Predation and biophysical context control long-term carcass nutrient inputs in an Andean ecosystem

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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. These patterns did not translate into higher plant N concentrations at kill sites, though such responses could have occurred immediately following carcass deposition, which our study did not capture. 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.

Keywords: carcasses, decomposition, predation, *Puma concolor*, *Vicugna vicugna*, High Andes, biogeochemical hotspots, nutrient cycling

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 (Barton 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, causing carcasses have minimal impacts on soil and plant nutrients in arid habitats

(Parmenter and MacMahon 2009; Barton 2016). Alternatively, pulsed additions of easily-decomposed animal matter and stomach contents in an otherwise nutrient-limited system with slow recycling of plant litter could have substantial impacts on ecosystem functioning (Schmitz and others 2010; McInturf and others 2019). To resolve these questions, we use a large long-term dataset of kill sites distributed across habitats throughout the landscape and relate 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 sought to assess 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 (e.g. Bump and others 2009a); however, we predicted 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 and thus even small carrion inputs could have substantial impacts. Alternatively, decomposition could be facilitated in moist environments, rendering carcass impacts greater 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, 2200-5467m elevation). Annual temperatures range from a mean of 1° C in the winter to a mean of 15° C in the summer, and annual precipitation is <200mm/year, in the form of rain in the summer and snow in the winter. 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 much lower densities (Martínez Carretero 2007; Donadio and others 2010). Vicuñas are heavily predated 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; while other, smaller avian scavengers and foxes will scavenge vicuña remains, condors are heavily subsidized by puma-predated vicuña carcasses and generally outcompete other scavengers when they descend upon a carcass (Perrig and others 2016, 2023). However, condors are also wary of pumas, and while they search and detect carcasses in areas of high puma predation risk, they are more likely 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 location (see Smith and others 2020 for more detailed methods on puma capture and cluster investigation). During this study, 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 20m of the GPS location (within the normal range of handheld GPS error), within the same setting recorded by the original observer, and 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 per habitat as adequate for sampling, for a total of 90 carcasses sampled.

At each sampled carcass site, 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 (e.g. on rock), and that whenever carcasses were on slopes, reference samples were collected at the same elevation along the slope. 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. Points were randomly generated within selected polygons in QGIS, and soil and plant sampling was conducted in the same manner as at reference points described above.

Each day, collected soil samples were immediately sieved to 2mm and weighed on a digital pocket scale (American Weigh Scale Blade ®). 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 gravimetric moisture by subtracting sample dry mass from wet mass and dividing by total wet mass. Plant samples were similarly air dried within coin envelopes.

All sampling was conducted under Permit #353 and subsequent renewals issued by the Argentine National Park Service. Samples were exported under permits issued by the Ministerio de Ambiente y Desarrollo Sostenible, Argentina, and imported to the United States under permits issued by the United States Department of Agriculture - Animal and Plant Health Inspection Service.

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 3.2mm 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 $\delta^{13}C$ and $\delta^{15}N$ using an elemental analyzer; other soil nutrients (P, Na, K, Fe, Mn, Mg, Zn, and Ca) were measured using an inductively coupled plasma - optical emissions spectrometer (ICP-OES).

Statistical analyses

After the removal of samples that could not be properly analyzed or outliers confirmed to be due to sampling error, 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). To investigate differences in soil and plant nutrient content between carcass, stomach, and reference samples, we analyzed soil and plant nutrient data 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 percent N and percent C as dependent variables specified a beta distribution with a logit link function, while models using all other nutrient concentrations as well as gravimetric moisture as dependent variables specified a gamma distribution with a log link function to constrain predictions to positive values. $\delta^{15}N$ and temperature data were normally distributed and these models specified a Gaussian distribution with 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.

When 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” (i.e., 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. Two fresh carcasses were opportunistically encountered in plains during fieldwork, and were less than a month in age. 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 data set and on a subset of the data with the two fresh carcasses removed to test whether patterns were unduly manifest by the few carcasses with ages < 1 yr.

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). Because carcasses mainly affected soil nitrogen (Fig. 1) we compared soil % N measurements at reference sites (including at the 30 random sampling points) and puma kill site selection probabilities for those same coordinates (Smith and others 2020) to assess whether patterns of localized carcass deposition and decomposition were related to background N availability at larger scales. Puma kill site selection was derived from 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 (Fig. 1, Table S2). This effect of carcasses was 32% greater in canyons than in plains ($\beta = 0.45$ vs. $\beta = 0.33$, Fig. 1). Stomachs increased soil N and C in both plains (by 59% and 46%, respectively) and canyons (by 52% and 45%, respectively), and also increased P in plains by approximately 17% (Table S2, Fig. 1). Stomachs had a negative effect on soil Mg in canyons (by 16%; Table S2, Fig. 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, Fig. 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, Fig. 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, though results for models without these samples are shown in Fig. 2. Similarly, the impacts of stomachs on soil C and N did not vary with carcass age (Table S3, Fig. 2b,d).

