

# **Vicuña antipredator diel migration drives spatial nutrient subsidies in a high Andean ecosystem**

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## **Abstract**

Spatial subsidies of nutrients within and among ecosystems have profound effects on ecosystem structure and functioning. Large animals can be important drivers of nutrient transport as they ingest resources in some habitats and release them in others, even moving nutrients against elevational gradients. In high Andean deserts, vicuñas (*Vicugna vicugna*) navigate a landscape of fear by migrating daily between productive wet meadows, where there is abundant water and forage but high risk of predation by pumas (*Puma concolor*), and open plains, where soils are nutrient-poor and forage is less abundant but the risk of predation is low. As they move, vicuñas also defecate and urinate in communal latrines to maintain the cohesion of their family groups. We investigated whether these latrines impacted soil and plant nutrient concentrations across three habitats in the Andean ecosystem (meadows, plains, and high-risk rugged canyons), and used stable isotope analysis to determine the source of fecal nutrients in latrines. We found that latrines increased the concentrations of nitrogen, carbon, phosphorus, and other nutrients in soils across all habitats. These inputs also corresponded with an increase in plant quality (lower C:N) at latrine sites in plains and canyons, but not in meadows. As we predicted, stable isotope mixing models revealed that a substantial proportion (30%) of nutrients in latrines in plains originated from vegetation in meadows, even though meadows accounted for only 2.6% of the landscape. Thus, vicuña diel migrations, motivated by predator avoidance, drive nutrient subsidies from low-lying, nutrient-rich meadows to more elevated, nutrient-poor plains. Scaling these results up to the landscape scale, we found that the amount of additional nitrogen and phosphorus in plains latrines were of the same order of magnitude as estimates of annual atmospheric nitrogen and phosphorus deposition for this region. These results suggest that vicuña-mediated nutrient

cycling and deposition is an important process impacting ecosystem functioning in arid Andean environments, on par with other major inputs of nutrients to the system.

## **Introduction**

Ecosystems are inherently open systems, in which energy, organisms, resources, and information flow across porous boundaries (Loreau et al. 2003, Gravel et al. 2010a, Gounand et al. 2018, Little et al. 2022). These movements result in spatial subsidies that can have cascading effects on ecosystem structure and function by altering species coexistence (Leroux and Loreau 2008, Gravel et al. 2010b), plant community composition (Croll et al. 2005, Maron et al. 2006), and food web stability (Rosenzweig 1971, Gounand et al. 2014). In heterogeneous environments, spatial subsidies from high to low productivity sites can be particularly impactful, markedly altering numerous ecosystem properties in recipient habitats (Polis and Hurd 1995, Polis et al. 1997, Sanchez-Pinero and Polis 2000, Hocking and Reynolds 2011).

Animals can be key drivers of spatial subsidies when they move within and between ecosystems, particularly in terrestrial landscapes (McInturf et al. 2019, Ellis-Soto et al. 2021). These movements can be motivated by numerous ecological factors (Kauffman et al. 2021), most prominent among them spatiotemporal changes in resource availability (Fryxell and Sinclair 1988, Middleton et al. 2018) and predation risk (Courbin et al. 2018, Kohl et al. 2018, Smith et al. 2019b). Animals may act as vectors of nutrient transport whenever they consume resources in some ecosystems or habitats and excrete and egest them elsewhere (Subalusky et al. 2015, Doughty et al. 2016, Ellis-Soto et al. 2021). These spatial subsidies can recur frequently, as in diel migrations between habitats, or be episodic, as during seasonal migrations across broader landscapes (Kitchell et al. 1999, Bauer and Hoye 2014, Subalusky et al. 2017). Furthermore,

unlike passive geophysical transport of subsidies, animals can actively transport nutrients against strong environmental gradients, including from low to high elevation, from concave to convex surfaces, or against the flow of water or prevailing winds (McInturf et al. 2019).

Large mammalian herbivores may be important vectors in landscapes where habitats differ in resource availability. Their large body size allows these herbivores to range over large expanses while consuming, processing, transporting, and releasing large amounts of nutrients (Doughty et al. 2016, Subalusky and Post 2018). However, herbivores may also be vulnerable to predation, which can influence their diel and seasonal migration patterns and hence the spatial dynamics of resource subsidies (Schmitz et al. 2010, Monk and Schmitz 2022).

Here we report on the effects of predator-driven spatial nutrient subsidies across habitats in a high Andean ecosystem in San Guillermo National Park (SGNP) Argentina. The vicuña (*Vicugna vicugna*), a wild camelid, exhibits a diel migration driven by predator avoidance (Smith et al. 2019a,b, Karandikar et al. 2023). Vicuñas are drawn to highly productive, patchily distributed meadows because of their abundant nutritious forage and water availability. However, pumas (*Puma concolor*) select heavily for meadows at all times of day because the abundant tall vegetation provides cover that abets their ambush hunting strategy (Smith et al. 2019b, 2020). In response, vicuñas generally feed in meadows at midday, when pumas are less active and easier to detect, and spend nights and crepuscular hours in the safer, but less productive, open plains that surround the isolated meadows and make up most of the landscape (Donadio and Buskirk 2016, Smith et al. 2019b, 2020). Thus, the tradeoff between nutrition and fear of predation drives a diel migration (counter to the elevational gradient) between the fertile, low-lying wet meadows and less fertile, elevated arid plains.

Vicuñas congregate in family groups and release nutrients in communal latrines (Vila 1994, Cassini et al. 2009). These latrines may create biogeochemical hotspots, and there is evidence from similar montane ecosystems in Peru indicating that vicuña latrines influence plant diversity, plant quality, and successional stage (Koford 1957, Franklin 1983, 2022, Reider and Schmidt 2021). However, the effects of latrines on soil and plant nutrients and their spatial outcomes at the landscape level have not been systematically investigated.

