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Capybaras (*Hydrochoerus hydrochaeris*) Generate Grazing Lawns and Maintain Plant Diversity in Neotropical Savanna

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ABSTRACT

Questions: Herbivores can exert strong top-down control on vegetation structure and composition, which in turn can affect overall biodiversity and ecosystem processes. However, South American megafauna was largely driven to extinction in recent prehistory, and remaining species have suffered severe range reductions from human actions. The potential role of South American megafauna in shaping vegetation therefore remains unclear. We examined herbivore-driven top-down control of the vegetation, particularly impacts on plant diversity, structure and functional composition.

Location: Iberá Wetlands, Corrientes, Argentina.

Methods: We set up an herbivore exclosure experiment in a restoration area with 10 wild large-herbivore species. We compared vegetation dynamics in fenced plots with paired control plots to which herbivores had full access. Replicate plot pairs were established in three grassland types: characterized as short, medium-tall and tall grasslands. Grass height, plant biomass, functional types and community composition were measured at the start of the experiment and after 6, 13 and 18 months.

Results: We found that in short and medium-tall grasslands, herbaceous biomass and grass height increased significantly in no-grazing plots, while species richness decreased. Similarly, community dissimilarity between paired grazed and ungrazed plots increased over time for short and medium-tall grasslands. Camera trap images revealed that capybara (*Hydrochoerus hydrochaeris*) was the dominant grazer on the grazed plots.

Conclusion: Our results show a strong impact of native herbivores on the structure and composition of South American savannas akin to African grazing lawns, with higher plant species richness and dominance of grazing-tolerant growth forms. These results imply that South American grassy ecosystems, despite severely reduced herbivore richness and density, have retained plant taxa and functional trait complexes that tolerate intense herbivory. Further, they also show that herbivory can still play an

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important role in maintaining their plant diversity. The conservation and restoration of South American grassy ecosystems are likely to benefit from restoring functional grazing regimes.

1 | Introduction

Large mammal herbivory is a key ecosystem process that influences plant diversity, vegetation structure and plant species abundance (Staver et al. 2021; Dantas and Pausas 2022; Pringle et al. 2023; Svenning, Lemoine, et al. 2024). Large herbivores shape ecosystems through physical disturbance, consumption of biomass, and seed and nutrient dispersal (Waldram et al. 2008; Galetti et al. 2018; Johnson et al. 2018; Lundgren et al. 2018). The top-down effects of herbivory shape the structure of savanna ecosystems through various mechanisms, for example, browsing can suppress woody plants while grazing may promote woody plants by reducing competition from grasses (Staver et al. 2009). However, large grazers specifically can have significant effects on vegetation and ecosystem structure, including the suppression of fire and shaping the functional and taxonomic composition of plant communities (Macias et al. 2014; Staver et al. 2021; Karp et al. 2024).

A prominent pathway by which grazers affect ecosystem structure, processes and plant communities are grazing lawns, a short lawn-like vegetation state maintained through repeated grazing (Cingolani et al. 2003; Hempson et al. 2015). Grazing lawns have positive consumer-resource feedbacks, where continuous grazing maintains high forage quality (low C:N ratios) by preventing plants from accumulating structural biomass such as stems, while at the same time receiving increased nutrient input through dung deposition. The locally high biomass removal, nutrient input and exclusion of fire, along with the resulting compositional shifts in plant community composition, results in spatiotemporal heterogeneity at the scale of several meters square to several hectares, which ultimately is likely to promote biodiversity (McNaughton 1984; Cromsigt and Olff 2008; Waldram et al. 2008; Veldhuis et al. 2014).

The effects of wild large herbivores on ecosystem structure have been strongly reduced in many regions due to severe extinctions and extirpations from the Late Pleistocene to the present, with global human-driven extinctions strongly accelerating from 50,000 years ago. Some South American extinctions only occurred between 14,000 and 7000 years ago, after human colonization of the continent (Prado et al. 2015; Svenning, Lemoine, et al. 2024). Megafauna extinctions were particularly severe in South America with 82% of species over 44 kg going extinct (Sandom et al. 2014; Stuart 2015; Doughty et al. 2016; Malhi et al. 2016; Svenning and Faurby 2017; Prates and Perez 2021; Svenning, Lemoine, et al. 2024). Three orders of herbivores disappeared from the continent, two of which (Notoungulata, Litopterna) became globally extinct (Prado et al. 2015). The severe extinctions also had strong functional implications as South America's formerly rich community of large herbivores underwent a severe downsizing, with a complete loss of all megaherbivores with body mass ≥ 1000 kg (Lopes et al. 2020). These extinctions likely had strong consequences for ecosystem structure and functioning, for example, nutrient cycling (Doughty et al. 2013), plant dispersal (Janzen and Martin 1982; Galetti et al. 2018), and vegetation structure and functional composition (Doughty et al. 2016; Dantas and Pausas 2022).

Megafauna extinctions during the Pleistocene likely left a significant mark on current ecosystem biogeography (Svenning, Lemoine, et al. 2024), and may be responsible for shifts from savanna to forest ecosystems in the Neotropics (Dantas and Pausas 2022). Savanna ecosystems are defined by the coexistence of trees and C4 grasses, and are still widespread, occupying 45% of South America (Costa et al. 2008; Ratnam et al. 2011). Savanna vegetation is strongly influenced by top-down effects, particularly fire (Bond 2005; Staver et al. 2011; Dantas et al. 2016). The role of herbivory in determining large-scale vegetation patterns and alternative ecosystem states is more difficult to test, but at local to landscape scales there is strong evidence that herbivory is a major determinant of African savanna vegetation where largely complete herbivore assemblages are present at natural densities (Skarpe 1991; Staver et al. 2021).

To explore whether herbivores similarly shape savannas in South America, a largely defaunated continent where savannas and other ecosystems are increasingly lost to intensive agriculture (Sano et al. 2010; Baeza and Paruelo 2020), we quantified the strength of top-down herbivore control on South American savanna vegetation in a restoration area with a relatively diverse herbivore assemblage. The aim of this study is to (1) determine if the current large-herbivore assemblage has the capacity to generate top-down controls on vegetation structure and composition in South American savannas; and (2) identify which herbivore species are driving top-down control on vegetation in this South American savanna. Understanding herbivore effects on vegetation dynamics and biodiversity in South America is relevant to ecosystem management, since the restoration of herbivore regimes is a feasible management strategy that is implemented by ecosystem managers around the world.

