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 cycling and 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 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, and other nutrients in 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 ~7% of nutrients in latrines in plains originated from vegetation in meadows, even though meadows accounted for only 2.6% of the study area; in contrast, ~68% of nutrients in latrines in meadows originated from plains and canyon vegetation, though these habitats made up nearly 98% of the study area. Thus, vicuña diel migrations, motivated by predator avoidance, appear to drive reciprocal nutrient subsidies between low-lying, nutrient-rich meadows and more elevated, nutrient-poor plains, and latrines also recycle and concentrate nutrients within habitats. Scaling these results up to the landscape scale, we found that the amount of additional nitrogen and phosphorus in soil at plains latrines were of the same order of magnitude as estimates of annual

atmospheric nitrogen and phosphorus deposition for this region (albeit far more localized and patchy). 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 vertical migrations within a water column (Roman and McCarthy 2010), 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^2 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. 1c). 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 ~1.2 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 × 50 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 exclosure 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, 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 10-cm deep soil samples beneath each latrine (brushing aside fecal pellets and vegetation to expose soil) with a 2-cm diameter soil corer. We similarly collected soil samples at randomly chosen reference sites within each plot. We collected green, living leaves from graminoids growing out of latrines, and collected leaves from the same taxa 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 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 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 Trace Metal 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, $\delta^{13}C$, and $\delta^{15}N$ using an elemental analyzer, and soil samples were analyzed for P, Na, K, Fe, Mn, Mg, Zn, and Ca concentrations (mg/kg) using an inductively coupled plasma – optical emissions spectrometer (ICP-OES).

Research permits were issued by the Argentine National Parks Administration (APN). Samples were obtained from and property of the APN and were exported under permits issued by the Argentine Ministry of Environmental and Sustainable Development, 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. 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 family 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 ‘adonis2’ function to run PERMANOVAs to test for compositional dissimilarity between latrine and reference communities in each habitat, including plot ID as a random grouping in each model.

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 δ^{13}C, δ^{15}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) and "Plains and Canyons" (containing all samples from those two dry habitats). We ran ANOVAs to verify that $\delta^{13}C$ and $\delta^{15}N$ 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 used trophic enrichment factors of 2.9‰ ± 0.3 for $\delta^{15}N$ and -0.4‰ ± 0.5 for $\delta^{13}C$ based on observations for llamas (*Lama glama*) in controlled feeding trials (Sponheimer 2003a,b). 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 ± 0.38; plots have an area of 2500 m^2), while meadows averaged 1.5 latrines/plot (SE ± 0.51) and canyons averaged 1.1 latrines/plot (SE ± 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 ~3.1 m^2.

In plains, latrines had significantly greater soil percent N by 106%, percent C by 113%, P concentrations by 15%, and Na concentrations by 8% compared to adjacent reference sites

(Table S1, Fig. 3). Latrines did not significantly 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 34% higher percent N (2.0% vs. 1.5%, $p < 0.01$) and 32% lower C:N ratios (25 vs 37, $p < 0.001$) than plants at reference sites (Fig. 4).

Similarly, in canyons, latrines had significantly greater soil percent N by 110% and percent C by 90% compared to reference sites (Table S1, Fig. 3). Latrines also had 9% greater concentrations of soil P than reference soil, though this effect did not meet our $\alpha < 0.05$ threshold for statistical significance, but had no effect on any of the other elements we measured (Table S1, Fig. 3). Plant percent N was 38% greater at latrines than at reference sites (2.6% compared to 1.9%; $p < 0.01$), translating into a 33% decrease in plant C:N ($p = 0.001$; Fig. 4).

In meadows, latrines had significantly greater soil percent N by 119%, percent C by 58%, P concentrations by 22%, and Mg concentrations by 25% compared to adjacent reference sites (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 (both $p > 0.05$, Fig. 4).

