

ARTICLE

Vicuña antipredator diel movement drives spatial nutrient subsidies in a high Andean ecosystem

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Abstract

Large animals could be important drivers of spatial nutrient subsidies when they ingest resources in some habitats and release them in others, even moving nutrients against elevational gradients. In high Andean deserts, vicuñas (*Vicugna vicugna*) move daily between nutrient-rich wet meadows, where there is abundant water and forage but high risk of predation by pumas (*Puma concolor*), and nutrient-poor open plains with lower risk of predation. In all habitats, vicuñas defecate and urinate in communal latrines. We investigated how these latrines impacted soil and plant nutrient concentrations across three habitats in the Andean ecosystem (meadows, plains, and canyons) and used stable isotope analysis to explore the source of fecal nutrients in latrines. Latrine soils had higher concentrations of nitrogen, carbon, and other nutrients than did nonlatrine soils across all habitats. These inputs corresponded with an increase in plant quality (lower C:N) at latrine sites in plains and canyons, but not in meadows. Stable isotope mixing models suggest that ~7% of nutrients in plains latrines originated from vegetation in meadows, which is disproportionately higher than the relative proportion of meadow habitat (2.6%) in the study area. In contrast, ~68% of nutrients in meadow latrines appear to originate from plains and canyon vegetation, though these habitats made up nearly 98% of the study area. Vicuña diel movements thus appear to concentrate nutrients in latrines within habitats and to drive cross-habitat nutrient subsidies, with disproportionate transport from low-lying, nutrient-rich meadows to more elevated, nutrient-poor plains. When these results are scaled up to the landscape scale, the amount of nitrogen and phosphorus subsidized in soil at plains latrines was of the same order of magnitude as estimates of annual atmospheric nitrogen and phosphorus deposition for this region (albeit far more localized and patchy). Thus, vicuña-mediated nutrient redistribution and deposition appears to be an important process impacting ecosystem functioning in arid Andean environments, on par with other major inputs of nutrients to the system.

KEYWORDS

antipredator behavior, diel movement, high Andes, latrines, nutrient hotspots, *Puma concolor*, spatial subsidies, *Vicugna vicugna*

INTRODUCTION

Ecosystems are inherently open systems in which energy, organisms, resources, and information flow across porous boundaries (Gounand et al., 2018; Gravel, Guichard, et al., 2010; Little et al., 2022; Loreau et al., 2003). These movements can result in spatial subsidies with cascading effects on ecosystem structure and function by altering species coexistence (Gravel, Mouquet, et al., 2010; Leroux & Loreau, 2008), plant community composition (Croll et al., 2005; Maron et al., 2006), and food web stability (Gounand et al., 2014; Rosenzweig, 1971). In heterogeneous environments, spatial subsidies from high- to low-productivity sites can be particularly impactful, markedly altering numerous ecosystem properties in recipient habitats (Hocking & Reynolds, 2011; Polis & Hurd, 1995; Polis et al., 1997; Sanchez-Pinero & Polis, 2000), although reciprocal subsidies between such habitat types can also be impactful in both high- and low-productivity environments (Nakano & Murakami, 2001).

Animals can be vectors of spatial nutrient subsidies whenever they consume resources in some habitats and excrete and egest them elsewhere as they move within and between ecosystems (Doughty et al., 2016; Ellis-Soto et al., 2021; McInturf et al., 2019; Subalusky et al., 2015). These movements can be motivated by numerous ecological factors (Kauffman et al., 2021), most prominently spatiotemporal changes in resource availability (Fryxell & Sinclair, 1988; Middleton et al., 2018) and predation risk (Courbin et al., 2018; Kohl et al., 2018; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). These spatial subsidies can recur frequently, as in diel movements between habitats or vertical diel movements within a water column (Roman & McCarthy, 2010), or be episodic, as during seasonal migrations across broader landscapes (Bauer & Hoyer, 2014; Kitchell et al., 1999; Subalusky et al., 2017). Furthermore, unlike passive geophysical transport of subsidies, animals can actively transport nutrients against strong environmental gradients, including from lower to higher elevations, from concave to convex surfaces, or against the flow of water or prevailing winds (McInturf et al., 2019).

Large mammalian herbivores may be important nutrient vectors in landscapes where habitats differ in resource availability. Their large body size allows them to range over large expanses while consuming, processing, transporting, and releasing large amounts of nutrients (Doughty et al., 2016; Subalusky & Post, 2018). However, herbivores may also be vulnerable to predation, which can influence their diel and seasonal movement patterns and, hence, the spatial dynamics of nutrient subsidies (Augustine, 2003a; le Roux et al., 2018, 2020; Monk & Schmitz, 2022; Schmitz et al., 2010).

Here we report on the effects of spatial nutrient subsidies across habitats in a high Andean ecosystem in San Guillermo National Park (SGNP) in Argentina. The vicuña (*Vicugna vicugna*), a wild camelid, exhibits diel movements driven by predator avoidance (Karandikar et al., 2023; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019; Smith, Donadio, Pauli, Sheriff, Bidder, & Middleton, 2019). 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, likely because the combination of abundant prey and cover from tall vegetation abets their ambush hunting strategy (Smith et al., 2020; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). In response, vicuñas generally feed in nutrient-rich meadows at midday, when pumas are both less active and easier to detect, and spend nights and crepuscular hours in the safer, but more nutrient-poor, open plains that surround the isolated meadows (Donadio & Buskirk, 2016; Smith et al., 2020; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). Thus, the tradeoff between nutrition and fear of predation drives a diel movement (counter to the elevational gradient) between the nutrient-rich, low-lying wet meadows and nutrient-poor, elevated arid plains.

Vicuñas occur in family groups and release nutrients in communal dung heaps, called latrines (Cassini et al., 2009; Vila, 1994). Most defecation occurs in these latrines, which are thought to help maintain group cohesion and orient individuals within their territories (Franklin, 1983; Vila, 1994). These latrines likely create biogeochemical hotspots that promote plant productivity. In similar montane ecosystems in Peru, vicuña latrines have been associated with increased plant diversity, plant quality, and rates of succession in otherwise nutrient-poor habitats (Franklin, 1983, 2022; Koford, 1957; Reider & Schmidt, 2021). Additionally, in sandy glacial moraine habitat in Tierra del Fuego, latrine sites of guanacos (*Lama guanicoe*), a related camelid, had much higher soil nutrient levels and greater plant species diversity than surrounding sites (Henríquez, 2004). However, the effects of vicuña latrines on soil and plant nutrients and the spatial biogeochemical outcomes of vicuña landscape-scale movement have not been investigated.