2 | Methods

2.1 | Study Area

The Iberá wetland region in north-eastern Argentina contains large fresh-water marshes, while the terrestrial parts are a mosaic of savannas, grasslands, gallery forests and sandy plains (Úbeda et al. 2013; Corriale and Herrera 2014). The Iberá macrosystem represents a convergence of three phytogeographic provinces (Cabrera and Willink 1973): to the north, the Paranaense Province; to the west, the Chaco Province; and to the south and east, the Espinal Province. Each province contributes its unique floristic characteristics, resulting in a diversity of natural environments (Carnevali 2003; Roggiero et al. 2011). Vegetation communities in the study area are primarily stratified along a moisture gradient, (1) "Pirizal" (wetland dominated by tall species of Cyperaceae, Maranthaceae, Typhaceae) dominated by *Rynchospora corimbosa*, *Cyperus giganteus*, *Scirpus californianus*, *Typha dominguensis*, *Thalia* spp., (2) "Pajonales" (marshy areas/wetland dominated by tall and perennial grass species) dominated by *Paspalum durifolium*, *Eryngium* spp., *Zizaniopsis bonariensis*, *Cephalanthus glabratus*, (3) semi-flooded grasslands of *Paspalum modestum* and *Setaria geminata*, (4) very wet grasslands with *Cyperus obtusatus, Rhynchospora tenuis, Fimbristylis dichotoma, Axonopus fissifolius*, (5) wet meadows of *Axonopus fissifolius* and *Paspalum notatum*, with sparse *Andropogon lateralis*, (6) wet meadows with *Copernicia alba* (Carnevali 2003) with *Paspalum modestum, Luziola sp., Eleocharis sp., Sporobolus indicus, Sida anomala, Distichlis spicata, Paspalum virgatum*, (7) savannas on sandy hills (Arbo and Tressens 2002), with a herbaceous layer of dominant species: *Elionurus muticus* and *Andropogon lateralis*, accompanied by *Paspalum ionanthus, P. plicatulum, Axonopus suffultus*, and *A. argentinus* and eudicots such as *Stylosanthes* spp., *Desmodium* spp., *Arachis* spp., *Oxalis conorrhiza, Acmella grisea, Sida regnellii, Cuphea glutinosa*. The climate is humid subtropical with mean annual precipitation of 1400 mm, the majority (~2/3rds) of which falls in summer between October and March (Giménez et al. 2001). Monthly mean temperatures are 27°C in summer and 16°C in winter (Corriale and Herrera 2014).

Our field site is the reserve Rincón del Socorro (124 km^2; −28.637544, −57.345981), a part of the Iberá National Park in Corrientes province, Argentina. The reserve was a cattle ranch until 2002, when it became a private protected area that excluded livestock and hunting of native species (Di Blanco et al. 2015; Zamboni et al. 2017). One of the main terrestrial habitats are savannas, where the woody component is dominated by spiny legumes (*Neltuma affinis*, *N. nigra* and *Vachellia caven*), ranging from very open to dense woodlands, accompanied by other tree species such as *Scutia buxifolia* and *Sideroxylon obtusifolium* as well as Cactaceae (*Opuntia elata, Cereus argetinensis, Harrisia tortuosa*), combined with large open grassland areas of *Andropogon lateralis, Sorghastrum setosum* and a herbaceous stratum with *Selaginella sellowii, Cuphea glutinosa, Cypella herbertii, Bromelia balansae* (Arbo and Tressens 2002; Carnevali 2003). While most herbaceous species in these grasslands are forbs, grasses dominate both the vegetation cover and biomass. The grasslands covering these ecosystems range from short and stoloniferous to tall and upright (Figure 1). These savannas are interspersed with clumps of broadleaved evergreen hygrophilous forests that line the