Here, we evaluate the impacts of vicuña latrines on soil and plant nutrients and plant diversity across habitats in SGNP. We expected that latrines would increase soil nutrient concentrations, plant diversity, and plant nutritional quality across habitats. We also test the hypothesis that predator avoidance drives a nutrient subsidy from high- to low-productivity habitats as vicuñas migrate daily between meadows and plains in a dynamic landscape of fear (Smith et al. 2019b, Monk and Schmitz 2022).

## **Methods**

### *Study area*

SGNP is a high elevation (2000-5600m) protected area encompassing 1660 km<sup>2</sup> on the western border of Argentina (29°14'S, 69°21'W). The park consists of three main habitats: open plains, which are arid expanses characterized by bare soil interspersed with sparse grasses and shrubs; canyons and mountain slopes, which have similar vegetation communities and soil to plains, but are characterized by rough terrain and rocky outcroppings; and meadows, which occur in riparian zones and where groundwater meets the surface, and are characterized by saturated, peaty soils and dense cover of rushes and sedges.

Interactions between pumas and vicuñas across these habitats create a dynamic landscape of fear (Smith et al. 2019b). Pumas have greatest success capturing vicuñas in meadows and canyons, both of which provide ample cover for ambush predation in the form of dense plant cover or complex terrain (Smith et al. 2019a, 2020; Fig. 1). Because of high risk, vicuñas tend to avoid canyons when possible; however, vicuñas are compelled to visit meadows despite high risk because of high availability of water and abundant nutritious forage (Donadio and Buskirk 2016, Smith et al. 2019b; Fig. 1). Accordingly, puma-vicuña encounter and kill rates in meadows are high (Smith et al. 2020). Vicuñas mitigate this risk by being highly vigilant in meadows and visiting them during daylight hours, when pumas are easier to detect, returning to plains at night when risk of predation is higher (Donadio and Buskirk 2016, Smith et al. 2019a, 2019b).

Within the area of the park where GPS-collared vicuñas from prior research were active, plains make up roughly 48.9% of the landscape, whereas canyons make up 48.5% and meadows the remaining 2.6% (Monk et al. 2022). Meadows are thus limited in their size and extent, with the largest meadow (known as the *Vega de los Leones*, nestled in the center of the largest plains area, the *Llano de los Leones*) encompassing  $\sim 1.2 \text{ km}^2$ . Meadows tend to occur along rivers and springs at the bottom of canyons or in shallow valleys surrounded by plains, and thus are generally lower lying than the other habitats.

#### *Data collection and laboratory analyses*

In each habitat, we established 15,  $50 \times 50 \text{ m}$  plots (45 plots total) (Fig. 1). In each habitat, six plots were placed at the sites of smaller control plots established for a previous enclosure experiment (see Donadio and Buskirk 2016, Monk et al. 2022), while the remaining nine plots were established at random points generated in QGIS (version 2.18.15). We marked the corners of plots with stake flags, and recorded corner locations with handheld Garmin GPS

units. We comprehensively searched each plot for vicuña latrines and counted the number of latrines in each plot, marking each latrine with a stake flag to avoid recounting. We recorded whether dung in each latrine appeared fresh (with dark black, shiny fecal pellets), medium-fresh (black fecal pellets, though less dark than fresh pellets), or old/abandoned (fecal pellets faded to grey) and measured the diameter of each latrine with a tape measure. We measured plant cover at each latrine by placing a 50 × 50 cm quadrat in the center of each latrine, and visually estimating the percent cover of each plant family within the quadrat. We similarly estimated percent plant cover by family at randomly placed reference quadrats within each plot.

At each latrine, we collected fecal pellets, choosing relatively fresh ones that had not been directly exposed to the sun. We collected two 10-cm deep soil samples beneath each latrine (brushing aside fecal pellets and vegetation to expose soil) with a 2-cm diameter soil corer, and these two samples were immediately pooled into a single plastic bag. We similarly collected soil samples at randomly chosen reference sites within each plot. We collected green, living leaves from grasses, rushes, and sedges growing out of latrines, and collected leaves from the same species at reference sites > 6 m from latrines.

We immediately sieved all soil samples to 2 mm and weighed them on an American Weigh Scale Blade™ digital pocket scale. Soil samples were air-dried indoors in open bags for 3 days, which was a sufficient period to reach constant mass in the arid climate, and were re-weighed to obtain dry mass. Plant samples were air-dried for 3 days in paper coin envelopes. Fecal samples were oven-dried at 72° C for 1 hour according to import permit protocols.

All samples were shipped to Yale University for laboratory analysis, and nutrients were analyzed at the Yale Analytical and Stable Isotope Center and with the assistance of the Soil Biogeochemistry Lab at University of Massachusetts, Amherst. We ground soil samples with

3.2mm diameter chrome steel balls in microcentrifuge tubes using a SPEX Sample Prep 5100™ Mixer Mill. Fecal samples were first broken up manually and then ground to powder using the same methodology. We ground plant samples by hand using a mortar and pestle, occasionally applying liquid nitrogen to help break up tougher samples. All samples (soil, plants, and fecal matter) were analyzed for total carbon, total nitrogen,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  using an elemental analyzer, and soil samples were analyzed for P, Na, K, Fe, Mn, Mg, Zn, and Ca concentrations using an inductively coupled plasma – optical emissions spectrometer (ICP-OES).

Research permits were issued by the Argentine National Parks Administration. 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.

### *Statistical analyses*

We expected that the distribution and size of latrines would differ between habitats, with more or larger latrines in plains and meadows, where vicuñas tend to spend more of their time, than in canyons (Donadio and Buskirk 2016). We tested whether the number of latrines per plot differed between habitats using a generalized linear model specifying a Poisson distribution with a log link function. We tested for differences in latrine diameter between habitats using a generalized linear model specifying a Gamma distribution and a log link function to constrain predictions to positive values. We tested for differences in dung freshness (as a proxy for recent latrine activity) between habitats by recoding freshness values (fresh, medium, and old/abandoned) as proportion data (0.999, 0.5, and 0.001, respectively) and then running a beta regression with a logit link function using the ‘betareg’ package in R (Cribari-Neto and Zeileis

2010). For all models, we used the ‘emmeans’ package to run post-hoc tests of pairwise differences between habitats (Lenth et al. 2022).

