Applied Vegetation Science IAVS

RESEARCH ARTICLE

Multiple Effects of Capybaras on Vegetation Suggest Impending Impacts of Jaguar Reintroduction

Ana Belen Avila[1,2] | María Jose Corriale[3,4] | Debora Di Francescantonio[2,5] | Pablo Ignacio Picca[6] | Emiliano Donadio[7] | Mario Santiago Di Bitetti[1,2,5] | Agustín Paviolo[1,2] | Carlos De Angelo[2,8]

[1]Instituto de Biología Subtropical (IBS), Universidad Nacional de Misiones (UNaM) – CONICET, Puerto Iguazú, Argentina | [2]Asociación Civil Centro de Investigaciones del Bosque Atlántico, Puerto Iguazú, Argentina | [3]Departamento de Genética, Ecología y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Buenos Aires (UBA), Capital Federal, Argentina | [4]Instituto de Ecología, Genética y Evolución (IEGEBA), Universidad Nacional de Buenos Aires (UBA) – CONICET, Capital Federal, Argentina | [5]Facultad de Ciencias Forestales, Universidad Nacional de Misiones (UNaM), El dorado, Argentina | [6]Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Buenos Aires (UBA), Capital Federal, Argentina | [7]Rewilding Argentina, Estancia La Ascensión, Los Antiguos, Argentina | [8]Instituto de Ciencias de la Tierra, Biodiversidad y Ambiente (ICBIA), Universidad Nacional de Río Cuarto (UNRC) – CONICET, Rio Cuarto, Argentina

Correspondence: Ana Belen Avila (belenavila4@gmail.com)

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ABSTRACT

Aims: A key challenge in applied vegetation science is understanding the impact of herbivory on plant communities. Herbivores often reduce dominant species' abundance (biomass, cover), making resources available for new species and increasing plant diversity. This understanding is crucial in systems undergoing ecological restoration through trophic rewilding. In Iberá National Park, Argentina, jaguars (*Panthera onca*) are being reintroduced after a 70-year absence, and it is critical to assess the role of herbivores in shaping plant communities for evaluating future potential trophic cascades. Capybaras (*Hydrochoerus hydrochaeris*), the park's most abundant herbivore and an important prey for jaguars, likely exert significant pressure on vegetation. This study aims to investigate how capybara herbivory affects vegetation height, biomass, diversity, and composition, providing insights into how jaguar reintroduction might indirectly influence plant communities and restore ecosystem functionality through capybaras' demographic or behavioral responses.

Location: Iberá National Park, Corrientes, Argentina.

Methods: We simulated the absence of capybara foraging pressure by establishing 10 3 m x 3 m herbivore exclosures with adjacent unfenced control plots in the capybara's grazing lawns. Vegetation attributes—height, biomass, plant diversity, and species composition—were monitored over 4 years to assess the impact of capybara exclusion on plant communities.

Results: Excluding capybaras significantly increased vegetation height and biomass, which, in turn, altered plant diversity and species composition. The exclosures' vegetation height and biomass were consistently higher than those in control plots. A decrease in species diversity accompanied this shift, as the abundance of common species declined and the dominance of a few species increased, generating new communities.

Conclusions: Capybaras significantly influence vegetation dynamics, demonstrating their role in shaping plant communities. Excluding capybaras leads to species composition and structural shifts, highlighting herbivory's importance in maintaining

ecosystem heterogeneity. These findings provide critical baseline data for understanding the potential indirect impacts of the jaguar's reintroduction on plant communities and ecosystem processes. This study contributes valuable insights into the ecological mechanisms underlying plant–herbivore interactions, which are essential for guiding restoration practices and rewilding strategies.

1 | Introduction

Herbivores play a central role in modifying plant communities by directly influencing height, biomass, and species composition (Lundgren et al. 2024; Trepel et al. 2024). The changes produced by herbivores on vegetation can impact broader ecosystem processes, such as nutrient cycling, carbon sequestration (Marquis 2010; Monk and Schmitz 2022) and wildfire regimes (Johnson et al. 2018; Karp et al. 2021). These dynamics highlight the broader ecological significance of herbivory in maintaining functional ecosystems and the key role that herbivores and vegetation ecology can play in restoration ecology and conservation.

Herbivory generally reduces the abundance of dominant plant species and concurrently increases biodiversity (Olff and Ritchie 1998). As dominant species decrease due to herbivore consumption, the availability of light, nutrients, and water increases, which enables the proliferation of less common species, the colonization of new species, and/or a reduction in local extinctions, modifying plant communities. However, the extent and nature of these effects are influenced by various factors, including ecosystem productivity and disturbance regimes (Kondoh 2001), as well as the palatability and consumption preferences of dominant species (Koerner et al. 2018). Consequently, grasping how plant communities respond to varying herbivory pressures within specific ecosystems is critical for effective ecosystem management and developing restoration strategies that prioritize biodiversity conservation and ecosystem resilience.

Rewilding has emerged as a strategy to restore ecosystem functionality by reintroducing species that can influence ecosystem processes disproportionately to their abundance (Paine 1995; Soorae 2021; Soulé and Noss 1998). Trophic rewilding aims to restore top-down interactions, such as reintroducing large predators (Svenning et al. 2016), which can indirectly affect plant communities through changes in herbivore populations and behavior (Estes et al. 2011). However, environmental conditions can buffer herbivory impacts (Ford et al. 2015; Morgan et al. 2017), potentially diluting indirect predator effects (Palmer et al. 2021; Pringle et al. 2007). Therefore, it is crucial to establish baseline data on herbivory and its effects on vegetation to effectively evaluate rewilding's potential to enhance biodiversity through trophic cascade restoration in specific ecosystems (Brice 2022).