Carcass and stomach effects on plant C, N, C:N, and $\delta^{15}N$ were not significant; nevertheless, they followed the same pattern as we expected, and plant % N was slightly higher and C:N slightly lower beneath carcasses and stomachs compared to reference sites in all habitats (Table S4, Fig. 3).

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, Fig. 4). This was largely driven by differences in predation risk between habitats – meadows had much higher nitrogen availability than plains and canyons (Fig. 4c), and are also the riskiest sites for vicuñas. We thus further examined these spatial correlations within the nutrient-poor habitats (plains and canyons combined) and within meadows to see if this pattern 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, Fig. 4c); while canyons had higher predation risk than plains due to rugged terrain and rocky outcroppings to shield hunting pumas (Donadio and Buskirk 2016; Smith and others 2019a), there was little variation in soil N within or between plains and canyons (% N largely ranging between 0.01% and 0.2%, Fig. 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, Fig. 4c).

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 stomachs had even greater effects on soil nitrogen, carbon, and phosphorus. However, these effects were habitat-dependent; carcasses and stomachs increased soil nutrients in plains and canyons, but 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. This effect of carcasses on soil N was greater in canyons than in plains (Fig. 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 that our study did not capture; nevertheless, biophysical setting seems to be more important than scavenger activity in determining long-term carcass impacts on soil nutrients.

Contrary to our expectations, increases in soil N at carcass sites did not in turn significantly increase plant nitrogen content, reduce plant C:N ratios, or alter foliar $\delta^{15}N$. 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 decomposition, 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. Alternatively, 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. However, 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. While smaller studies in more productive regions have provided important initial evidence for the biogeochemical impacts of vertebrate carcasses, our results add substantially to this emerging body of literature by confirming that these patterns hold in extremely arid, unproductive environments, with a large sample size, and for an extended period of time after carcass deposition.

We further demonstrate that across the landscape and within wet meadow environments, predation risk (i.e., probability of puma kill site selection) is correlated with soil nitrogen, suggesting that pumas select for N-rich sites that may attract susceptible vicuña prey. However, the lack of carcass impacts in meadow habitats does not support the hypothesis that this pattern of predation positively reinforces nutrient availability through the decomposition of predated carcasses at high-risk sites (Monk and Schmitz 2022; Peziol and others 2023). Instead, carcass and stomach decomposition seem to increase local soil N and P concentrations in nutrient-poor habitats, potentially increasing heterogeneity at smaller scales through the generation of biogeochemical hotspots (Carter and others 2007; Johnson-Bice and others 2022; Monk and Schmitz 2022).

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 (e.g. 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). Our results, while limited to one ecosystem, suggest that animals could, at least in some circumstances, have stronger effects than expected on ecosystem functioning in arid, nutrient-poor sites, because both heavy herbivory (Donadio and Buskirk 2016; Monk and others 2022) and the spatial concentration of essential nutrients in carcasses, urine, and feces can greatly impact the degree to which resources are limiting (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). 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. While we intended to investigate more recent carcasses, and thus have a more complete range of carcass ages to assess, the outbreak of mange and subsequent decline of the vicuña population (Ferreyra and others 2022; Monk and others 2022) rendered the detection of fresh carcasses via vehicular surveys far more difficult than it had been in previous field seasons, and we ultimately did not have 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).

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 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 >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 (Johnson-Bice and others 2022; Monk and Schmitz 2022).

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 Sarcoptic mange 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). Because the kill sites we investigated were created when there were ample vicuñas available to pumas, but it had already become rare to discover fresh vicuña carcasses by the time of the study, we were unable to directly examine the contrasting spatial and biogeochemical impacts of mange vs. puma-killed vicuña carcasses. 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.

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Fig. 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).

Fig. 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 grey regions represent 95% confidence intervals. Stomach effects on soil C and N did not vary over time.

Fig. 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 effects of treatment on plant nutrient content.

Fig. 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,b). 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; $p < 0.05$).