Here, we evaluate the impacts of vicuña latrines on soil and plant nutrients and plant diversity across habitats in SGNP. We predicted that soil nutrient concentrations, plant diversity, and plant nutritional quality would be higher in latrine sites than surrounding nonlatrine sites within each habitat. We also predicted that differences in the sources of latrine nutrients would reflect diurnal movements between meadows and plains as vicuñas forage and avoid predation, resulting in a

nutrient subsidy between high- and low-productivity habitats. We tested these predictions by comparing soil and plant nutrients and plant diversity at latrines and nonlatrine sites within survey plots in each habitat and by using stable isotopes of carbon and nitrogen to estimate the sources of nutrients in vicuña fecal matter at latrines.

METHODS

Study area

San Guillermo National Park (SGNP) is a high-elevation (2000–5600 m) protected area encompassing 1660 km² 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 vegetation communities and soil similar to those of plains but are characterized by rough terrain and rocky outcroppings; and meadows, which occur in riparian zones and where groundwater reaches 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, Donadio, Pauli, Sheriff, & Middleton, 2019). Pumas are most successful at 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., 2020; Smith, Donadio, Pauli, Sheriff, Bidder, & Middleton, 2019; Figure 1c). Because of high predation risk, vicuñas tend to avoid canyons when possible; however, vicuñas are compelled to visit meadows despite the high predation risk because water and nutritious forage are highly abundant (Donadio & Buskirk, 2016; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019). 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 open plains (where vicuñas are better able to detect and escape from pumas) at night when risk of predation is generally higher (Donadio & Buskirk, 2016; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019; Smith, Donadio, Pauli, Sheriff, Bidder, & Middleton, 2019).

Within the area of the park where Global Positioning System (GPS)-collared vicuñas were previously studied to assess their responses to predation risk (Smith, Donadio, Pauli, Sheriff, & Middleton, 2019; Smith, Donadio, Pauli, Sheriff, Bidder, & Middleton, 2019), 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 ~1.2 km². Meadows tend to occur along rivers and springs at the bottom of canyons or in shallow valleys surrounded by plains and are generally lower lying than surrounding habitats.

Data collection and laboratory analyses

In each of the three habitats, we established fifteen 50 × 50 m survey plots (45 plots total) (Figure 1). In each habitat, six plots were placed at the sites of smaller control plots established for a previous enclosure experiment (Donadio & 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. During the 2020 growing season, 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. Latrines were fairly clearly delineated circles with densely packed fecal pellets at their centers. We measured the diameter of each latrine with a tape measure, counting the edge of the latrine as the border of the area with densely packed fecal pellets. We measured plant cover at each latrine by placing a 50 × 50 cm quadrat in the center of each latrine and visually estimating the percentage cover of each plant family within the quadrat. We similarly estimated percentage plant cover by family at randomly placed quadrats within each plot.

We collected fecal pellet samples from the center of latrines, choosing pellets that had not been directly exposed to the sun ($n = 33$ plains latrines, $n = 16$ canyon latrines, $n = 19$ meadow latrines). We collected 10-cm-deep soil cores from the center of each latrine (brushing aside fecal pellets and vegetation to expose soil) with a 2-cm-diameter soil corer ($n = 36$ plains latrines, $n = 17$ canyon latrines, $n = 20$ meadow latrines). Where graminoids were growing within the area covered by a latrine and touching fecal matter, we collected green, living leaves from one individual/latrine (sampling was conducted during the growing season; $n = 22$ plains latrines, $n = 11$ canyon latrines, $n = 15$ meadow latrines). We also gathered soil and plant samples from nonlatrine reference sites within each survey plot, aiming to collect at least two reference samples in plots where multiple latrines were present (soil $n = 26$ plains samples, $n = 16$ canyon samples, $n = 20$ meadow samples;

