

Predation and Biophysical Context Control Long-Term Carcass Nutrient Inputs in an Andean Ecosystem

Julia D. Monk,^{1,2*}  Emiliano Donadio,³ Justine A. Smith,⁴ Paula L. Perrig,⁵ Arthur D. Middleton,² and Oswald J. Schmitz¹

¹School of the Environment, Yale University, 370 Prospect St., New Haven, Connecticut 06511, USA; ²Department of Environmental Science, Policy, and Management, University of California - Berkeley, 130 Hilgard Way, Berkeley, California 94709, USA; ³Fundación Rewilding Argentina, Scalabrini Ortiz 3355 4J, 1425 Buenos Aires, CP, Argentina; ⁴Department of Wildlife, Fish, and Conservation Biology, University of California - Davis, 1088 Academic Surge, 455 Crocker Lane, Davis, California 95616, USA; ⁵INIBIOMA (CONICET-Universidad Nacional del Comahue), San Carlos de Bariloche R8400FRF, Río Negro, Argentina

ABSTRACT

Animal carcass decomposition is an often-overlooked component of nutrient cycles. The importance of carcass decomposition for increasing nutrient availability has been demonstrated in several ecosystems, but impacts in arid lands are poorly understood. In a protected high desert landscape in Argentina, puma predation of vicuñas is a main driver of carcass distribution. Here, we sampled puma kill sites across three habitats (plains, canyons, and meadows) to evaluate the impacts of vicuña carcass and stomach decomposition on soil and plant nutrients up to 5 years after carcass deposition. Soil beneath both carcasses and stomachs had significantly higher soil nutrient content than adjacent reference sites in arid, nutrient-poor plains and canyons, but not in moist, nutrient-rich meadows. Stomachs had greater effects on soil nutrients than carcasses. However, we did not detect higher plant *N* concentrations at kill

sites. The biogeochemical effects of puma kills persisted for several years and increased over time, indicating that kills do not create ephemeral nutrient pulses, but can have lasting effects on the distribution of soil nutrients. Comparison to broader spatial patterns of predation risk reveals that puma predation of vicuñas is more likely in nutrient-rich sites, but carcasses have the greatest effects on soil nutrients in nutrient-poor environments, such that carcasses increase localized heterogeneity by generating nutrient hotspots in less productive environments. Predation and carcass decomposition may thus be important overlooked factors influencing ecosystem functioning in arid environments.

Key words: carcasses; decomposition; predation; *Puma concolor*; *Vicugna vicugna*; high Andes; biogeochemical hotspots; nutrient cycling.

Received 31 May 2023; accepted 3 December 2023

Supplementary Information: The online version contains supplementary material available at <https://doi.org/10.1007/s10021-023-00893-7>.

Author Contributions: DM and OJS conceived of and designed the study; JDM, ED, and ADM provided materials; JDM, ED, PLG, and ADM collected data; JDM and JAS analyzed the data; JDM and OJS wrote the paper with revisions from all authors.

*Corresponding author; e-mail: julia.monk@berkeley.edu

HIGHLIGHTS

- Vicuña carcasses and especially stomachs can increase soil nutrients in the high Andes
- These effects were context-dependent and only occurred in arid, nutrient-poor habitats

- Carcass effects in these habitats persist for several years and increase over time

INTRODUCTION

Classic ecological theory holds that predators can have positive indirect effects on plant diversity and productivity by capturing and killing herbivore prey, which in turn reduces live herbivore abundance and associated foraging impacts on plants (Schmitz and others 2000; Ripple and others 2016). Several recent studies have expanded the concept of cascading predator effects on ecosystems to include the ecosystem effects of predator deposition of prey carcasses and their embodied nutrients (Bump and others 2009a; Schmitz and others 2010; Monk and Schmitz 2022; Peziol and others 2023).

In terrestrial ecosystems, prey carcasses could have an outsized impact on ecosystem functioning over time and space because they provide inputs of high concentrations of nutrients (Benbow and others 2016). This input can elevate soil nutrients and increase plant quality, diversity and productivity (Bump and others 2009b; Barton and others 2013; de Miranda and others 2023). However, studies of nutrient release from predated carcasses among different kinds of ecosystems have revealed positive (Bump and others 2009a; Gharajehdaghipour and others 2016; de Miranda and others 2023; Peziol and others 2023) as well as neutral (Teurlings and others 2020) effects. Hence, as with classical trophic cascades of predators on plant biomass (Chase 2003), the ecosystem effects of carcass nutrient release could be highly context-dependent, determined by variation in biophysical conditions of carcass deposition sites within and among ecosystems (Hocking and Reynolds 2012; Monk and Schmitz 2022).

Here, we report on an exploration of the context-dependent fate of nutrients from predated vertebrate carcasses in the arid Andean ecosystem of San Guillermo National Park (SGNP) in Argentina. The potential for context dependency in SGNP arises from a patchwork of three habitat types that vary in topography, aridity, nutrient availability, and productivity: plains (open, sparsely vegetated flatlands with low nutrient availability), canyons (slopes and rugged terrain, also sparsely vegetated with low nutrient availability), and meadows (moist, nutrient-rich patches with dense vegetation). SGNP has a single apex predator, the puma (*Puma concolor*), which predominantly preys on one main large herbivore, the vicuña (*Vicugna vicugna*). Vicuña carcasses are further consumed by an obligate scavenger, the Andean condor (*Vultur gryphus*).

Puma predation has historically accounted for 91% of adult vicuña mortality (Donadio and others 2012), making puma predation a main source of carcasses. Predation and scavenging both vary spatially across these habitats. Predation risk is highest in meadows, which provide dense cover for stalking pumas, but pumas succeed in killing vicuñas in all habitats (Donadio and Buskirk 2016; Smith and others 2020). Open plains with high visibility provide some refuge for vicuñas from stalking pumas, and condors similarly avoid encounters with pumas by feeding most heavily at carcasses in plains (Perrig and others 2023). Thus, pumas and condors together play a substantial role in determining the location, quantity, and quality of vertebrate detritus that decomposes across the heterogeneous desert landscape.

Overall, carcasses are generally highly consumed by pumas and condors, and when scavenging occurs little but bone, hide, and fur are left in the days after a kill. However, these remaining carcass elements persist on the landscape, remaining identifiable at kill sites for years after a predation event. Pumas often remove vicuña stomachs before feeding, leaving what are essentially large piles of partially digested plant matter at kill sites. Stomach contents are consumed only in small quantities by vertebrate scavengers (Barceló and others 2022), and similarly can remain at kill sites for years. The dry, cold conditions of this ecosystem may limit microbial activity and slow the release of labile nutrients from carcasses to the surrounding environment. Thus, carcasses could have minimal impacts on soil and plant nutrients in arid habitats (Parmenter and MacMahon 2009; Benbow and others 2016). Alternatively, pulsed additions of easily decomposed animal matter and partially digested stomach contents could have substantial impacts on ecosystem functioning in an otherwise nutrient-limited system with slow recycling of plant litter (Schmitz and others 2010; McInturf and others 2019). To resolve these questions, we used a large long-term dataset of kill sites distributed across habitats throughout the landscape and related those kill sites to their nutrient legacies. Specifically, we sought to determine (a) whether vicuña carcasses impact soil and plant biogeochemistry in SGNP, given high carcass utilization by predators and scavengers, and (b) how carcass impacts might vary across habitat contexts that differ in aridity, nutrient availability, and predation risk.

First, we hypothesized that puma-killed carcasses and stomachs would increase local soil and plant nutrient content, but that stomachs would have more pronounced effects because they are not

heavily consumed by predators and scavengers. We expected that carcasses could also impact soil moisture and temperature by physically trapping condensation and shading soils. We also assessed how carcass impacts on soils changed over time. Most studies of carcass biogeochemical hotspots follow the fate of nutrients for a few months to a few years (but see Barton and others 2016); however, our dataset included carcass sites persisting up to 5 years. In some systems, the magnitude of carcass impacts decreases with carcass age as the initial flush of nutrient inputs tapers off (for example, Bump and others 2009a). We predicted instead that carcass effects would increase over time due to the slow release of nutrients from the recalcitrant tissues left behind after puma and scavenger consumption of soft tissue.