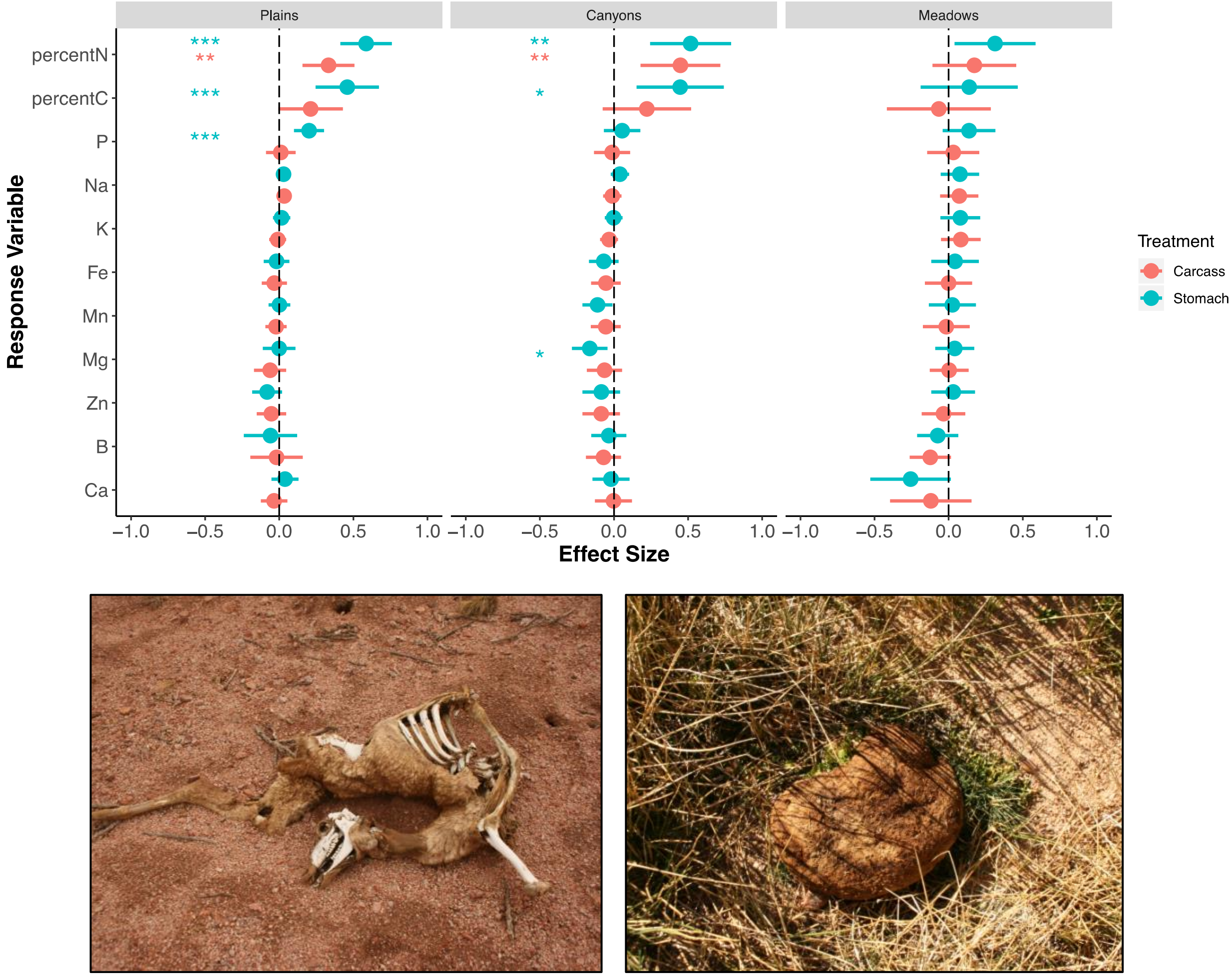

Plains
Canyons
Meadows
Response Variable
percentN
percentC
P
Na
K
Fe
Mn
Mg
Zn
B
Ca
***
**
***
***
**
**
*
*
−1.0
−0.5
0.0
0.5
1.0
Effect Size
Treatment
Carcass
Stomach