Iberá National Park (INP), Argentina, is the focus of a rewilding process, where the reintroduction of the jaguar (*Panthera onca*) after 70 years of being extinct (Donadio et al. 2022) represents a unique opportunity to investigate how apex predators can shape vegetation dynamics via trophic cascades (Ripple et al. 2016). The capybaras (*Hydrochoerus hydrochaeris*), being the most abundant herbivore in INP, potentially exert significant pressure on vegetation through grazing activities. Additionally, they are a crucial prey for the jaguar in other regions where this predator is present (Cavalcanti and Gese 2010; Foster et al. 2013; McBride et al. 2010), thus representing an important potential prey for this reintroduced carnivore (Donadio et al. 2022). Given the high abundance of capybaras in INP and their relative naivety to predator cues, significant changes in their densities, behavior, and foraging patterns are expected in response to jaguar presence (Avila et al. 2022). These changes could subsequently affect plant community composition and structure, but for this trophic cascade to occur, capybaras must play an important role in consuming vegetation (Ford and Goheen 2015). Therefore, assessing how changes in capybara grazing impact plant communities is crucial for understanding the potential broader impacts of this rewilding strategy on INP restoration.

To assess the direct influence of capybara herbivory on vegetation at INP, we simulated the absence of grazing by establishing herbivore exclosures and monitoring vegetation attributes over 4 years before jaguars were reintroduced. We hypothesized that if capybaras play a key role in controlling vegetation dynamics, excluding them would lead to increased vegetation height and biomass, as well as changes in species diversity and composition. This would result in a less diverse grassland dominated by a few dominant species. Understanding the effect of capybara grazing on vegetation should enable us to assess whether the reintroduction of jaguars may indirectly influence plant communities and to better understand the potential impacts of trophic rewilding as a conservation strategy.

2 | Materials and Methods

2.1 | Study Area

We conducted this study in Iberá National Park (Corrientes, Argentina), a 195,094-ha protected area in the extensive Iberá Wetland. Iberá, the second largest wetland in South America, is a 13,000 km^2 depression located in a paleo-river bed of the Paraná River (Neiff and Poi de Neiff 2006) (Figure 1). The region's mean annual precipitation is 1700 mm, concentrated in the warm season (November to March) (Ligier et al. 2004). Mean annual temperatures range from 28°C in summer to 16°C in winter.

From December 2017 to December 2021, we implemented our fieldwork in San Alonso (28°18′23.2″ S, 57°27′15.9″ W), a 10,459-ha island surrounded by marshes in the center of INP (Figure 1). Jaguars were eradicated from Iberá in the mid-20th century, whereas pumas (*Puma concolor*) had not been recorded in San Alonso until the end of this study. Therefore, large felid predation of capybaras has likely been absent for over 70 years. San Alonso is the area of INP where the jaguar reintroduction program is focused. Therefore, this is a key area for understanding herbivore –vegetation relationships to predict potential indirect effects of jaguars, and this is why our experiment was focused on this area to establish a pre-reintroduction baseline.