We hypothesized that carcass impacts could differ between habitats in two alternative ways. First, carcasses could have greater effects on soil and plant nutrients in plains and canyons, where background soil nutrient concentrations are low, thus enabling even small carrion inputs to have substantial impacts. Alternatively, decomposition could be facilitated in moist environments, causing greater carcass impacts in meadows compared to plains and canyons. Furthermore, higher rates of condor scavenging could further reduce the impacts of carcasses in plains, where condors are safer from pumas (Perrig and others 2023).

We finally considered how localized carcass deposition might relate to landscape-scale patterns of nutrient availability. We hypothesized that if carcasses increase soil nutrients, sites with high predation risk should have higher background nutrient levels due to regular carcass inputs; indeed, greater nutrient availability may attract vicuñas to otherwise high-risk sites, spurring a positive feedback between resources and risk (Monk and Schmitz 2022; Peziol and others 2023).

METHODS

Study Area

San Guillermo National Park (SGNP) is a 166,000 ha reserve located in the central Andes on the western edge of Argentina (29° 13' S, 69° 21' W, 2200–5467 m elevation). Annual temperatures range from a mean of 1 °C in the winter to a mean of 15 °C in the summer. Annual precipitation is < 200 mm/year, mainly falling in the form of rain in the summer growing season (November–March) (Martínez Carretero 2007). The time period of our study was within the range of normal temperature

and precipitation for the region (see Monk and others 2022). There are three main habitats that characterize the park: plains, canyons, and meadows. Both environmental factors and trophic interactions differ between these habitats. Plains (48.9%) and canyons (48.5%) make up the majority of the area inhabited by vicuñas (Monk and others 2022), and are characterized by dry, exposed soil interspersed with sparse grasses and shrubs. Productivity in these Andean puna habitats is limited by nitrogen and phosphorus (Cueto and Ponce 1985). Lush wet meadows make up 2.6% of the study area (ranging in size from several square meters to 120 ha; Monk and others 2022), occurring where water is available, and are highly vegetated with rushes and sedges. These three habitats create a variable landscape of risk and reward over which vertebrate trophic interactions play out.

Vicuñas are among the park's only large mammalian herbivores; while guanacos (*Lama guanicoe*), another camelid species, also exist in the park, they occur at very low densities (Martínez Carretero 2007; Donadio and others 2010). Vicuñas are heavily preyed upon by pumas (Donadio and others 2010, 2012), and predation risk drives a strong landscape of fear in SGNP (Donadio and Buskirk 2016). Pumas are highly successful at hunting vicuñas in meadows, where dense vegetation provides ample cover for stalking predators, and in canyons, where rocky outcroppings and sloping terrain similarly facilitate ambush predation (Donadio and Buskirk 2016; Smith and others 2019a). As a result, vicuñas tend to avoid canyons, which pose a high risk, but continue to visit meadows when pumas are least active due to the high availability of otherwise limited water and nutritious forage (Smith and others 2019b, 2020). Vicuñas spend a substantial amount of time in open plains, where they can more easily detect and evade predators. However, pumas do occasionally kill vicuñas in plains as well, despite conditions being less conducive to successful kills (Smith and others 2020). Andean condors are the dominant scavengers in SGNP, but other, smaller avian scavengers and foxes also consume vicuña remains. Condors rely heavily on puma-predated vicuña carcasses and generally displace and outcompete other scavengers when they descend upon a carcass (Perrig and others 2016, 2023). Invertebrates in principle may also consume some carcass material. However, we rarely observed signs of invertebrate scavenging carcasses, suggesting that vertebrate scavenging was predominant in this system (Barceló and others 2022). Condors, like vicuñas, are wary of pumas, and while they detect carcasses in

areas of high puma predation risk, they tend to descend and feed on carcasses in open habitats farther from cover, such as plains (Perrig and others 2023).

Data Collection

We identified carcass locations using an extensive historical database of kill sites extending from 2014 to 2017 collected as part of a previous study (Smith and others 2019b, 2020). Kill sites had been identified by investigating GPS clusters from nine collared pumas. Whenever carcasses were found at clusters, information on prey species, body condition, and physical setting was recorded along with the GPS coordinates (see Smith and others 2020 for more detailed methods on puma capture and cluster investigation). In January–March 2019, we revisited the GPS locations of these previously identified puma-killed carcasses. Carcass sites were deemed appropriate for sampling if carcasses were again found within 20 m of the GPS location recorded by the original observer (within the normal range of handheld GPS error) and only if stomach contents were found within a similar radius. We also opportunistically searched for freshly killed carcasses during fieldwork each day, and accordingly found and sampled several new carcasses in plains. We thus identified 30 carcasses in each habitat that we deemed adequate for sampling, for a total of 90 carcasses sampled.

At each sampled carcass location, we sampled at the carcass itself (where bones were scattered, we chose the vertebral column and thoracic cavity as the point for sampling), beneath the stomach material, and at a reference point six meters from the carcass. The cardinal direction of each reference point was randomly determined, with the proviso that we excluded random directions if they placed the reference point on a different substrate (for example, on rock). Whenever carcasses were on slopes, we collected reference samples at the same elevation along the slope. We did not collect reference samples from beneath shrubs, where nutrient hotspots can form in desert environments (Johnson and others 2016), instead collecting reference samples from open areas with low vegetation similar to the carcass microenvironment. At each sampling point (carcass, stomach, and reference), we collected two 10 cm-deep soil cores using a 2 cm-diameter soil corer. Each pair of cores was pooled into the same sample. If plants were growing directly beneath or adjacent to the carcass or stomach, we collected living green leaves of these plants as well as leaves from the same species at the

reference point. At each sampling point, we also measured soil temperature using a probe thermometer (the thermometer broke midway through the field season, and thus temperature data were only collected for 21 carcasses.) To examine broader patterns of background nutrient availability for comparison to predation risk, we further sampled at 30 random points on the landscape to fill gaps in the spatial distribution of sampling within the study area. Random points were generated within selected polygons in QGIS, and soil and plant samples were collected in the same manner as at reference points described above.

All collected soil samples were immediately sieved to 2 mm and weighed on a digital pocket scale (American Weigh Scale Blade®). Clumps and aggregates were manually broken up to allow soil to pass through the sieve, such that only rocks and roots were retained by the sieve. Sieved samples were then air-dried in a glass-roofed room for three days (a sufficient period to reach constant mass in the arid climate). After drying, we re-weighed all samples and calculated air-dried moisture content by subtracting sample dry mass from wet mass and dividing by total wet mass. Plant samples were similarly air-dried within coin envelopes.

All laboratory analyses were conducted at the Yale School of the Environment and the Yale Analytical and Stable Isotope Center, and with the assistance of the Soil Biogeochemistry Lab at University of Massachusetts, Amherst. We ground subsamples of soil using a SPEX Sample Prep 5100 Mixer Mill® (samples were ground in microcentrifuge tubes with 3.2 mm diameter chrome steel balls). Plant samples were ground using a mortar and pestle, with the occasional application of liquid nitrogen to aid pulverization. All soil and plant samples were analyzed for total C and N as well as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using an elemental analyzer coupled with an isotope ratio mass spectrometer; total concentrations of other soil nutrients (P, Na, K, Fe, Mn, Mg, Zn, and Ca, expressed in mg/kg) were digested using HF-HNO₃ (Zhang and others 2012) and measured using an inductively coupled plasma—optical emissions spectrometer (ICP-OES).

