



Linking predation risk, ungulate antipredator responses, and patterns of vegetation in the high Andes

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Whether large carnivores indirectly influence vegetation via prey behavior remains controversial because available evidence is largely correlational, and recent field experiments have found weak associations between risk experienced by prey and vegetative responses to herbivory. We combined observational data and a field experiment to test whether an ambush predator—the puma (*Puma concolor*)—affected the antipredator behavior of its primary ungulate prey—the vicuña (*Vicugna vicugna*)—which in turn had cascading effects on vegetation. We predicted that strong protective effects of pumas on vegetation would be most apparent in habitats where cover and terrain (i.e., physical complexity) facilitated the ambushing strategy of pumas. In 3 different habitats, we evaluated the relationships among predation risk, vicuña behavior, and—by deploying vicuña exclosures—vegetation structure and productivity. We also examined habitat-specific rates of vegetative regrowth. Risky habitats presented high physical complexity, a disproportionately large number of vicuñas killed by pumas, and high relative abundance of pumas. In these habitats, vicuñas displayed strong antipredator behaviors and exclosures did not affect vegetation, suggesting that pumas indirectly protected plants. Conversely, a safe habitat presented low structural complexity, a disproportionately low number of vicuñas killed by pumas, and low relative abundance of pumas. Here, vicuñas relaxed antipredator behaviors and exclosures had strong effects on vegetation. In 1 habitat deemed as risky, however, cascading effects were offset likely because water and nutrients were readily available to plants and regrowth was rapid. Our results show that large ambush carnivores can positively affect vegetation via nonconsumptive effects on their prey, and that these effects are habitat mediated. However, primary productivity modulated the strength of such effects, with high primary productivity dampening the observed cascading effects.

Si los grandes carnívoros terrestres afectan indirectamente la vegetación vía cambios en el comportamiento de sus presas es controversial porque la evidencia existente es largamente correlacional, y experimentos de campo recientes encontraron una débil asociación entre el riesgo de depredación y las respuestas de la vegetación a la presión de pastoreo. En este trabajo evaluamos si un depredador de emboscada—el puma (*Puma concolor*)—afecta las respuestas antidepredador de su presa principal—la vicuña (*Vicugna vicugna*)—con efectos de cascada sobre la vegetación (i.e., gramínoideas). Predijimos que el efecto protector de los pumas sobre la vegetación sería más evidente en hábitats donde la cobertura y el terreno (i.e., complejidad estructural) facilitan la estrategia de emboscada del puma. En tres hábitats diferentes, evaluamos las relaciones entre el riesgo de depredación, el comportamiento de las vicuñas y—mediante la utilización de clausuras—la estructura y productividad de la vegetación. También examinamos tasas de rebrote en cada hábitat. Los hábitats riesgosos presentaron gran complejidad estructural, un número desproporcionadamente alto de vicuñas depredadas por pumas, y una alta abundancia relativa de pumas. En estos hábitats, las vicuñas mostraron fuertes comportamientos antidepredador y las clausuras afectaron levemente la vegetación, sugiriendo que los pumas indirectamente protegen las plantas. Contrariamente, el hábitat definido como seguro presentó poca complejidad estructural, un número desproporcionadamente bajo de vicuñas depredadas por pumas, y una baja abundancia relativa de pumas. Aquí, las vicuñas relajaron sus comportamientos antidepredador y las clausuras tuvieron un fuerte efecto sobre la vegetación. Sin embargo, en un hábitat definido como riesgoso los efectos de cascada fueron neutralizados, probablemente porque el agua y los nutrientes estaban disponibles para las plantas permitiendo un rápido rebrote. Nuestros resultados muestran que los grandes carnívoros pueden beneficiar a los productores primarios vía cambios en el comportamiento de sus presas, y que estos efectos están mediados por el tipo de hábitat. No

obstante, la productividad primaria modula la intensidad de estos efectos, con altos niveles de productividad primaria amortiguando los efectos de cascada iniciados por el depredador tope.

Key words: community ecology, fear ecology, predation risk, puma, South American camelids, trophic cascades

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It has been long recognized that predators can directly influence ecological systems by numerically reducing prey populations (Hairston et al. 1960; Paine 1966). However, predators affect ecological patterns and processes by mechanisms that extend beyond the simple killing of prey (Schmitz et al. 2004). One such mechanism, termed the behaviorally mediated trophic cascade (BMTC), occurs when prey respond to the risk of predation by shifting the habitats they occupy or increasing costly vigilance at the expense of foraging (Lima 1998). These antipredator responses can release plants from heavy herbivory, modifying the attributes of plant communities and altering ecosystem function (Schmitz 2008; Schmitz et al. 2010).

Behaviorally mediated trophic cascades have been reported for a diverse array of aquatic and invertebrate systems (Werner and Peacor 2003; Schmitz et al. 2004). However, in systems involving large terrestrial carnivores and their ungulate prey, the occurrence and strength of BMTCs remains controversial (Mech 2012; Peterson et al. 2014) because evidence is largely correlational (Ripple and Beschta 2012) and lacks experimental support (Hebblewhite et al. 2005; Kauffman et al. 2010; Winnie 2012; Marshall et al. 2013). Thus, how large carnivores may—via BMTCs— influence plant communities is unclear, which hinders ecological theory and conservation practice, while society debates the importance of vanishing large predators to the ecological integrity of vast landscapes (Estes et al. 2011; Ripple et al. 2014).

The strongest BMTCs are expected to occur in systems featuring ambush predators (Preisser et al. 2007). Unlike active predators (e.g., wolves *Canis lupus*), which roam widely to increase encounter rates, ambush predators are tied to specific habitat features that increase their hunting success. In a given landscape, the distribution of such features would provide potential prey a mosaic of spatially consistent information about the risk of ambush (Andruskiw et al. 2008). Hence, prey should display strong antipredator responses in habitats where they perceive a high risk of being killed, with consequently beneficial effects on plants. Although controlled mesocosm experiments (Schmitz 2008) and behavioral studies of African ungulates (Valeix et al. 2009; Thaker et al. 2011) suggest strong effects of ambush predators, little is known about the ability of large ambushing vertebrate predators to indirectly affect vegetation structure and function via a BMTC.