Fig. 1

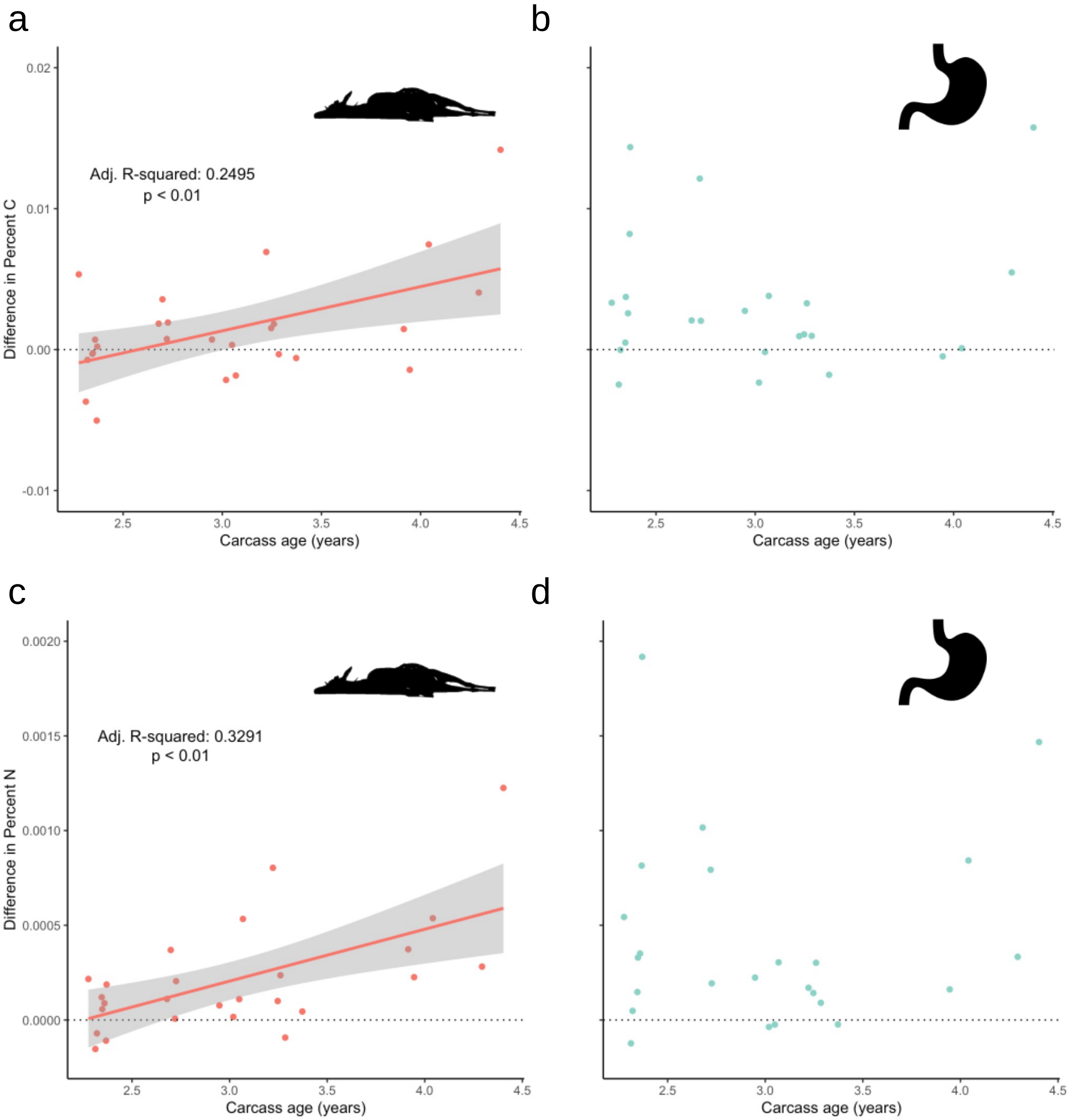