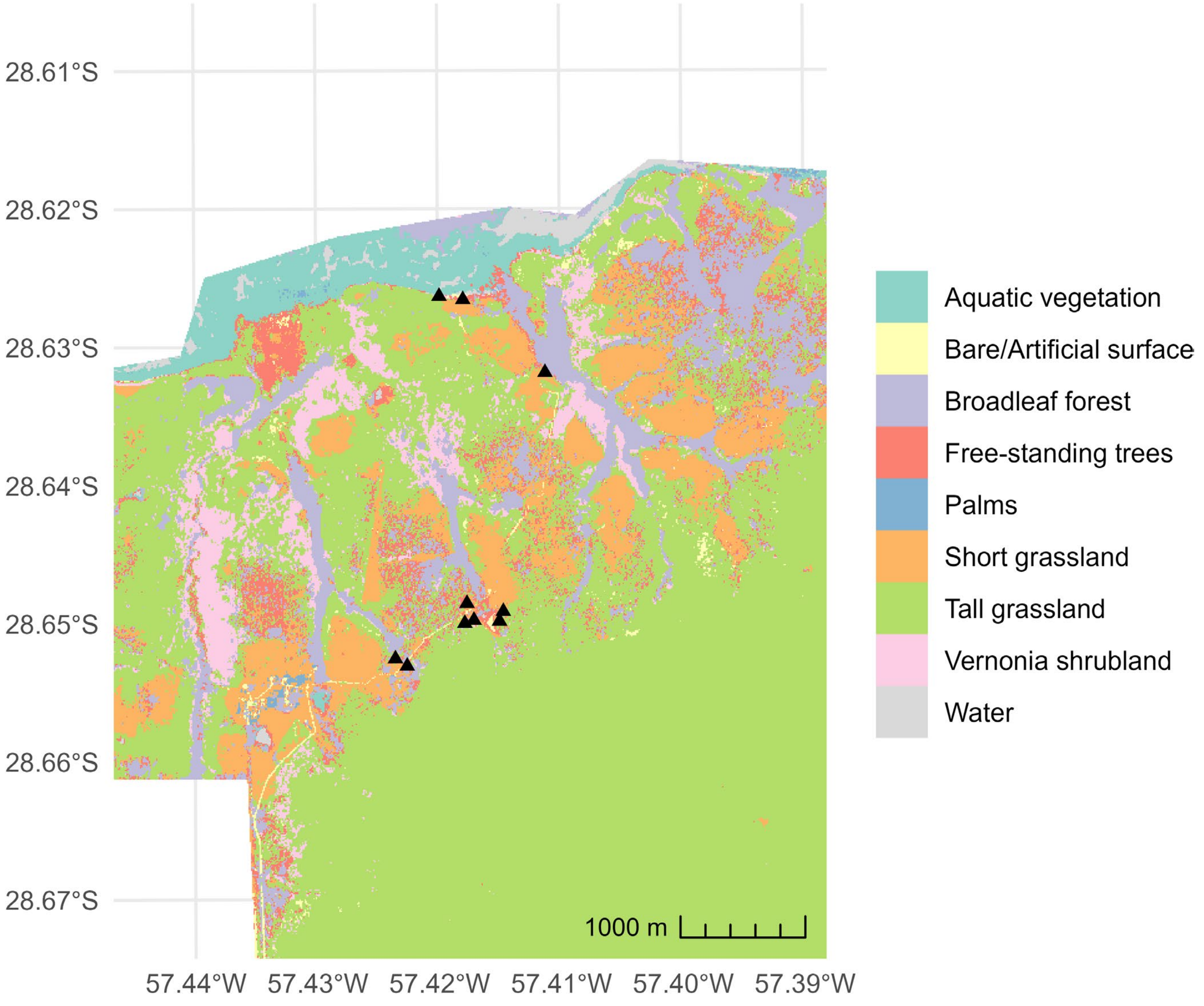

FIGURE 1 | A map of the study area showing vegetation types (adapted from Mata et al. 2021) and the location of the 10 study sites.

stream banks. Significant areas are occupied by dense monodominant thickets of asteraceous shrubs and tall grasslands. A large estuary defines the northern boundary of the reserve and is lined with seasonally flooded grasslands, sometimes with tall palm stands (*Copernicia alba*) (Di Blanco et al. 2015). Capybara (*Hydrochoerus hydrochaeris*), a large semi-aquatic and social rodent, are the most abundant native herbivores in the area. Capybara are grazers (Moreira et al. 2012). Other herbivores in the area are plains vizcacha (*Lagostomus maximus*), greater rhea (*Rhea americana*), marsh deer (*Blastocerus dichotomus*), and brocket deer (*Mazama gouazoubira*), a selective browser. As part of a reintroduction program to increase trophic complexity, populations of pampas deer (*Ozotoceros bezoarticus*) a medium-sized grazer, collared peccary (*Dicotyles tajacu*), and lowland tapir (*Tapirus terrestris*) have been established (Zamboni et al. 2017). Additionally, two exotic species are common, the Axis deer (*Axis axis*) and wild boar (*Sus scrofa*). With the exception of tapir, these species can leave the protected area, but densities outside the protected area are far lower for all native herbivores (pampas deer are virtually absent), with the possible exception of the non-native axis deer and wild boar, which are very actively controlled in the protected area (although also hunted outside).

2.2 | Experimental Design

We tested the impact of grazing in three different vegetation communities using a full-factorial experiment. In April 2018 we established 30 pairs of 2×2 m plots, where each pair consisted of an ungrazed fenced plot, and a grazed control plot. At each of the 10 replicate sites, one plot pair was established in each of the three grassland types: short grass, medium-tall grass and tall grass (Figure 2). Short grassland was defined as areas with creeping grasses that on average do not exceed 20 cm in height. Medium-tall grassland were defined as areas with a herbaceous height of 20–70 cm, with at least some caespitose grasses, typically with tuft diameters < 20 cm. Tall grasslands were defined as areas with grasses over 70 cm height on average, dominated by coarse bunchgrasses, typically with tuft diameters > 50 cm. The patch size of these grassland types varied from several tens of m^2 to hectares.

We selected sites where the three grassland types occurred within a distance of 100 m from each other, to minimize topographic and edaphic gradients within each site (Figure 1). Plot pairs were always at least 2 m apart to avoid the fenced plot affecting herbivore visitation to the grazed control plot, but within 10 m from each other to minimize environmental differences within plot pairs. The distance between sites ranged from 77 to 3000 m.

The ungrazed plots were fenced using four wooden posts approximately 1.2 m in height, with a 0.7 m tall metal mesh fence and an additional metal wire at approximately 1 m (Figure 2). Although the deer species would be able to jump over this fence, the relatively small plot size was expected to discourage this, which we confirmed using camera trap images. The grazed control plots were marked with four short wooden posts.

2.3 | Data Collection

2.3.1 | Vegetation

To quantify the impact of grazing on vegetation structure and composition, we recorded several variables at the start of the experiment and at 6, 13 and 18 months.

To quantify vegetation structure, we measured the height and estimated biomass of the herbaceous layer. Height was measured as grass leaf-table height (Wigley et al. 2020) at eight equally spaced points along the perimeter of a 1 m^2 square positioned at the center of the plot. We also estimated biomass at the four corners of each plot, keeping 50 cm away from the fence to avoid potential edge effects. Biomass was estimated non-destructively with a disc pasture meter (Bransby and Tainton 1977; Zambatis et al. 2006), which consists of a flat disc of standard dimensions and mass, which is dropped on the vegetation from a set height (exact specifications in Appendix S1, Figure S1). The depth to which the disc drops is determined by the amount and structure of the vegetation underneath. The falling depth of the disc is translated to biomass by constructing a calibration curve using destructive harvesting on similar vegetation outside the experiment. To construct the calibration curve, we took 25 samples along a biomass gradient, where we related the falling depth of the disc to the clipped and dried biomass of all the vegetation underneath the disc. The resulting curve was best described by a linear regression (Figure S2).

FIGURE 2 | Ungrazed exclosure plots in the three studied grassland types (a) short grassland; (b) medium-tall grassland; and (c) tall grassland, at the time they were erected.

