences in total N concentration was best explained by season ($P < 0.01$, $\beta = --0.24 \pm 0.09$ SE, reference summer), rather than time ($P < 0.46$) or weight ($P < 0.29$). Differences in δ^{15}N were best explained by carcass weight ($P = 0.03$, $\beta = 0.009 \pm 0.004$ SE), rather than time ($P = 0.16$) or season ($P = 0.97$).

We did not detect a difference between paired samples for GE (mean difference $= --6.55$; paired *t*-test, $t_{64} = --0.26$, $P < 0.60$), DE (mean difference $= -0.02$;

Fig. 3 Mean and 95% CI for total nitrogen (**A**) and $\delta^{15}N$ (**B**) of soils collected from mountain lion (*Puma concolor*) kill sites in the southern Greater Yellowstone Ecosystem in 2014–2018 as a function of time since carcass deposition, based on our top-ranked model. Total nitrogen was elevated for all months after the initial (control) month, with peak total nitrogen at 12 months after carcass deposition. All months had elevated $\delta^{15}N$ compared to the control month, with a peak $\delta^{15}N$ at 3 months after carcass deposition
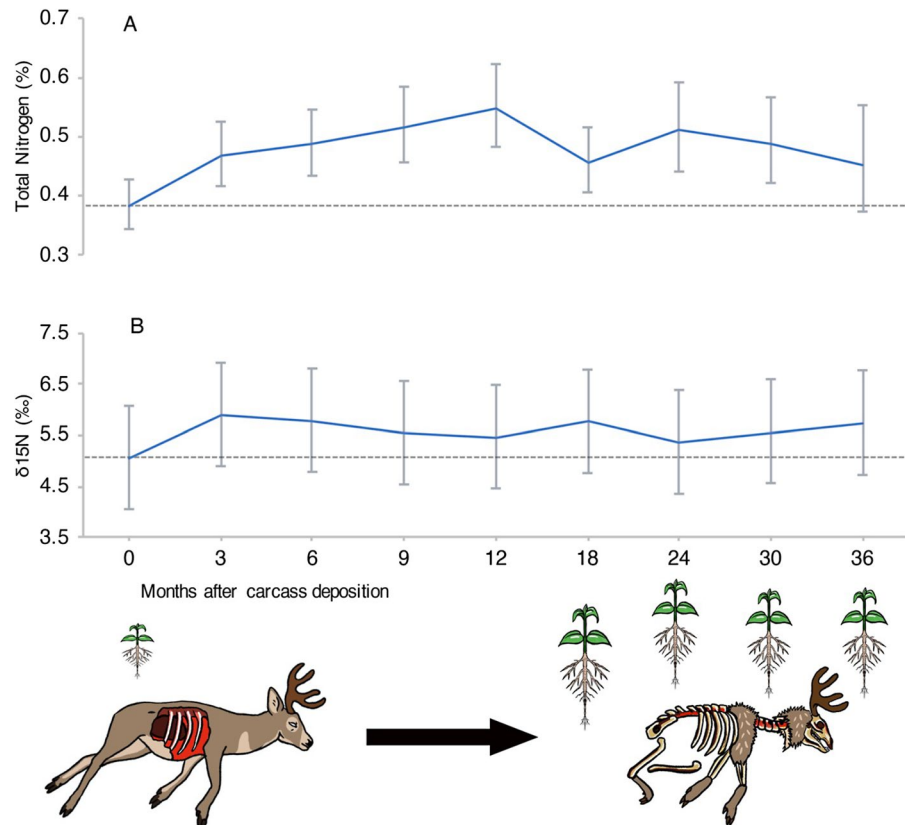
paired *t*-test, $t_{64} = -0.09$, $P < 0.93$), NDF (mean difference $= -1.01$; paired *t*-test, $t_{64} = -0.93$, $P < 0.82$), cellulose (mean difference $= -1.37$; paired *t*-test, $t_{64} = -1.46$, $P < 0.15$), or ADL (mean difference $= -0.46$; paired *t*-test, $t_{64} = -1.24$, $P < 0.89$).