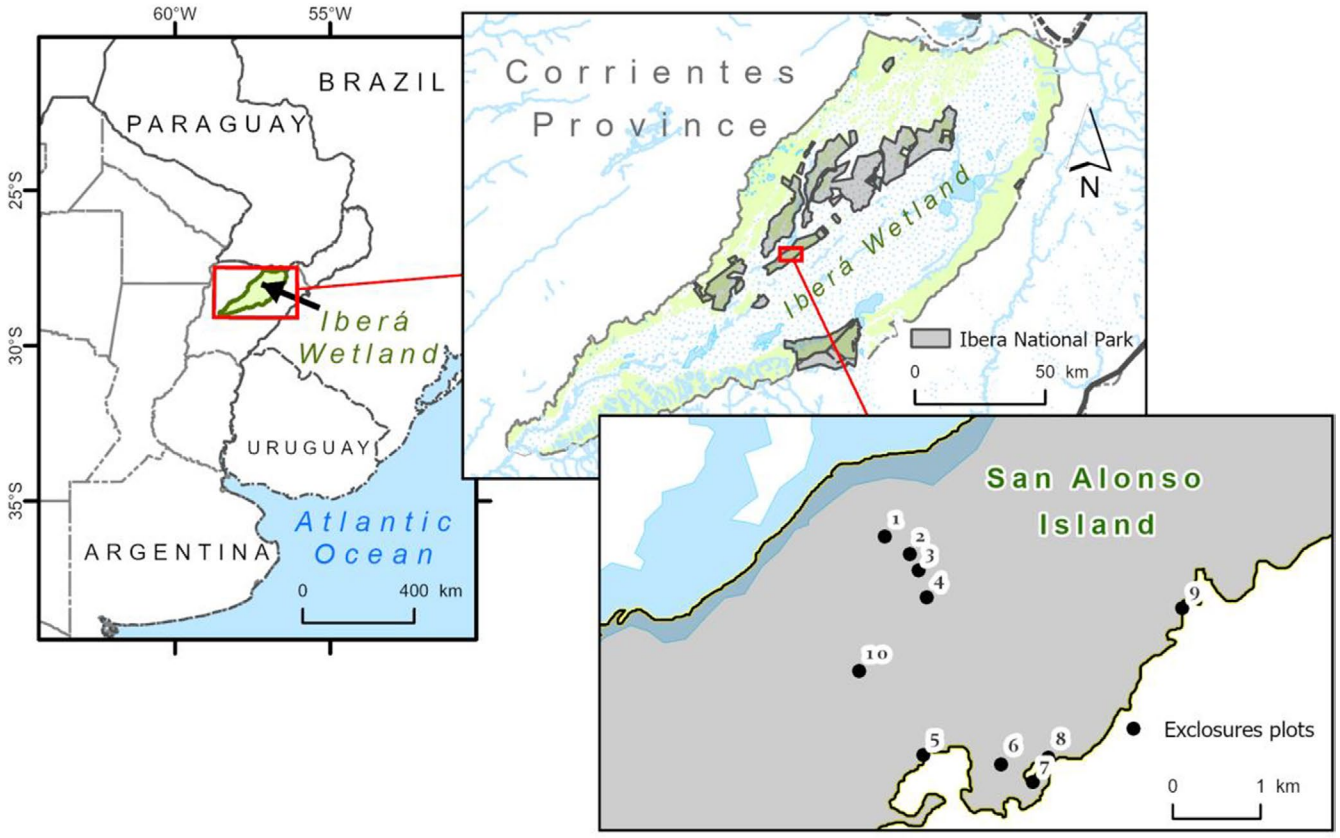

FIGURE 1 | Geographical location of the Ibera Wetland, Iberá National Park, and San Alonso Island (Corrientes, Argentina).

Capybaras are large social rodents of about 35–70 kg (Ojasti 1973) and they are the most abundant herbivores at INP with densities over 50 individuals per square km (Avila 2017). Other large herbivores, such as marsh deer (*Blastocerus dichotomus*) and pampas deer (*Ozotoceros bezoarticus*), have much lower densities (Avila 2017). Roads are absent and overall human influence is negligible on the island.

2.2 | Physiognomy of the Vegetation and Areas Used by Capybaras

San Alonso presents a mosaic of grasslands, lagoons, marshes, and forests. The landscape is dominated by 'espartillo' grasslands (*Elionurus muticus*) in upland areas with deep and well-drained soils, 'paja colorada' grasslands (*Andropogon lateralis*) in mid-elevation areas, where water drains incompletely, and floodplains of 'paja azul' grasslands (*Paspalum durifolium*) in the low areas. There are small patches of hygrophilous forests locally called mogotes and small stands of yatay poñí palms (*Butia paraguayensis*) in well-drained sandy areas (Corriale et al. 2013).

The habitats most frequently utilized by capybaras as foraging grounds are those located in the transition between the mid-elevation lands and the lagoons or marshes (Corriale 2010; Herrera and Macdonald 1989) and the uplands located between mid-elevation and high areas that are unlikely to become flooded. Capybaras mainly consume soft-leaved, low-statured Poaceae and Cyperaceae (Quintana et al. 1994, 1998a, 1998b), including species from the genera *Paspalum*, *Steinchisma*, and *Axonopus* (Barreto and Quintana 2013; Mata 2021).

Transitional areas feature up to 15-cm tall plants, like *P. pumilum, Oldenlandia salzmannii*, *Eleocharis minima*, and *Hydrocotyle verticillata*, which are the dominant species (Corriale et al. 2013) (Figure 2). Upland areas present patches of 30–160 cm tall grasses dominated by *A. lateralis*, and patches of ≤10-cm tall grasses dominated by *Axonopus fissifolius* (Poaceae), *P. pumilum*, and *P. almum* (Poaceae). In the uplands, capybaras concentrate their foraging mainly in the afternoon (Corriale et al. 2013) (Figure 2). In our experiment, we established 10 exclosures in these upland areas, since these areas furthest from water are expected to be the first to be abandoned by capybaras in response to the presence of jaguars, and where the first changes in vegetation structure and composition would be observed (Avila et al. 2022).

2.3 | Experimental Design and Data Collection

We tested the effects of capybaras on vegetation by establishing 10 pairs of 3 × 3 m exclosure and control plots in the upland areas used for foraging by 10 different capybara groups that were monitored and subjected to behavioral studies (Avila et al. 2022). The exclosures were created in 2017 (Year 0) and we include in this study the measurements until 2021 (Year 4), the year when jaguars were reintroduced to the study site. Three female jaguars (two of them with their cubs) were sequentially soft-released (in January, April, and September,

respectively) and monitored as part of the INP rewilding program (Donadio et al. 2022). Therefore, to avoid potentially confusing effects of jaguar presence in our control plots, we ended this stage of the experiment in December 2021 when we started noticing jaguar activity in the surroundings of our experimental areas.

Each exclosure consisted of a 1 m-high fence that excluded medium and large herbivores (Figure 3). Paired treatment-control plots were 1–5 m apart to ensure consistency in plant community composition. This design assumed that vegetation was primarily affected by capybaras given their high densities compared to other herbivores in the study area (Avila 2017). To test this assumption, we deployed a trail camera (Bushnell Trophy Cam) facing the control plot in each site at the beginning of the experiment. Then, we estimated the number of photographs/day for different herbivore species and averaged this value across all 10 sites. Cameras were active 24 h a day, taking one photograph per activation event with a 10-s interval between events. Cameras operated 122 ± 71 days ($\bar{x} \pm \text{SD}$, $n = 10$).