Statistical Analyses

After the removal of samples that could not be properly analyzed, we analyzed data for 28 carcass sites in plains, 30 carcass sites in canyons, and 29 carcass sites in meadows. Unless otherwise specified, data were analyzed separately for each habitat due to large differences in variance between samples from different habitats (variance of meadow

nutrient data was consistently at least one order of magnitude greater than variance of plains and canyon nutrient data, as determined using the “var” function in R). We tested for differences in soil and plant nutrient content between carcass, stomach, and reference samples using generalized linear mixed-effects models using the “glmmTMB” package in R (Brooks and others 2017), with kill site as a random effect and treatment (reference, carcass, and stomach) as a fixed effect. Models using %N and %C as dependent variables specified a beta distribution with a logit link function. Models using all other nutrient concentrations as well as air-dried moisture as dependent variables specified a gamma distribution with a log link function to constrain predictions to positive values. $\delta^{15}\text{N}$ and temperature data were normally distributed, enabling these models to be specified with a Gaussian distribution via an identity link function. When treatment effects were significant ($p < 0.05$), we used the “emmeans” package for post hoc pairwise comparisons (Lenth and others 2022). Models were inspected graphically for patterns in residuals.

Whenever significant impacts on soil nutrients were detected, we further assessed whether the magnitude of these impacts was influenced by the age of the carcass. We calculated “carcass age” (that is, the amount of time a carcass had been on the landscape) by taking the difference between the date of the GPS cluster associated with a puma kill and the date of sampling at the carcass. Because puma kill locations were monitored between 2014 and 2017, and field sampling for this study was conducted in 2019, all but two sampled carcasses ranged in age between 2 and 5 years. We opportunistically encountered two fresh carcasses (< 1 month old) in plains. We ran linear models to evaluate the effects of carcass age on treatment–control differences for each habitat. For this, we calculated the difference in each relevant soil nutrient variable between treatment (carcass, stomach) and reference samples at each carcass site. In plains, we ran the model on the full dataset and on a subset of the data with the two fresh carcasses removed to test whether patterns were unduly influenced by the fresh carcasses.

We evaluated the spatial correlation between risk and soil nutrient content at the landscape level using spatially modified t tests, using the “SpatialPack” package in R (Vallejos and others 2020). Carcasses mainly affected soil nitrogen (Figure 1). Therefore, we compared soil %N measurements at reference sites (including at the 30 random sampling points) and puma kill site selection probabili-

ties for those same reference coordinates (Smith and others 2020) to assess whether patterns of localized carcass deposition and decomposition were related to background N availability at larger scales. Kill site selection analysis was performed for pumas using a resource selection function of predicted kill sites applied to the study area. Predicted kill sites were determined from a mixed-effects logistic regression model that distinguished field-investigated kills from non-kills using puma movement parameters (more detail can be found in Smith and others 2020).

RESULTS

Neither carcasses nor stomachs had significant effects on soil moisture in any habitat (Table S1). Soil beneath carcasses was significantly cooler than reference soil in plains and canyons, but soil temperature did not differ between treatments in meadows (Table S1).

Carcasses significantly increased soil percent N in both plains and canyons, but not in meadows; carcasses did not influence any other nutrient we measured (Figure 1, Table S2). This effect of carcasses was 1.3 times greater in canyons than in plains ($\beta = 0.45$ vs. $\beta = 0.33$, Figure 1). Stomachs increased soil N and C in both plains (by 1.6 and 1.5 times, respectively) and canyons (by 1.5 and 1.4 times, respectively) and increased P in plains by 1.2 times (Table S2, Figure 1). Stomachs had a negative effect on soil Mg in canyons (decreasing Mg by 16%; Table S2, Figure 1).

Because carcasses significantly impacted soil N and had marginal effects on soil C ($\beta = 0.22$ in plains and 0.21 in canyons; Table S2, Figure 1), we further investigated whether the magnitude of these effects varied with carcass age. The difference in soil %C and %N between carcasses and reference sites significantly increased with carcass age in plains (Table S3, Figure 2a, c); however, in canyons there was no change in carcass effects on soil C and N over time (Table S3). These patterns remained consistent when we included the two fresh carcasses (< 1 month old) we sampled in plains (model results without these samples are shown in Figure 2). The impacts of stomachs on soil C and N also did not vary with carcass age (Table S3, Figure 2b, d).

Carcass and stomach effects on plant C, N, C/N, and $\delta^{15}\text{N}$ were not significant, though they trended in the direction we expected, with plant %N slightly higher and C/N slightly lower at carcass and stomach sites compared to reference sites in all habitats (Table S4, Figure 3).

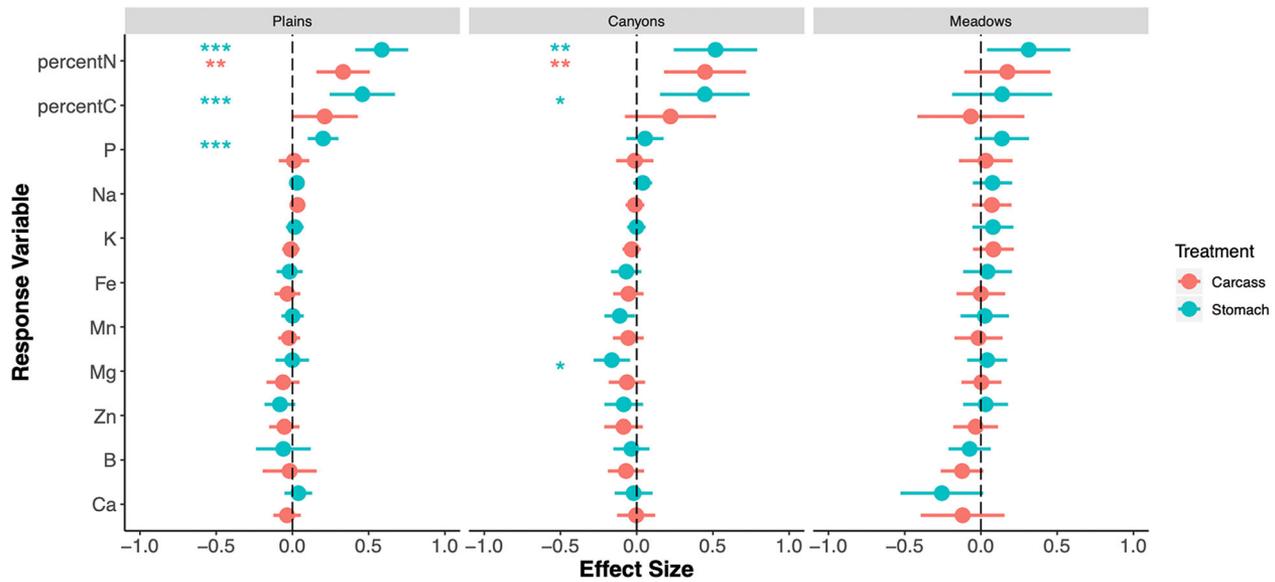


Figure 1. Effects of puma-predated vicuña carcasses and stomachs on percent *N*, percent *C*, and concentrations of 13 additional nutrients in soil across habitats in San Guillermo National Park. Here, effect size is represented by the β -estimate for each treatment (carcass, stomach) of each generalized linear mixed-effects model; because the models all specified the reference treatment as the intercept, β -estimates for non-intercept treatments reflect the effect of treatment relative to the reference estimates (corrected for the localized effects of carcass site). Vertical dashed lines represent an effect of 0, closed circles represent the β -estimate, and horizontal lines on either side of the estimates represent the 95% confidence intervals. Asterisks to the left of β -estimates denote statistically significant effects ($*p < 0.05$; $**p < 0.01$; $***p < 0.001$). Photos show a decomposing vicuña carcass in canyon soil (left) and a vicuña stomach in meadow habitat (right).