Plant cover was significantly lower at latrines (29% estimated mean plant cover) than at adjacent reference sites in meadows (81% estimated mean plant cover; $p < 0.001$), but plant cover did not differ significantly 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 references sites in plains ($p = 0.89$ and $p = 0.91$, respectively) or canyons ($p = 0.92$ and $p = 0.35$, respectively), nor were the plant communities significantly dissimilar between treatments in these habitats ($p = 0.12$ in plains and $p = 0.35$ in canyons). In meadows, mean family 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 lower Juncaceae and Cyperaceae cover in quadrats than adjacent reference sites (though Poaceae 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}N and less enriched in ^{13}C than vegetation from plains and canyons (Fig. 5a, c). Stable isotope mixing models revealed that meadow vegetation contributed ~7% (95% CI 2%-13%) to fecal nutrient subsidies in plains, disproportionately greater (by almost double) than the proportional representation of meadow habitat across the landscape (Fig. 5b). Meadow vegetation contributed slightly less to fecal nutrient subsidies in canyons (~3%, 95% CI 1%-7%). In meadows, models estimated that ~68% (95% CI 57%-78%) of fecal nutrients were derived from plains and canyon vegetation – a substantial subsidy, but slightly less than expected given their combined proportion on the landscape.

Discussion

By systematically investigating latrine soil, plants, and fecal pellets across the landscape, we determined that vicuña latrine use increases local soil nutrient concentrations and, in arid habitats, plant nutritional quality. This likely increases spatial heterogeneity as nutrients consumed from across the landscape become concentrated into localized deposits. We also found some evidence that vicuña diel migrations – likely motivated by the need to balance food and water acquisition and predator avoidance – transport nutrients between high- and low-risk sites, with reciprocal subsidies between fertile, low-lying meadows and 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.

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 (Sitters and Olde Venterink 2015, Sitters et al. 2017, Monk and Schmitz 2022). Thus, the impacts of nutrient deposition by animals vary depending on the extent to which those nutrients are (co)limiting in a given environment (Sitters et al. 2017, Subalusky and Post 2018, le Roux et al. 2020). 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 could seem insignificant within the context of a vast landscape, latrines are prevalent throughout the vicuña home range in the park, particularly in plains. With an average of 2.5 latrines per 2500 m^2 plot in the plains (Fig. 2), and plains making up roughly 48% (547.2 km^2) 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 547,000 latrines in plains alone where vicuñas were active at the time of this study (in contrast, meadows make up only 19.6 km^2, with ~ 11,800 latrines). With an area of ~3.1m^2 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/cm^3 in plains), the presence of the latrines on the landscape likely contributed approximately 97,500 additional kg of N and 18,500 kg of P to the top 10 cm of plains soils within the area where vicuñas were active – nutrient inputs 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 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 (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 additional phosphorus in plains latrine soil (~0.34 kg/ha or 0.034g/m^2 at the latrine densities in our plains survey plots) 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 where vicuñas are active.

Isotopic data showed that ~7% of fecal nutrients in plains derived from meadows, and ~68% of fecal nutrients in meadows originated in arid habitats, suggesting that vicuñas transport and deposit nutrients across habitat boundaries in both directions as they move across the landscape. Theory predicts 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). Indeed, we found that latrines were associated with greater plant nitrogen content in plains, suggesting that this reciprocal subsidy may have had differential impacts in habitats where nutrients were limiting. 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 spatial extent of these habitats on the landscape. Thus, we found some support for our hypothesis that vicuña diel migrations drive nutrient subsidies from meadows to plains, though the reciprocal subsidy from plains (and canyons) to meadows was large; accordingly, this diel migration may contribute more to nutrient recycling and distribution in high-risk sites. Nevertheless, latrines were far more numerous in plains, as meadows are quite limited in extent, suggesting the overall quantity of vicuña-mediated nutrient inputs in these refuge habitats was greater. Furthermore, this mode of transport represents a counter-elevational subsidy, in contrast to most abiotic nutrient flows. Generally, vicuñas appear to redistribute nutrients within and between all habitats, concentrating resources in latrine hotspots that may increase heterogeneity and, where nitrogen availability is low, increase plant quality.

Our research suggests that diel migrations of large mammals in terrestrial systems transports nutrients between fertile, low-lying, high-risk zones and safer, elevated, more nutrient-poor 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 transport between, for example, watering holes and open savanna habitats. Thus, antipredator responses can drive the redistribution of nutrients at the landscape level, with effects that cascade up to primary producers.

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 in plains and canyons 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 (Ferreyra et al. 2022, Monk et al. 2022). As vicuña densities have rapidly declined, the transport and deposition of nutrients from at latrine sites 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 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 and plant 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 reciprocal nutrient transport between nutrient-rich and nutrient-poor habitats; 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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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 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 the middle of dense meadow vegetation.