To assess community composition, we used a 0.5×0.5 m pin-point frame at the center of each plot, within which we dropped 16 pins on a regular grid and recorded the species at the first hit (Levy and Madden 1933; Kent and Coker 1992). This method generates data on the relative abundances of species. In addition, we identified all species with the 0.5×0.5 m sample square to generate a species list for each plot.

To assess the impact of grazing on the dominance of different growth forms, we measured the relative abundance of plant functional types within four 0.5×0.5 m sample squares placed at the center of each quadrant of the plot with a pin-point frame. Grasses were classified as: (1) short stoloniferous grasses, with prostrate growth and soft leaves, typically *Paspalum* spp. (2) palatable-looking grasses with soft leaves, likely annuals or biennials growing in upright tufts, (3) less palatable-looking grasses with tougher leaves and dead leaves still attached to the plant, suggesting they were perennial, growing in larger and denser tufts than (2); and (4) tall unpalatable-looking grasses with hard leaves, perennial, growing in very large tufts, predominantly *Andropogon lateralis* or *Sorghastrum setosum*.

Overall, we gathered full time series on 48 plots, and included 93.3% of all plot-date combinations in our analysis. Three of the 60 plots were excluded from the last data collection as they were disturbed by management activities (site 4, short grassland, grazed plot and site 5, short grassland, grazed and ungrazed plots). A further four plots were severely disturbed by prolonged flooding between the second and third data collection (site 1 and site 2 short grazed and ungrazed) and were therefore excluded from the third measurement onwards. Finally, five plots were burned in a wildfire before the last measurement and consequently excluded for the last data collection (site 4 tall grazed and ungrazed, site 7 tall ungrazed, site 8 tall grazed and ungrazed).

2.3.2 | Camera Trap Images

We set up camera traps to determine herbivore activity on the experiment. Three camera traps were distributed across the site in a 6-month rotation. Cameras monitored the grazed control plots of either short or medium grass and, where possible, the paired ungrazed plot was included in the field of view to detect whether the fences kept out animals. Cameras were Browning Dark Ops 940 HD (Model BTC-6HD-940) with a passive infrared motion sensor (0.4 s trigger speed, 24 m detection range) and a no glow infrared flash (24 m flash range). They were programmed to take two photos (4 MP) 2 s apart day and night when motion was detected, with an interval of 20 s between trigger events. Cameras were installed at a height of 0.6 m, on either a wooden pole or tree, and angled slightly downward. All sites except site one and nine were monitored for approximately 6 months.

2.3.3 | Data Analysis

We used linear mixed models from the lme4 package (Bates et al. 2015) in R version 4.0.2 (R Core Team 2024) to analyze how the height and biomass of herbaceous vegetation in the plots were affected by the experimental treatment (grazed vs. ungrazed), the time since the exclosure fences were erected, season (autumn or spring), and the type of grassland (short, medium-tall and tall). The random variables were the plots, nested in the plot pair (three plot pairs per site), nested in the replicate site ($n = 10$).

To quantify temporal change in the dominance of plant functional types we ranked the functional types from short and palatable to tall and un-palatable: (1) short stoloniferous grasses, (2) tufted palatable grasses, (3) bunch grasses, and (4) tall tough grasses. For each plot, we calculated the weighted average of these ranks over the pinpoint measurements within the plot, where a low value indicates dominance of creeping lawn grasses, while a high value indicates dominance of tall unpalatable bunch grasses. We used the general linear mixed models with treatment, time, season and type of grass plots as fixed factors. The random variables were the plots, nested in the plot pair (a total of 30 plot pairs). We did not include the replicate site as a random variable because the variance and standard deviation of this variable were zero.

To quantify plant diversity, we calculated species richness per plot and used general linear mixed models with treatment, time, season and type of grass plots as fixed factors. The random variables were the plots, nested in the plot pair, nested in the replicate site.

To assess community dissimilarity between paired grazed and ungrazed plots, we calculated Bray-Curtis pairwise distance with the vegan package (Oksanen et al. 2019). We used general linear mixed models to model the relationship between the community dissimilarity with time, season and type of grass plots. Through calculating the pairwise distance between paired plots, we lose the plot variable, as a result the random variables for our analysis were plot pairs (three plot pairs per site) nested in the replicate site ($n = 10$). When calculating dissimilarity from relative abundance, we assigned an abundance value of one to species that were present in the community composition list but were not abundant enough to be caught by the assessment with the pin-point frame. Plant taxonomic nomenclature was standardized using the Taxonomic Name Resolution Service v4.0 from iPlant Collaborative (IPlant Collaborative; Missouri Botanical Garden; National Plant Data Team).

We included the season as an explanatory variable in the models to account for the potential impact of species phenology on detectability in the field. For all models we started with the full model and eliminated interactions without significant effects. We also checked that the AIC for the final model was lower than for more complex models. We assessed the overall ability of the model to explain the data using R^2 for LMMs, which includes conditional and marginal R^2 (Nakagawa and Schielzeth 2013; Lüdecke et al. 2021).

We used a manual annotation software, the VGG Image Annotator (Dutta and Zisserman 2019), to record the presence of herbivores and omnivores in the camera trap images from our replicate sites. For each replicate site, we randomly selected 200 images from all images captured by that camera trap. We reviewed and annotated a total of 1600 images, for eight replicate sites (site 2–8 and site 10). We recorded all herbivores that could be identified, including multiple per image, small birds were not included. We checked that the randomly selected images did not include both of the consecutive multi-pchotos and replaced one with another random image if necessary. We extracted the animal occurrence data from our annotations of the camera trap images using the rjson (Couture-Beil 2024) package in R. We calculated the percentage of individuals of each herbivore species, in relation to the total number of herbivores identified in the randomly selected camera trap images at each replicate set.

3 | Results

Plant species richness decreased significantly in the ungrazed plots throughout the experiment for all grass types, but remained constant in the grazed plots ($p<0.003$, conditional $R^2=0.63$, marginal $R^2=0.27$). Ungrazed plots lost on average 3–4 species, around 40% of the average species richness, over the course of 18 months. The short grasslands richness was significantly higher than that of tall grasslands ($p<0.005$), but did not differ from the medium-tall grasslands (Figure 3a). Consistent with the finding of reduced richness in ungrazed plots, we found that plant community dissimilarity increased over time between pairs of ungrazed and grazed plots within the same grassland type and site ($p<0.005$, cond. $R^2=0.52$, mar. $R^2=0.41$). This dissimilarity between paired plots was significantly higher in short grasslands than in tall grasslands at the end of the experiment ($p<0.05$), but did not differ from medium-tall grasslands (Figure 3b).