Background soil nitrogen (%*N* of soil at reference points and random sampling locations) was significantly spatially correlated with predation risk at the landscape scale ($F_{(1,92.9)} = 76.1$, $p < 0.001$, corrected Pearson’s correlation for spatial autocorrelation: 0.671, Figure 4). This was largely driven by differences in predation risk between habitats—meadows, which are the riskiest sites for vicuñas, had much higher nitrogen availability than plains and canyons (Figure 4c). We further examined whether these spatial correlations within the nutrient-poor habitats (plains and canyons combined) and within meadows held independently of the strong inter-habitat differences. There was no

relationship between soil *N* and risk within nutrient-poor habitats ($F_{(1,80.3)} = 0.475$, $p = 0.493$, corrected Pearson’s correlation for spatial autocorrelation: 0.077, Figure 4c). Even though canyons had higher predation risk than plains, there was little variation in soil *N* within or between plains and canyons (%*N* largely ranging between 0.01 and 0.2%, Figure 4c). In contrast, soil *N* in meadows varied widely, ranging as high as 1%, and there was a positive spatial correlation between soil *N* and predation risk within meadow habitats $F_{(1,28.2)} = 4.635$, $p = 0.04$, corrected Pearson’s correlation for spatial autocorrelation: 0.376, Figure 4c).

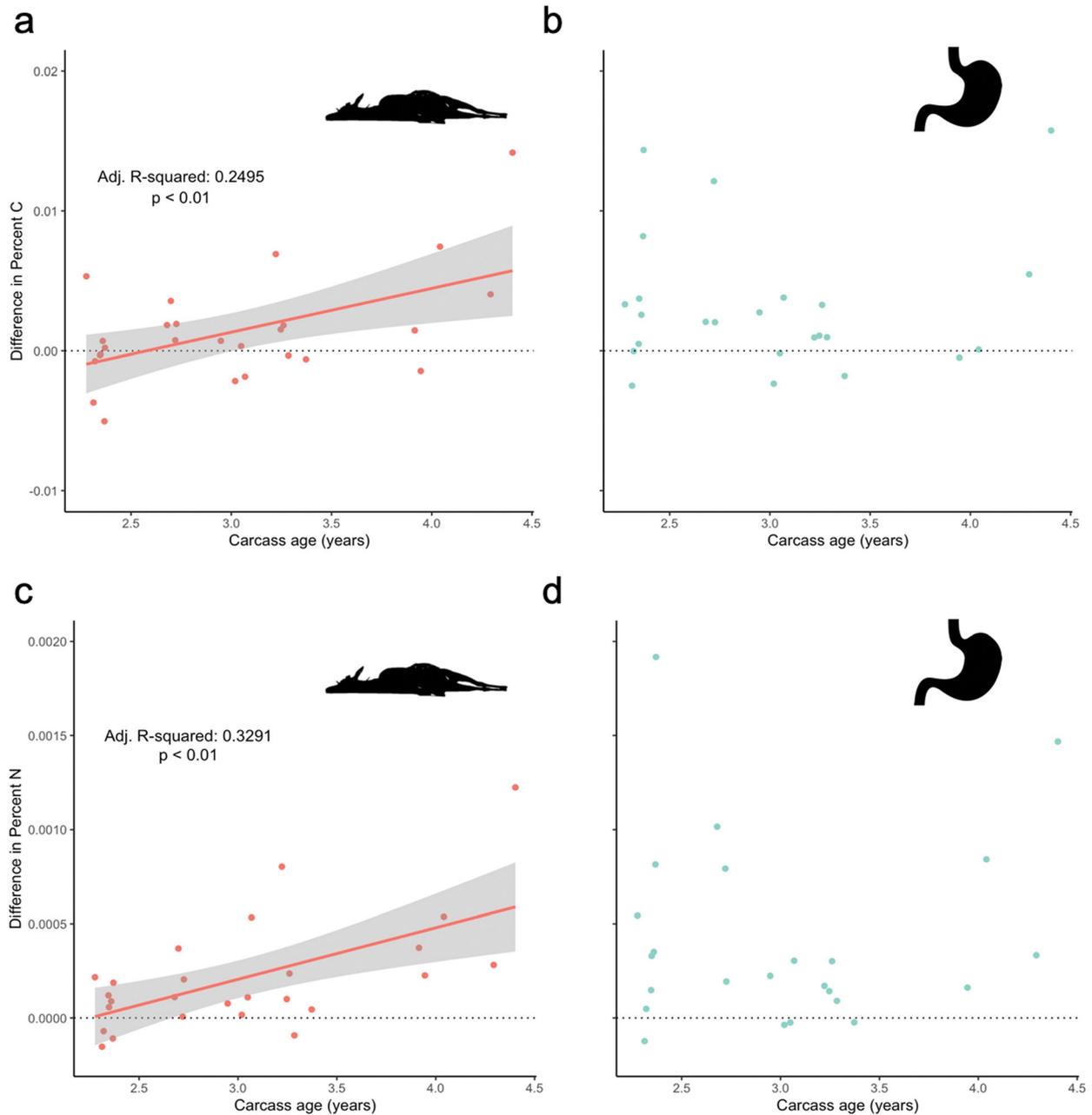


Figure 2. Relationships between carcass age (in years) and the difference in percent carbon (**A, B**) and percent nitrogen (**C, D**) between reference soil and soil beneath puma-predated vicuña carcasses (**A, C**) and stomachs (**B, D**) in plains habitat in San Guillermo National Park. Percent *N* and *C* are expressed on a scale from 0 to 1 (e.g., 0.01 = 1%). The effects of carcasses on soil percent *C* and *N* increased significantly with carcass age (both $p < 0.01$); solid lines show linear model predictions, and the shaded gray regions represent 95% confidence intervals. Stomach effects on soil *C* and *N* did not vary over time.

DISCUSSION

By analyzing soil and plant nutrients at 87 vicuña carcass sites across the high Andean desert, we demonstrate that vertebrate carcass decomposition can create biogeochemical hotspots with elevated soil carbon and nitrogen in arid regions. As we

predicted, puma-killed vicuña carcasses significantly increased soil nitrogen, and vicuña stomachs had even greater effects on soil nitrogen, carbon, and phosphorus. However, these effects were habitat-dependent; carcasses and stomachs increased soil nutrients only in plains and canyons,