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 m^2, or 0.25 km^2) in plains, canyons, and meadows. Circles and vertical lines denote means ± 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 higher % N, % 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 % 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). 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.

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 ± one standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values of vegetation (sources), following correction with a trophic enrichment factor. Open orange circles represent $\delta^{13}C$ and $\delta^{15}N$ 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 7% of nutrients in plains fecal samples were likely derived from meadow vegetation, while roughly 68% of nutrients in meadow fecal samples were likely derived from plains vegetation.

Figure 1.

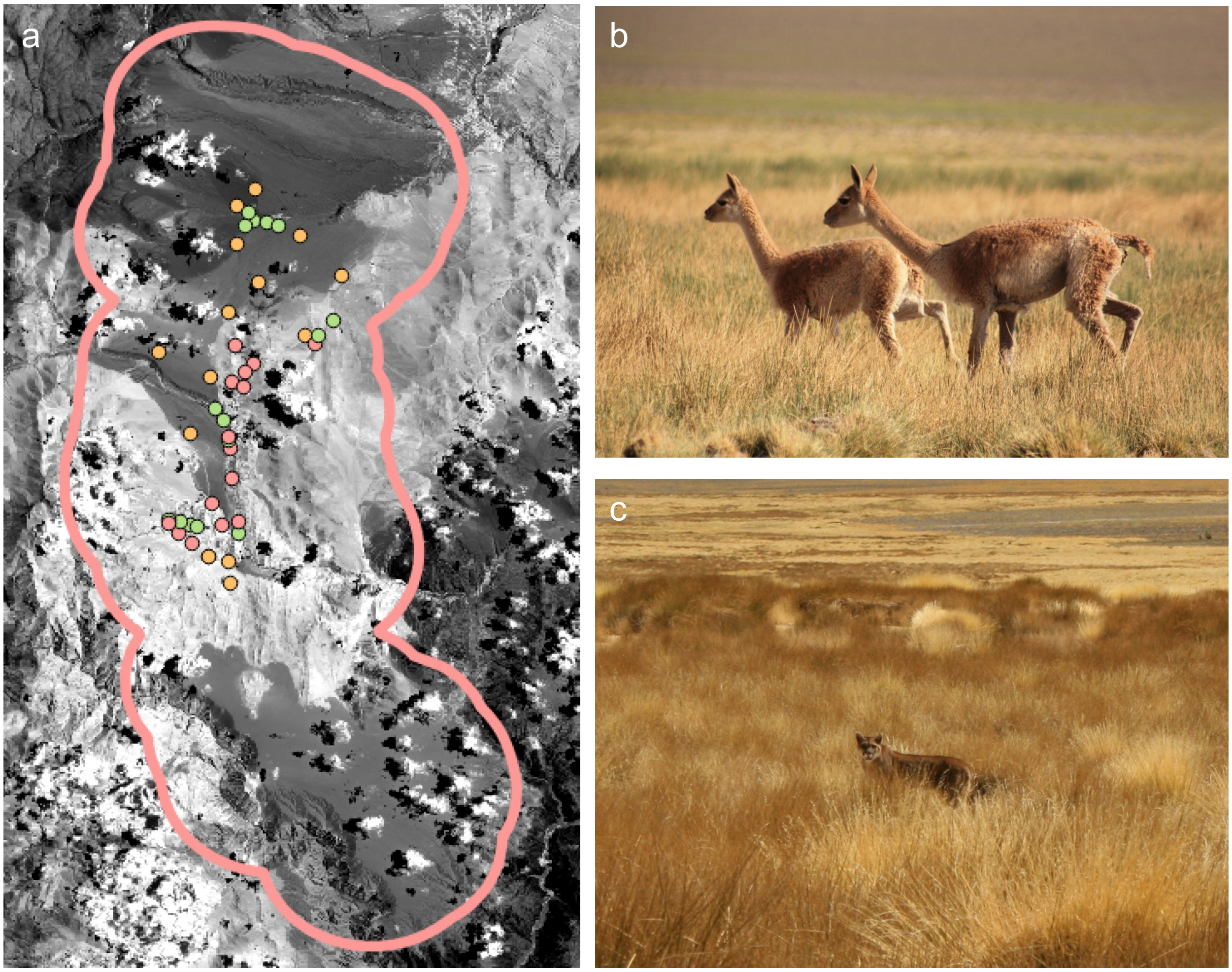


Figure 2.