In each plot, we evaluated the vertical structure of the vegetation, plant diversity, and plant species composition. We carried out these evaluations annually in December (spring/summer) from 2017 to 2021. The measure for December 2020 had to be delayed due to the COVID-19 outbreak and was taken in March 2021. In exclosure and control plots, we assessed vertical structure using four 0.5×0.5 m quadrats and recorded the vegetation height (cm), the number of plant species, and cover (%) inside each quadrat. Near the end of the experiment in 2021, we estimated plant biomass (g/m^2) as a proxy of primary productivity by placing a 0.25×0.25 m quadrat in the center of each plot and clipping all plant samples within. Samples were dried in an oven for 3 days at 70°C and weighed with a precision scale to the nearest gram.

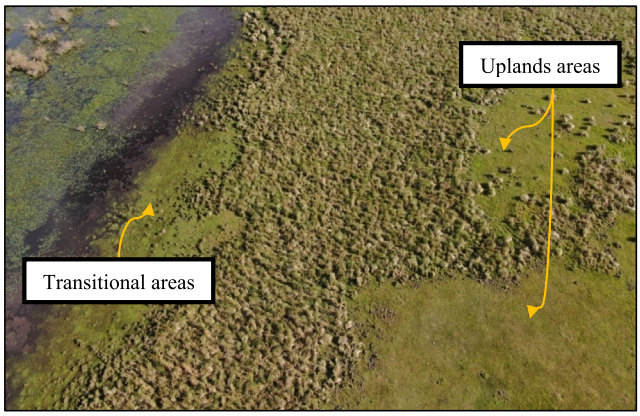

FIGURE 2 | Transitional and upland areas; both represent the main foraging habitats for capybaras. San Alonso Island, Iberá National Park (Esteros del Iberá, Corrientes).

2.4 | Data Analysis

2.4.1 | Vertical Structure of the Vegetation and Plant Biomass

We evaluated differences in vegetation height among exclosures and control plots by year, using a generalized linear mixed model (GLMM). Each pair of plots (exclosure + control) was used as a random factor. We included vegetation height from 2017 (Year 0) as a covariate. Post hoc mean comparisons were conducted using a Tukey test. To evaluate the impact of capybara exclosure on biomass, we used average dry weight as the response variable, and we fitted this variable to a linear model with a normal distribution. We assessed distribution adjustment graphically from complete model residuals. The variance of dry weight was modeled using the Fixed function (varFixed) to correct for heterogeneity. All analyses were performed using R version 4.2.2 (R Core Team 2024) utilizing the '*lme4*' package (Bates et al. 2015) and the '*nlme*' package (Pinheiro et al. 2022). Differences were considered significant at $p < 0.05$.

2.4.2 | Plant Diversity

We estimated plant diversity per year for exclosure and control plots using incidence data (presence/absence of each species in the total 0.5×0.5 m grids, 40 per treatment). To represent the effective number of species within a specific community, we used Hill numbers (Hill 1973):

- q0 (species richness): it counts species equally without regard to their relative abundances. Therefore, it reflects the total number of species, including rare species (Chao et al. 2016; Jost 2007).

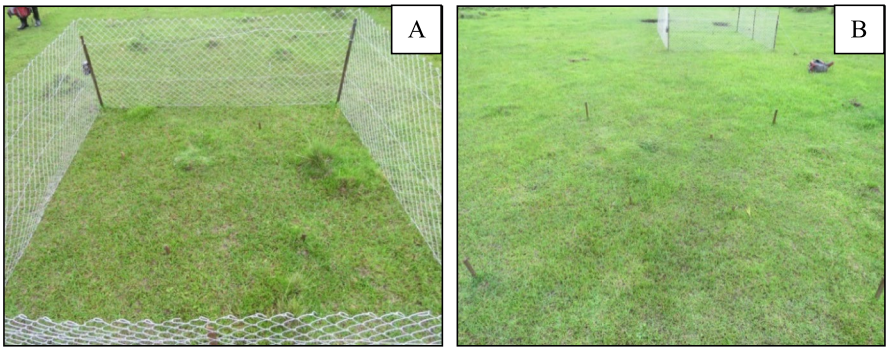

FIGURE 3 | Exclosure (A) and control (B) plots in the foraging area of a capybara group in San Alonso Island, Iberá National Park (Corrientes, Argentina), February 2018. Note the stakes defining the control plot.

- q1 (the exponential of the Shannon index): it weights species proportionally to their incidence frequency, giving more importance to species with moderate to high occurrence. This metric is associated with the 'effective number of common species', as it reduces the influence of rare species (Chao et al. 2016; Jost 2007)
- q2: (the inverse of Simpson diversity index): it gives higher weight to the most frequent species, highlighting those that dominate the community and can be interpreted as the 'effective number of dominant species' (Chao et al. 2016; Jost 2007).

To assess how well the sample represented the community, we estimated sampling completeness for each year using rarefaction curves based on sample coverage (Chao et al. 2016). Coverage is considered a measure of sample completeness, indicating the proportion of the frequency of individuals in a community that belong to the species represented in the sample (Chao and Jost 2012). We compared the values of q between years using a 95% confidence interval obtained from bootstrapping the original data, at the same coverage value (the minimum value of treatment and control per year) (Chao et al. 2016). These analyses were conducted using the iNEXT package (Chao et al. 2016).