Scaling carcass effects

Our global model inclusive of all relevant biological covariates was the top-ranked model in our RSF analyses (Supporting Materials, Table S1, Fig. 4A). Our AUC value for the receiver operating characteristic curve analyses was 0.73. The global model had high predictive power when tested against validation data and Spearman rank correlations of selection probabilities between training and validation data was 1.0 ($P < 0.001$). Mountain lions were more likely to kill prey in areas of high tree canopy and southerly aspects, at low elevations and with steeper slopes and were also more likely to make a kill in areas closer to forest edge, roads, and streams (Supporting Materials, Table S4). Mountain lions selected habitats in which

to hunt prey in the following order: 1) deciduous forest 2) mixed forest 3) grassland 4) shrub-steppe 5) riparian 6) other 7) developed.

When we mapped the relative probability of a mountain lion killing prey across our study area, we detected clear spatial heterogeneity in the probability that any given area would host hunting mountain lions. Most of the landscape exhibited low probability of being selected by mountain lions for foraging. If we only consider sites with a medium to high relative probability of being a kill site location (which we defined as a relative probability of > 0.40), these sites only accounted for 4% of the total study area (Fig. 4B).

We followed 9 adult mountain lions for 81.6 ± 37.8 (SD) weeks, recorded 746 ungulate kills, and estimated average kill rates of 1.033 ± 0.2 ungulates/wk (Supporting Materials, Table S5). On average, each mountain lion produced 54 ungulate carcasses per year, creating 8,478 kg of carrion per year per resident mountain lion (of which mountain lions eat approximately 33% themselves; Elbroch et al. 2014).
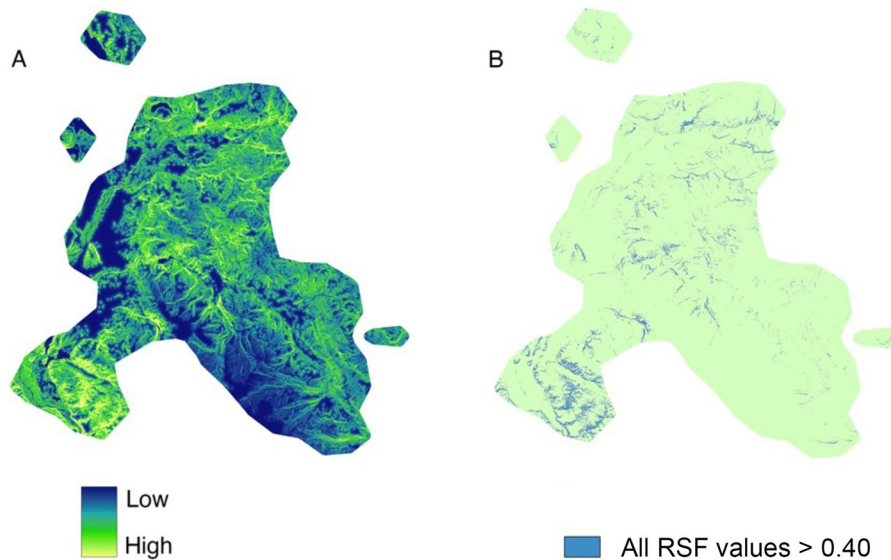
Fig. 4 A Proportional probability of habitat selection for carcass deposition of ungulates killed by mountain lions (*Puma concolor*) in southern Greater Yellowstone Ecosystem during 2001–2016. Map represents RSF model averaged coefficient estimates for aspect, slope, tree canopy, elevation, distance to forest, distance to roads, distance to streams, and vegetation according to *AICc*. **B** Predicted probability of habitat selection with RSF values > 0.40 for carcass deposition of ungulates killed by mountain lions (*Puma concolor*) in southern Greater Yellowstone Ecosystem during 2001–2016

Based on the estimate of mountain lion density in our 2,314 km^2 study area (0.52/100 km^2; Elbroch et al. 2018), we calculated that resident adult mountain lions redistributed 102,026 kg of ungulate carrion and 3,249 kg of N annually (Robbins et al. 1974), or 44.1 kg of carrion and 1.4 kg of N per km^2.