In our study, we investigated whether a BMTC occurred in a tritrophic-level system, where the predator was a large ambushing carnivore. We conducted this work in the high deserts (3,000–3,800 m elevation) of the Puna ecosystem in the Andes of South America, where native camelids—vicuñas (*Vicugna vicugna*) and guanacos (*Lama guanicoe*)—are the

only medium-sized to large herbivores. Vicuñas, which are medium-sized (38–40 kg) grazers (Cajal 1989; Franklin 2011), were at least 10 times more abundant than guanacos in our study site (Puig and Videla 2007). Here, vicuñas graze almost exclusively on grasses, rushes, and sedges (grasses hereafter), which represent $\geq 65\%$ of their diet (Cajal 1989). Pumas (*Puma concolor*) were the only predators capable of killing vicuñas and accounted for most vicuña mortality. During our study, 91% of adult and subadult vicuña carcasses and at least 49% of radiomarked vicuña crías showed signs of puma predation (Donadio et al. 2012), and camelids represented the bulk of puma diet (Donadio et al. 2009). Pumas and vicuñas occupied a landscape of 3 distinct habitats: open plains, canyons, and meadows, which differed in levels of putative predation risk to vicuñas. Rugged terrain in canyons and tall vegetation in meadows suggested that these habitats were riskier than open plains.

The strong ecological interactions observed between pumas and vicuñas and vicuñas and grasses suggest a potential for pumas to indirectly influence the structure and productivity of the grass community. As ambushing predators, pumas rely on physical features (e.g., irregular terrain, dense vegetation cover) to approach and conceal themselves from large prey (Bank and Franklin 1998). In turn, prey can identify these physical features to organize spatial information about predation risk and respond accordingly (Lima and Dill 1990; Lima 1998). Consequently, the interaction among predation risk, physical features, and prey antipredator responses might create areas where plants are freed from intensive herbivory (Riginos and Grace 2008).

We hypothesized that puma predation would affect the antipredator behavior of vicuñas with cascading effects on grasses. These effects, however, would be observed only in those habitats where physical features facilitate hunting by pumas (Fig. 1). We sought to evaluate this hypothesis by simultaneously studying relationships among predation risk, vicuña antipredator behavior, and the structure and productivity of the grass community in plains, canyons, and meadows. In each habitat, we evaluated predation risk by measuring habitat features that would increase the hunting success of pumas, by analyzing the spatial distribution of vicuñas killed by pumas and by estimating relative puma abundance. We further assessed vicuña responses to varying levels of predation risk by measuring, across habitats, their relative abundance and time spent vigilant versus foraging.

Available reports of large carnivores (i.e., wolves) triggering a BMTC offer detailed observational data on prey antipredator behavior and their presumed effects on vegetation but give little attention to alternative explanations (Mech 2012). For instance,

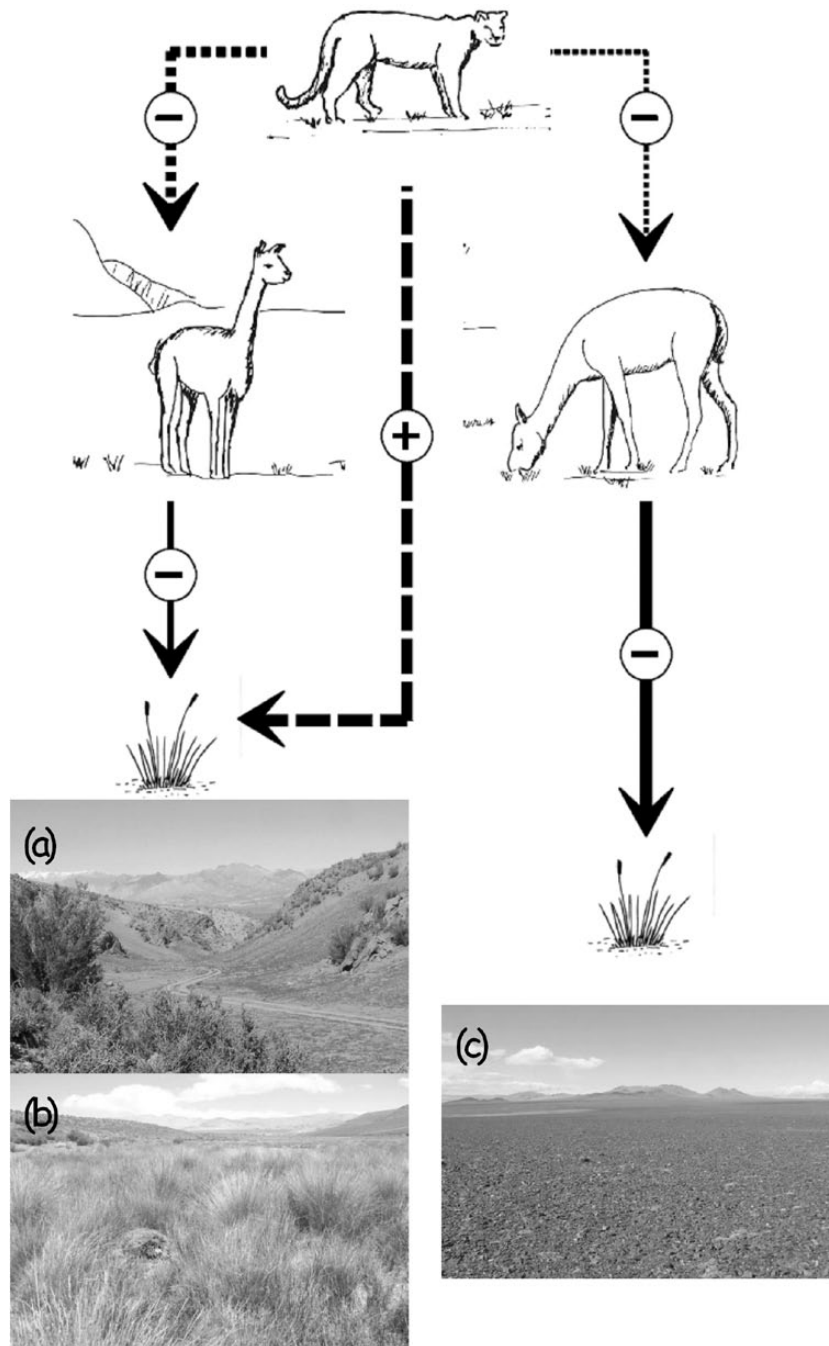


Fig. 1.—Hypothesized risk-mediated effects, in 3 different habitats, of an ambush predator on its herbivore prey (dotted lines) and vegetation (dashed line). An ambush predator is most lethal where brush and uneven topography enhance hunting success. In turn, these physical features provide prey with spatially predictable information about predation risk. We predicted that vicuñas would be less abundant, and spend less time foraging and more time vigilant in canyons (a) and meadows (b) than in plains (c). These responses should in turn release vegetation in canyons and meadows from heavy grazing; the opposite should occur in plains. If pumas were, indeed, protecting vegetation via a behaviorally mediated trophic cascade, then construction of vicuña exclosures in risky habitats (a and b) should have little effect on vegetation, because pumas—not exclosures—protect vegetation. Conversely, similar exclosures in safe habitats (c) should have a large effect on vegetation. Thick and thin lines represent strong and weak effects, respectively.

experimental work has recently shown that plant recovery in riparian areas of Yellowstone National Park depended heavily on hydrological conditions, a bottom-up mechanism, rather than reduced ungulate browsing induced by wolves (Bilyeu et al. 2008; Marshall et al. 2013), a top-down mechanism.