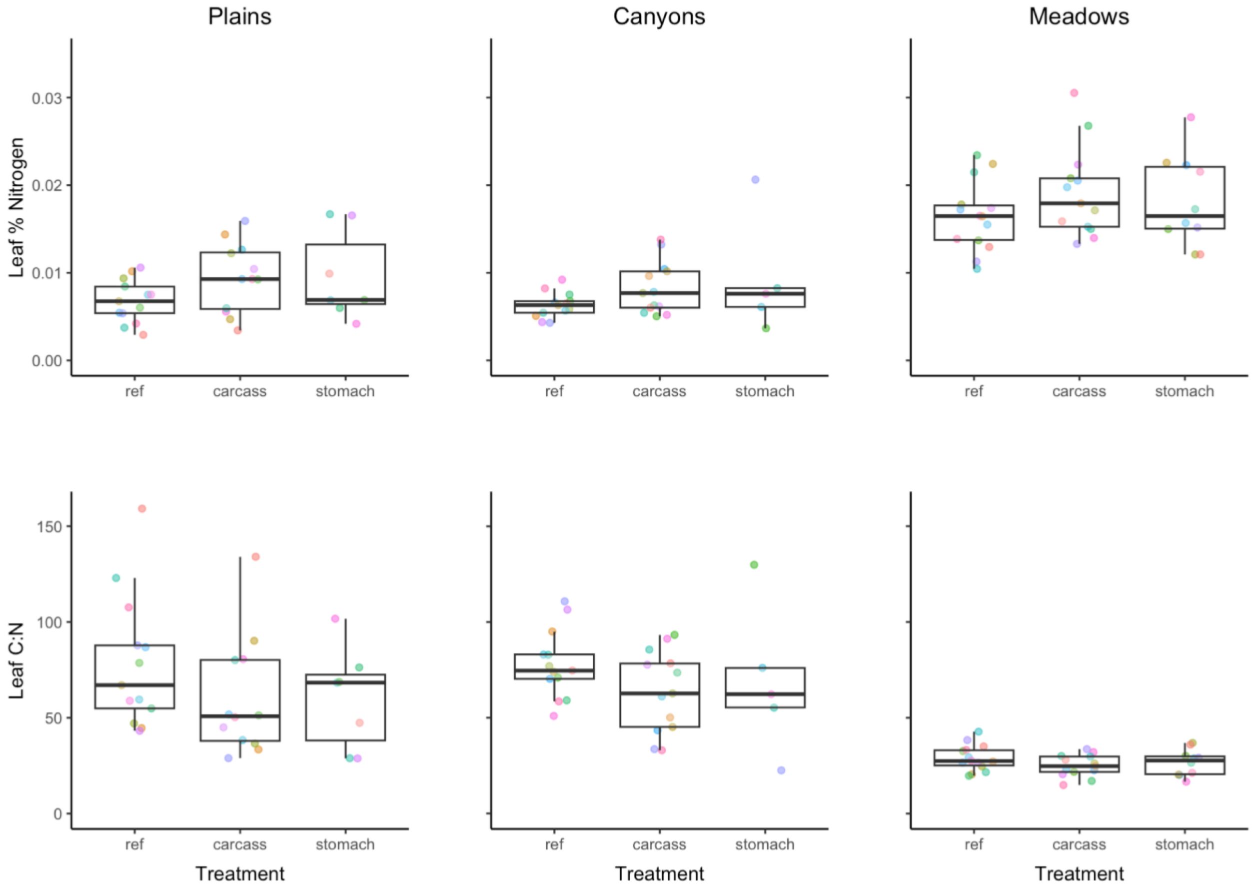