Discussion

We found strong evidence that carcasses provided by mountain lions impact soil and plant chemistry, as well as evidence to support Monk and Schmitz's (2022) hypothesis that carnivore foraging contributes to widescale heterogeneity in nutrient cycling and biogeochemistry. Mountain lion foraging provided 44.1 kg of ungulate carrion and 1.4 kg of N per square kilometer to the GYE each year. These are conservative estimates because they are based on our minimum mountain lion density estimates for resident adults, and do not include transient mountain lions that forage as they pass through the system. Mountain lion effects on N cycling were not uniform; rather, they were limited to predictable locations in a very small proportion of the study area, suggesting that ambush predators, in particular, may enhance resource heterogeneity at scale that may have diverse cascading effects on local community assemblages.

Mountain lion prey changed soil biogeochemistry during decomposition, including altered pathways of nutrient flow and modifications to stable isotopic composition. Soils at carcass sites exhibited an increase in total N and δ^{15}N for the duration of our 3-year study, suggesting long-lasting effects of carcass deposition on N cycling. Soil δ^{15}N peaked almost immediately, indicating a rapid contribution of isotopically heavy carcass components to local communities. We also documented large differences in δ^{15}N in soils and plants at control plots versus kill sites (e.g., ~40% higher for plants collected at 18 months), suggesting that plants are uptaking a significant portion of N contributions from carcass remains (Bump et al. 2009a). Plant δ^{15}N increased by 2.3 ‰, which is large when one considers that the range of variation in plants across xeric and mesic systems in the GYE is only 6.3 ‰ (Frank and Evans 1997).

Previous research has shown that increases in plant N can alter plant chemistry and increase protein content (Leghari et al. 2016), and therefore increase the likeliness that a plant is selected by herbivores

(Dostaler et al. 2011). Neverthelss, we did not find that increased N in plants led to a reduction in cell wall constituents or plant fiber. Our inability to detect differences in plant fiber between carcass and control plants may reflect structural differences in the different individual plants and plant species collected at each location, along with differences in microbial and soil properties at collection sites (Barton et al. 2013). In our plant samples, we did not control for the proportion of fibrous stems and less-fibrous leaves, and digestibility of plant tissues vary dramatically depending on the part of the plant collected (Buxton and Marten 1989).

We found support for our hypotheses that season and carcass weight would affect N and δ^{15}N concentrations in soils and plants, although these effects were smaller than time, as determined via model selection. The summer season was characterized by higher values of total N in both soils and plants, which we attribute to faster carcass decomposition times (Towne 2000), and the potential for leaching to reduce N concentrations during the wet, winter season. Prey size may not have been influential on total N as we sampled actual mountain lion kills rather than placed whole carcasses as part of an experiment. Mountain lions fed from carcasses along with a diverse vertebrate scavenger community (Elbroch et al. 2017), and therefore prey remains may have been more comparable in size regardless of the initial size of carcasses. Moreover, because we assessed ungulate carcasses and ignored smaller prey such as American beavers (*Castor canadensis*), we may have limited our ability to discern the effect of carcass size on total N deposition. Both soil and plant δ^{15}N, in contrast, saw increases with carcass size but no effect of season. Greater δ^{15}N enrichment may simply reflect greater N assimilation via volatilization and other processes associated with larger sources of organic N, or in plants, an efficient uptake system utilizing amino acid transporters or other mechanisms we have yet to understand (Näsholm et al. 2009) in the nutrient poor soil environments characteristic of northwestern Wyoming (Griffin et al. 2011).

We estimated that each mountain lion in our study system created approximately 482 ephemeral hotspots of nutrient rich soils over a 9-year lifespan, and that each year, 12 resident mountain lions produced 101,736 kg of carrion, a mass comparable to that of a blue whale (*Balaenoptera musculus*). Our RSF analysis based on kill site locations revealed that this biomass was being placed in only a tiny fraction of the overall study region, in areas which favored the stalk-and-ambush foraging strategy of solitary felids (Holmes and Laundré 2006; Cristescu et al. 2019). This is perhaps strong support for Monk and Schmitz's hypothesis that carnivores that hunt disproportionately in small areas will create positive feedback loops via carcass deposition that in turn increases plant quality and then attracts ungulates to feed, beginning the cycle all over again. This is particularly feasible for mountain lions because they are considered "land-tenure" species, and new mountain lions in populations generally exhibit home range characteristics very similar to their predecessors that they replaced (Seidensticker et al. 1973); in this way generations of mountain lions might hunt, and "garden," the very same areas.