We ran a series of generalized linear mixed-effects models to evaluate the effects of latrines on soil and plant nutrient content. We used the ‘glmmTMB’ package in R (Brooks et al. 2017), and for all models we specified treatment (latrine vs. reference) as a fixed effect and plot ID as a random intercept. We ran models separately for each habitat due to large differences in variance between data from distinct habitats, as determined using the ‘var’ function in R. Models analyzing soil % C and N and plant % N specified a beta distribution with a logit link function, while models analyzing soil P, Na, K, Fe, Mn, Mg, Zn, and Ca concentrations and plant C:N specified a Gamma distribution with a log link function to constrain predictions to positive values. We assessed all models graphically to identify patterns in residuals.

To determine whether plant cover differed between latrines and reference sites, we ran a generalized linear mixed-effects model with plot ID as a random intercept, specifying a beta distribution with a logit link function, again using R package ‘glmmTMB’ (Brooks et al. 2017). We used the ‘vegan’ package in R to investigate the effects of latrines on plant diversity (Oksanen et al. 2018). We calculated richness and Shannon diversity using the ‘specnumber’ and ‘diversity’ functions and ran ANOVAs to test for differences in these metrics between latrine and reference quadrats. We also used the ‘adonis’ function to run PERMANOVAs to test for dissimilarity between latrine and reference communities in each habitat.

If vicuña diel migrations fuel a nutrient subsidy from meadows to plains, we would expect to find that a substantial proportion of fecal nutrients from latrines in plains would originate from meadow vegetation (at least greater than 5%, which is double the proportion of the landscape meadows represent). To determine the source of latrine nutrients, we first isolated

all plant reference  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ , percent C, and percent N data, using reference samples collected for this study as well as those used in a related research project (Monk 2022). We classified plant samples into two source categories: “Meadows” (containing all meadow samples, including mainly Juncaceae and Cyperaceae species in addition to a few Poaceae samples from genus *Festuca*) and “Plains and Canyons” (containing all samples from those two dry habitats, all Poaceae species mainly from genera *Jarava* and *Stipa*) (Martínez Carretero 2007). We ran ANOVAs to verify that  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for the two source categories differed significantly (both  $p < 0.001$ ). We then ran separate stable isotope mixing models for each habitat, using “Meadow” and “Plains and Canyon” vegetation as the two source datasets and dung collected in each habitat as the mixture datasets, using the ‘simmr’ package in R (Parnell et al. 2013, Parnell 2021), which runs Markov chain Monte Carlo functions to determine the proportion of sources in each mixture based on C and N stable isotope ratios. We did not specify prior means, thus defaulting to uninformative priors. We did use reference sample percent C and N data to specify elemental concentration means. We used the ‘diagnostics’ summary function in the ‘simmr’ package to assess model fit. We conducted all statistical analyses in R software (v. 3.6.3).

## Results

Latrine density was highest in plains, with a mean of 2.5 latrines/plot (SE  $\pm$  0.38; plots have an area of 2500 m<sup>2</sup>), while meadows averaged 1.5 latrines/plot (SE  $\pm$  0.51) and canyons averaged 1.1 latrines/plot (SE  $\pm$  0.43); plains latrine counts were significantly higher than canyon latrine counts ( $p < 0.05$ ; Fig. 2). There was no difference in latrine diameter between habitats ( $p > 0.05$ ), and latrines were on average 2 m in diameter and covered an area of  $\sim$ 3.1 m<sup>2</sup>. There was no significant difference in dung freshness between habitats ( $p > 0.05$ ), though the mean

freshness score for canyons (0.09) was much lower than for the other two habitats (0.34 for plains and 0.37 for meadows), suggesting that latrines in plains and meadows were more recently active.

In plains, latrines significantly increased soil percent N (by 113%,  $p < 0.001$ ), and C (59%,  $p < 0.001$ ), and concentrations of P (16%,  $p < 0.05$ ) and Na (11%,  $p < 0.001$ ) compared to adjacent reference sites, which had 0.047% soil N, 0.454% soil C, 653.2 mg/kg P, and 18230.8 mg/kg Na on average (Supplementary Table 1, Fig. 3). Latrines also had slight effects on soil K (increasing concentrations by 5.7%,  $p = 0.057$ ; Table S1). Latrines did not influence concentrations of any other soil nutrients that were measured in plains (Table S1). Increases in soil nutrients at plains latrine sites in turn impacted plants at latrines, which had 26% higher percent N (mean of 1.9% vs. 1.5%,  $p < 0.01$ ) and 32% lower C:N ratios ( $p < 0.001$ ) than plants at reference sites (Fig. 4).

Similarly, in canyons, latrines increased soil percent N by 130% ( $p < 0.001$ ) and C by 113% ( $p < 0.001$ ) compared to reference sites, which had 0.037% soil N and 0.447% soil C on average (Table S1, Fig. 3). Latrines also increased soil P concentrations by 13% in canyons ( $p < 0.05$ ), but had no effect on any of the other elements we measured (Table S1, Fig. 3). Plant percent N was 53% greater at latrines than at reference sites (2.9% compared to 1.9%;  $p < 0.01$ ), translating into a 38% decrease in plant C:N ( $p < 0.001$ ; Fig. 4).

In meadows, latrines increased soil percent N by 52% ( $p < 0.01$ ) and C by 31% ( $p < 0.05$ ), and also increased concentrations of P by 53% ( $p < 0.05$ ) and Mg by 59% ( $p < 0.05$ ) compared to adjacent reference sites, which had 0.249% N, 4.63% C, 710.97 mg/kg P, and 9265.76 mg/kg Mg on average (Table S1, Fig. 3). Latrines did not influence concentrations of any other soil nutrients that were measured in meadows (Table S1). However, these effects of

latrines on soil N did not correspond to changes in plant quality, as plant percent N and C:N did not differ between latrine sites and reference sites in meadows (Fig. 4).