Grass was significantly taller in the ungrazed plots than in the grazed plots ($p<0.005$, cond. $R^2=0.85$, mar. $R^2=0.69$) (Figure 4). In the grazed plots, grass height remained constant throughout the 18-month study period, while in the ungrazed plots height increased significantly over time (interaction between time and treatment is $p<0.001$, Figure 3). The difference in grass height between grazed and ungrazed plots was significantly modulated by grassland type (interaction between short and intermediate grass type and treatment was $p=0.04$, interaction between time, grass type and treatment was $p<0.05$), with strong herbivore exclusion effects in short and medium grasslands, but not in tall grasslands (Figure 4a).

Herbivore exclusion affected plant biomass in a similar way as height (Figure 4b). Over the 18 months of the study, ungrazed plots had higher biomass compared to grazed plots through time ($p<0.001$, cond. $R^2=0.78$, mar. $R^2=0.55$), and this effect was stronger for short and medium grasslands (Figure 4b).

The composition of grass functional types shifted toward more upright (caespitose) and taller functional types in the ungrazed plots through time ($p<0.001$, cond. $R^2=0.94$, mar. $R^2=0.87$), consistent with observed increases in vegetation height and biomass. However, after 18 months the initially short and medium-tall grasslands did not acquire the tallest and coarsest grass functional types (category 4) that dominate tall grasslands (Figure 5). In contrast, grazed plots remained dominated by the same grass functional types (Figure 5).

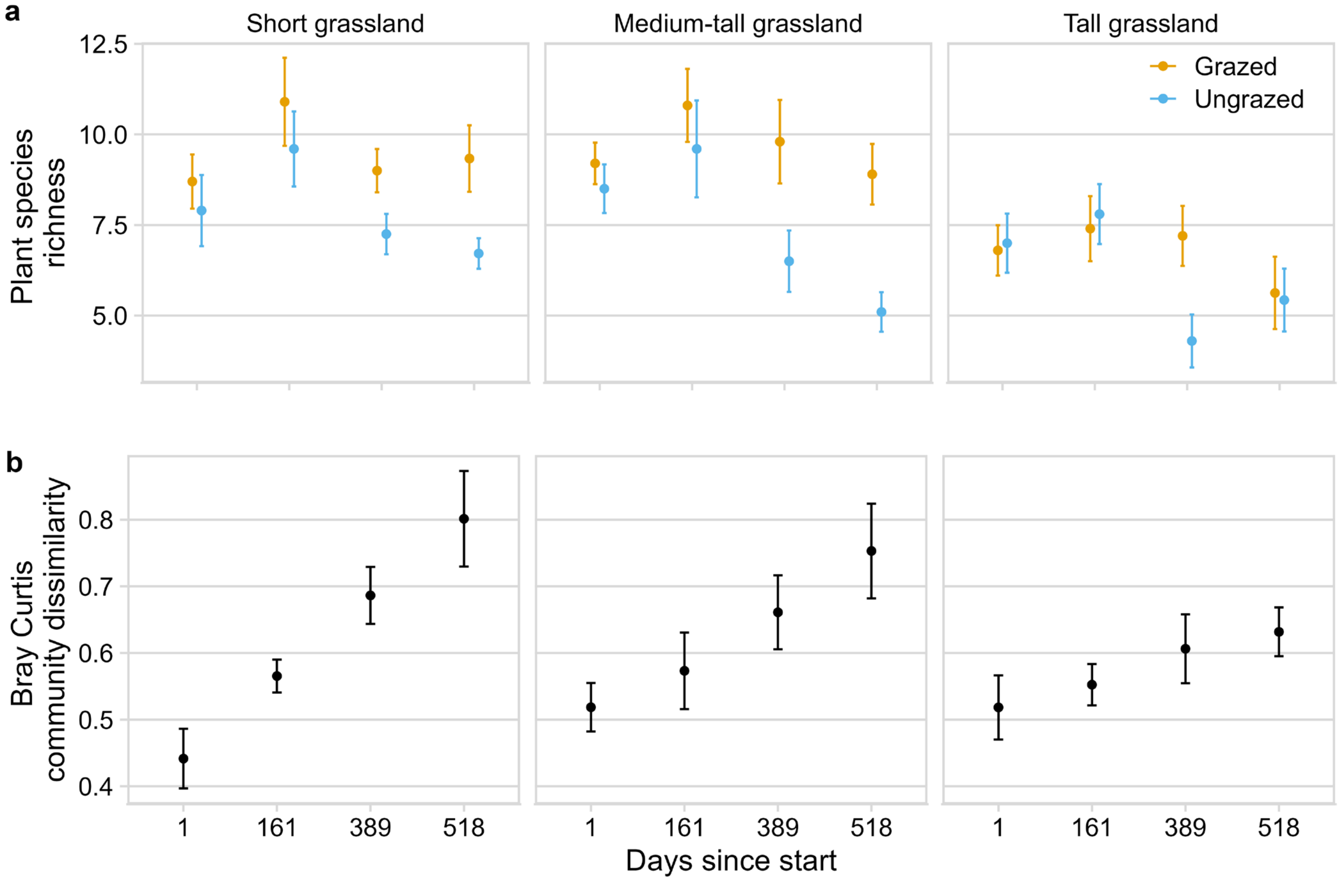

FIGURE 3 | Herbivore exclusion reduces plant species richness in an 18-month exclosure experiment (a) and increases plant community dissimilarity between paired grazed and ungrazed plots (b). Error bars are standard errors.