Nevertheless, risk experienced by prey species is context dependent (e.g., impacted by topography and prey behaviors; Heithaus et al. 2009) and may not follow clean patterns as proposed by Monk and Schmitz (2022). Carcasses give woody trees a competitive advantage over herbaceous plants, for example, and therefore plant N enrichment via carcass deposition could alter plant communities as well as plant structure (Bump et al. 2009b); structural changes could in turn influence prey vulnerability and hunting behaviors of carnivores, both of which impact the hunting success of carnivores vital to completing the predation-enrichment cycle. Humans also alter species interactions, and in systems where anthropogenic impacts are large, predator–prey interactions may be even more difficult to predict (Haswell et al. 2017). Therefore, we expect that field experiments will need to be very carefully planned to test whether herbivores preferentially select past predation sites to forage, beginning the cycle all over again (Monk and Schmitz 2022) (Fig. 1). In terms of field sampling, we also encourage an exploration of C:N ratios and stored forms of N in areas where carnivores forage more frequently, to test for potential long-term effects of carnivore foraging on N cycles.

Our research supports a growing body of evidence that large carnivores affect ecosystem function via the redistribution of carrion resources that spread nutrients via diverse environmental and consumer pathways. Carrion produced by carnivores, for example, affects the distribution and diversity of invertebrates

(Barry et al. 2019), structures vertebrate scavenger communities (Allen et al. 2015), impacts plant community diversity and physical structure (Bump et al. 2009b), as well as affects soil and plant chemistry (Hilderbrand et al. 1999; Bump et al. 2009a). This research provided novel insights into complex ecology, as well as supports conservation practitioners faced with improving public support for large carnivores and prioritizing "strongly interacting species" that play disproportionately important roles in maintaining ecosystem function (Brodie et al. 2018).

Data availability The data are archived in the following archive: https://figshare.com/s/eb800917542576038c1d.

Declarations

References

Allen ML, Elbroch LM, Wilmers CC, Wittmer HU (2015) The comparative effects of large carnivores on the acquisition of carrion by scavengers. Am Nat 185:822–833

Augustine DJ, McNaughton SJ, Frank DA (2003) Feedbacks between soil nutrients and large herbivores in a managed savanna ecosystem. Ecol Appl 13:1325–1337

Barry JM, Elbroch LM, Aiello-Lammens ME, Sarno RJ, Seelye L, Kusler A, Quigley HB, Grigione MM (2019) Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. Oecologia 189:577–586

Barton PS, Bump JK (2019) Carcass decomposition. In: Olea PP, Mateo-Tomás P, Sánchez-Zapata JA (eds) Carcass ecology and management. Springer, Cham., pp 101–124

Barton PS, Cunningham SA, Lindenmayer DB, Manning AD (2013) The role of carcass in maintaining biodiversity and ecological processes in terrestrial ecosystems. Oecologia 171:761–772

Barton PS, Evans MJ, Foster CN, Pechal JL, Bump JK, Quaggiotto MM, Benbow ME (2019) Towards quantifying carcass biomass in ecosystems. Trends Ecol Evol 34(10):950–961

Benninger LA, Carter DO, Forbes SL (2008) The biochemical alteration of soil beneath a decomposing carcass. Forensic Sci Int 180:70–75

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK (2002) Evaluating resource selection functions. Ecol Model 157:281–300

Brenna JT, Corso TN, Tobias HJ, Caimi RJ (1997) High-precision continuous-flow isotope ratio mass spectrometry. Mass Spectrometry Rev 16:227–258

Brodie JF, Redford KH, Doak DF (2018) Ecological function analysis: incorporating species roles into conservation. Trends Ecol Evol 33:840–850

Bump JK, Peterson RO, Vucetich JA (2009a) Wolves modulate soil nutrient heterogeneity and foliar nitrogen by configuring the distribution of ungulate carcasses. Ecology 90:3159–3167