Plant cover was significantly lower at latrines (22% plant cover) than at adjacent reference sites in meadows (73% plant cover;  $p < 0.001$ ), but plant cover did not differ between latrines and reference sites in plain and canyon habitats ( $p > 0.05$ ). Contrary to our expectations, plant family richness and Shannon diversity did not differ between latrines and reference sites in plains ( $p = 0.885$  and  $p = 0.905$ , respectively) or canyons ( $p = 0.348$  and  $p = 0.941$ , respectively), nor were the plant communities significantly dissimilar between treatments in these habitats ( $p = 0.195$  in plains and  $p = 0.159$  in canyons). In meadows, mean species richness was significantly higher at reference sites (2) than at latrines (1.5,  $p < 0.05$ ), and these communities were significantly dissimilar ( $p < 0.01$ ), largely driven by the fact that latrines in meadows had lower cover overall, and thus had fewer Juncaceae and Cyperaceae species in quadrats than adjacent reference sites (though Poaceae species were still commonly found in latrine quadrats).

Vegetation from meadows (a wet habitat) and plains and canyons (dry habitats) differed in isotopic space, with vegetation from meadows more enriched in  $^{15}\text{N}$  and less enriched in  $^{13}\text{C}$  than vegetation from plains and canyons (Fig. 5a, c). Stable isotope mixing models revealed that meadow vegetation contributed substantially (33.2%, 95% CI 24.9%-41.8%) to fecal nutrient subsidies in plains (Fig. 5b). Meadow vegetation contributed far less to fecal nutrient subsidies in canyons (14.7%, 95% CI 6.2%-24.1%). In meadows, models estimated that fecal nutrients were derived almost equally from meadow vegetation and plain and canyon vegetation (52.6%, 95% CI 41.2%-66.5%; and 47.4%, 95% CI 33.5%-58.8%; Fig. 5d).

## Discussion

By systematically investigating latrine soil, plants, and fecal pellets across the landscape, we were able to determine that vicuña latrine use increases local soil nutrient concentrations and, in arid habitats, plant nutritional quality. Furthermore, we determined that vicuña diel migrations – motivated by the need to balance food and water acquisition and predator avoidance – transport nutrients from fertile, low-lying meadows to nutrient-poor, elevated plains. Latrine use as a driver of biogeochemical hotspot formation has been documented in several other systems. River otters in Alaska subsidized nutrients from marine to terrestrial environments by consuming marine fauna and defecating and urinating in latrines on land (Ben-David et al. 1998). Similarly, rabbit latrines can contribute to local soil fertility in semi-arid environments in Spain (Willott et al. 2000). Here, we show that latrine hotspots in arid montane habitats can act as subsidies from isolated nutrient-rich environments to the surrounding matrix, substantially increasing the extent of nutrient-elevated soils and plants in otherwise less productive habitats.

Latrines were slightly more abundant in plains and meadows than in canyons, though latrine size was consistent across the landscape. While latrines increased soil C, N, and P in both dry and wet habitats (as well as soil Na, K, and Mg in certain habitats), only plants in the arid plains and canyons displayed concomitant increases in plant % N and decreases in plant C:N. These results support the findings of recent studies suggesting that animal biogeochemical effects may be particularly impactful in dry, nutrient-limited habitats with scarce vegetation (Sitters et al. 2017, Monk 2022), where microbially-mediated plant litter decomposition is slow to replenish the supply of plant-available nutrients (Monk and Schmitz 2022). We did not observe the changes in plant community composition and diversity at vicuña latrine sites that have been documented at sites further north in the Andes (Koford 1957, Franklin 1978, 2022,

Reider and Schmidt 2021). However, these studies were also conducted at higher elevations than SGNP (most of our study area ranged between 3500-3800 m), including along glacial fronts. Montane plant communities can turn over quickly with elevation (Carilla et al. 2018, Smithers et al. 2020), and thus vegetation in these other systems may have been more sensitive to localized increases in fertility.

Latrines had profound effects on the ecosystem in SGNP, increasing soil nutrient availability and plant nutritional quality. While such localized effects – concentrated in roughly 3 m<sup>2</sup> patches – could seem insignificant within the context of a vast landscape, latrines are remarkably prevalent throughout the vicuña home range in the park (approximately 1140 km<sup>2</sup>, Fig. 1a; see Monk et al. 2022 for study area definition). With an average of 2.5 latrines per 2500 m<sup>2</sup> plot in the plains (Fig. 2), and plains making up roughly 48% (547.2 km<sup>2</sup>) of the home range of GPS-collared vicuñas in the park, there were likely at least 547,700 latrines in plains alone at the time of this study. While not all latrines would have been in active use, based on our results (and accounting for a mean bulk density of 1.15 g soil/cm<sup>3</sup> in plains), the presence of the latrines on the landscape likely contributed approximately 98,700 additional kg of N, 1.02 million kg of C, and 18,700 kg of P to the top 10 cm of plains soils – a substantial subsidy that cascaded up to increase plant quality (C:N) in arid plains and canyons, where soil nitrogen availability is generally low. To put these numbers into context, this nitrogen subsidy represents 1.8 kg/ha, and estimated atmospheric nitrogen deposition rates for this region range between 1 and 5 kg/ha (Galloway et al. 2004). Thus, even accounting for the fact that nitrogen in latrine soil is deposited over a few years rather than in a single year, nitrogen deposition by vicuñas in plains occurs at a comparable order of magnitude to atmospheric nitrogen deposition (the other main input of nitrogen to the system). Furthermore, the quantity of phosphorus in plains latrines (also

expressed as 0.34 kg/ha or 0.034g/m<sup>2</sup>) is greater than global mean annual total phosphorus deposition rates (Tipping et al. 2014), suggesting that subsidies from vicuña latrines are likely a major source of phosphorus on the landscape.