a
b
c
d
Adj. R-squared: 0.2495
p < 0.01
Adj. R-squared: 0.3291
p < 0.01
Difference in Percent C
Difference in Percent N
Carcass age (years)
0.02
0.01
0.00
-0.01
0.0020
0.0015
0.0010
0.0005
0.0000
2.5
3.0
3.5
4.0
4.5

Fig. 2



669
670
671 **Fig. 3**

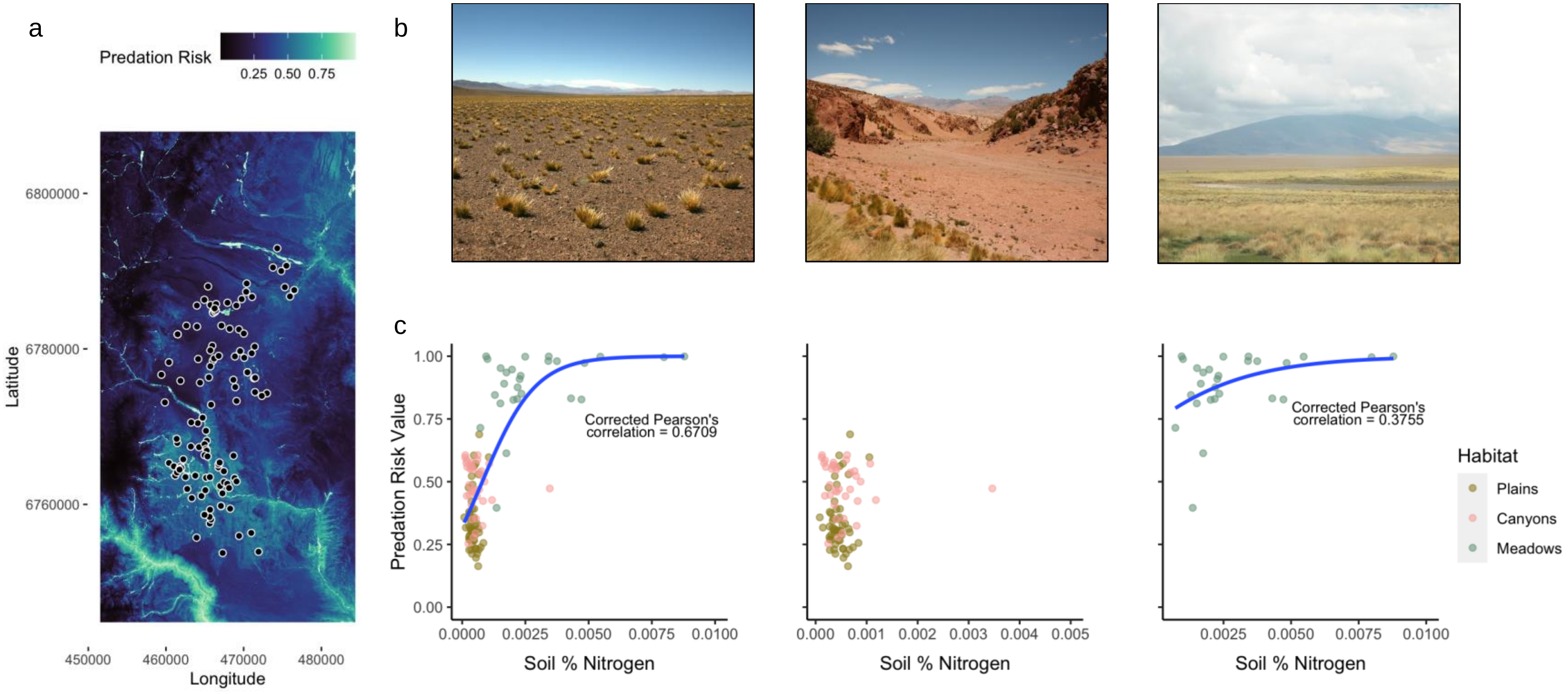

a
Predation Risk
0.25 0.50 0.75
6800000
6780000
6760000
Latitude
450000 460000 470000 480000
Longitude
b
c
1.00
0.75
0.50
0.25
0.00
Predation Risk Value
0.0000 0.0025 0.0050 0.0075 0.0100
Soil % Nitrogen
Corrected Pearson's correlation = 0.6709
0.000 0.001 0.002 0.003 0.004 0.005
Soil % Nitrogen
0.0025 0.0050 0.0075 0.0100
Soil % Nitrogen
Corrected Pearson's correlation = 0.3755
Habitat
Plains
Canyons
Meadows

Fig. 4

Supplementary Material

Table S1. Results of generalized linear mixed-effects models examining effects of vicuña carcasses and stomachs (compared to adjacent reference sites [intercepts]) on soil moisture and temperature in plains, canyons, and meadows in San Guillermo National Park, Argentina. Full model results are shown in the top table section, and results from pairwise post-hoc tests for models with significant treatment effects are shown in the bottom section. Significant p values (p<0.05) are shown in bold; rows with significant pairwise differences between treatments are shaded.

Variable	Habitat	Treatment	Estimate	Std. Error	z value	Pr(>|z|)	df
Soil Moisture	Plains	(Intercept)	-4.146	0.223	-18.615	<0.001	78
Soil Moisture	Plains	Carcass	-0.092	0.138	-0.67	0.503	78
Soil Moisture	Plains	Stomach	-0.208	0.143	-1.456	0.145	78
Soil Moisture	Canyons	(Intercept)	-4.362	0.284	-15.358	<0.001	84
Soil Moisture	Canyons	Carcass	0.072	0.162	0.446	0.655	84
Soil Moisture	Canyons	Stomach	-0.168	0.163	-1.031	0.302	84
Soil Moisture	Meadows	(Intercept)	-1.167	0.182	-6.429	<0.001	82
Soil Moisture	Meadows	Carcass	-0.126	0.16	-0.783	0.433	82
Soil Moisture	Meadows	Stomach	-0.011	0.161	-0.068	0.946	82
Soil Temperature	Plains	(Intercept)	18.627	2.076	8.974	<0.001	19
Soil Temperature	Plains	Carcass	-3.649	1.04	-3.509	**<0.001**	19

Soil Temperature	Plains	Stomach	-1.797	1.097	-1.639	0.101	19
Soil Temperature	Canyons	(Intercept)	17.55	1.45	12.101	<0.001	17
Soil Temperature	Canyons	Carcass	-3.775	1.258	-3.001	**0.003**	17
Soil Temperature	Canyons	Stomach	-2.483	1.402	-1.771	0.076	17
Soil Temperature	Meadows	(Intercept)	7.971	0.773	10.316	<0.001	16
Soil Temperature	Meadows	Carcass	-1.3	0.968	-1.343	0.179	16
Soil Temperature	Meadows	Stomach	-1.286	0.968	-1.328	0.184	16