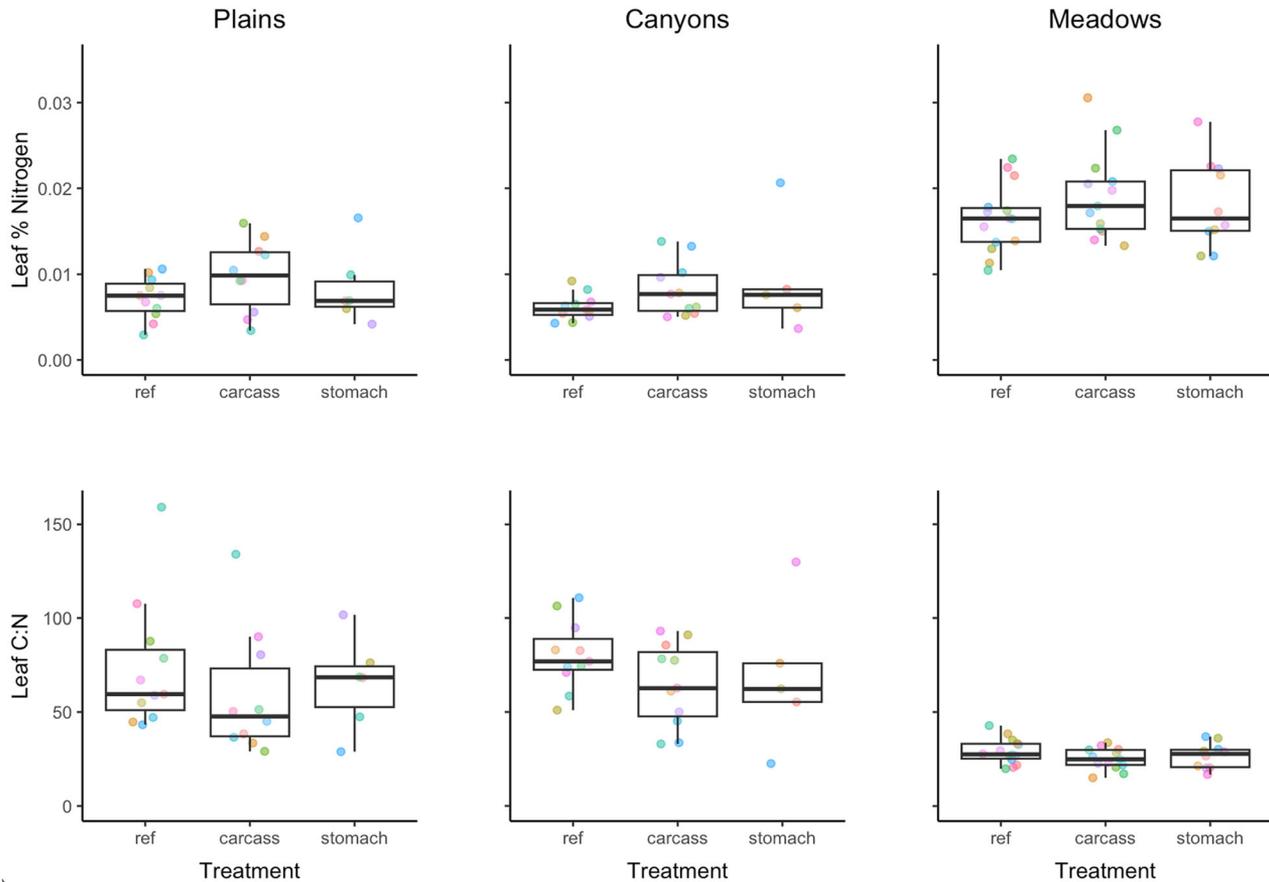


Figure 3. Effects of treatment (vicuña carcass, vicuña stomach, and reference) on percent nitrogen (top row) and C/N (bottom row) of graminoid plants across habitats in San Guillermo National Park. Percent nitrogen is expressed on a scale from 0 to 1. Full data are shown beneath boxplots; dots of the same color within each panel represent samples taken from the same carcass site. Generalized linear mixed-effects models revealed no significant pairwise differences in plant nutrient content between treatments.

not in meadows, supporting the hypothesis that carcass inputs have greater impacts in dry, nutrient-poor soils with otherwise slow recycling of nutrients. While stomachs had greater effects on soil nutrients than carcasses, carcasses themselves increased soil nitrogen despite high consumption by pumas and scavengers. The magnitude of these carcass effects on soil % N in plains (carcass: 0.062% vs. reference: 0.044%; Table S2) were remarkably similar to those from a semiarid steppe in the western USA where, three years after carcass deposition, soil N beneath mule deer carcasses was 0.064% whereas reference soil N was 0.045%) (Parmenter and McMahon 2009). Alternatively, carcasses of elk and bison did not significantly influence soil % N in grasslands in Yellowstone National Park, USA, where background soil N values (~ 0.2 – 1%) were more similar to our meadow habitats (Risch and others 2020). Accordingly, our conclusions that carcasses have greater impacts on

soil N in nutrient-poor environments may hold in other systems, and at broader scales.

The effect of carcasses on soil N was greater in canyons than in plains (Figure 1); this may be attributable to the fact that condors scavenge more heavily on carcasses in plains, and thus more carcass material may have been left to decompose in canyons, where condors are more reluctant to land (Perrig and others 2023). However, under this logic, the greatest carcass effects should have been observed in meadows, where condor use of carcasses should be lowest. Given that very little soft tissue remained on any carcasses after several years of exposure, condors may play a more important role in mediating carcass inputs in the early periods following carcass deposition, which our study was unable to capture. Even so, biophysical setting seems to be more important than scavenger activity in determining long-term carcass impacts on soil nutrients. We did not measure some attributes of

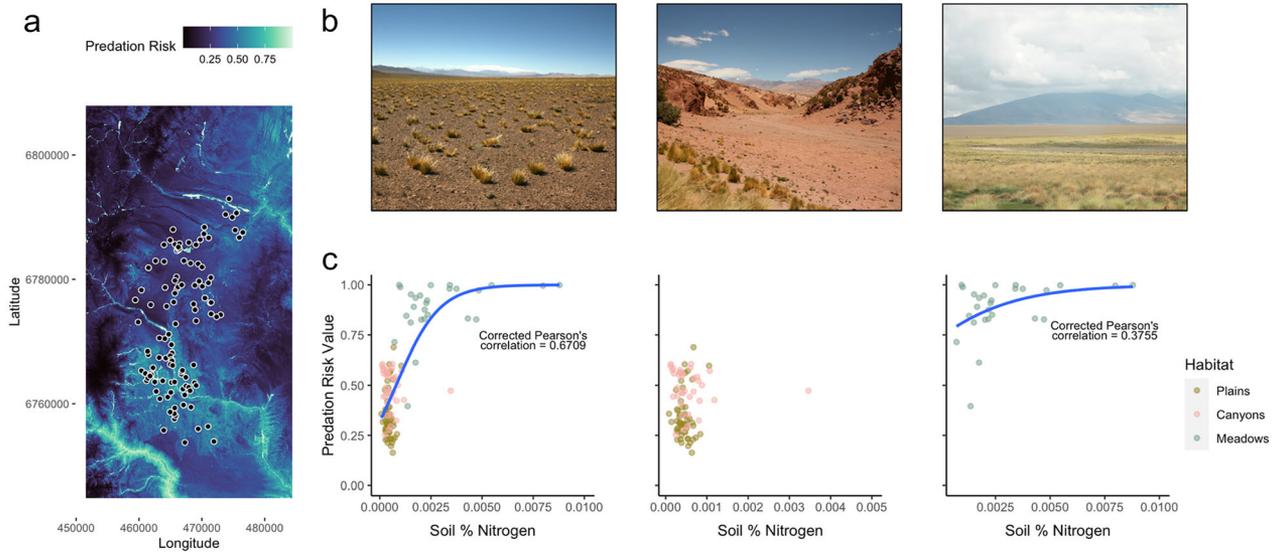


Figure 4. Relationship between predation risk and soil nitrogen across the landscape in San Guillermo National Park. **A** Distribution of predation risk throughout the park; predation risk values are the probability of puma habitat selection as determined by a resource selection function using data from 9 GPS-collared pumas (Smith and others 2019a, 2019b). Dots indicate soil sampling locations. **B** Photographs of the three main habitats in SGNP; from left to right, plains, canyons, and meadows. **C** Spatial correlation between soil percent nitrogen and predation risk across habitats. Soil percent nitrogen is expressed on a scale from 0 to 1. Across the entire landscape, soil nitrogen and predation risk were significantly positively correlated in space (left panel; $p < 0.001$); however, this appears largely driven by differences between habitats, as meadows have both higher predation risk and higher soil nitrogen. Soil %N and predation risk were not spatially correlated within the dry habitats alone (plains and canyons, middle panel; $p = 0.4926$). However, within meadows there remained a significant positive spatial correlation between soil N and predation risk (right panel; $p < 0.05$).

biophysical setting (soil texture and water-holding capacity) in our study. Texture and water-holding capacity likely differ between habitats (particularly between plains and canyons, with sandier soils, and meadows, with peaty organic soils). These soil property differences could exacerbate long-term differences in the impacts of carcass nutrient inputs between habitats, especially in total amounts of nutrients retained vs. leached (vs. simply differences in % soil N and C content). However, texture and water-holding capacity likely do not explain differences between carcass and reference sites within habitats, given the similarity in biophysical and topographic conditions between those sites. Thus, within habitats, any significant differences in soil nutrient contents between treatments are likely predominantly attributable to carcass and stomach inputs.