Isotopic data showed that ~30% of fecal nutrients in plains derived from meadows, and ~50% of fecal nutrients in meadows originated in arid habitats, suggesting that vicuñas transport and deposit nutrients across habitat boundaries as they move across the landscape. Theory predicts that high-productivity habitats should exert significant effects upon recipient habitats even if material flows are reciprocal (Holt 2004). Indeed, we did find that latrines exerted strong effects on soil and plant nutrient availability in plains, which contained a disproportionate amount of nutrients derived from meadows. This subsidy is particularly notable given that meadows comprise less than 3% of the study area within SGNP (Monk et al. 2022) – yet these isolated, productive habitats with minimal extent contribute substantially to the recycled nutrients deposited by vicuñas in the surrounding, less productive environments. These data support our hypothesis that vicuña nutrient subsidies from meadows to plains result from diel migrations, and also support recent theory suggesting that herbivore-mediated nutrient transport can play an important role in increasing nutrient availability in nutrient-poor recipient ecosystems (Sitters and Olde Venterink 2015, Stark et al. 2015).

Our research suggests that diel migrations of large mammals in terrestrial systems transports nutrients from fertile, high-risk zones to safer, more nutrient-poor environments. These terrestrial subsidies, like well-documented marine vertical subsidies (Roman and McCarthy 2010, Roman et al. 2014), can also transport nutrients against gravity. In SGNP, meadows are often low-lying compared to surrounding plains; thus, vicuña nutrient transport from meadows to plains is an important counter-gradient flow replenishing nutrients in arid

montane environments. Previous work in SGNP shows that movement between meadows and plains results from antipredator behavior (Smith et al. 2019a,b). Daily movements between habitats driven by predator avoidance have been documented in several other mammalian herbivores (Valeix et al. 2009, Courbin et al. 2018, Kohl et al. 2018); our results suggest that these daily movements may similarly drive nutrient subsidies from, for example, watering holes to open savanna habitats. Thus, antipredator responses can drive the redistribution of nutrients at the landscape level, with effects that cascade up to primary producers (Monk et al. 2022).

Whether these effects propagate beyond the soil and vegetation to further impact the Andean food web merits further study. The prevalence of more nutritious plants at latrine sites could supplement forage resources for vicuñas and other, smaller herbivores in the ecosystem (Koford 1957, Franklin 1978, Reider and Schmidt 2021), though vicuñas may also avoid feeding at latrine sites due to the potential risk of disease (Weinstein et al. 2017). Indeed, the rapid spread of mange has already severely impacted the vicuña population in SGNP in recent years (Ferreira et al. 2022, Monk et al. 2022). As vicuña densities have rapidly declined, the subsidy of nutrients from meadows to plains has likely been disrupted. Ongoing research in SGNP should investigate not only how plants and other interacting species respond to declines in vicuña herbivory in the wake of the mange outbreak (Monk et al. 2022), but also how the reduction in latrine formation may impact plains food webs by potentially decreasing nutrient availability or altering the spatial distribution of nutrients on the landscape.

Our study confirms that vicuña latrine use generates hotspots with elevated soil and plant nutrients. It further demonstrates that the daily movement of vicuñas between high-risk meadows and low-risk plains drives a nutrient subsidy counter to the elevational gradient, from more productive, lower elevation to less productive, higher elevation habitats. Thus, predator-prey

interactions may play an important role in the cycling and redistribution of nutrients in the Andean ecosystem. While large herbivores would consume and deposit resources regardless of predation pressures, puma predation and the spatial distribution of risk seem to fuel the flow of resources away from fertile, high-risk sites to more nutrient-poor, arid refuge habitats.

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**Figure 1.** Study system in San Guillermo National Park (SGNP), Argentina. a) Satellite imagery of the study area within SGNP. The pink outline represents the study area boundary (defined using data on vicuña home ranges from GPS collars; see Monk et al. 2022). Orange dots indicate latrine plots in plains (n = 15), pink dots represent plots in canyons (n = 15), and green dots represent plots in meadows (n = 15). b) Vicuñas entering a meadow to forage. c) An adult puma in the middle of dense meadow vegetation.

**Figure 2.** Vicuña latrine density in San Guillermo National Park, Argentina, sampled in March 2020. a) The number of latrines per  $50 \times 50$  m plot ( $2500 \text{ m}^2$ , or  $0.25 \text{ km}^2$ ) in plains, canyons, and meadows. Circles and vertical lines denote means  $\pm$  standard error; latrine density was significantly higher in plains than in canyons ( $p < 0.05$ ). b) Photograph of latrines on a slope descending into plains, as seen from the top of a hill. Arrows point to two latrines.

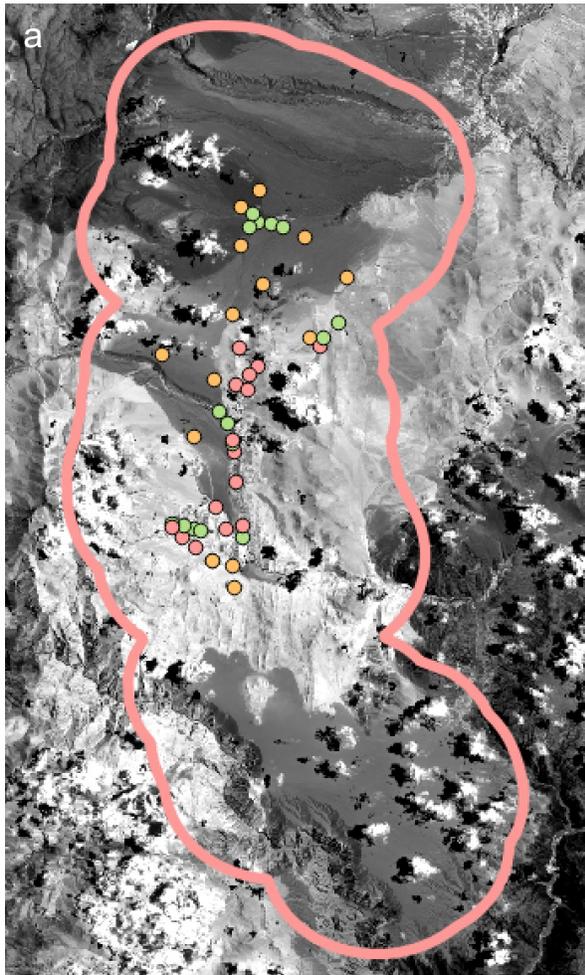
**Figure 3.** Effects of vicuña latrines on soil nitrogen, carbon, and phosphorus in plains, canyons, and meadows in San Guillermo National Park, Argentina, sampled in March 2020. Soil beneath latrines had significantly higher % N, % C, and P concentrations than reference soil in all three habitats; p-values of generalized linear mixed-effects models are shown above boxplots. The y-axes for % N and % C are on a scale from 0 to 1 (e.g. 0.05 = 5%). Photographs on the right show, from top to bottom, latrines in plains, canyons, and meadows.