Bump JK, Webster CR, Vucetich JA, Peterson RO, Shields JM, Powers MD (2009b) Ungulate carcasses perforate ecological filters and create biogeochemical hotspots in forest herbaceous layers allowing trees a competitive advantage. Ecosystems 12:996–1007

Buxton DR, Marten GC (1989) Forage quality of plant parts of perennial grasses and relationship to phenology. Crop Sci 29:429–435

Cook RC, Shipley LA, Cook JG, Camp MJ, Monzingo DS, Robatcek SL, Berry SL, Hull IT, Myers WL, Denryter KA, Long RA (2022) Sequential detergent fiber assay results used for nutritional ecology research: Evidence of bias since 2012. Wildlife Society Bulletin 46(4):e1348

Cristescu B, Bose S, Elbroch LM, Allen ML, Wittmer HU (2019) Habitat selection when killing primary versus alternative prey species supports prey specialization in an apex predator. J Zool 309:259–268

Danell K, Berteaux D, Bråthen KA (2002) Effect of muskox carcasses on nitrogen concentration in tundra vegetation. Arctic 55:389–392

Day TA, Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. Ecology 71:180–188

DeVault TL, Rhodes OE Jr, Shivik JA (2003) Scavenging by vertebrates: behavioral, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems. Oikos 102:225–234

Dostaler S, Ouellet JP, Therrien JF, Côté SD (2011) Are feeding preferences of white-tailed deer related to plant constituents? J Wildl Manage 75:913–918

Elbroch LM, Allen ML, Lowrey BH, Wittmer HU (2014) The difference between killing and eating: Ecological shortcomings of puma energetic models. Ecosphere 5:1–16

Elbroch LM, O'Malley C, Peziol M, Quigley HB (2017) Vertebrate diversity benefiting from carcass provided by pumas and other subordinate, apex felids. Biol Conserv 215:123–131

Elbroch LM, Marescot L, Quigley H, Craighead D, Wittmer HU (2018) Multiple anthropogenic interventions drive puma survival following wolf recovery in the Greater Yellowstone Ecosystem. Ecol Evol 8:7236–7245

Evans RD (2007) Soil Nitrogen isotopic composition. Stable Isotopes Ecol Environ Sci 2:83–98

Frank DA, Evans RD (1997) Effects of Native Grazers on Grassland N Cycling in Yellowstone National Park. Ecology 78:2238–2248

Goering HK, Van Soest PJ (1970) Forage fiber analyses (apparatus, reagents, prcedures, and some applications). USDA Agr Handb

Griffin JM, Turner MG, Simard M (2011) Nitrogen cycling following mountain pine beetle disturbance in lodgepole pine forests of Greater Yellowstone. For Ecol Manag 261:1077–1089

Hanley JA, McNeil BJ (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology143:29–36

Hanley TA, Robbins CT, Hagerman AE, McArthur C (1992) Predicting digestible protein and digestible dry matter in tannin-containing forages consumed by ruminants. Ecology 73:537–541

Heithaus MR, Wirsing AJ, Burkholder D, Thomson J, Dill LM (2009) Towards a predictive framework for predator risk effects: the interaction of landscape features and prey escape tactics. J Anim Ecol 78:556–562

Hilderbrand GV, Hanley TA, Robbins CT, Schwartz CC (1999) Role of brown bears in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546–550

Holmes BR, Laundré JW (2006) Use of open, edge and forest areas by pumas Puma concolor in winter: are pumas foraging optimally? Wildl Biol 12:201–209

Keenan SW, Schaeffer SM, Jin VL, DeBruyn JM (2018) Mortality hotspots: nitrogen cycling in forest soils during vertebrate decomposition. Soil Biol Biochem 121:165–176

Knopff KH, Knopff AA, Kortello A, Boyce MS (2010) Cougar kill rate and prey composition in a multiprey system. J Wildl Manage 74:1435–1447

Leghari SJ, Wahocho NA, Laghari GM, HafeezLaghari A, MustafaBhabhan G, HussainTalpur K et al (2016) Role of nitrogen for plant growth and development: A review. Adv Environ Biol 10:209–219