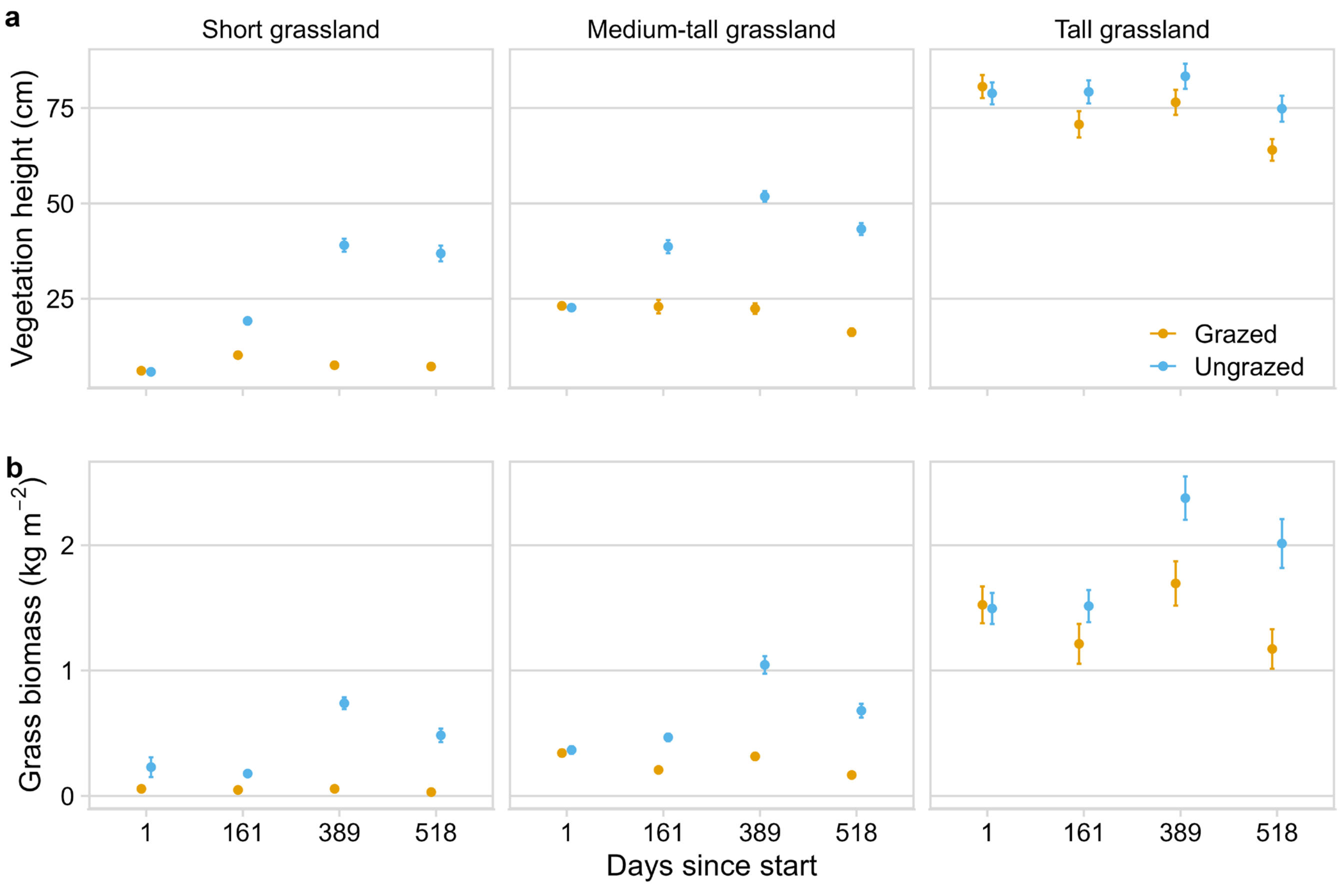

FIGURE 4 | Herbivore exclusion affects vegetation structure in an 18-month exclosure experiment, specifically herbaceous vegetation height (a) and herbaceous biomass (b). Error bars show standard errors.

Camera trap images showed that capybara (an obligate grazer) was the dominant herbivore in our study area, with smaller contributions by gray brocket deer and greater rhea (Figure 6). For all replicate sets analyzed through camera trap data, between 47% and 81% of the individuals identified in the images were capybara (Appendix S1, Table S1).

4 | Discussion

We examined herbivore-driven top-down control of vegetation structure and composition in a South American savanna where the majority of native megafauna has recently gone extinct, in several cases only 7000–8000 years ago (Barnosky and Lindsey 2010; Prado et al. 2015; Doughty et al. 2016). We found that removing large herbivores decreased alpha diversity of the herbaceous layer, likely by reducing light competition from taller and fast-growing species. Specifically, areas with shortly cropped vegetation generated by capybara, the dominant grazing herbivore in the system, appear analogous to grazing lawns in African savannas. In Africa grazing lawns strongly influence local plant diversity, animal movement and landscape-scale ecosystem processes such as nutrient (re)distribution and patterns of fire spread (Waldram et al. 2008). These results imply that South American grassy ecosystems, despite severely reduced herbivore richness and density, have retained plant taxa and plant functional trait complexes that tolerate intense herbivory and, importantly, that herbivory is required to maintain biodiversity in South American savannas (Dantas and Pausas 2022). The conservation and restoration of South American grassy ecosystems is therefore likely to benefit from restoring natural grazing regimes.

We found that in plots without herbivory, species richness decreased over time as herbaceous vegetation height and biomass increased. As a consequence, dissimilarity between grazed and ungrazed plots increased over the duration of the experiment. Fast growing, taller plants often out-shade smaller light-demanding plants in the absence of disturbance and become dominant (Archibald 2008; Timmermann et al. 2015). Herbivores can reduce this competition by consuming some of the faster-growing plants and providing space for light-demanding plants (Borer et al. 2014). These results highlight the importance of herbivory for maintaining or increasing plant species richness in South American grasslands.