**Figure 4.** Effects of vicuña latrines on plant nutritional quality (carbon to nitrogen ratio) in plains, canyons, and meadows in San Guillermo National Park, Argentina, sampled in March 2020. High plant nutritional quality corresponds to lower C:N (higher proportional nitrogen

concentrations). Where plants at latrine sites had significantly lower C:N in leaves than plants at reference sites, p-values from generalized linear mixed-effects models are shown above boxplots.

**Figure 5.** Results of stable isotope mixing models determining the source of nutrients in vicuña feces collected in plains (a, b) and meadows (c, d). In all panels, data from plants from arid habitats (plains and canyons) are shown in brown and data from meadow plants are shown in green. The left panels plot the raw data in isospace. Green circles (meadows) and brown triangles (plains and canyons) represent means  $\pm$  one standard deviation of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of vegetation (sources). Open orange circles represent  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of individual vicuña fecal samples (mixtures) collected in plains (a) and meadows (c). The right panels display modeled probabilities of the proportion of nutrients derived from each source [plains and canyons vegetation (brown) and meadow vegetation (green)] in fecal samples collected in plains (b) and meadows (d). Thus, roughly 33% of nutrients in plains fecal samples were likely derived from meadow vegetation, while roughly 47% of nutrients in meadow fecal samples were likely derived from plains vegetation.

Figure 1.



**Figure 2.**

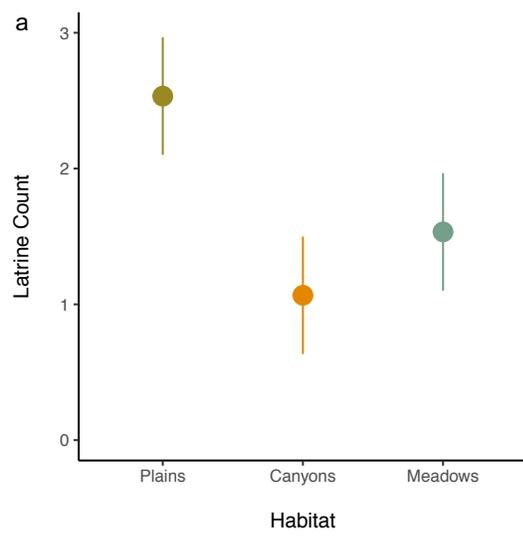


Figure 3.

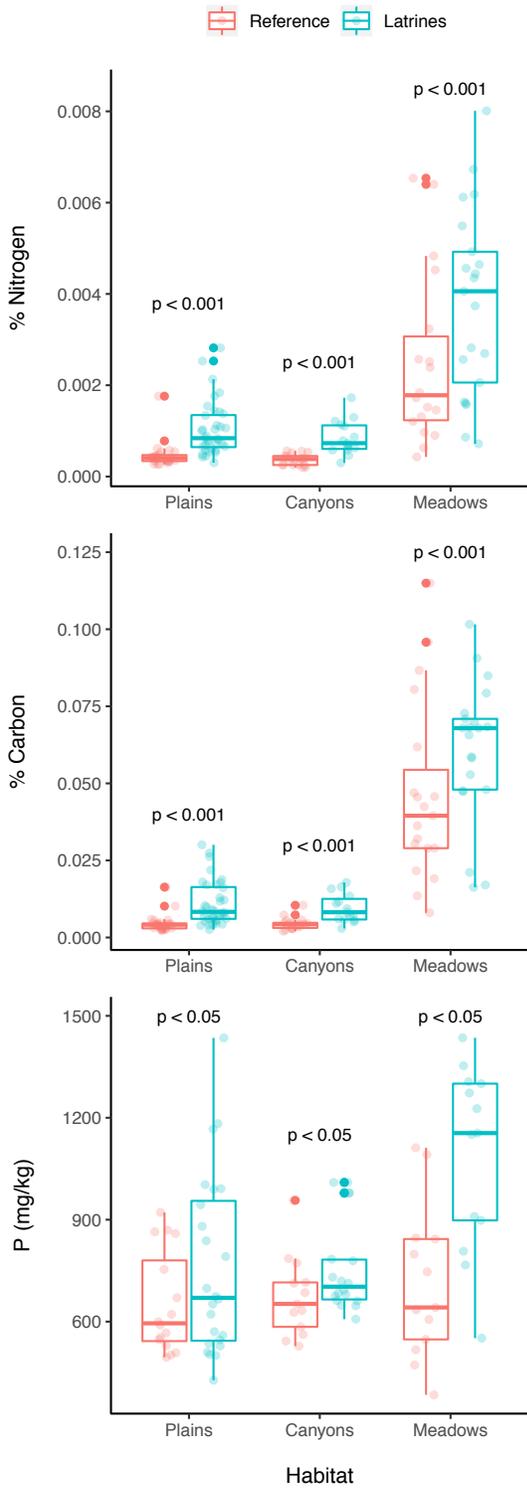


Figure 4.