Pairwise post-hoc tests

Variable	Habitat	Contrast	Estimate	SE	t ratio	P value	df
Soil Temperature	Plains	ref - carcass	3.649	1.04	3.509	**0.006**	19
Soil Temperature	Plains	ref - stomach	1.797	1.097	1.639	0.254	19
Soil Temperature	Plains	carcass - stomach	-1.852	1.093	-1.694	0.233	19
Soil Temperature	Canyons	ref - carcass	3.775	1.258	3.001	**0.021**	17
Soil Temperature	Canyons	ref - stomach	2.483	1.402	1.771	0.209	17
Soil Temperature	Canyons	carcass - stomach	-1.292	1.402	-0.922	0.634	17

Table S2. Results of generalized linear mixed-effects models examining the effects of vicuña carcasses and stomachs (compared to adjacent reference sites) on soil nutrients in plains, canyons, and meadows in San Guillermo National Park, Argentina. Estimates shown are back-transformed estimated means for each treatment level (reference, carcass, and stomach), as well as associated test statistics; letters indicate significant differences between treatments determined by pairwise post-hoc tests using Tukey's adjusted p-value for multiple comparisons. Significant p values (p<0.05) are shown in bold; rows with significant pairwise differences between treatments are shaded.

		GLMM treatment effect								Pairwise post-hoc test treatment		
Response Variable	Habitat	Reference Estimate	Carcass Estimate	Carcass P Value	Carcass Z Value	Stomach Estimate	Stomach P Value	Stomach Z Value	df	Reference	Carcass	Stomach
% N	Plains	0.044	0.062	**<0.001**	3.715	0.079	**<0.001**	6.61	77	**a**	**b**	**c**
% C	Plains	0.45	0.556	0.056	1.907	0.71	**<0.001**	4.195	77	**a**	**a**	**b**
P	Plains	679.808	686.843	0.84	0.201	831.06	**<0.001**	3.875	77	**a**	**a**	**b**
K	Plains	27186.257	26906.195	0.724	-0.353	27614.673	0.6	0.525	78	a	a	a
Ca	Plains	12584.664	12152.186	0.447	-0.76	13079.462	0.408	0.827	78	a	a	a
Fe	Plains	36827.961	35622.056	0.443	-0.767	36148.874	0.673	-0.423	78	a	a	a
Mg	Plains	8283.255	7785.174	0.262	-1.122	8276.777	0.989	-0.014	78	a	a	a
Mn	Plains	652.79	638.591	0.551	-0.597	653.332	0.982	0.022	78	a	a	a
B	Plains	61.647	60.531	0.84	-0.202	58.073	0.516	-0.65	78	a	a	a
Na	Plains	15034.571	15538.092	0.187	1.32	15480.535	0.248	1.156	78	a	a	a
Zn	Plains	79.88	75.755	0.297	-1.043	73.583	0.111	-1.594	78	a	a	a

% N	Canyons	0.051	0.08	**0.001**	3.267	0.086	**<0.001**	3.703	83	**a**	**b**	**b**
% C	Canyons	0.618	0.77	0.146	1.455	0.963	**0.003**	2.975	83	**a**	**ab**	**b**
P	Canyons	667.304	659.102	0.843	-0.199	704.945	0.38	0.877	83	a	a	a
K	Canyons	34506.177	33381.404	0.282	-1.075	34435.322	0.947	-0.067	83	a	a	a
Ca	Canyons	11168.472	11130.815	0.958	-0.053	10947.145	0.753	-0.314	83	a	a	a
Fe	Canyons	30158.379	28562.391	0.285	-1.068	28145.41	0.176	-1.355	83	a	a	a
Mg	Canyons	6476.855	6074.72	0.293	-1.051	5499.657	**0.007**	-2.676	83	**a**	**ab**	**b**
Mn	Canyons	548.578	519.064	0.284	-1.071	490.928	**0.032**	-2.146	83	a	a	a
B	Canyons	47.919	44.66	0.244	-1.164	46.267	0.563	-0.579	83	a	a	a
Na	Canyons	21370.457	21127.929	0.717	-0.362	22237.656	0.208	1.259	83	a	a	a
Zn	Canyons	68.701	63.007	0.182	-1.336	63.084	0.189	-1.313	83	a	a	a
% N	Meadows	0.292	0.348	0.23	1.2	0.4	**0.025**	2.244	79	a	a	a
% C	Meadows	6.207	5.832	0.711	-0.371	7.064	0.408	0.828	80	a	a	a
P	Meadows	711.513	734.02	0.729	0.347	816.513	0.13	1.514	82	a	a	a
K	Meadows	22296.45	24193.496	0.232	1.196	24119.753	0.252	1.146	82	a	a	a
Ca	Meadows	37927.845	33633.751	0.392	-0.856	29338.491	0.064	-1.851	82	a	a	a
Fe	Meadows	24313.872	24292.658	0.991	-0.011	25382.374	0.599	0.526	82	a	a	a