2.4.3 | Floristic Composition

To visualize and detect yearly differences in floristic composition among exclosure and control plots, we used non-metric multidimensional scaling (NMDS). This analysis was based on species cover averaged per site using a Bray–Curtis similarity matrix and permutational multivariate ANOVA (PerMANOVA) (Anderson 2001) with 9999 permutations. We used the 'vegan' package (Oksanen et al. 2019) in R version 4.2.2 (http://www.r-project.org) to perform both analyses. We conducted comparisons upon building the exclosures in 2017 (Year 0), and then in 2019 (Year 2) and 2021 (Year 4). We included as covariates the cover of dry matter (%), bare soil (%), and the height in cm of vegetation. Covariates were not included in the distance matrix, so their significance does not explain group formation but rather the association of the covariates with the groups formed.

We applied a classification method to evaluate the number and similarity of plant communities at the beginning and after 4 years of excluding capybaras. We used average species abundance values to perform a cluster analysis with Ward's clustering method and the Bray–Curtis similarity coefficient for Years 0 and 4. We then described the clusters formed in terms of dominant (species with the highest abundance and/or species with abundance greater than 25%) and companion species (second most abundant species, but less than 25%). Clustering and choosing the optimal number of groups were carried out using the *cluster* package in R version 4.2.2 (http://www.r-project.org).

3 | Results

Capybaras were the most frequent herbivores recorded where the experiments were deployed. They represented 94% of the total individual mammals recorded by the cameras ($\bar{x}[\pm SD] = 56 \pm 28$ capybara records day^{-1}; $n = 10$).

We identified 33 plant species from 20 families in capybara foraging areas (Appendix S1). Poaceae (8 species) and Cyperaceae (6 species) were the best-represented families.

3.1 | Vertical Structure of the Vegetation and Plant Biomass

3.1.1 | Height

From 2017 to 2021, vegetation height increased in the exclosures, but not in the control plots ($F = 8.39$, df = 3, $p = 0.001$) (Figure 4). The largest difference in plant height between exclosures and control plots was observed after 2 years (year 2019: $\bar{x}$ exclosure [95% CI] = 54 [47–62] cm; $\bar{x}$ control = 11 [4–17] cm), with up to a 4-fold increase in some plots compared to the first year (year 2018: $\beta = -21.8$, $p < 0.001$).

3.1.2 | Biomass

Mean dry biomass inside exclosures increased by 2.3-fold compared to the control plots after 3 years and 4 months of excluding medium and large herbivores ($\beta = 209.3$, $t = 5.58$, $p < 0.05$) (Figure 5).

3.1.3 | Plant Diversity

Experimental protection of vegetation from grazing led to a reduction in plant diversity, primarily driven by the decline of the richness of common and dominant species. In all years, sampling completeness exceeded 90%, indicating that the majority of species present in the area were successfully detected during sampling. Over the 4 years, the total effective number of species ($q0$) was relatively constant in both exclosure and control plots (Figure 6). The effective number of common species ($q1$) decreased by 50% inside exclosures from the second year onwards, whereas in control plots it declined by 10% (Figure 6). The effective number of dominant species decreased by 12% in the first year in exclosures and controls. From the second year onward, exclosures showed a 40% reduction in the number of dominant species, indicating a shift towards the dominance of a few species that increased in abundance (Appendix S2). At the same time, control plots maintained a stable high number, suggesting greater evenness (Figure 6).

3.1.4 | Floristic Composition

3.1.4.1 | Non-Metric Multidimensional Scaling Analysis (NMDS). During the first year, we noted a unified group encompassing both exclosure and control plots, displaying plant communities with no significant differences in composition (PerMANOVA, $F_{1,18} = 0.63$, $p = 0.69$) (Figure 7, A).