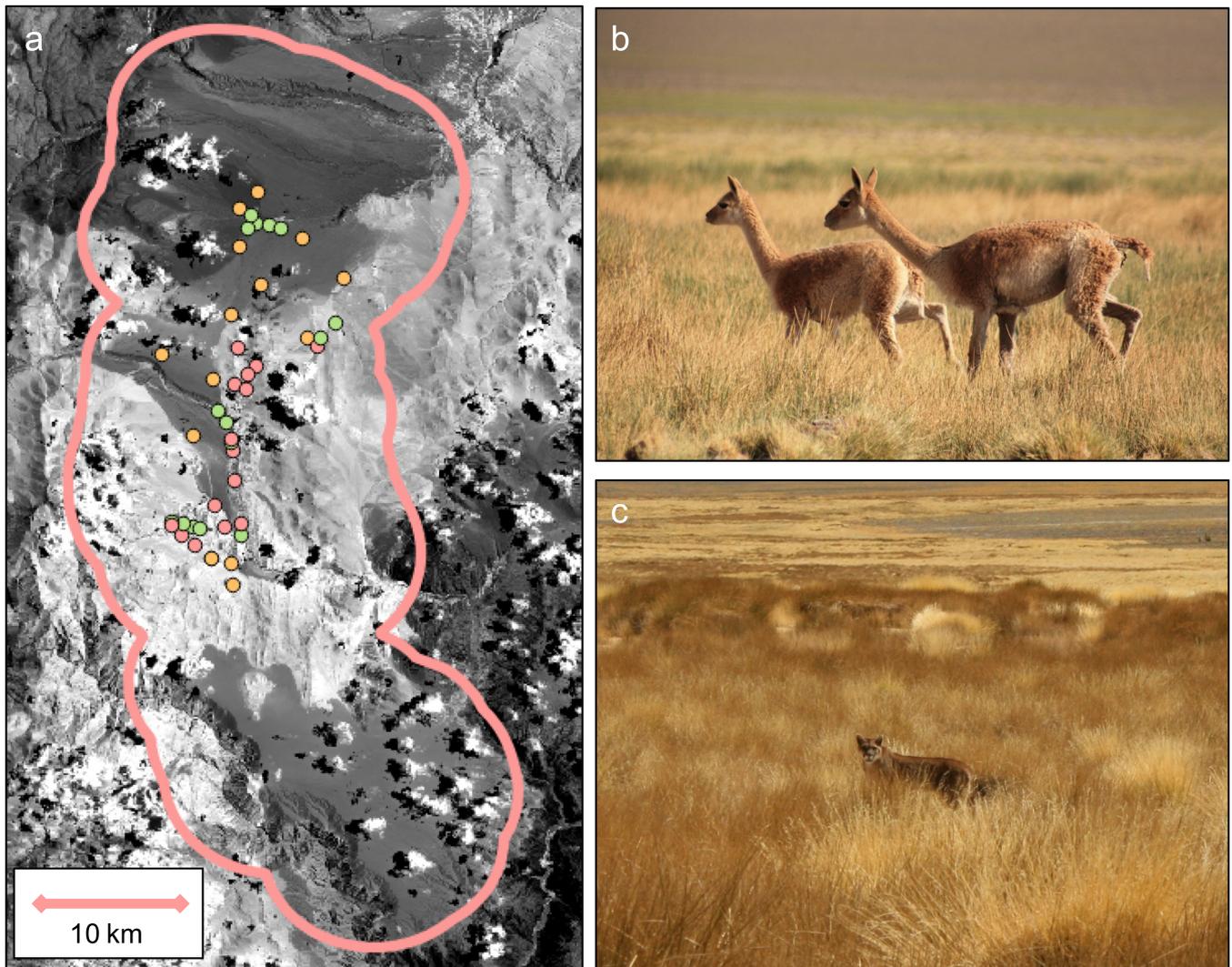


FIGURE 1 Study system in San Guillermo National Park, Argentina. (a) Satellite imagery of study area within SGNP. The pink outline represents the study area boundary (based on the outer bound of the amalgam of individual vicuña home ranges estimated using GPS collar data; see Monk et al., 2022; Landsat-8 imagery courtesy of the U.S. Geological Survey). Orange dots indicate survey 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 dense meadow vegetation. (Photographs by Julia D. Monk).

plant $n = 19$ plains samples, $n = 15$ canyon samples, $n = 21$ meadow samples). We selected nonlatrine sites by spinning a pencil to randomly choose a direction, then walking 6 m from the edge of a latrine in that direction; where latrines were positioned on slopes, we collected reference samples at the same elevational position along the slope. Where latrines were not present, we selected within-plot reference sites by walking 6 m toward the center of the plot from its southeast corner. At nonlatrine sites, we collected soil and plant samples following the same methodology as latrine sampling, selecting the nearest plant individuals of the same genus as the latrine plant samples.

We immediately sieved all soil samples to 2 mm, breaking up soil so only pebbles and roots were retained

on the sieve, and weighed them on an American Weigh Scale Blade digital pocket scale to 0.1 g accuracy. 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 reweighed to obtain air-dried mass. Plant samples were air-dried for 3 days in paper coin envelopes. Fecal samples were oven-dried at 72°C for 1 h 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 Trace Metal Biogeochemistry Lab at the University of Massachusetts, Amherst. We ground soil samples with 3.2-mm-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 a Costech ECS 4010 elemental analyzer (Costech Analytical Technologies) interfaced with a Thermo Delta Plus Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific); $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ ratios are expressed in the δ notation in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite (VPDB) international standard for C and the atmospheric nitrogen (AIR) international standard for N, calibrated with internal laboratory standards. Soil samples were analyzed for P, Na, K, Fe, Mn, Mg, Zn, and Ca concentrations (in milligrams per kilogram) using an inductively coupled plasma-optical emissions spectrometer (ICP-OES); a subset of soil samples was accidentally disposed of prior to ICP-OES analysis, so results are presented for $n = 40$ plains (24 latrine, 16 nonlatrine), $n = 32$ canyons (17 latrine, 13 nonlatrine), and $n = 26$ meadows (13 latrine, 13 nonlatrine).

Statistical analyses

We expected the density and size of latrines to 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 & Buskirk, 2016). We tested whether the number of latrines per 50×50 m plot differed between habitats using a generalized linear model specifying a Poisson distribution with a log-link function. We used the emmeans package to run post hoc tests of pairwise differences between habitats (Lenth et al., 2022). We tested for differences in latrine diameter between habitats using generalized linear models specifying a Gamma distribution and a log-link function to constrain predictions to positive values. Because the number of latrines differed between habitats, with the lowest number ($n = 16$) in canyons, we bootstrapped results by running 1000 iterations of this generalized linear model, sampling (with replacement) 16 diameter values per habitat for each model run, and calculating means and 95% CIs for model test statistics.

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 percentage C and N and plant percentage 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 nonlatrine reference sites, we ran generalized linear mixed-effects models, with plot ID as a random intercept (again with separate models for each habitat), specifying a beta distribution with a logit link function, again using the 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., 2022). We calculated family richness, Shannon diversity, and the inverse Simpson index using the “specnumber” and “diversity” functions and ran ANOVAs to test for differences in these metrics between latrine and reference quadrats, analyzed separately for each habitat. We also used the “adonis2” function to run permutational multivariate ANOVAs (PERMANOVAs) to test for Bray–Curtis compositional dissimilarity between latrine and reference communities in each habitat, using relative cover values and including plot ID as a random grouping in each model.