The strong effects of grazing exclusion on plant community dynamics were most pronounced in short and medium-tall grasslands, whereas community effects in tall grasslands were either weak or absent. We hypothesize that the current, strongly downsized herbivore assemblage cannot consume enough of these coarse, less palatable grasses to have a measurable effect in our exclosure experiment. Larger bulk grazers, currently not present in the system but continuously present in the system since the early Cenozoic and up until the mid-Holocene (Table S2), may be required to establish top-down herbivore control in these

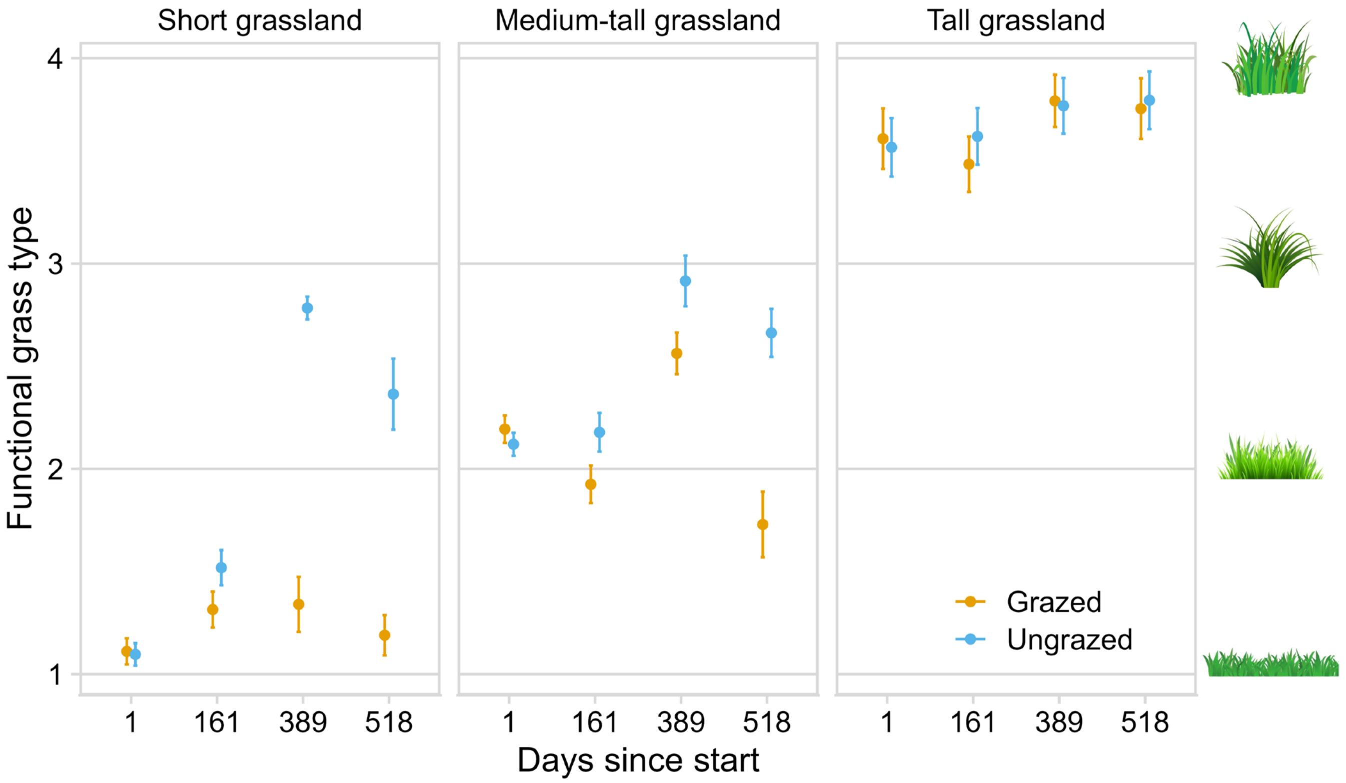

FIGURE 5 | An 18-month herbivore exclusion leads to shifts in the dominance of grass functional types. The values on the y-axis are the weighted mean of an ordinal variable where short grass = 1, tufted grass = 2, bunch grass = 3, tall grass = 4, and the weights are the relative abundance of each type per plot. A small value indicates that a plot is dominated by short prostrate grasses, whereas plots dominated by tall and coarse grasses get a large value. Error bars show standard errors.

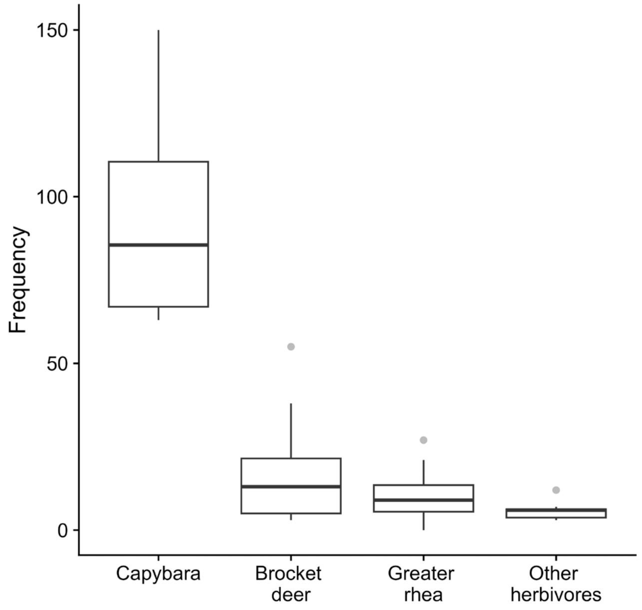

FIGURE 6 | Frequency of herbivore species detected in 1600 camera trap images on grazed plots of an 18-month exclosure experiment. Other herbivores include: Marsh deer, feral pig, axis deer, lowland tapir and collared peccary.

tall grasslands. Alternatively, vegetation fires followed by high-intensity grazing from locally abundant smaller herbivores may be able to keep currently tall vegetation in a shorter state as can be observed in African ecosystems (Cromsigt and Olff 2008; Donaldson et al. 2018). Both of these ideas remain to be tested in South American savannas and grasslands.

In addition to impacts on vegetation composition and species richness, we found strong impacts of grazing on vegetation structure, where grazing reduced vegetation height, and decreased the relative abundance of taller-growing grass functional types. There are several grass traits that indicate tolerance to grazing, including prostrate growth, clonal growth, short-stature, small leaves and seeds, and higher specific leaf area (Cayssials and Rodríguez 2018; Archibald et al. 2019; Fischer et al. 2019). In fenced short-grass plots, the vegetation shifted from a grazing lawn, that is, a structure and functional composition indicative of grazing tolerance, to upright caespitose grasses.