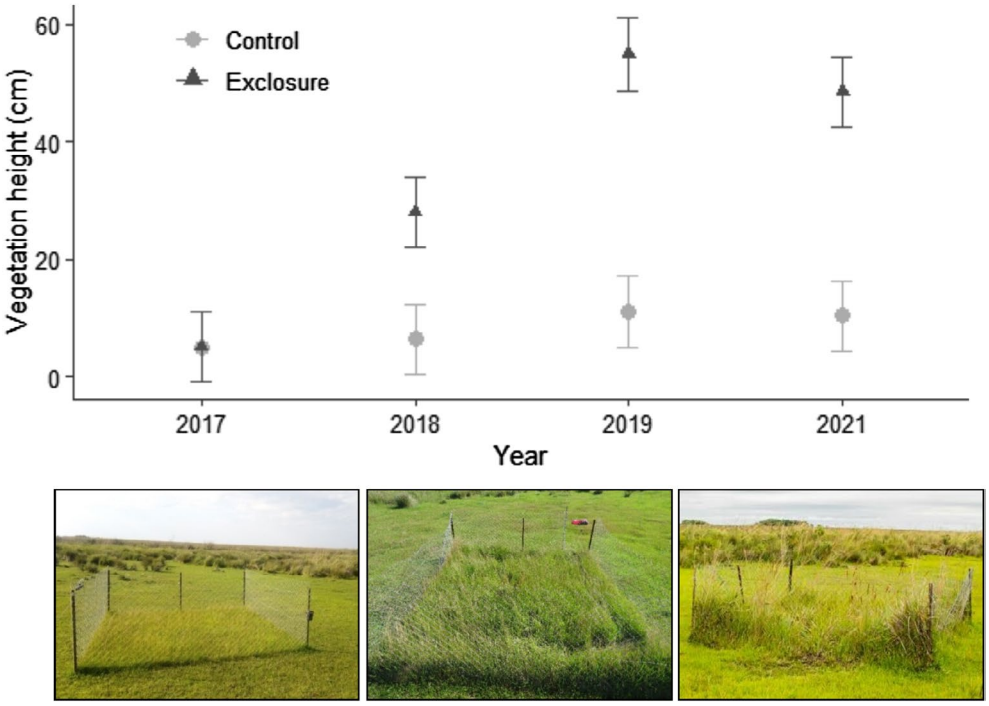

FIGURE 4 | Vegetation height (cm) in exclosure and control plots on San Alonso Island, Iberá National Park (Esteros del Iberá, Corrientes), at the start of the experiment (2017) and one (2018), two (2019), and four (2021) years after excluding herbivores. Vertical bars indicate 95% confidence intervals. Photos were obtained in 2017 (Figure 3), 2018 (left), 2019 (center), and 2021 (right) when measuring the plots. In 2020, we could not measure vegetation height due to restrictions related to the COVID-19 outbreak.

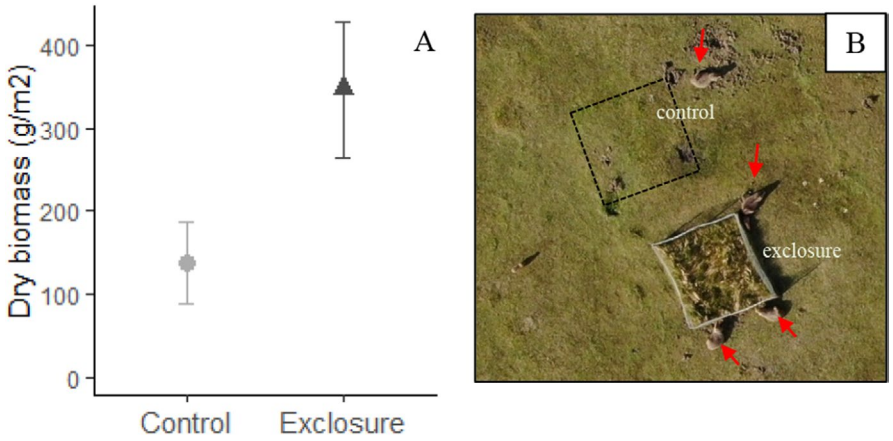

FIGURE 5 | (A) Dry plant biomass (g/m2) after 3 years and 4 months (March 2021) after excluding medium and large herbivores in San Alonso Island, Iberá National Park (Argentina, Corrientes). Vertical bars indicate 95% confidence intervals ($N = 10$). (B) Aerial view of an exclosure and its control plot (black rectangle) after 2 years of excluding herbivores showing the height and biomass differences. Several capybaras can be seen grazing near the plots (red arrows).

Two years after capybara exclusion, we observed two well-defined groups (PerMANOVA, $F = 2.83$, $p = 0.008$), with exclosures characterized by higher *Andropogon lateralis* cover and higher dry matter cover and vegetation height than control plots (Figure 7B). In turn, the latter were characterized by low grasses, such as *P. pumilum*, and a high percentage of bare soil.

Four years after capybara exclusion, differences in vegetation composition between exclosure and control plots persisted (PerMANOVA, $F = 4.61$, $p < 0.006$) (Appendix S2). Increased cover of *A. lateralis* continued to define the exclosures, together with increased cover of *P. maculosum* and some species that had very low abundance in Year 0, such as *Trichanthecium schwackeanum, Chaetogastra gracilis*, and *Steinchisma decipiens*. An increase in dry matter cover and vegetation heights characterized this group (Figure 7C).

3.1.4.2 | **Cluster Analysis.** The cluster analysis revealed two main groups at the beginning of the experiment (Figure 8). The first group (Group 0.1), consisting of exclosure and control plots, was dominated by *A. fissifolius*, with *Fimbristylis dichotoma* and *Andropogon lateralais* as accompanying species (species with lower abundance than the dominant one but with higher abundance compared to the rest of the species). The second