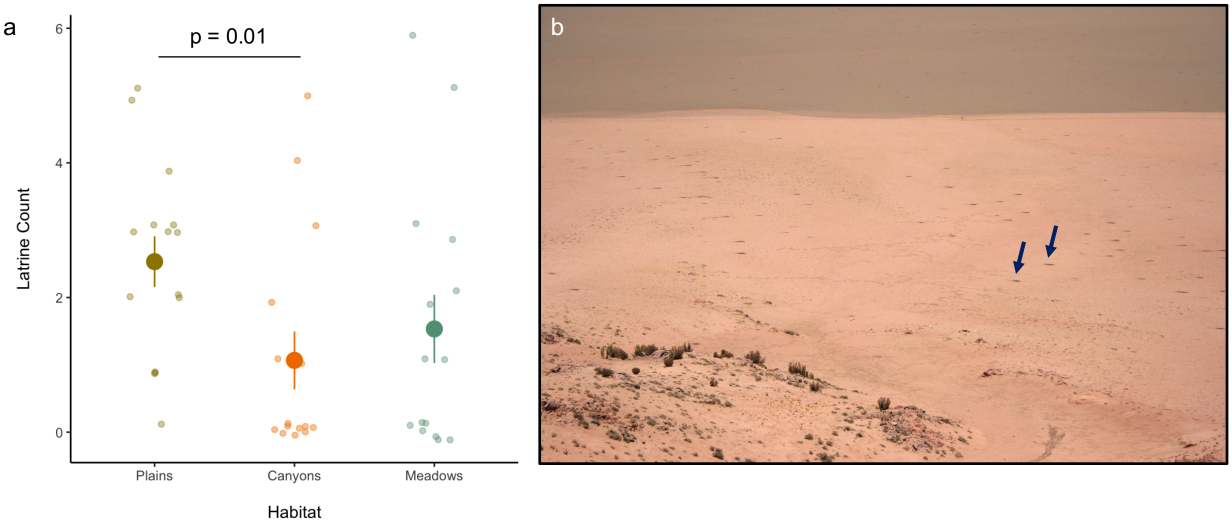
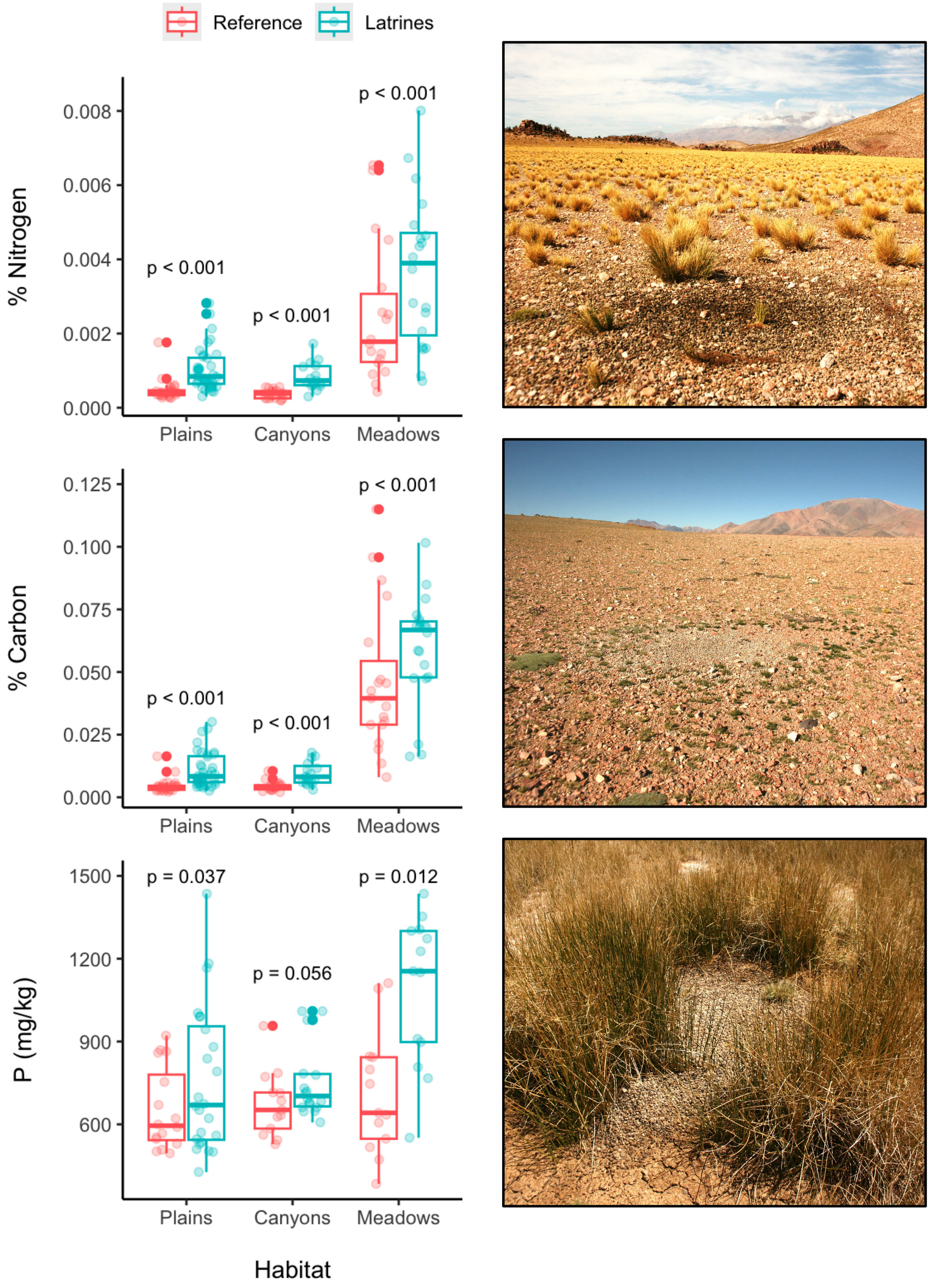