Contrary to our expectations, increases in soil N at carcass sites did not significantly increase plant nitrogen content, reduce plant C/N ratios, or alter foliar $\delta^{15}\text{N}$. It is possible that our sampling missed the time period when carcass and stomach decomposition had the greatest effect on plants; an initial flush of plant-available nutrients may have been deposited at the beginning of carcass decom-

position, whereas we sampled soil and plants 2–5 years after carcass deposition. Additionally, the seasonality of our sampling (January–February) came slightly before peak green-up (late February–March), and the weak trends in plant nutrient availability at carcass sites may have been more evident during peak seasonal productivity. Similarly, fluctuations in rainfall may have impacted plant nutrient uptake, with rain events either facilitating plant uptake by mineralizing N or triggering N losses via leaching or gas loss (Austin and others 2004). Furthermore, soil nutrients at carcass sites may remain in recalcitrant forms largely unavailable for plant uptake, particularly as the more labile soft tissue from vicuña carcasses was likely largely consumed by pumas and scavengers. Even so, our results confirm that the effects of puma kills on soil carbon, nitrogen, and phosphorus in arid habitats remain detectable for at least 5 years. Earlier studies localized in more productive regions have provided important evidence for the biogeochemical impacts of wild vertebrate carcasses, and the study of human cadavers has contributed significantly to our understanding of the ecology of carcass decomposition (Carter and others 2007; MacDonald and others 2014; Benbow

and others 2016). Our results, based on a comparatively large sample size across a landscape, add substantially to this emerging body of evidence by confirming that these patterns hold in extremely arid, unproductive environments, and for an extended period of time after carcass deposition.

The heightened effects of carcass decomposition on soil nutrients in arid, nutrient-poor habitats compared to moist, nutrient-rich environments suggests a reconsideration of classic conceptions of the importance of top-down vs. bottom-up forces along environmental gradients. It has frequently been argued that “bottom-up” controls (for example, water and nutrient availability) should largely drive ecosystem dynamics in arid, low-productivity environments, given that resource variation should have outsized effects when these resources are scarce. Simultaneously, a series of theoretical works have argued that “top-down effects,” or primary resource regulation by large predators and herbivores, should be strongest in ecosystems with intermediate productivity and resource availability, as these systems are more likely to support populations in multiple, higher trophic levels (Oksanen and others 1981; Schoener 1989; Schmitz 1992). However, many of these theoretical works have not accounted for feedbacks whereby animals recycle resources within a system, potentially engineering their own food webs via consumer-driven nutrient recycling (Schmitz 2008). Such feedbacks may thus account for why attempts to investigate potential correlations between trophic cascade strength and ecosystem productivity (Chase 2003; Borer and others 2005; Daskin and Pringle 2016; Letnic and others 2017) have yielded mixed results. Accounting for animal impacts on ecosystems beyond herbivory, including animal-mediated nutrient cycling, complicates these assumptions and blurs the conceptual divide between “top-down” and “bottom-up” effects (Schmitz 2008; Sitters and Olde Venterink 2015). Instead, as our research demonstrates, animals can greatly impact the degree to which resources are limiting in otherwise nutrient-poor, arid environments by influencing the spatial concentration of essential nutrients deposited in carcasses, urine, and feces (Sitters and others 2017; Ferraro and others 2022; Monk and Schmitz 2022; Monk and others 2023).

Indeed, in highly arid systems like SGNP, where microbial activity is low and plant decomposition slow, mammal bodies may be important microclimates for decomposition as well as sources of high-quality nutrients (Leroux and Loreau 2010; Monk and others 2023), priming the processing of large

quantities of plant matter more rapidly and efficiently than the surrounding environment. In wetter, more fertile environments, these effects may be smaller in comparison to rapid decomposition by microbes, fungi, and invertebrates in the external environment. However, emerging evidence suggests that vertebrate microbiomes may also strongly impact biogeochemical cycling in the external environment in aquatic systems, further justifying greater consideration of vertebrate bodies as micro-systems of decomposition across biomes (Dutton and others 2021; Yang and others 2022). Further study comparing decomposition across ecosystems should begin to shed light on the relative importance of animal-mediated nutrient cycling across aridity and productivity gradients.

In contrast to previous studies of carrion biogeochemistry (Melis and others 2007; Bump and others 2009b), we found that the effects of carcasses on soil *C* and *N* in plains increased with carcass age. This could again be attributable to abiotic differences across study sites—in more productive biomes, carcasses may decompose quickly and thus have more ephemeral effects, whereas in our arid system, decomposition may be a slower and steadier process, yielding smaller but more persistent effects. However, this discrepancy may also be due to differences in study duration. We did not encounter enough recent carcasses in our study to meaningfully investigate decomposition effects in the initial post-predation period. Thus, we likely missed an early pulse of nutrients deposited by carcasses and subsequently taken up by plants—explaining both the temporal patterns we observed and the lack of carcass effects on plants. However, by failing to sample carcass sites more than a year or two after deposition, some other studies may also have missed longer-term effects of carrion decomposition as more recalcitrant components of carcasses such as hide and bone break down over the course of years (Barton and others 2016; Quaggiotto and others 2019). In this respect, our sampling may have been too early to detect carcass effects on soil nutrients such as calcium and phosphorus; in an arid environment lacking specialized bone scavengers, these elements likely remain trapped in bone for far longer than 5 years (Barton and others 2016). Thus, vertebrate bodies may sequester essential nutrients such as phosphorus and calcium in cold and arid environments with slow decomposition rates, as has been documented in other systems, altering the recycling of these recalcitrant nutrients (le Roux and others 2020; Subalusky and others 2020; Abraham and others 2021).

Our spatial analyses yielded evidence that puma predation risk (that is, probability of puma kill site selection) is higher where soil nitrogen availability is greater, both across the landscape and within high-risk meadows. This supports prior conclusions that pumas select for more fertile areas when hunting vicuñas, likely because of both greater cover, which facilitates ambush predation, and the fact that vicuñas are compelled to visit spatially constrained meadows to obtain water and higher quality forage (Smith and others 2019b, 2019a, 2020). However, carcass decomposition did not appear to in turn reinforce soil nitrogen availability in nitrogen-rich meadows, and we found no evidence to support this hypothesized positive feedback mechanism (Monk and Schmitz 2022; Peziol and others 2023). This could seem to suggest that while predation and carcass decomposition have localized effects on soil biogeochemistry in nutrient-poor plains and canyons, these hotspots would have minimal impacts at the broader landscape scale. However, puma predation rates in San Guillermo are among the highest documented throughout the puma's range (Cristescu and others 2022). For the 9 adult pumas instrumented with GPS collars whose kill sites were monitored (Smith and others 2019a), the vicuña kill rate averaged around 8 vicuñas/month (Monk and others 2022). Roughly 75% of these kills occurred in nutrient-poor environments, and more than half occurred in canyons (Monk and others 2022). Under these parameters, and based on the extremely conservative assumption that collared pumas were the only puma individuals present in the park, a minimum of 864 vicuña carcasses should be deposited in the study area by puma predation annually, with more than 600 of these in canyons and plains, where they can have significant impacts on soil carbon, nitrogen, and phosphorus.

Thus, high rates of predation may have consistently contributed to patchiness and small-scale heterogeneity in dry, nutrient-poor habitats by generating hotspots with persistent elevated nutrients at carcass sites (Carter and others 2007; Keenan and others 2018; Monk and Schmitz 2022; Johnson-Bice and others 2023).