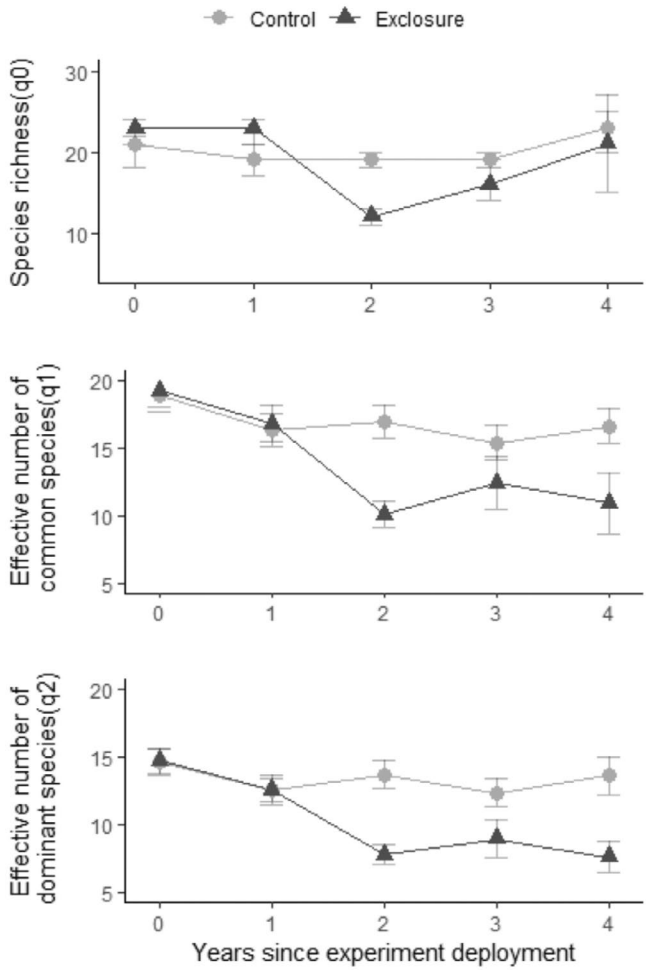

FIGURE 6 | The effective number of plant species for the diversity indices of order q0 (Species richness), *q*1 (common species), and *q*2 (dominant species) in exclosure and control plots in San Alonso Island, Iberá National Park (Argentina, Corrientes), between 2017 and 2021 (0–4). Vertical bars indicate 95% confidence intervals.

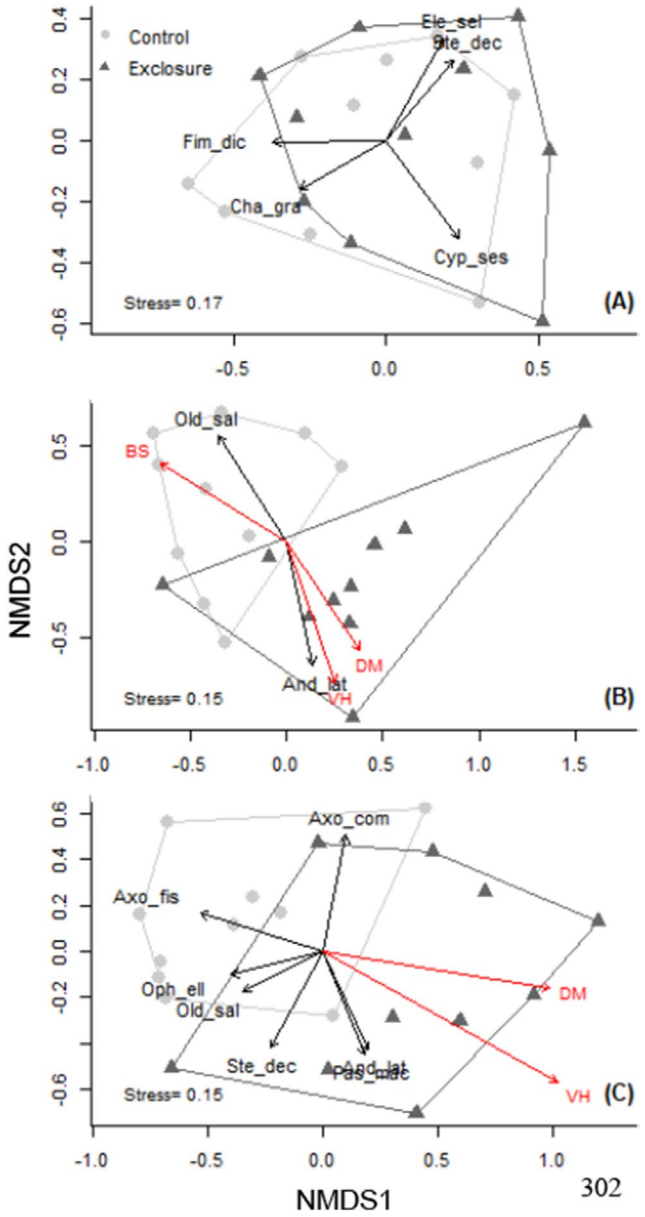

FIGURE 7 | Clustering of control and exclosures plots in San Alonso Island, Iberá National Park (Argentina, Corrientes) in years 0 (2017, A), 2 (2019, B), and 4 (2021, C) based on non-metric multidimensional scaling (NMDS). Minimum convex polygons circumscribe the plots in each treatment. The stress value is displayed, indicating the goodness of fit (<0.2=good fit). Variables (percentage of coverage per plant species) with $p<0.01$ in NMDS models are displayed and included. The proximity of points indicates similarity between plant communities. The direction and length of the arrows indicate the association of each variable and covariable with each group of points and the strength of this association, respectively. Abbreviations: And_lat, *Andropogon laterialis*; Axo_com, *A. compressus*; *Axo_fis*, *A. fissifolius*; BS, bare soil; Cha_gra, *Chaetogastra gracilis*; Cyp_ses, *Cyperus sesquiflorus*; DM, dry matter; Ele_sel, *Eleocharis sellowiana*; Fim_dic, *Fimbristylis dichotoma*; Old_sal, *Oldenlandia salzmannii*; *Oph_ell*, *Ophioglossum ellipticum*; *Pas_mac*, *P. maculosum*; Ste_dec, *Steinchisma decipiens*; VH, Vegetation height.

group (Group 0.2), also composed of both exclosure and control plots, was dominated by *A. compressus*, with *A. fissifolius* as an accompanying species (Appendix S3A).