In this study, we linked several independent estimates of predation risk and vicuña antipredator behavior across habitats to vicuña effects on vegetation via a field experiment (Fig. 1), which also controlled for the effects of habitat-specific rates of grass regrowth (i.e., bottom-up mechanisms). We excluded

vicuñas, but not small herbivores, from 6 fenced exclosures that were replicated across 3 habitats, and we measured the functional (biomass and seed production) and structural (cover and height) responses of the grass community relative to paired, unfenced controls. Each paired treatment–control plot was in turn related to a 3rd plot where we mowed grasses and estimated grass regrowth.

MATERIALS AND METHODS

Study area and species.—We collected field data at San Guillermo National Park (SGNP) during January 2008–April 2011. Located in the central Andes of Argentina (29°14'S, 69°21'W), SGNP protects 166,000 ha of arid landscapes at 2,000–5,600 m elevation (see [Supporting Information S1](#)). The park's remote location and its lack of reliable road access result in extremely low visitation rates (< 100 tourists/year). Moreover, previous work on vicuña flight behavior suggests that poaching is negligible ([Donadio and Buskirk 2006](#)). Thus, in the park, human impacts on vicuña behavior are insignificant.

In this region of the Andes, rainfall averages 240 mm/year and falls mainly in summer, December–March. Warm temperatures (mean = 14°C) and rains allow a pulse of plant growth during mid-January–March. Low temperatures (mean = -1°C) and water limitation define the nongrowing season of 9 months ([Salvioli 2007](#)).

Three habitats characterize the landscape: extensive open plains (~3,400-m elevation) surrounded by hills and mountain peaks represent 81% of the study area. Narrow (10–300 m wide) canyons with steep rocky walls dissect the plains and mountains and represent 15% of the area. Isolated meadows are located in the plains or along rivers and streams and represent 4% of the area. Plains and canyons are xeric habitats with sandy soils, where water availability is low and depends exclusively on precipitation ([Pruel and Sala 1995](#)). Meadows are mesic habitats with soils rich in organic matter, where water availability is high and depends on precipitation and ground water flowing onto the surface ([Perotti et al. 2005](#); [Irisarri et al. 2012](#)); consequently, meadows are more productive than plains or canyons ([Irisarri et al. 2012](#)). Vegetation in plains and canyons is similarly characterized by a short-grass steppe dominated by perennial grasses (*Jarava* spp. and *Stipa* spp.). Meadows are dominated by relatively tall rushes (*Juncus* spp.), sedges (*Carex* spp. and *Scirpus* spp.), and fescues (*Festuca* spp.).

South American camelids—vicuñas and guanacos—are the only large mammalian herbivores present at SGNP. Mean densities of vicuñas and guanacos were 10/km² [95% confidence interval (CI) 5–22] and 1/km² (95% CI 0.2–4), respectively ([Puig and Videla 2007](#)). We rarely saw guanacos during the duration of the study; thus, we assumed that all the grazing responses measured during the study could be attributed to vicuñas. Absolute densities of pumas in the area are unknown, but pumas were sufficiently abundant that they were observed 1–3 times per month incidentally to field activities.

Assessing habitat-related levels of predation risk.—Pumas are ambush predators whose hunting efficiency improves in habitats with tall vegetation, extensive shrubs, and rugged

topography ([Wilson 1984](#); [Bank and Franklin 1998](#)). Thus, habitats with these characteristics should increase the risk to vicuñas of being preyed upon. Although canyons and meadows could be considered *a priori* as risky habitats (as opposed to safe [plains]), we developed 3 independent lines of evidence to corroborate this classification. First, we quantitatively evaluated physical habitat features that should favor the ambushing strategy of pumas. In each habitat, we surveyed thirty 15-m-long transects to measure vegetation (grasses and shrubs) cover and height, slope, and distance to rocky outcrops. We estimated vegetation cover and height using the point-intercept method; we recorded both variables every 0.5 m. At each starting point, we estimated the slope (from a digital elevation model using the Spatial Analyst extension in ArcView 3.2) and distance to the nearest rocky outcrop (using a Bushnell Pro 1000 range-finder and satellite photographs). We used a stratified random design to select starting points (Random Point Generator 3.1 [[Jenness 2005](#)] in ArcView 3.2) and directions of transects.

Second, we evaluated the spatial distribution of puma kills as a function of habitat area ([de Boer et al. 2010](#)). Relative to area, puma kills should be more frequent than expected in risky than in safe habitats. We searched for carcasses year-round by surveying permanent transects from a vehicle. We conducted on-foot searches in meadows 1–5 times per month, because of the difficulty of detecting carcasses in this habitat with relatively tall vegetation. We performed on-site necropsies on all carcasses found; we classified proximate cause of death as puma predation if we found clear signs of predation-caused trauma. If dragging marks were absent, we assumed the animal had been killed where we found it; otherwise, we followed dragging marks to their origin. For each carcass, we recorded the habitat type where it was killed. We surveyed all habitats daily while in the field (~60% of the 3.4 years of field work). We collected a total of 82 puma kills: 80 vicuñas and 2 guanacos. All carcasses belonged to animals that were > 9 months old. We estimated the area surveyed for each habitat using satellite imagery (Landsat 7 ETM+) and ArcView software v. 3.2 (ESRI, Redlands, California; [Supporting Information S2](#) for details and [Supporting Information S3](#)). Third, we derived a crude relative estimate of puma abundance in each habitat by counting puma scats along strip transects (see below).

Relative abundances of pumas and vicuñas.—We evaluated puma and vicuña relative abundances in each habitat by surveying 500-m-long strip transects that were 7 m wide, within which we recorded the number of puma scats and vicuña dung piles ([Buckland et al. 2001](#); [Donadio et al. 2009](#)). We surveyed 60 transects in the extensive plains, and 30 in each of the other habitats. In an effort to meet the key assumption that detection probability within the strip was 1, we assigned 2 (canyons and plains) and 4 (meadows) observers to simultaneously survey each transect. We used a stratified random design to select starting points (Random Point Generator 3.1 [[Jenness 2005](#)] in ArcView 3.2; [Supporting Information S4](#)) and directions of transects.