Lendrum PE, Elbroch LM, Quigley H, Thompson DL, Jimenez M, Craighead D (2014) Home Range characteristics of a subordinate predator; selection for refugia or hunt opportunity? J Zool 294:58–66

Manly BFL, McDonald L, Thomas DL, McDonald TL, Erickson WP (2007) Resource selection by animals: Statistical design and analysis for field studies. Springer Science & Business Media, Dordrecht

McClain ME, Boyer EW, Dent CL, Gergel SE, Grimm NB, Groffman PM et al (2003) Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–312

Melis C, Selva N, Teurlings I, Skarpe C, Linnell JD, Andersen R (2007) Soil and vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland. Ecol Res 22:807–813

Monk JD, Schmitz OJ (2022) Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. Oikos 2022:e08554

Näsholm T, Kielland K, Ganeteg U (2009) Uptake of organic nitrogen by plants. New Phytol 182:31–48

Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A (2013) Ecological and evolutionary implications of food subsidies from humans. Ecol Lett 16:1501–1514

Parmenter RR, MacMahon JA (2009) Carcass decomposition and nutrient cycling in a semiarid shrub–steppe ecosystem. Ecol Monogr 79:637–661

Pojar TM, Bowden DC (2004) Neonatal mule deer fawn survival in west-central Colorado. J Wildl Manage 68:550–560

Qi XM, Zhang LD, Du XL, Song ZJ, Zhang Y, Xu SY (2003) Quantitative analysis using NIR by building PLS-BP model. Spectrosc Spectral Anal 23:870–872

Robbins C (2012) Wildlife feeding and nutrition. Elsevier

Robbins CT, Moen AN, Reid JT (1974) Body composition of white-tailed deer. J Anim Sci 38:871–876

Robbins CT, Hanley TA, Hagerman AE, Hjeljord O, Baker DL, Schwartz CC, Mautz WW (1987) Role of tannins in defending plants against ruminants: reduction in protein availability. Ecology 68:98–107

Robbins CT, Spalinger DE, van Hoven W (1995) Adaptation of ruminants to browse and grass diets: are anatomical-based browser-grazer interpretations valid? Oecologia 103:208–213

Robinson D (2001) δ15N as an integrator of the nitrogen cycle. Trends Ecol Evol 16:153–162

Schimel JP, Bennett J (2004) Nitrogen mineralization: challenges of a changing paradigm. Ecology 85:591–602

Sebastián-González E, Morales-Reyes Z, Botella F, Naves-Alegre L, Pérez-García JM et al (2020) Network structure of vertebrate scavenger assemblages at the global scale: drivers and ecosystem functioning implications. Ecography 43:1143–1155

Schmitz OJ, Hawlena D, Trussell GC (2010) Predator control of ecosystem nutrient dynamics. Ecol Lett 13:1199–1209

Seidensticker JC, Hornocker MG, Wiles WV, Messick JP (1973) Mountain lion social organization in the Idaho Primitive Area. Wildl Monogr 35:3–60

Smith JA, Donadio E, Bidder OR, Pauli JN, Sheriff MJ, Perrig PL, Middleton AD (2020) Where and when to hunt? Decomposing predation success of an ambush carnivore. Ecology 101:e03172

Towne EG (2000) Prairie vegetation and soil nutrient responses to ungulate carcasses. Oecologia 122:232–239

Wikenros C, Sand H, Ahlqvist P, Liberg O (2013) Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. PLoS ONE 8:e77373

Wilmers CC, Stahler DR, Crabtree RL, Smith DW, Getz WM (2003) Resource dispersion and consumer dominance: scavenging at wolf-and hunter-killed carcasses in Greater Yellowstone, USA. Ecol Lett 6:996–1003

Wilmshurst JF, Fryxell JM (1995) Patch selection by red deer in relation to energy and protein intake: a re-evaluation of Langvatn and Hanley's (1993) results. Oecologia 104:297–300

Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carcass structure communities. Trends Ecol Evol 26:129–135

Yang LH (2004) Periodical cicadas as resource pluses in North American forests. Science 306:1565–1567