CONCLUSIONS

Much evidence demonstrating predator impacts on biogeochemical cycling has stemmed from research in invertebrate systems, which lend themselves well to short-term manipulative experiments (e.g., Hawlena and others 2012; Strickland and others 2013). Vertebrate predators are more difficult to

experimentally manipulate due to logistical, financial, and ethical constraints; yet as predators experience rapid anthropogenic declines worldwide, understanding their impacts on ecosystem functioning is critical (Estes and others 2011; Ripple and others 2014). Here, we demonstrate that kill sites resulting from puma predation of vicuñas increase soil nitrogen, carbon, and phosphorus in arid habitats in the high Andes, generating patches with persistent elevated nutrients compared to the surrounding desert soil with low nutrient availability. Yet, even in this remote protected area, these patterns of predator-mediated nutrient cycling via carcass decomposition have been recently disrupted. An outbreak of Sarcocystis mangle began to seriously affect the vicuña population in 2015, ultimately causing a severe population crash by 2019 (Ferreyra and others 2022; Monk and others 2022). We were unable to directly examine the contrasting spatial and biogeochemical impacts of mange vs. puma-killed vicuña carcasses, as the puma kill sites we investigated were created when there were ample vicuñas available to pumas and fresh vicuña carcasses (regardless of the cause of mortality) had become rare by the time of our sampling. Nevertheless, there is substantial evidence that mange dramatically restructured the ecosystem in SGNP, causing large increases in grass biomass and cover in plains and leading to the functional abandonment of the park by Andean condors (Monk and others 2022). Further study will be necessary to determine whether these impacts of the disease outbreak extend to the recycling and distribution of nutrients. As vegetation biomass has increased by 900% across nearly half of the study area after release from intensive vicuña herbivory (Monk and others 2022), soil nutrient availability may become the more salient factor regulating plant growth and community composition on the plains, and the disruption of consumer-mediated nutrient recycling may thus have even more profound effects on ecosystem functioning in the arid Andean ecosystem.

ACKNOWLEDGEMENTS

We thank Martin Fileni, Morena Fernandez, Pablo Gregorio, and Adam Roddy for their assistance with fieldwork. We thank all the staff of San Guillermo National Park, as well as San Guillermo Provincial Reserve, the Argentine National Parks Administration, the Administration of Provincial Reserves for San Juan Province, CONICET, and Conservación Patagónica Asociación Civil for logistical support. We thank B. Erkkila for assistance with

stable isotope analyses, and J. Richardson for assistance with other nutrient analyses. We also thank Evan Parker, Ben Girgenti, and Franklin Bertolotti for assistance processing samples in the lab. We thank Mark Bradford for lab support and substantial intellectual guidance throughout this project. All sampling was conducted under Permit #353 and subsequent renewals issued by the Argentine National Park Service (APN). Samples were obtained from and property of the APN and were exported under permits issued by the Ministerio de Ambiente y Desarrollo Sostenible, Argentina, and imported to the USA under permits issued by the United States Department of Agriculture—Animal and Plant Health Inspection Service. Funding for this project was supported by a Yale Dean’s Emerging Scholars Fellowship, the Yale Institute for Biospheric Studies, the Tropical Resources Institute at Yale, the Schiff Fund for Wildlife, Habitat, and the Environment, the Yale Council on Latin American and Iberian Studies, the Yale School of the Environment, and the Prince Albert II of Monaco Foundation.

OPEN ACCESS

This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

DATA AVAILABILITY

Data are available on Dryad Digital Repository at <https://doi.org/https://doi.org/10.5061/dryad.kkwh70s8t>.

REFERENCES

Abraham AJ, Webster AB, Prys-Jones TO, le Roux E, Smith D, McFayden D, de Jager PC, Clauss M, Doughty CE. 2021. Large predators can mitigate nutrient losses associated with off-site removal of animals from a wildlife reserve. *Journal of Applied Ecology* 58:1360–1369.

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.

Barceló G, Perrig PL, Dharampal P, Donadio E, Steffan SA, Pauli JN. 2022. More than just meat: Carcass decomposition shapes trophic identities in a terrestrial vertebrate. *Functional Ecology* 36:1473–1482.

Barton PS, Cunningham SA, Macdonald BCT, McIntyre S, Lindenmayer DB, Manning AD. 2013. Species traits predict assemblage dynamics at ephemeral resource patches created by carrion. *PLoS ONE* 8:e53961.

Barton PS, McIntyre S, Evans MJ, Bump JK, Cunningham SA, Manning AD. 2016. Substantial long-term effects of carcass addition on soil and plants in a grassy eucalypt woodland. *Ecosphere* 7:e01537.

Benbow ME, Tomberlin JK, Tarone AM, Eds. 2016. *Carrion Ecology, Evolution, and Their Applications*. Boca Raton, FL: CRC Press.

Borer ET, Seabloom EW, Shurin JB, Anderson KE, Blanchette CA, Broitman B, Cooper SD, Halpern BS. 2005. What determines the strength of a trophic cascade? *Ecology* 86:528–537.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal* 9:378–400.

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.

Carter DO, Yellowlees D, Tibbett M. 2007. Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften* 94:12–24.

Chase JM. 2003. Strong and weak trophic cascades along a productivity gradient. *Oikos* 101:187–195.

Cristescu B, Elbroch LM, Dellinger JA, Binder W, Wilmers CC, Wittmer HU. 2022. Kill rates and associated ecological factors for an apex predator. *Mammalian Biology* 102:291–305.

Cueto LJ, Ponce CF. 1985. Management of vicuña: its contribution to rural development in the High Andes of Peru. Rome: Food & Agriculture Organization of the United Nations.

Daskin JH, Pringle RM. 2016. Does primary productivity modulate the indirect effects of large herbivores? A global meta-analysis. *Journal of Animal Ecology* 85:857–868.

de Miranda EBP, Peres CA, Oliveira-Santos LGR, Downs CT. 2023. Long-term concentration of tropical forest nutrient hotspots is generated by a central-place apex predator. *Scientific Reports* 13:4464.

del Ferreyra H, V, Rudd J, Foley J, Vanstreels RET, Martín AM, Donadio E, Uhart MM. 2022. Sarcoptic mange outbreak decimates South American wild camelid populations in San Guillermo National Park, Argentina. *Plos ONE* 17:e0256616.

Donadio E, Buskirk SW. 2016. Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes. *Journal of Mammalogy* 97:966–977.

Donadio E, Novaro AJ, Buskirk SW, Wursten A, Vitali MS, Monteverde MJ. 2010. Evaluating a potentially strong trophic interaction: pumas and wild camelids in protected areas of Argentina. *Journal of Zoology* 280:33–40.