If vicuña nutrient subsidies in plains reflected diel movements in response to predation risk, we would expect to find that the proportion of fecal nutrients in plains latrines that originate from meadows would be higher than the proportional representation of meadows (2.6%) on the landscape. We estimated the source of latrine nutrients by first isolating all nonlatrine plant $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, percentage C, and percentage N data, using reference samples collected for this study as well as those used in a related research project (Monk, Donadio, Smith, et al., 2024). 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) and “Plains and Canyons” (containing all samples from those two dry habitats, mainly Poaceae species). We ran ANOVAs to verify that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the two source categories differed significantly (both $p < 0.001$, $F_{(1,89)} = 34.7$ and $F_{(1,89)} = 82.81$, respectively). We then ran separate stable isotope mixing models for each habitat, using “Meadows” and “Plains and Canyon” vegetation as the two source data sets and dung collected in each habitat as the mixture data sets, using the simmr package in R (Govan et al., 2023), which runs Markov chain Monte Carlo (MCMC) functions to determine the proportion of

sources in each mixture based on C and N stable isotope ratios. We used trophic enrichment factors of $2.9‰ \pm 0.3$ for $\delta^{15}\text{N}$ and $-0.4‰ \pm 0.5$ for $\delta^{13}\text{C}$ based on observations for llamas (*Lama glama*) in controlled feeding trials (Sponheimer, Robinson, Ayliffe, et al., 2003; Sponheimer, Robinson, Roeder, et al., 2003). We did not specify prior means, thereby defaulting to uninformative priors. We also used the default number of chains, size of burn-in period, and amount of thinning; we ran 50,000 iterations of each MCMC. We used reference sample percentage C and N data to specify elemental concentration means. To assess model fit, we used the “diagnostics” summary function in the *simmr* package to check convergence, assuring that all values were close to 1. We also used the “posterior_predictive” function to check that ~50% of observations were within the 50% posterior predictive distribution. We conducted all statistical analyses in R software (version 3.6.3), and all figures were produced using the “ggplot2” package (Wickham, 2016).

RESULTS

Latrine densities were highest in plains, with a mean of 2.5 latrines per 50×50 m plot (SE ± 0.4 , or 10/ha), while meadows averaged 1.5 latrines/plot (SE ± 0.5 , or 6/ha) and canyons averaged 1.1 latrines/plot (SE ± 0.4 , or 4.4/ha). Latrine densities were significantly higher in plains than in canyons ($Z = 2.90$, $p = 0.01$;

Appendix S1: Table S1; Figure 2), but latrine densities did not significantly differ between meadows and either plains or canyons ($Z = 1.19$, $p = 0.14$ and $Z = -1.12$, $p = 0.51$, respectively; Appendix S1: Table S1; Figure 2). There were no significant differences in latrine diameter in pairwise comparisons between habitats (all $p > 0.05$; Appendix S1: Table S2). Latrines were on average 2 m in diameter and covered an area of ~ 3.1 m².

In plains, latrines (compared to adjacent reference sites) had 2.06 times the soil percentage N ($Z = 5.74$, $p < 0.001$), 2.13 times the soil percentage C ($Z = 5.22$, $p < 0.001$), 1.15 times the P concentrations ($Z = 2.09$, $p = 0.037$), and 1.08 times the Na concentrations ($Z = 4.22$, $p < 0.001$) (Appendix S1: Table S3; Figure 3). Latrines also had 1.06% higher concentrations of soil K than reference sites, although this difference was not quite statistically significant ($Z = 1.90$, $p = 0.057$; Appendix S1: Table S3). Latrines were not significantly associated with concentrations of any other soil nutrients that were measured in plains (all $p > 0.05$; Appendix S1: Table S3). Increases in soil nutrients at plains latrine sites in turn impacted plants at latrines, which had 1.34 times the percentage N (2.0% vs. 1.5%; $Z = 2.78$, $p = 0.005$) and 0.68 times lower C:N ratios (25 vs. 37; $Z = -3.96$, $p < 0.001$) compared to plants at reference sites (Appendix S1: Table S4; Figure 4).

Similarly, in canyons, latrine soil (compared to adjacent reference sites) had 2.1 times the percentage N ($Z = 5.27$, $p < 0.001$) and 1.9 times the percentage C

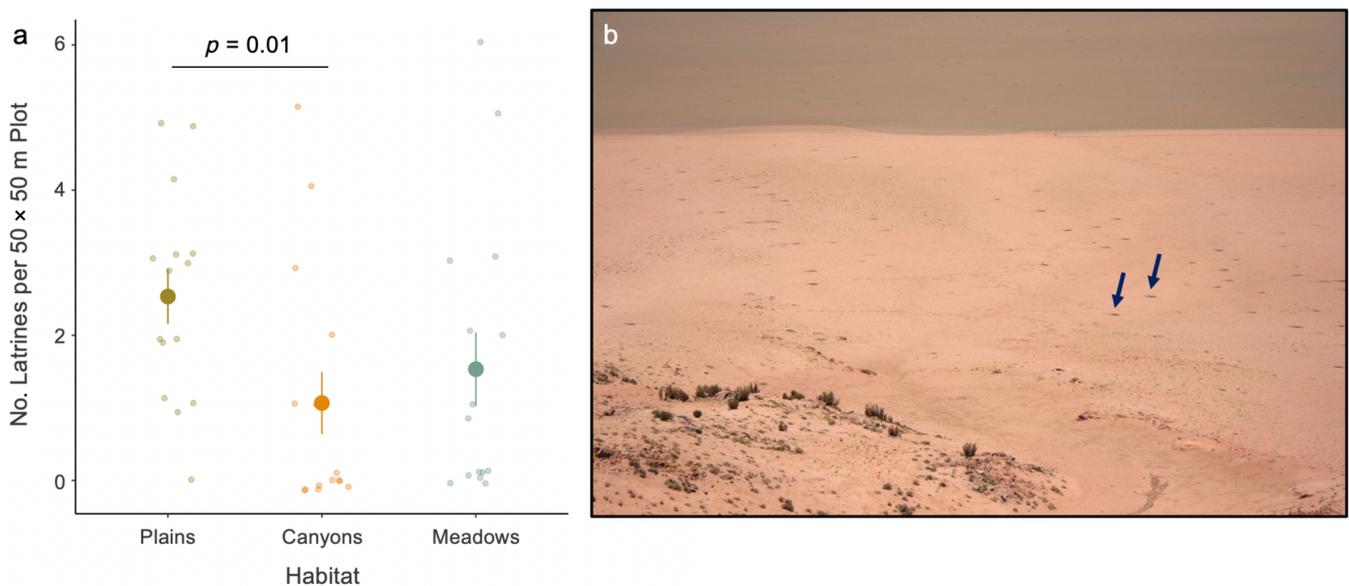


FIGURE 2 Vicuña latrine counts in San Guillermo National Park, Argentina, sampled in March 2020. (a) The number of latrines per 50×50 m plot (2500 m², or 0.25 ha) in plains, canyons, and meadows ($n = 15$ plots/habitat). Large circles and vertical lines denote means \pm SEs; smaller, translucent points show individual counts/plot. Latrine counts were significantly higher in plains than in canyons ($p = 0.01$). (b) Photograph of latrines on slope descending into plains, as seen from top of a hill (photograph by Julia D. Monk). Arrows point to two latrines roughly 20 m apart.