Forage quality.—Ungulate use of certain habitats is strongly influenced not only by risk of predation (e.g., [Creel et al. 2005](#)), but also by the availability and quality of forage (e.g., [Hopcraft](#)

et al. 2012). Consequently, we evaluated forage quality in the 3 habitats by analyzing nitrogen content in grasses collected during the growing season (January–March). We randomly selected plants near enclosures and clipped them at 1 cm above ground level. We stored samples in paper bags, and dried them at room temperature (25–38°C) for 2 to 7 days. We subsequently froze samples until we analyzed them at the Laboratorio de Evaluación de Forrajes (Instituto Nacional de Tecnología Agropecuaria Bariloche, Río Negro province, Argentina). We ground each sample in a laboratory knife mill through a 1-mm screen and used subsamples of 0.2 g for nitrogen (Göering and van Söest method) and 0.5 g for fiber (Kjeldhal method) analyses (Haufler and Servello 1996).

Diel occupancy of meadows and plains by vicuñas.—Our observations showed that vicuñas were most abundant in meadows. Thus, in January–February 2011, we counted the number of vicuñas in a meadow and contiguous plain at different times of the day to evaluate whether puma hunting success in meadows was a function of either prey abundance or prey vulnerability (i.e., presence of habitat features that favor the ambushing strategy of pumas). In the region, pumas are mostly nocturnal and crepuscular (Lucherini et al. 2009). Consequently, if puma hunting success were a function of vicuña abundance, then pumas should be active at the same time that abundance of vicuñas was highest. We counted the number of vicuñas in a section of a meadow and the contiguous plain at 1-h intervals from dawn to dusk. Sample size per 1-h interval ranged from 8 to 10 counts (i.e., 8–10 counts were conducted at the same time on 10 different days). We conducted all counts from the same fixed point with the aid of 8-power binoculars. We assumed that after all vicuñas had left the meadow at dark, they did not reenter it at night. The meadow contained zero vicuñas at 1st morning light.

Vicuña behavior.—We conducted behavioral observations during the nongrowing season (mid-March–early November) from 0900 to 1700 h in all 3 habitats. In an effort to avoid pseudoreplication, we never recorded vicuña behavior from the same observation point. Indeed, we recorded data on individual and group behavior over an area ~60 km². Furthermore, the high density of vicuñas together with their territorial behavior (Franklin 1982) likely strengthened our efforts to avoid repeated measures on the same individual or group. We considered animals to be members of the same group if they exhibited cohesive behavior (e.g., they presented synchronized movements), and stayed within 100 m of each other. We initiated observations only if the group could be clearly identified and after waiting ~15 min for acclimation. We abandoned observations if individuals showed signs of being disturbed by the observer, moved into a different habitat or out of sight, and groups either split or mixed with other groups.

We defined 2 types of vigilant behaviors. We considered that individuals were scanning for predators (i.e., predator vigilance) if standing looking around with their heads raised and ears erect and pointing forward. If individuals with heads raised directed their attention to other vicuñas moving their ears back and forward, then we considered them to be monitoring conspecifics (i.e., conspecific vigilance—Svendsen and Bosch 1993). Thus, we isolated scanning for predators from other vigilance

behaviors. We considered that individuals were foraging when standing or walking with the head below the shoulder, either handling food or not. Other behaviors recorded included walking, chasing, resting, and grooming.

We evaluated individual and group behaviors using focal and scan techniques, respectively (Altmann 1974). We conducted focal observations on solitary and randomly selected adults (> 1 year old) in groups (group size range: 2–13). Average distance to focal individuals was 268 m (range: 64–560). We filmed individuals for 1 min every 10 min over 1 h (seven 1-min sessions) using a camcorder (Sony DCR-DVD108 with 40× Optical Zoom, Sony Corporation, Shanghai, China). We analyzed videos in the lab and recorded the duration of each behavior (in seconds) during each 1-min session. Vigilance metrics represent the proportion of time (e.g., time foraging [s]/7 × 60 s) that 1 individual spent either foraging or vigilant over 1 h. For each observation, ancillary information included habitat type, group size (number of adults), number of juveniles (< 1 year old) in the group, and distance of the focal individual to its nearest neighbor measured in vicuña body lengths (Marino and Baldi 2008). For the latter, we estimated the distance of the focal individual at the beginning of each 1-min session and obtained an average distance over the seven 1-min sessions.

Behavioral observations on groups complemented data on individual behavior. Group size ranged from 2 to 15 individuals; average distance from observer to group was 306 m (range: 56–800). We conducted scans every 10 min through 1 h (7 scans) using binoculars if necessary. We recorded only the behaviors of adults. Data represent the mean proportion of adults displaying a given behavior over the 7 scans during 1 h. We collected ancillary information as for focal observations with the exception of distance to the nearest neighbor, which we did not record for group observations.

Exclosures.—Under the BMTC hypothesis, the construction of vicuña exclosures in habitats with high predation risk should have little effect on enclosed vegetation. Similar exclosures in safe habitats should have a large effect. We tested this prediction by quantifying the effects of vicuñas on vegetation using 6 pairs of 20 × 20-m treatment and control plots in each habitat (18 pairs total). Paired plots were 50 m apart to ensure consistency in plant community composition between treatments and controls. All treatment plots (vicuña exclosures hereafter) consisted of 1.5-m-high fences that excluded vicuñas but not other small herbivores. The locations of paired plots spanned ~24.5 km (Supporting Information S4). We built all vicuña exclosures in January–March 2009 and checked them at least biweekly. We never observed vicuñas or signs of vicuña activity inside exclosures. We sampled grasses during the peak of the growing season (February) of 2010 and 2011. We present data only from 2011. In 2009, logistic constraints and park regulations precluded random placement of vicuña exclosures and associated control plots in the landscape. However, structural (cover and height) characteristics of the grass community were similar in control plots and randomly placed transects (i.e., those surveyed to evaluate physical features of each habitat), suggesting that vegetation in control and treatment plots was representative of the habitats we evaluated (Supporting Information S5).

We measured grass cover, height, and proportion of plants with spikes (as a proxy for seed production) using the point-intersect method (Barbour et al. 1998). In each plot, we placed five 20-m-long transects 3 m apart and recorded the presence and height of grasses with and without spikes every 0.5 m. We estimated green standing grass biomass (g/m^2) by randomly placing in each plot six 1×1 -m quadrats. We clipped and weighed all grasses inside each quadrat. We estimated biomass only in 2011. In each plot, values for each variable obtained from each transect or quadrat were averaged ($n = 5$ for transects; $n = 6$ for quadrats). We did not sample spikes in meadows because spikes of rushes (dominant in this habitat) branch out from the side of the plant, at some distance below the tip, and our observations suggested that they were not highly responsive to vicuña grazing.