Figure 3.



Reference
Latrines
% Nitrogen
0.008
0.006
0.004
0.002
0.000
p < 0.001
p < 0.001
p < 0.001
Plains
Canyons
Meadows
% Carbon
0.125
0.100
0.075
0.050
0.025
0.000
p < 0.001
p < 0.001
p < 0.001
Plains
Canyons
Meadows
P (mg/kg)
1500
1200
900
600
p = 0.037
p = 0.056
p = 0.012
Plains
Canyons
Meadows
Habitat

Figure 4.

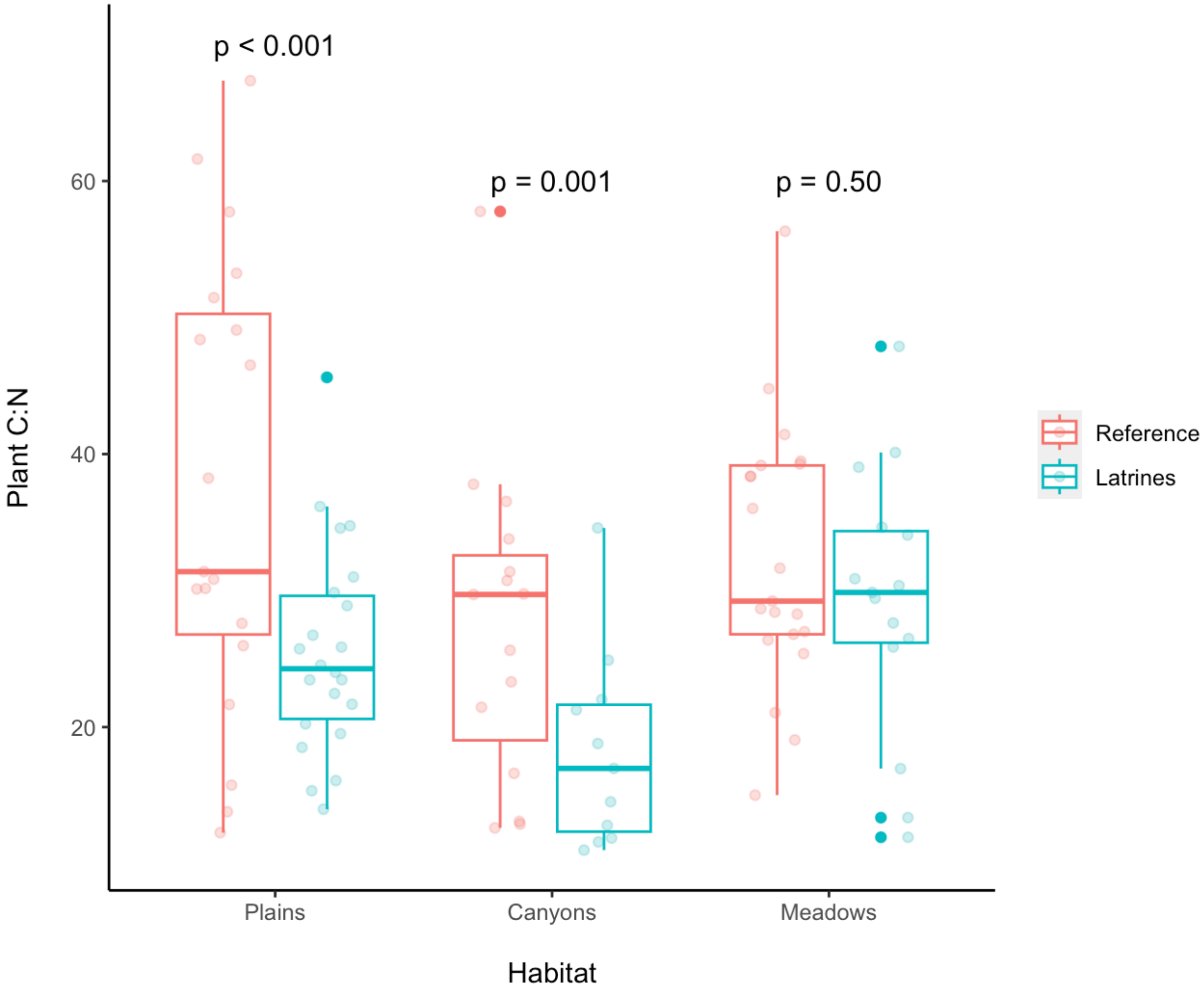
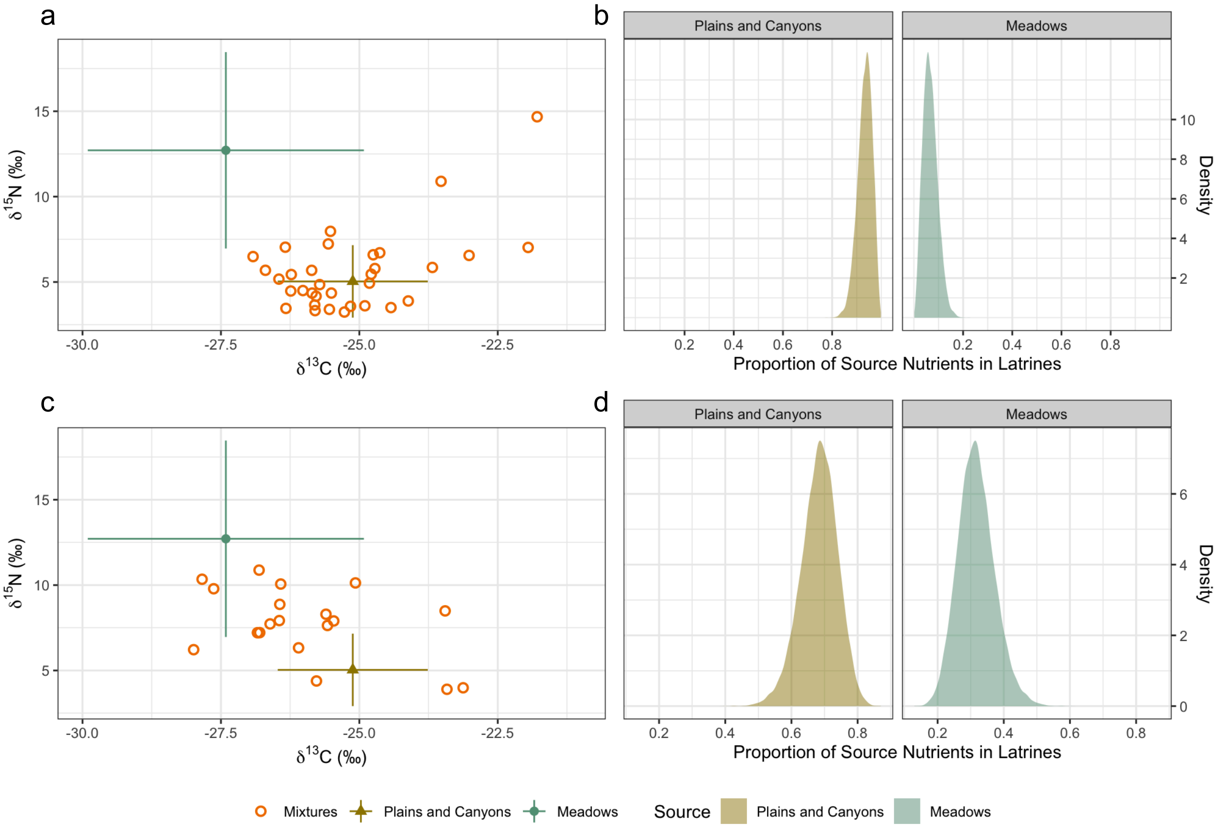