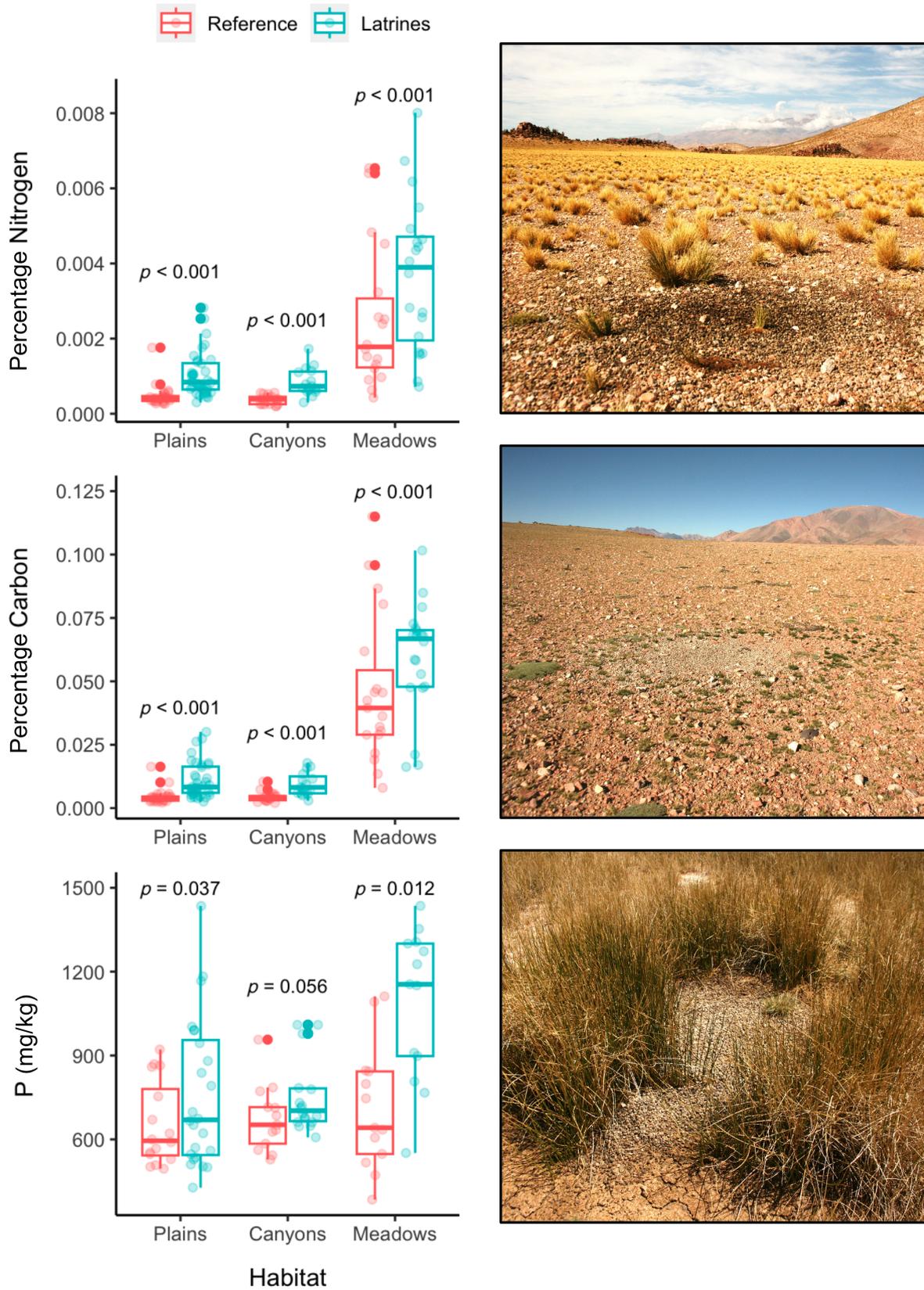


FIGURE 3 Effects of vicuña latrines on soil nitrogen, carbon, and phosphorus in plains, canyons, and meadows in San Guillermo National Park, Argentina, sampled in March 2020. Soil beneath latrines had higher percentage N, percentage C, and P concentrations than reference soil in all three habitats; *p*-values denote results from generalized linear mixed-effects models analyzing differences between latrine and reference treatments. The y-axes for percentage N and percentage C are on a scale from 0 to 1 (e.g., 0.05 = 5%). Photographs on right show (top to bottom) latrines in plains, canyons, and meadows (photographs by Julia D. Monk).

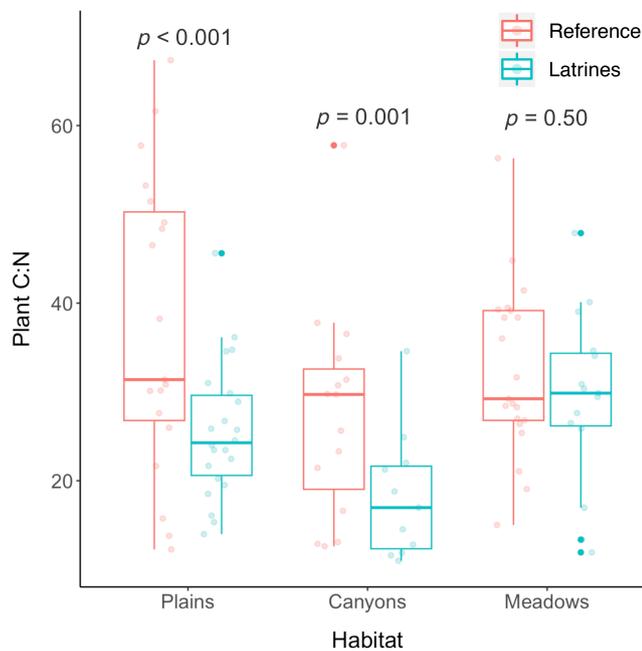


FIGURE 4 Effects of vicuña latrines on plant nutritional quality (carbon to nitrogen ratio) in plains, canyons, and meadows in San Guillermo National Park, Argentina, sampled in March 2020. High plant nutritional quality corresponds to lower C:N (higher proportional nitrogen concentrations). Plants at latrine sites had significantly lower C:N in leaves than plants at reference sites in plains and canyons habitats; p -values denote results from generalized linear mixed-effects models analyzing differences between latrine and reference treatments.