In risky habitats, a lack of effect of exclosures on vegetation could be a result of plants outside exclosures regrowing rapidly rather than being protected from herbivory by predators. To test this alternative explanation, we built a 2nd exclosure (20×20 m, 50 m apart) next to each of the paired treatment-control plots (i.e., an additional 18 exclosures). In these exclosures ("vicuña exclosures + clipping plots" hereafter), we mowed vegetation to ground level at the onset of the growing season. At the peak of the growing season, we measured grass height (as we did for the other plots) and compared it with that of the paired vicuña exclosure. If rapid plant regrowth was responsible for the lack of effect of vicuña exclosures in risky habitats, then grass height should be similar in vicuña exclosure and vicuña + clipping exclosure plots.

Statistical analysis.—We used a chi-square test to evaluate the hypothesis that puma kills would be distributed in each habitat in proportion to habitat area. After a significant ($\alpha \leq 0.05$) result, we constructed 95% individual CIs for each proportion of occurrence and determined whether expected values lay within the range of significant effects. We constructed confidence intervals by adjusting the z statistics by $1 - \alpha/K$, where $\alpha = 0.05$ and K is the number of simultaneous estimates being made (Neu et al. 1974; Manly et al. 2002). We used the Brown–Forsythe robust test (B–F) for equality of means to evaluate differences in habitat features, and puma and vicuña abundances among habitats. Significant results ($\alpha \leq 0.05$) were followed by post hoc Tamhane's T2 tests for pairwise differences. We constructed 95% CIs by bootstrapping (1,000 replicates) the raw data.

We used multivariate analysis of covariance (MANCOVA) tests to evaluate the effects of the fixed factor habitat type as well as the covariates group size (i.e., number of individuals > 1 year old), number of juveniles (≤ 1 year old), distance to the nearest neighbor, and the interaction between group size and habitat on individual and group vigilance and foraging behavior. Significant MANCOVA results ($\alpha \leq 0.05$) were followed by the B–F test and post hoc Tamhane's T2 tests for pairwise differences. We constructed 95% CIs as before. We evaluated differences between controls and vicuña exclosures for each habitat using 1-way paired t -tests on grass cover, height, and proportion of plants with spikes and biomass. We evaluated differences between vicuña exclosures and vicuña exclosures

+ clipping plots in each habitat using 2-way paired t -tests on grass height.

RESULTS

Distribution of puma kills (Fig. 2a), relative abundance of pumas (Fig. 2b), and habitat physical features (Supporting Information S6) supported our *a priori* classification of plains as safe, and canyons and meadows as risky habitats. Kills by pumas were observed at a 30% lower frequency than expected from the relative area of the plains, where pumas were relatively least abundant, and low vegetation cover and plant height, even terrain and lack of rocky outcrops might hinder the ambushing strategy of pumas. Conversely, puma kills were observed 90% more frequently than expected based on area in canyons and 480% more frequently than expected based on area in meadows. Both habitats showed frequent use by pumas and exhibited physical features (extensive tall shrubs, steep slopes, and rocky outcrops in canyons; high vegetation cover and tall grasses in meadows) that favored ambushing.

Habitat-dependent levels of predation risk were correlated with behavioral responses of vicuñas. Vicuñas were about 4.7 times more abundant in plains than in canyons, but contrary to our expectations, they were most abundant in meadows (Fig. 2c). However, vicuñas heavily utilized meadows during the day and avoided them from dusk to dawn (Supporting Information S7). As predicted, individual and group foraging times were 20% to 30% lower in canyons and meadows, and vigilance showed a 3.7 (canyons) to 6.2 (meadows) times increase compared to plains (Figs. 3a–d). Both foraging and vigilance budgets were independent of group size, number of juveniles, and distance to the nearest neighbor (MANCOVA: all $P \geq 0.26$; Supporting Information S8 and S9).

Experimental protection of grasses from vicuña grazing led to habitat-specific effects on the grass community. In canyons and meadows, vicuña exclosures had weak or no effect on attributes of grasses relative to controls. By contrast, in the plains, vicuña exclosures resulted in a 28 times increase in seed production, a 6.6 times increase in biomass, a 2.6 times increase in height, and a 2.2 times increase in cover of grasses (Figs. 4a–d; Supporting Information S10 and S11).

In canyons, the weak effects of vicuña exclosures on grasses were not related to rapid grass regrowth. Indeed, at the peak of the growing season, grasses were 2.6 times taller in vicuña exclosures than in vicuña exclosure + clipping plots, where grasses did not recover from mowing. Conversely, in meadows, the weak effects of exclosures on grasses seemed to be a consequence of rapid grass regrowth. At the peak of the growing season, grass height in meadows within vicuña exclosures and vicuña exclosure + clipping plots was similar. Finally, as observed in canyons, grasses in plains regrew slowly: grasses were 1.6 times taller in vicuña exclosures than in vicuña exclosure + clipping plots (Fig. 5).

DISCUSSION

Whether large terrestrial predators can trigger BMTCs is currently being questioned because recent field tests failed to find