Mg	Meadows	7507.688	7532.076	0.961	0.048	7821.292	0.543	0.609	82	a	a	a
Mn	Meadows	498.755	490.816	0.842	-0.199	511.274	0.76	0.305	82	a	a	a
B	Meadows	71.796	63.438	0.082	-1.738	66.663	0.296	-1.046	82	a	a	a
Na	Meadows	14195.286	15246.465	0.279	1.082	15313.78	0.251	1.148	82	a	a	a
Zn	Meadows	63.403	61.232	0.642	-0.464	65.371	0.685	0.406	82	a	a	a

Table S3. Results of linear models examining the effects of vicuña carcass age (i.e. the amount of time since a carcass was deposited) on carcass and stomach impacts on soil % C and N (compared to adjacent reference sites) in San Guillermo National Park, Argentina. Models analyzed data for plains and canyons, and we also ran separate models on the full plains dataset and on the dataset with the two fresh carcasses (carcass age < 1 year) removed. Significant p values ($p < 0.05$) are shown in bold, and rows with significant positive effects of carcass age on treatment-reference differences in soil % C and N are shaded.

Response Variable	Habitat	F value	df (numerator)	df (denominator)	P value	Adj. R-Squared
Carcass-Reference Difference in %C	Plains (All)	6.461	1	26	**0.017**	0.168
Carcass-Reference Difference in %N	Plains (All)	10.509	1	26	**0.003**	0.26
Stomach-Reference Difference in %C	Plains (All)	0.547	1	24	0.467	-0.018
Stomach-Reference Difference in %N	Plains (All)	0.674	1	24	0.42	-0.013
Carcass-Reference Difference in %C	Plains (w/o Fresh Carcasses)	9.31	1	24	**0.005**	0.249
Carcass-Reference Difference in %N	Plains (w/o Fresh Carcasses)	13.263	1	24	**0.001**	0.329
Stomach-Reference Difference in %C	Plains (w/o Fresh Carcasses)	0.146	1	22	0.706	-0.039
Stomach-Reference Difference in %N	Plains (w/o Fresh Carcasses)	0.099	1	22	0.756	-0.041
Carcass-Reference Difference in %C	Canyons	0.04	1	27	0.844	-0.036
Carcass-Reference Difference in %N	Canyons	0.003	1	27	0.954	-0.037
Stomach-Reference Difference in %C	Canyons	0.243	1	26	0.626	-0.029
Stomach-Reference Difference in %N	Canyons	0.005	1	26	0.944	-0.038

Table S4. Results of generalized linear mixed-effects models examining the effects of vicuña carcasses and stomachs (compared to adjacent reference sites) on plant % N, C:N, and δ^{15}N in plains, canyons, and meadows in San Guillermo National Park, Argentina. Estimates shown are back-transformed estimated means for each treatment level (reference, carcass, and stomach), as well as associated test statistics; letters indicate significant differences between treatments determined by pairwise post-hoc tests using Tukey's adjusted p-value for multiple comparisons. Significant p values ($p<0.05$) are shown in bold; however, as indicated by the letters, none of the pairwise differences between treatments were significant in these models.

		GLMM treatment effect								Pairwise post-hoc test treatment		
Response Variable	Habitat	Reference Estimate	Carcass Estimate	Carcass Z Value	Carcass P Value	Stomach Estimate	Stomach Z Value	Stomach P Value	df	Reference	Carcass	Stomach
% N	Plains	0.69	0.922	1.912	0.056	0.934	1.65	0.099	27	a	a	a
C:N	Plains	76.671	57.978	-1.859	0.063	58.095	-1.516	0.13	27	a	a	a
δ^{15}N	Plains	2.138	2.404	0.187	0.851	2.153	0.009	0.993	27	a	a	a
% N	Canyons	0.644	0.821	1.806	0.071	0.865	1.495	0.135	26	a	a	a
C:N	Canyons	77.979	63.741	-1.528	0.127	69.192	-0.675	0.499	26	a	a	a
δ^{15}N	Canyons	0.389	0.803	0.498	0.618	1.129	0.65	0.515	26	a	a	a
% N	Meadows	1.637	1.918	2.02	**0.043**	1.81	1.161	0.246	32	a	a	a
C:N	Meadows	28.761	24.554	-2.086	**0.037**	26.158	-1.145	0.252	32	a	a	a
δ^{15}N	Meadows	11.738	10.144	-2.537	**0.011**	11.175	-0.809	0.418	32	a	a	a