($Z = 4.14$, $p < 0.001$) (Appendix S1: Table S3; Figure 3). Latrine soil also had 1.09 times the P concentrations of reference soil, although this difference was not quite statistically significant ($Z = 1.91$, $p = 0.056$; Figure 3). Latrines were not significantly associated with any of the other elements we measured in canyons (all $p > 0.05$; Appendix S1: Table S3). Plant percentage N was 1.38 times greater at latrines than at reference sites (2.6% compared to 1.9%; $Z = 2.83$, $p = 0.005$), translating into a significant decrease in plant C:N (18 vs. 27; $Z = -3.22$, $p = 0.001$; Appendix S1: Table S4; Figure 4).

In meadows, latrine soil (compared to adjacent reference sites) had 2.19 times the percentage N ($Z = 6.24$, $p < 0.001$), 1.58 times the percentage C ($Z = 4.89$, $p < 0.001$), 1.22 times the P concentrations ($Z = 2.52$, $p = 0.012$) (Figure 3), and 1.25 times the Mg concentrations ($Z = 2.11$, $p = 0.035$) (Appendix S1: Table S3). Latrines were not significantly associated with concentrations of any other soil nutrients that were measured in meadows (all $p > 0.05$, Appendix S1: Table S3). However, higher soil N at latrines did not correspond to changes in plant quality, as plant percentage N and C:N did not differ significantly between latrine sites and reference sites

in meadows ($Z = 0.57$, $p = 0.57$ and $Z = -0.68$, $p = 0.50$, respectively; Appendix S1: Table S4; Figure 4).

Plant cover was significantly lower at latrines (29% mean plant cover) than at adjacent reference sites in meadows (81% mean plant cover; $Z = -4.97$, $p < 0.001$), but plant cover did not differ significantly between latrines and nonlatrine sites in plains (9% vs. 12%, $Z = -1.18$, $p = 0.24$) or in canyons (9% vs. 13%, $Z = -1.45$, $p = 0.15$). Contrary to our expectations, plant family richness, Shannon diversity, and compositional evenness (inverse Simpson index) did not differ between latrines and nonlatrine sites in plains or canyons (all $p > 0.70$), nor were the plant communities significantly compositionally dissimilar (using the Bray–Curtis dissimilarity index) between treatments in these habitats ($F_{1,47} = 1.55$, $p = 0.12$ in plains and $F_{1,25} = 2.01$, $p = 0.09$ in canyons). In meadows, mean family richness was significantly higher at nonlatrine sites (2.0) than at latrines (1.5, $F_{1,30} = 5.11$, $p = 0.03$), though Shannon diversity and compositional evenness did not significantly differ between latrines and nonlatrine sites (both $p > 0.40$). Meadow latrine and reference plant communities were significantly compositionally dissimilar (using the Bray–Curtis dissimilarity index) ($F_{1,30} = 4.98$, $p = 0.016$), with higher relative Poaceae cover and lower relative Juncaceae cover at latrine sites compared to nonlatrine sites.

Vegetation from meadows (wet habitat) and plains and canyons (dry habitats) differed in isotopic space, with vegetation from meadows more enriched in ^{15}N and less enriched in ^{13}C than vegetation from plains and canyons (Figure 5a,c). Stable isotope mixing models estimated that meadow vegetation contributed $\sim 7\%$ (95% CI 2%–13%) to fecal nutrient subsidies in plains, which is disproportionately greater (by more than double) than the proportional representation of meadow habitat across the landscape (2.6%, Figure 5b). Meadow vegetation contributed slightly less to fecal nutrient subsidies in canyons ($\sim 3\%$, 95% CI 1%–7%). In meadows, models estimated that $\sim 68\%$ (95% CI 57%–78%) of fecal nutrients were derived from plains and canyon vegetation, but slightly less than expected given the combined proportional representation of these habitats (97.4%) on the landscape.

DISCUSSION

By investigating soil, plants, and fecal pellets among habitats across the landscape, we revealed that vicuña latrines increased local soil nutrient concentrations and, at latrines in plains and canyons, plant nutritional quality. Deposition of fecal nutrients to create locally