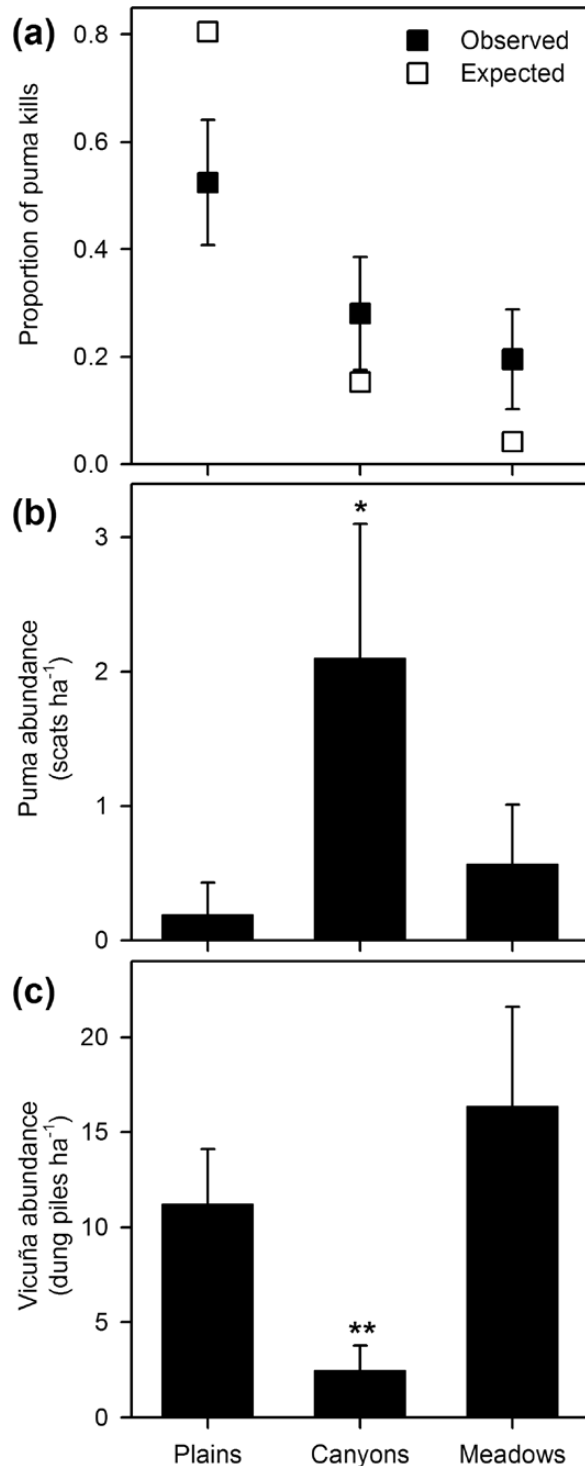


Fig. 2.—Distribution of puma kills, and surveyed abundance of pumas and vicuñas in safe (plains) and risky (canyons and meadows) habitats. (a) Relative to area, vicuñas were more likely to be killed in risky (canyons: $n = 23$ puma kills; meadows: $n = 16$) than in safe (plains: $n = 43$) habitats ($\chi^2_2 = 15.6$, $P < 0.001$). (b) Puma abundance (Brown–Forsythe robust test [B–F]: $F_{2,43} = 10.9$, $P < 0.001$). (c) Vicuña abundance (B–F: $F_{2,53} = 11.3$, $P < 0.001$). Bars show mean estimates; error bars show 95% confidence interval (CI) from bootstrap resampling with 1,000 replicates. Determinations of differences in puma and vicuña abundances between habitats were based on the B–F followed by post hoc Tamhane’s T2 contrasts. * $P \leq 0.021$, ** $P < 0.001$.

strong links between risk factors and vegetation responses (Kauffman et al. 2010; Winnie 2012; Marshall et al. 2013). However, these studies derive mostly from systems in which the focal predator is an active hunter (i.e., wolf—Ripple and Beschta 2012), which has been predicted to elicit weak anti-predator responses in prey and consequently in vegetation (Preisser et al. 2007). We tested if a large terrestrial predator that ambushes its prey triggered a BMTC, and we evaluated the strength of any such mechanism in 3 habitats that differed in their levels of predation risk. We found strong relationships among predation risk, ungulate antipredator behaviors, and plant community structure and function. However, other habitat attributes such as high primary productivity attenuated or even cancelled strong top-down effects.

As predicted, in canyons and meadows, habitat features that increased vulnerability of vicuñas enhanced the hunting success of pumas. Indeed, pumas killed vicuñas more in canyons and meadows and less in plains than expected on the basis of area. Vicuñas responded strongly to this variation in levels of predation risk across habitats. They were less abundant in canyons, and became more vigilant and spent less time foraging in canyons. Relatively low use of canyons was not a function of food availability because forage quantity was similar and quality was higher in canyons than in plains (Supporting Information S6). Conversely, vicuñas were more abundant in plains where they decreased markedly their vigilance for predators, and increased their foraging times. These results suggest that by creating variation in predation risk across habitats, pumas altered vicuña antipredator responses, leading to habitat-dependent effects on the structure and productivity of vegetation. In canyons, pumas imparted high predation risk, which resulted in strong antipredator responses by their prey and protective effects for grasses. In the plains, low predation risk resulted in the relaxation of herbivore antipredator responses, which led to intense grazing pressure that depressed the productivity and simplified the structure of the grasses. These habitat-specific indirect effects of puma on grasses reveal how a large ambush predator and its ungulate prey interact with habitat features to produce spatially heterogeneous, but simultaneous, responses that result in structural and functional variation in grass communities across the landscape.

Contrary to our predictions, high risk of predation did not prevent vicuñas from occupying meadows, presumably because meadows offered abundant, high-quality forage. This result contrasts sharply with most data from African and North American systems, where ungulates tend to select safe habitats, but often poor quality ones nutritionally (Creel et al. 2005; Fortin et al. 2005; Riginos and Grace 2008; Thaker et al. 2011). At SGNP, meadows are scarce and represent a small fraction (~4%) of the total area of the park. We think that this shortage of patches with high-quality forage leaves vicuñas with no option but to use meadows. Indeed, complete avoidance of risky meadows likely would be detrimental to the nutritional condition of vicuñas; they use meadows, but respond by enhancing vigilant behaviors during the day and departing at dusk, when pumas become harder to detect (Sarno et al. 2008). This result