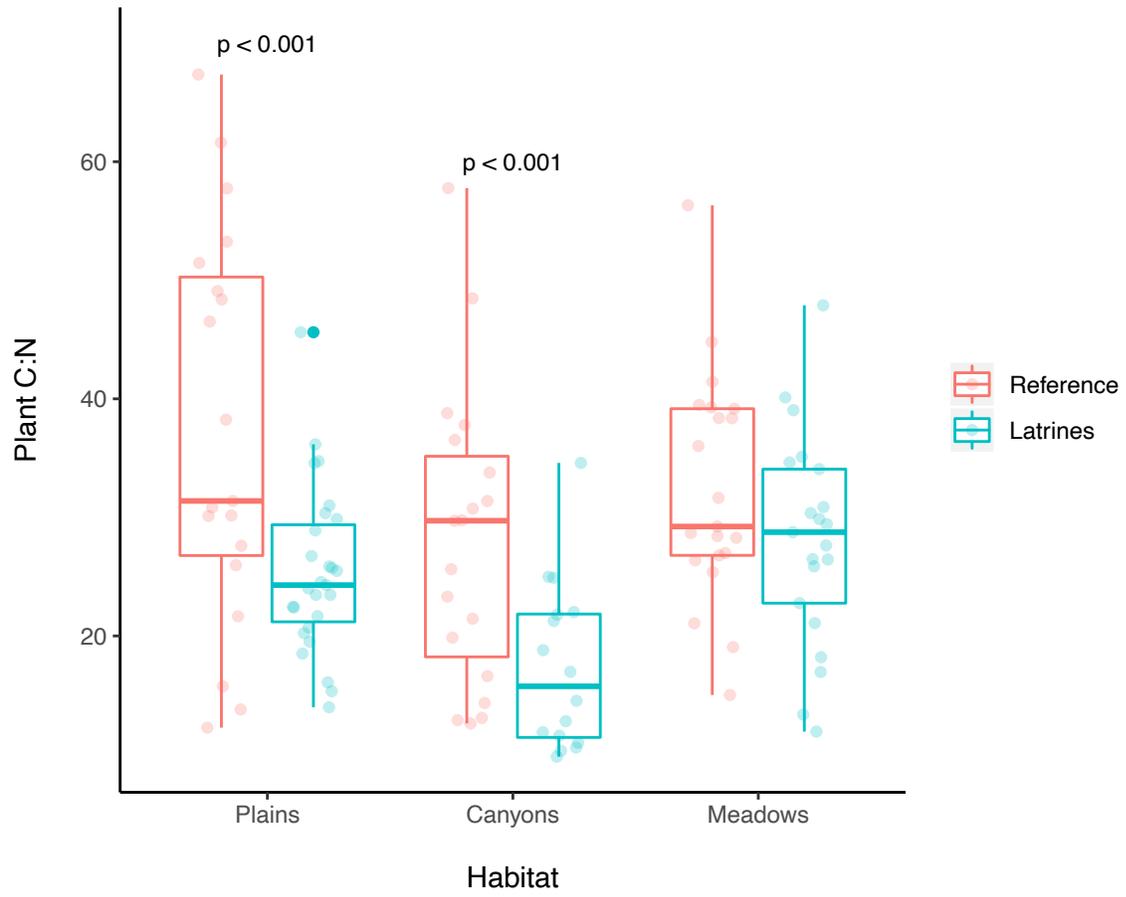
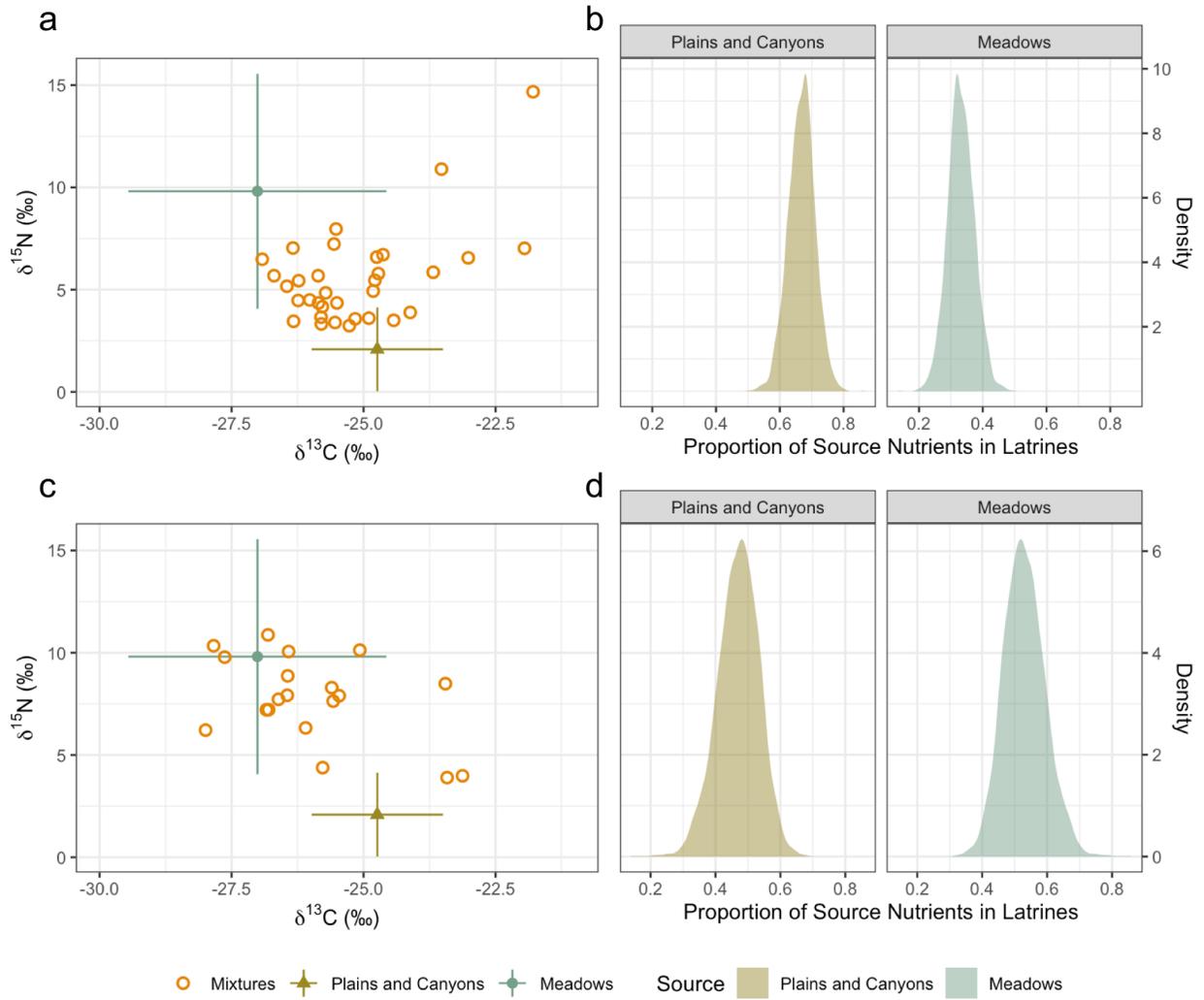