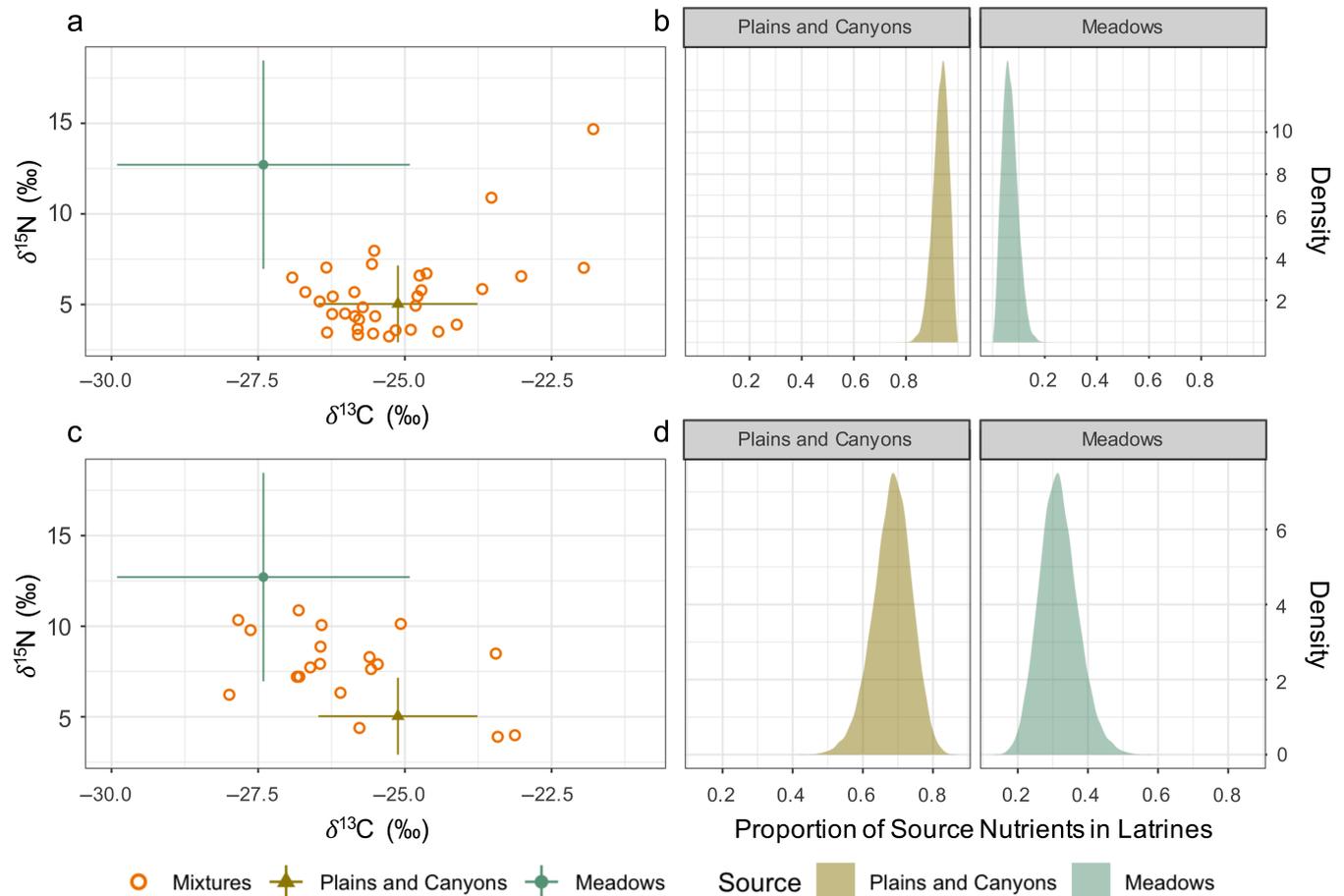


FIGURE 5 Results of stable isotope mixing models determining source of nutrients in vicuña feces collected in plains (a, b) and meadows (c, d). In all panels, data from plants from arid habitats (plains and canyons) are shown in brown, and data from meadow plants are shown in green. The left panels plot the raw data in isospace. Green circles (meadows) and brown triangles (plains and canyons) represent means \pm one SD of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of vegetation (sources), following correction with a trophic enrichment factor. 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). Panels on right display kernel density estimates of modeled probabilities of 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 7% of nutrients in plains fecal samples were primarily derived from meadow vegetation, while roughly 68% of nutrients in meadow fecal samples were primarily derived from plains vegetation.

concentrated soil nutrient inputs increased the spatial heterogeneity within these habitats across the landscape. Generally, large grazing herbivores can play an important role in generating patchiness in ecosystems by concentrating herbivory and nutrient deposition into such localized hotspots, increasing overall landscape heterogeneity (Augustine, 2003a, 2003b; del Ferreyra et al., 2022; Veldhuis et al., 2018). 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 semiarid environments in Spain (Willott et al., 2000).

We found that vicuña diel movements between habitats—likely motivated by the need for large herbivores in dryland habitats to balance food and water acquisition and predator avoidance in dryland areas (see also Augustine et al., 2003; Riginos, 2015; Smith, Donadio, Pauli, Sheriff, & Middleton, 2019)—led to the transportation of nutrients between high-risk meadows and low-risk plains habitats, with reciprocal subsidies between nutrient-rich, low-lying meadows and nutrient-poor, elevated plains. Consequently, latrine sites became biogeochemical hotspots in otherwise less productive plains habitats by increasing the local density and extent of nutrient-elevated soils and plants. Latrines exhibited increased soil C, N, and P in all habitats (as well as soil Na, K, and Mg in certain habitats) and

had elevated plant quality (higher percentage N and lower C:N) in plains and canyons. This finding is a counterexample to the suggestion that herbivores should have negative impacts on soil and plant N availability in nutrient-poor environments (Bardgett & Wardle, 2003; Pastor et al., 2006) and supports the suggestion that animal-mediated nutrient cycling can be particularly impactful for plants in nutrient-limited habitats with lower productivity, where microbially mediated plant litter decomposition is slow to replenish the supply of plant-available nutrients (Monk & Schmitz, 2022; Sitters et al., 2017; Sitters & Olde Venterink, 2015). Similar nutrient-enhancing effects due to herbivore-mediated subsidies to nutrient-poor environments have been documented in the Brazilian Atlantic forest (Villar et al., 2021, 2022), in European farm–forest matrices (Abbas et al., 2012), and in Arctic tundra (Sitters et al., 2017). In contrast, a substantial body of literature suggests that large herbivores can reinforce the disparity between nutrient-rich and nutrient-poor environments by continually using and, thus, recycling and concentrating nutrients in productive patches that they have created (Augustine, 2003a; Augustine et al., 2003; McNaughton et al., 1997). Consistent with this suggestion, we found that vicuñas also moved nutrients from nutrient-poor environments to sustain soil in nutrient-rich meadows as they forage there. However, this subsidy did not impact plant nutrient content in the nutrient-rich meadows, suggesting that vicuña impacts merely contribute to sustaining, but not enhancing, the abundance and quality of plants in meadows.

The flow of nutrients occurred in both directions, and the proportion of meadow-derived nutrients was slightly greater than expected and the proportion of plain- and canyon-derived nutrients was slightly less than expected based on the proportional representation of these habitats in the study area. Thus, we found some support for our hypothesis that vicuña diel movements drive nutrient subsidies to nutrient-poor habitats, although this diel movement also contributes to nutrient deposition in high-risk, nutrient-rich sites. As such, our results support theoretical predictions and other empirical evidence that high-productivity habitats should exert significant effects upon recipient low-productivity habitats even if material flows are reciprocal (Holt, 2004; Stark et al., 2015; Villar et al., 2021).