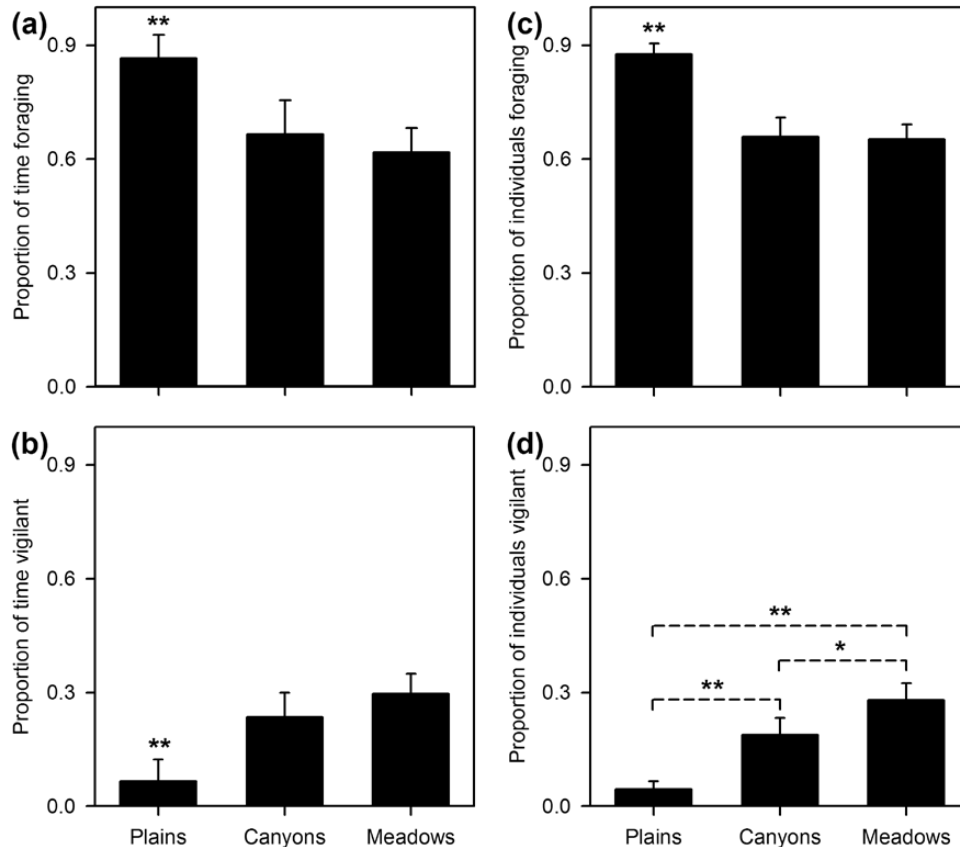


Fig. 3.—Individual and group behavioral budgets in safe [plains: individual ($n = 25$), group: $n = 47$] and risky (canyons: $n = 27$ and 46 ; meadows: $n = 26$ and 49) habitats. (a) Proportion of time individuals spent foraging (Brown–Forsythe robust test [B–F]: $F_{2,69} = 11.7$, $P < 0.001$). (b) Proportion of time individuals spent vigilant ($F_{2,108} = 42.9$, $P < 0.001$). (c) Proportion of individuals foraging in a group (B–F: $F_{2,120} = 29.7$, $P < 0.001$). (d) Proportion of individuals vigilant in a group (B–F: $F_{2,108} = 42.9$, $P < 0.001$). Bars show mean estimates; error bars show 95% confidence interval (CI) from bootstrap resampling with 1,000 replicates. Determinations of differences in behaviors among habitats were based on MANCOVA tests (Supporting Information S8 and S9) and subsequent B–F followed by post hoc Tamhane’s T2 contrasts. * $P = 0.01$, ** $P \leq 0.002$.

shows how risk effects produced by predators are offset by prey venturing into risky but highly productive habitats to avoid starvation, and suggests that patches of high-quality habitat in a low-quality matrix would be less prone to top-down regulation.

Intensive use of meadows by vicuñas during daylight resulted in high grazing pressure there. However, this pressure neither depressed the productivity nor simplified the structure of the grasses. Meadows are mesic habitats with rich soils, where—in contrast to canyons and plains—water and nutrients are abundant (Perotti et al. 2005) and likely increase grass tolerance to herbivory (Strauss and Agrawal 1999; Chase et al. 2000; Hawkes and Sullivan 2001). Therefore, high primary productivity allows for rapid compensatory regrowth of plants and renders meadows less susceptible to cascading effects than canyons. Indeed, experimental mowing of grasses in the vicuña exclosures + clipping plots showed that grasses in meadows were capable of rapid recovery. Thus, in this particularly productive habitat, bottom-up mechanisms overrode top-down ones. This result is consistent with that observed in the African savannas, where increasing primary productivity attenuates the effects of herbivory by ungulates (Pringle et al. 2007), and suggests that predator regulation of plant communities through indirect mechanisms is more likely to occur in low-productivity

systems. Our results also revealed how bottom-up mechanisms could be masked as top-down mechanisms if bottom-up factors are not explicitly accounted for when evaluating the potential indirect effects of predators on primary producers. For instance, plants exposed to abundant water and nutrients could be affected little by herbivory. If so, the observed pattern might be mistakenly interpreted as protective effects of predators on plants if only antipredator responses of prey are considered (i.e., observed small effects of herbivores on plants are correlated with high levels of herbivore vigilance). Specifically in our study area, had we left untested the importance of bottom-up factors, we would have wrongly concluded that pumas were strongly influencing the structure and function of the grass community in meadows.

Two alternative explanations also might account for the lack of effect of vicuña exclosures in canyons. First, as observed in meadows, grasses in canyons could present rates of regrowth that are sufficient to compensate for vicuña grazing. Indeed, bottom-up mechanisms such as availability of water and nutrients and resulting high primary productivity are known to moderate the impacts of large mammalian herbivores on vegetation (Pringle et al. 2007; Bilyeu et al. 2008; Marshall et al. 2013). Under this scenario, at the end of the growing season, we would