Figure 5.



## Supplementary Information

**Table 1.** Mixed-effects model estimates, confidence intervals, and p-values documenting the effects of vicuña latrines (compared to reference sites) on a variety of soil nutrients across plains, canyons, and meadows in San Guillermo National Park, Argentina sampled in March 2020.

Shaded rows with bolded p-values indicate soil variables significantly impacted by latrines. All mixed-effects models included Plot ID as a random intercept.

Response Variable	Habitat	Reference Estimate	Reference Lower CI	Reference Upper CI	Latrine Estimate	Latrine Lower CI	Latrine Upper CI	P-Value
% N	Plains	0.04826	0.03786	0.06151	0.09923	0.06086	0.16173	< <b>0.001</b>
% C	Plains	0.48587	0.36505	0.64642	1.03896	0.5875	1.83093	< <b>0.001</b>
P	Plains	643.29301	546.80137	756.81211	738.41246	551.54739	988.58769	<b>0.03653</b>
K	Plains	27899.11348	24923.00348	31230.60725	29478.63855	24880.57605	34926.4474	0.05728
Ca	Plains	14129.54712	11833.01437	16871.78731	14403.04351	11123.85973	18648.89233	0.64261
Fe	Plains	40829.22441	33853.55409	49242.26158	37791.42278	28023.56485	50963.95278	0.17483
Mg	Plains	8769.95637	7276.17172	10570.41224	8535.88434	6399.66882	11385.17062	0.6007
Mn	Plains	699.52779	602.71194	811.89552	664.9498	516.50919	856.05106	0.33777
Na	Plains	17956.52013	16256.20746	19834.67645	19344.04961	16916.89345	22119.4427	< <b>0.001</b>
Zn	Plains	87.82458	78.10628	98.75208	85.91083	69.19237	106.66885	0.66319
% N	Canyons	0.03901	0.03121	0.04875	0.08168	0.05002	0.13334	< <b>0.001</b>
% C	Canyons	0.47988	0.37835	0.6085	0.91274	0.53518	1.55251	< <b>0.001</b>
P	Canyons	674.23381	609.7985	745.47777	746.16451	612.42025	909.11669	<b>0.0407</b>
K	Canyons	30719.32259	28174.76157	33493.6918	31602.70767	27321.61794	36554.61159	0.3471
Ca	Canyons	12987.21234	11524.08813	14636.0981	12865.94704	10839.31402	15271.50086	0.72303

<b>Fe</b>	Canyons	37517.0216 3	33745.2469 6	41710.3752	36859.1963 3	30344.2048 9	44772.9758 8	0.6953 8
<b>Mg</b>	Canyons	7698.41975	6709.78558	8832.7214	7647.87714	6218.10106	9406.41269	0.8526 7
<b>Mn</b>	Canyons	622.28105	563.32506	687.4072	618.49533	525.03129	728.59748	0.8524 3
<b>Na</b>	Canyons	22395.9575 4	20100.2330 7	24953.8854 7	22333.4114 4	19172.1607 1	26015.9130 8	0.9019 1
<b>Zn</b>	Canyons	81.78523	75.41348	88.69534	85.75488	72.2105	101.83975	0.3062 6
<b>% N</b>	Meadow s	0.19672	0.12884	0.30027	0.43154	0.22127	0.83995	<b>&lt;0.001</b>
<b>% C</b>	Meadow s	4.18843	2.95936	5.89692	6.60637	3.91573	10.93544	<b>&lt;0.001</b>
<b>P</b>	Meadow s	668.21416	555.3494	804.01666	814.0276	580.36768	1141.76058	<b>0.0116 3</b>
<b>K</b>	Meadow s	21850.9062 1	17206.0121 9	27749.7247 4	22067.7369 1	16086.3479 2	30273.1866	0.8019 6
<b>Ca</b>	Meadow s	34720.5286 4	23964.5756 8	50304.0456 5	36510.5788 6	18627.3389 3	71562.6839 2	0.7444 1
<b>Fe</b>	Meadow s	30318.0783 1	25412.6576 8	36170.3952 5	27722.3049 8	19958.8893 6	38505.4588 7	0.2486 5
<b>Mg</b>	Meadow s	8584.15796	6983.51607	10551.6715 6	10714.1699 6	7095.38482	16178.6063 6	<b>0.0347 4</b>
<b>Mn</b>	Meadow s	464.75678	379.78891	568.734	483.99349	335.1207	699.00098	0.6313 8
<b>Na</b>	Meadow s	16000.8337	12347.1413 9	20735.7048 1	15351.6597 5	10272.3175 7	22942.5789 5	0.5690 6
<b>Zn</b>	Meadow s	77.56212	69.03273	87.14537	74.38816	60.67641	91.1985	0.3479