Nutrient subsidies to plains and canyons did not result in changes in plant diversity or community composition at the family level, unlike in other studies that documented changes in plant community composition and diversity at vicuña latrine sites in nutrient-poor habitats further north in the Andes (Franklin, 1983, 2022; Koford, 1957; Reider & Schmidt, 2021) and at guanaco

latrine sites in southern Chile (Henríquez, 2004). The lack of effect in SGNP may stem from plant diversity in these habitats already being low, or it may be that our taxonomic resolution was too coarse to discern shifts in difficult-to-distinguish graminoid species. Additionally, the vicuña studies in the northern Andes were conducted at higher elevations than SGNP (most of our study area ranged between 3500 and 3800 m), and both the vicuña and the guanaco studies occurred along glacial fronts. Plant communities can turn over quickly with elevation in high montane settings (Carilla et al., 2018; Smithers et al., 2020), so vegetation in these other systems may have been more sensitive to localized increases in soil nutrient inputs. Furthermore, plant communities along the edges of receding glaciers may be in a more active stage of assembly (Pothula & Adams, 2022), such that small changes in local nutrient availability coupled with potential animal-mediated seed dispersal may be more important determinants of community composition where plants are being newly established on recently exposed ground (Henríquez, 2004).

The localized effects of latrine nutrient inputs could seem insignificant when considering the context of the vast SGNP landscape. However, latrines are prevalent throughout the vicuña range within the park, particularly in plains. With a mean of 10 latrines per hectare in the plains (Figure 2) and plains making up roughly 48% (547.2 km²) of the home range of GPS-collared vicuñas in the park, and assuming these latrine densities held constant within vicuña home ranges, there were likely at least 500,000 latrines in plains alone where vicuñas were active at the time of this study (in contrast, meadows make up only 19.6 km², with ~12,000 latrines). With an area of ~3.1 m² each, latrines thus likely cover ~0.3% of the plains landscape (a relatively small area). Nevertheless, based on our results (and accounting for an approximate bulk density of 1.15 g soil/cm³ in plains), latrines likely deposited approximately an additional 97,500 kg N and 18,500 kg P to the top 10 cm of plains soil within the areas where vicuñas were active—nutrient inputs that cascaded up to increase plant quality (lower C:N) in arid plains and canyons, where soil nitrogen availability is generally low. To put these numbers into context, this nitrogen subsidy of ~1.8 kg/ha (at the latrine densities in our plains survey plots) and estimated atmospheric nitrogen deposition rates for this region range between 1 and 5 kg/ha annually (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, vicuñas transport and deposit nitrogen in plains at comparable orders of magnitude to atmospheric nitrogen deposition. Similar scales of herbivore-mediated nitrogen transport and deposition have been documented

in South African savannas (Veldhuis et al., 2018) and North American forests (Murray et al., 2014). Furthermore, the phosphorus subsidy in plains latrine soil (~ 0.34 kg/ha or 0.034 g/m² at the latrine densities in our plains survey plots) is greater than global mean annual total phosphorus deposition rates (Tipping et al., 2014), as has been documented for primate-mediated phosphorus deposition in the Amazon (Stevenson & Guzmán-Caro, 2010), suggesting that vicuñas play a substantial role of determining the distribution of phosphorus in SGNP, transporting and depositing high concentrations of the essential nutrient in latrine sites.

The spatiotemporal development of latrine sites and their biogeochemical impacts with fluctuating use by vicuñas merit further study. The spatial distribution of latrine sites and the magnitude of their impacts may fluctuate as latrines are established, added to, abandoned, and revisited by vicuñas over time (vicuñas will often reuse previously established latrines; Franklin, 1983). Although we attempted to determine which latrines appeared recently used based on the presence and amount of dark, fresh-looking fecal pellets (compared to gray, desiccated fecal pellets), estimating this consistently was difficult and could be flawed due to differences in environmental factors (e.g., sun exposure in open habitats, seasonality of dung deposition) that may have influenced the rate at which fecal pellets dried out. Marking, revisiting, and resampling latrines for soil and plant nutrient content over time would shed important light on the duration of latrine biogeochemical impacts and the extent to which these hotspots are relatively stable or ephemeral over time (Butterworth et al., 2023). Furthermore, latrine nutrient inputs may leach out and diffuse into the surrounding environment over time, particularly on slopes, where precipitation may wash latrine nutrients downhill; such diffusion and subsequent visible influence on latrine-associated vegetation was previously documented in Peru (Franklin, 1983). Because of this, we did not collect nonlatrine samples downhill from latrines on slopes; however, it is also possible that our results somewhat underestimate latrine impacts if nutrients from older latrines diffused >6 m from latrine edges without visible impacts on soil and vegetation.

Whether latrine 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 in plains and canyons could locally supplement forage resources for vicuñas and other, smaller herbivores in the ecosystem (Franklin, 1983; Koford, 1957; Reider & Schmidt, 2021), though vicuñas may also avoid spending time at latrine sites due to the potential risk of disease (Weinstein et al., 2017). Indeed, the rapid spread of sarcoptic mange has already severely impacted the

vicuña population in SGNP in recent years (del Ferreyra et al., 2022; Monk et al., 2022). As vicuña densities have plummeted, the transport and deposition of nutrients at latrine sites have likely declined similarly. Future research should investigate not only how plants and other interacting species respond to declines in vicuña herbivory in the wake of the disease outbreak (Monk et al., 2022) but also how the reduction in latrine formation may impact the ecosystem by potentially slowing nutrient cycling or altering the spatial distribution of nutrients on the landscape.

Our study confirms that vicuña latrine use generates hotspots with elevated soil nutrients and that these hotspots increase plant nitrogen content where nitrogen availability is low. It further demonstrates that the daily movement of vicuñas between high-risk meadows and low-risk plains appears to drive nutrient transport between nutrient-rich and nutrient-poor habitats, with disproportionate transport from low-lying, productive meadows to elevated, less-productive plains. In all habitats, latrines clearly concentrate nutrients into localized patches, increasing spatial heterogeneity. Thus, herbivore latrine use and, to a certain extent, predator–prey interactions may play an important role in the cycling and redistribution of nutrients in the Andean ecosystem.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Monk, Donadio, Gregorio, et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.kh18932dq>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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