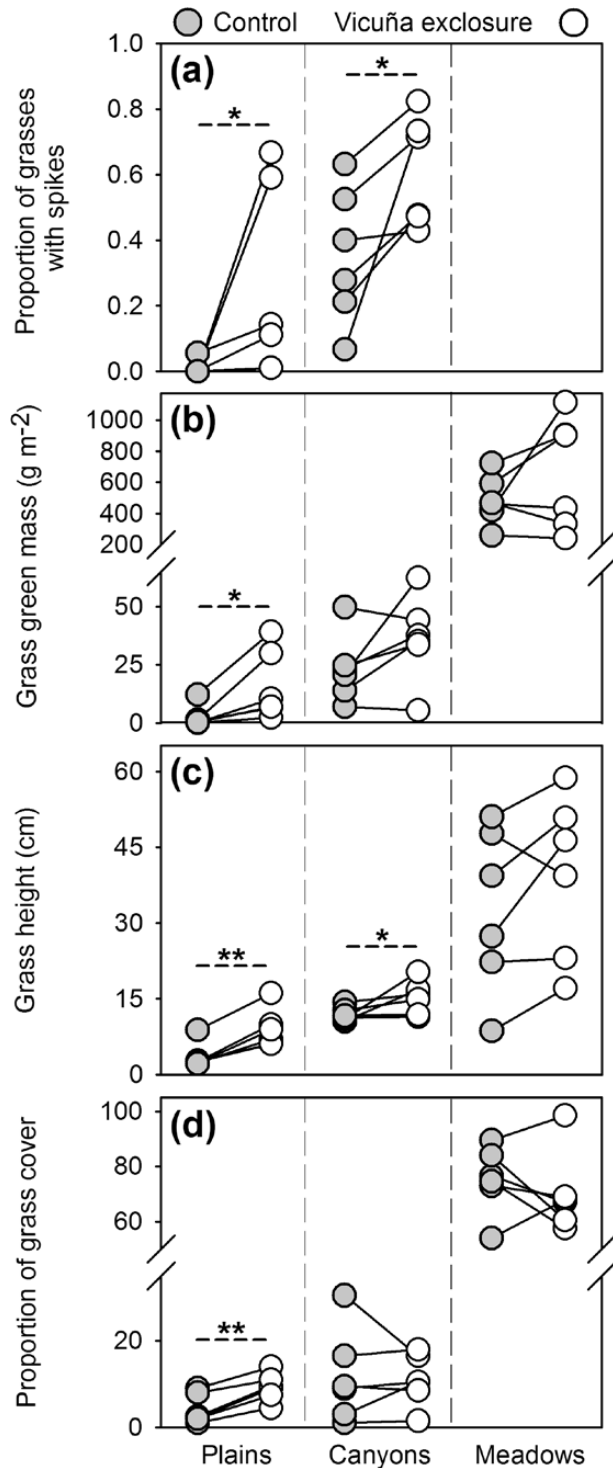


Fig. 4.—Effects of manipulating vicuña grazing on vegetation productivity and structure in 3 habitats with different levels of predation risk. Experimental exclusion of vicuñas had stronger effects in safe (plains) than in risky (canyons) habitats for grass seed production (a), biomass (b), height (c), and cover (d). Lack of effect in meadows was likely a result of bottom-up control rather than high levels of predation risk (see text and Fig. 5). Spikes were not measured in meadows (see “Materials and Methods”). Determinations of treatment differences were based on 1-way paired *t*-tests, $n = 6$ replicates per habitat (Supporting Information S11). * $0.02 < P \leq 0.05$, ** $P < 0.001$.

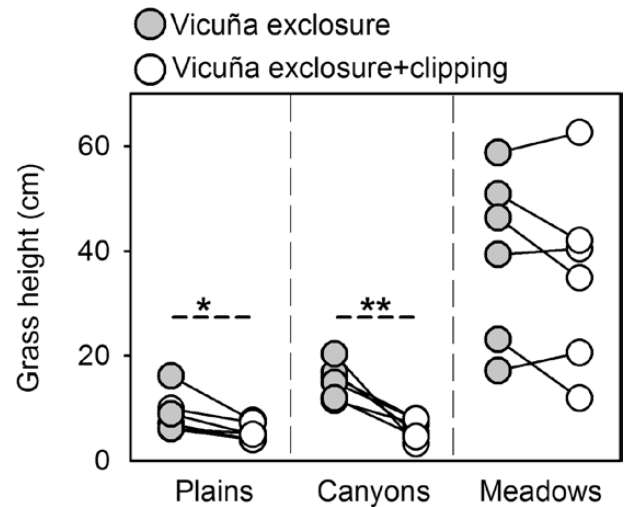


Fig. 5.—Measures of grass regrowth in 3 habitats with different levels of predation risk. In the safe plains ($t_5 = 3.3$, * $P = 0.02$, $n = 6$) and risky canyons ($t_5 = 5.1$, ** $P = 0.004$, $n = 6$), grasses clipped at the onset, and measured at the peak of the growing season, were significantly shorter than unclipped grasses; in risky meadows, clipped grasses regrew to heights similar to those of unclipped ones ($t_5 = 1.3$, $P = 0.26$, $n = 6$).

expect grasses clipped in the vicuña exclusion + clipping plots to regrow to heights similar to those observed in the vicuña exclusions where clipping was not conducted. However, we did not find such response in grasses suggesting that bottom-up mechanisms were not the main drivers of the structure and productivity of the grass community in canyons.

Second, grasses could be benefited by pumas reducing vicuña numbers rather than solely affecting vicuña behavior in canyons. For instance, high rates of puma predation might reduce vicuña survival and fecundity indirectly, by negatively influencing vicuña nutritional condition (i.e., vicuñas increase vigilance at the expense of foraging), or directly, through killing. For this numerical mechanism to occur, it should be assumed that within the vicuña population there are individuals that inhabit only canyons or plains. However, vicuñas move daily across multiple habitats in search of food, water, and safety (Koford 1957; Franklin 1974). Moreover, the nutritional status of vicuña carcasses in our study site appeared to be a function of temporal (i.e., phenological changes in forage) rather than spatial factors (i.e., habitat where the carcass was found—Donadio et al. 2012). Thus, the operation of numerical mechanisms seems an unlikely explanation for the lack of effect of vicuña exclusions in canyons. Yet, a limitation of our study is that we lack detailed information on vicuña habitat use and selection at SGNP. The recent deployment of GPS collars in adult vicuñas in our study site will provide this information explicitly.

Our results are consistent with data derived from small-scale experiments (Schmitz 2008) and a recent synthesis (Preisser et al. 2007), which have suggested that ambushing predators could have strong effects on prey behaviors, community structure, and ecosystem function. Although the risk cues produced by ambush predators are restricted to spatially localized

terrain features, the resulting cascading effects can spill across a much larger area. For instance, puma predation indirectly, but strongly, enhanced vegetation structure and biomass, and seed production in the risky canyons. These positive effects on vegetation could enhance plant reproduction and indirectly maintain genetic diversity in grass populations via seed dispersal from risky (i.e., canyons) to safe (i.e., plains) habitats. Furthermore, complex vegetation structure and abundant seed banks in canyons could be important for the maintenance of biodiversity of other taxa, including assemblages of invertebrates and small vertebrates. Finally, the interplay between pumas and vicuñas also might affect plant diversity. Low predation risk and subsequent high levels of vicuña grazing in the plains limits dominant grasses with potential beneficial effects on short-lived annual plants.

Observational and experimental data from 3 trophic levels strongly suggested the operation of a BMTC in a carnivore–ungulate–grass system. We found cascading effects that were substantial and attributable to the heterogeneous landscape of predation risk that is created when prey individuals respond to the strategy of an ambush predator. Our research also showed that such top-down effects were weakened by high primary production in 1 habitat type (i.e., meadows) and suggested how differences in environmental factors among habitats could switch between top-down and bottom-up processes as drivers of plant communities. Indeed, high structural complexity and low primary productivity appeared to be critical habitat conditions for an ambush carnivore to elicit protective effects on vegetation by influencing ungulate antipredator behaviors. Overall, our findings highlight the importance of considering predator hunting mode and differences in habitat attributes when predicting the relative strength with which predators might structure the communities they inhabit.

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SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (j mammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Study area location.

Supporting Information S2.—Estimation of area surveyed for puma kills.

Supporting Information S3.—Spatial distribution of puma kills by habitat.

Supporting Information S4.—Locations of control–treatment plots and starting points of animal sign and vegetation transects.

Supporting Information S5.—Statistics comparing vegetation attributes between random locations and experimental plots.

Supporting Information S6.—Main attributes of the 3 habitats surveyed.

Supporting Information S7.—Temporal patterns in habitat use by vicuñas.

Supporting Information S8.—MANCOVA statistics for the effect of habitat and other covariates on the behavior of focal vicuñas.

Supporting Information S9.—MANCOVA statistics for the effect of habitat and other covariates on the behavior of vicuña groups.

Supporting Information S10.—Effects of exclosures in plains, canyons, and meadows.

Supporting Information S11.—*t*-test statistics comparing vegetation attributes between vicuña exclosures and controls.

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