p < 0.001
p = 0.001
p = 0.50
60
40
20
Plant C:N
Plains
Canyons
Meadows
Habitat
Reference
Latrines

Figure 5.


a
b
c
d
δ15N (‰)
δ13C (‰)
-30.0
-27.5
-25.0
-22.5
5
10
15
Plains and Canyons
Meadows
0.2
0.4
0.6
0.8
Proportion of Source Nutrients in Latrines
Density
2
4
6
8
10
0
Mixtures
Plains and Canyons
Meadows
Source
Plains and Canyons
Meadows

Supplementary Information

Table 1. Mixed-effects model estimates, 95% 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 that differ significantly between latrines and reference sites at an $\alpha < 0.05$ significance threshold; shaded rows without bolded p-values indicate variables for which $p \sim 0.05$. 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	0.048	0.038	0.062	0.099	0.061	0.16	**<0.001**
% C	Plains	0.49	0.37	0.65	1.04	0.59	1.83	**<0.001**
P	Plains	643	547	757	738	552	989	**0.037**
K	Plains	27899	24923	31231	29479	24881	34926	0.057
Ca	Plains	14130	11833	16872	14403	11124	18649	0.64
Fe	Plains	40829	33854	49242	37791	28024	50964	0.18
Mg	Plains	8770	7276	10570	8536	6340	11385	0.60
Mn	Plains	700	603	812	665	517	856	0.34
Na	Plains	17957	16256	19835	19344	16917	22119	**<0.001**
Zn	Plains	88	78	99	86	69	107	0.66
% N	Canyons	0.04	0.031	0.049	0.082	0.049	0.14	**<0.001**
% C	Canyons	0.48	0.37	0.61	0.92	0.53	1.6	**<0.001**
P	Canyons	674	611	744	734	610	884	0.056
K	Canyons	30717	28154	33512	31643	27300	36677	0.34
Ca	Canyons	12990	11522	14644	12854	10811	15283	0.70
Fe	Canyons	37514	33681	41784	36347	30164	43798	0.43
Mg	Canyons	7699	6696	8853	7582	6185	9293	0.64
Mn	Canyons	622	562	689	614	522	723	0.67

Na	Canyons	22390	20088	24956	22414	19255	26092	0.96
Zn	Canyons	82	76	88	84	73	98	0.46
% N	Meadows	0.20	0.12	0.30	0.43	0.22	0.84	**<0.001**
% C	Meadows	4.1	2.8	5.9	6.6	3.9	11	**<0.001**
P	Meadows	668	555	804	814	580	1142	**0.012**
K	Meadows	21851	17206	27750	22068	16086	30273	0.80
Ca	Meadows	34721	23965	50304	36511	18627	71563	0.74
Fe	Meadows	30318	25413	36170	27722	19959	38505	0.25
Mg	Meadows	8584	6984	10552	10714	7095	16179	**0.035**
Mn	Meadows	465	380	569	484	335	699	0.63
Na	Meadows	16001	12347	20736	15352	10272	22943	0.57
Zn	Meadows	78	69	87	74	61	91	0.35