Grazing lawns are short-grass areas dominated by low-statured grass species that can tolerate heavy grazing. High intensity and recurrent grazing on lawns selects for grazing-tolerant plant species, while preventing the build-up of senescent plant material and keeping the vegetation in state of continuous regrowth, with higher nutrient concentrations. This attracts more grazing and associated nutrient input from urine and dung, further strengthening the grazer-vegetation feedback (McNaughton 1984; Archibald 2008; Hempson et al. 2015). In addition to plant communities, grazing lawns can affect biodiversity and ecosystems in various ways. For example, certain bird and insect species depend on shortly grazed grasslands (Krook et al. 2007; Hempson et al. 2015). Lawns also contribute heterogeneity in the amount and continuity of herbaceous biomass and therefore act as natural firebreaks (Waldram et al. 2008; Leonard et al. 2010), and can lower predation risk for herbivores (Riginos and Grace 2008; Anderson et al. 2010). Grazing lawns have been linked to accelerated nutrient cycling through grazers returning plant-available nutrients as dung and urine (Hempson et al. 2015). Our results suggest that the short grasslands in our South American study site are analogous and function similarly to African grazing lawns, promoting overall biodiversity and heterogeneity in South American grassy ecosystems.

However, the creation and maintenance of African grazing lawns are often ascribed to very large herbivores with relatively broad muzzles such as hippopotamus (*Hippopotamus amphibius*) and white rhino (*Ceratotherium simum*), while all very large grazers have gone extinct from South America. Instead, we identified capybara, a 50 kg animal, as the main grazer that maintains these grazing lawns. This is consistent with more recent work on African grazing lawns, which shows that medium-sized grazers such as blue wildebeest (*Connochaetes taurinus*) and warthog (*Phacochoerus africanus*) can have equally large, or larger roles in maintaining lawns (Cromsigt and Olff 2008; Donaldson et al. 2018).

Capybara are highly gregarious and relatively sedentary in our study system, exerting a high grazing pressure locally, regardless of their size (Moreira et al. 2012). While capybara depend on the presence of water in the landscape, in our study system they exploit smaller ponds and wetlands which are ubiquitous in these landscapes, especially in areas with natural hydrology. Since capybaras have a wide potential distribution near water in South America, but have disappeared from much of their former range (Moreira et al. 2012) there may be considerable potential for reintroducing capybara as a top-down control on grassy vegetation in South America, especially since they have high reproductive rates and new populations should be relatively easy to establish. Furthermore, because of their plasticity in resource use, capybaras are able to thrive in diverse environment types, including heavily human influenced environments (Magioli et al. 2023). Especially in combination with fire, which might enable smaller-bodied grazers like capybara to maintain short-grass areas in otherwise tall grasslands, capybara expansion may be a promising and relatively cost-effective approach to reinstating herbivory in (seasonally) wet South American grassy ecosystems.

However, since capybara had negligible impacts on the tall grasslands in our study system, which make up 64% of the study area (Mata et al. 2021), the reintroduction of a larger grazer may be needed if the management objective is to increase plant diversity and vegetation heterogeneity in these areas. Since all large native grazers in this South American savanna have been driven to extinction (Table S2), a functional replacement species would be required to perform this ecological function. Horses may be interesting to consider as a large grazer in this context, since South America has had native horses for the past 900,000 years and were driven to extinction by humans only around 12,000 years ago (de Villalobos and Zalba 2010; Naundrup and Svenning 2015; Scorolli 2018; Di Bitetti et al. 2022). South American plant species and vegetation formations have thus been exposed to, and evolved under, horse herbivory for a very long time.

While we are not aware of any studies on horse impacts in South American grassy ecosystems, there is indeed evidence that larger grazers may benefit South American grassy ecosystems. Low-intensity cattle grazing has been shown to limit woody and exotic grass invasion compared to cattle exclusion sites (Durigan et al. 2022; Abrigo et al. 2024; Sandoval-Calderon et al. 2024). In other areas, complete cattle exclusion with sporadic fires was shown to lead to increased plant species diversity compared to traditional cattle farming (Batista et al. 2018), suggesting that livestock grazing intensity may be important in predicting impacts on plant diversity. Regardless, our results highlight the need for more work that better quantifies the impact of large, possibly non-native, grazers in South American grassy ecosystems, and how herbivore impacts may vary along environmental and biogeographic gradients.

Another societally-relevant reason to better quantify the potential of herbivores in regulating vegetation is their potential to limit the risk of severe wildfires (Di Bitetti et al. 2022; Karp et al. 2024), not least considering the large potential for vegetation fires in this region with the capacity for large economic damages, as happened in 2022, when 800,000 ha burned in Corrientes province. Since fire is perceived as a growing threat to human well-being in the region (Saucedo et al. 2022), low-cost nature-based solutions to reducing fuel loads and fuel continuity may become increasingly important. It is thus crucial to further unravel the interactions between herbivory and fire in South American savannas with increasingly novel climates (Johnson et al. 2018; Svenning, Buitenwerf, and Le Roux 2024).

Our results show that herbivory promotes local plant diversity in a South American grassy ecosystem. There is strong evidence on the impacts of herbivory in South American savannas, supporting our suggestion that restoring natural grazing and fire regimes should benefit biodiversity in these ecosystems (Koerner et al. 2014; Bernardi et al. 2016; Doughty et al. 2016), consistent with the reported impacts of trophic rewilding around the world (Svenning, Lemoine, et al. 2024). This view is increasingly adopted and rewilding projects are emerging around South America as a means to restore ecological function to landscapes historically affected by human-driven megafauna extinctions (Galetti et al. 2017; Zamboni et al. 2017; Svenning, Lemoine, et al. 2024).

Author Contributions

J.C.M., J.-C.S. and R.B. conceived of the research idea; J.C.M., R.B., R.N.C., M.D., R.S. and A.V. collected data. J.C.M. and R.B. performed statistical analyses; J.C.M. and R.B., with contributions from J.-C.S. and R.N.C., wrote the paper; all authors discussed the results and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data can be downloaded at https://doi.org/10.5281/zenodo.14288542.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.