- Donadio E, Buskirk SW, Novaro AJ. 2012. Juvenile and adult mortality patterns in a vicuña (*Vicugna vicugna*) population. *Journal of Mammalogy* 93:1536–1544.
- Dutton CL, Subalusky AL, Sanchez A, Estrela S, Lu N, Hamilton SK, Njoroge L, Rosi EJ, Post DM. 2021. The meta-gut: community coalescence of animal gut and environmental microbiomes. *Scientific Reports* 11:23117.
- Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE, Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen R, Wardle DA. 2011. Trophic downgrading of planet Earth. *Science* 333:301–306.
- Ferraro KM, Schmitz OJ, McCary MA. 2022. Effects of ungulate density and sociality on landscape heterogeneity: a mechanistic modeling approach. *Ecography* 2022:e06039.
- Gharajehdaghpour T, Roth JD, Fafard PM, Markham JH. 2016. Arctic foxes as ecosystem engineers: increased soil nutrients lead to increased plant productivity on fox dens. *Scientific Reports* 6:24020.
- Hawlena D, Strickland MS, Bradford MA, Schmitz OJ. 2012. Fear of predation slows plant-litter decomposition. *Science* 336:1434–1438.
- Hocking MD, Reynolds JD. 2012. Nitrogen uptake by plants subsidized by Pacific salmon carcasses: a hierarchical experiment. *Canadian Journal of Forest Research* 42:908–917.
- Johnson BG, Verburg PSJ, Arnone JA. 2016. Plant species effects on soil nutrients and chemistry in arid ecological zones. *Oecologia* 182:299–317.
- Johnson-Bice SM, Gable TD, Roth JD, Bump JK. 2023. Patchy indirect effects of predation: predators contribute to landscape heterogeneity and ecosystem function via localized pathways. *Oikos* 2023:e10065.
- Keenan SW, Schaeffer SM, Jin VL, DeBruyn JM. 2018. Mortality hotspots: nitrogen cycling in forest soils during vertebrate decomposition. *Soil Biology and Biochemistry* 121:165–176.
- le Roux E, van Veenhuisen LS, Kerley GIH, Cromsigt JPGM. 2020. Animal body size distribution influences the ratios of nutrients supplied to plants. *Proceedings of the National Academy of Sciences* 117:22256–22263.
- Lenth RV, Buerkner P, Herve M, Love J, Miguez F, Riebl H, Singmann H. 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://CRAN.R-project.org/package=emmeans>. Last accessed 03/03/2022.
- Leroux SJ, Loreau M. 2010. Consumer-mediated recycling and cascading trophic interactions. *Ecology* 91:2162–2171.
- Letnic M, Feit A, Forsyth DM. 2017. Strength of a trophic cascade between an apex predator, mammalian herbivore and grasses in a desert ecosystem does not vary with temporal fluctuations in primary productivity. *Ecosystems* 21:153–165.
- Macdonald BCT, Farrell M, Tuomi S, Barton PS, Cunningham SA, Manning AD. 2014. Carrion decomposition causes large and lasting effects on soil amino acid and peptide flux. *Soil Biology and Biochemistry* 69:132–140.
- Martínez Carretero E. 2007. Diversidad biológica y cultural de los altos Andes centrales de Argentina: línea de base de la reserva de biosfera San Guillermo, San Juan. San Juan, Argentina: Editorial Fundación Universidad Nacional de San Juan.
- McInturf AG, Pollack L, Yang LH, Spiegel O. 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biological Reviews* 94:1761–1773.
- Melis C, Selva N, Teurlings I, Skarpe C, Linnell J, Andersen R. 2007. Soil and vegetation nutrient response to bison carcasses in Białowieża Primeval Forest, Poland. *Ecological Research* 22:807–813.
- Monk JD, Schmitz OJ. 2022. Landscapes shaped from the top down: predicting cascading predator effects on spatial biogeochemistry. *Oikos* 2022:e08554.
- Monk JD, Smith JA, Donadio E, Perrig PL, Crego RD, Fileni M, Bidder OR, Lambertucci SA, Pauli JN, Schmitz OJ, Middleton AD. 2022. Cascading effects of a disease outbreak in a remote protected area. *Ecology Letters* 25:1152–1163.
- Monk JD, Donadio E, Gregorio PF, Schmitz OJ. 2023. Vicuña antipredator diel migration drives spatial nutrient subsidies in a high Andean ecosystem. *EcoEvoRxiv*. <https://doi.org/10.32942/X2HC7Q>.
- Oksanen L, Fretwell SD, Arruda J, Niemela P. 1981. Exploitation ecosystems in gradients of primary productivity. *American Naturalist* 118:240–261.
- Parmenter RR, MacMahon JA. 2009. Carrion decomposition and nutrient cycling in a semiarid shrub-steppe ecosystem. *Ecological Monographs* 79:637–661.
- Perrig PL, Donadio E, Middleton AD, Pauli JN. 2016. Puma predation subsidizes an obligate scavenger in the high Andes. *Journal of Applied Ecology* 54:846–853.
- Perrig PL, Lambertucci SA, Donadio E, Smith JA, Middleton AD, Pauli JN. 2023. Risk effects cascade up to an obligate scavenger. *Ecology* 104:e3871.
- Peziol M, Elbroch LM, Shipley LA, Evans RD, Thornton DH. 2023. Large carnivore foraging contributes to heterogeneity in nutrient cycling. *Landscape Ecology* 38:1497–1509.
- Quaggiotto M-M, Evans MJ, Higgins A, Strong C, Barton PS. 2019. Dynamic soil nutrient and moisture changes under decomposing vertebrate carcasses. *Biogeochemistry* 146:71–82.
- Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG, Hebblewhite M, Berger J, Elmhagen B, Letnic M, Nelson MP, Schmitz OJ, Smith DW, Wallach AD, Wirsing AJ. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- Ripple WJ, Estes JA, Schmitz OJ, Constant V, Kaylor MJ, Lenz A, Motley JL, Self KE, Taylor DS, Wolf C. 2016. What is a trophic cascade? *Trends in Ecology & Evolution* 31:842–849.
- Risch AC, Frossard A, Schütz M, Frey B, Morris AW, Bump JK. 2020. Effects of elk and bison carcasses on soil microbial communities and ecosystem functions in Yellowstone, USA. *Functional Ecology* 34:1933–1944.
- Schmitz OJ. 1992. Exploitation in model food chains with mechanistic consumer-resource dynamics. *Theoretical Population Biology* 41:161–183.
- Schmitz OJ. 2008. Herbivory from individuals to ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 39:133–152.
- Schmitz OJ, Hambäck PA, Beckerman AP. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* 155:141–153.
- Schmitz OJ, Hawlena D, Trussell GC. 2010. Predator control of ecosystem nutrient dynamics. *Ecology Letters* 13:1199–1209.
- Schoener TW. 1989. Food webs from the small to the large. *Ecology* 70:1559–1589.

- Sitters J, Olde Venterink H. 2015. The need for a novel integrative theory on feedbacks between herbivores, plants and soil nutrient cycling. *Plant and Soil* 396:421–426.
- Sitters J, te Beest M, Cherif M, Giesler R, Olofsson J. 2017. Interactive effects between reindeer and habitat fertility drive soil nutrient availabilities in Arctic tundra. *Ecosystems* 20:1266–1277.
- Smith JA, Donadio E, Pauli JN, Sheriff MJ, Bidder OR, Middleton AD. 2019a. Habitat complexity mediates the predator–prey space race. *Ecology* 100:e02724.
- Smith JA, Donadio E, Pauli JN, Sheriff MJ, Middleton AD. 2019b. Integrating temporal refugia into landscapes of fear: prey exploit predator downtimes to forage in risky places. *Oecologia* 189:883–890.
- 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.
- Strickland MS, Hawlena D, Reese A, Bradford MA, Schmitz OJ. 2013. Trophic cascade alters ecosystem carbon exchange. *Proceedings of the National Academy of Sciences* 110:11035–11038.
- Subalusky AL, Dutton CL, Rosi EJ, Puth LM, Post DM. 2020. A river of bones: wildebeest skeletons leave a legacy of mass mortality in the Mara River, Kenya. *Frontiers in Ecology and Evolution* 8:31.
- Teurlings IJM, Melis C, Skarpe C, Linnell JDC. 2020. Lack of cascading effects of Eurasian lynx predation on roe deer to soil and plant nutrients. *Diversity* 12:352.
- Vallejos R, Osorio F, Bevilacqua M. 2020. *Spatial Relationships Between Two Georeferenced Variables: With Applications in R*. Switzerland: Springer Cham.
- Yang J, Su W, Yu Q, Shi Z, Huang X, Heděnc P, Zhou H, Qu J, Li H. 2022. The long-term decomposition of wild animal corpses leads to carbon and phosphorus accumulation and disturbs the ecological succession of the denitrification community encoded by *narG*. *Applied Soil Ecology* 175:104455.
- Zhang W, Hu Z, Liu Y, Chen L, Chen H, Li M, Zhao L, Hu S, Gao S. 2012. Reassessment of HF/HNO₃ decomposition capability in the high-pressure digestion of felsic rocks for multi-element determination by ICP-MS. *Geostandards and Geoanalytical Research* 36:271–289.