After excluding capybaras for 4 years, exclosures and control plots showed differences in plant species composition (Figure 8). Four groups emerged: Group 4.1, composed of only one exclosure plot, where there was a 200% increase in *Trichanthecium schwackeanum*; Group 4.2, consisting of seven plots, all but one of them corresponding to exclosures, that was now dominated by *Andropogon laterialis*, with a 40%–50% increase to time 0; Group 4.3, including three control and two exclosure plots that showed a 20%–50% increase in *A. compressus*; and Group 4.4, comprising seven control plots displaying little change in plant composition and proportions of the dominant species *A. fissifolius* and *A. compressus* similar to those of Year 0 (Appendix S3B).

4 | Discussion

Using a paired treatment–control experimental design, we showed that capybaras exert multiple and strong effects on vegetation through grazing. Indeed, excluding capybara grazing resulted in changes in vegetation height, dry aboveground biomass, plant diversity, and species composition. Camera-trap surveys showed these changes could be

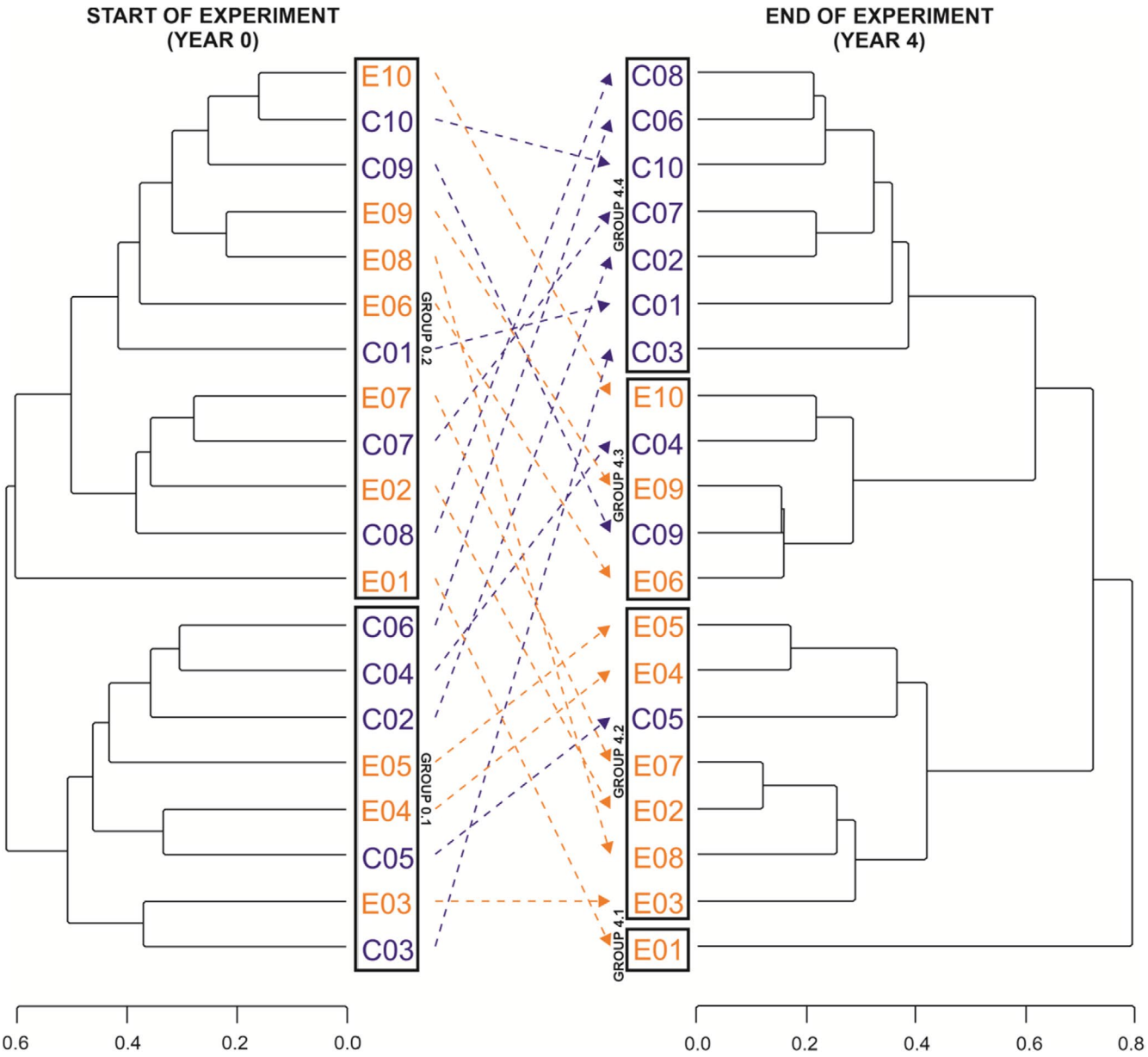

FIGURE 8 | Dendrogram of cluster analysis based on mean coverage data of plant species obtained from control (C-Blue) and exclosure (E-Orange) plots at the start of the experiment (Year 0, 2017) and at the end of the experiment (Year 4, 2021) on San Alonso Island. The analysis used average linkage as the agglomeration criterion and the Bray–Curtis dissimilarity index. Cophenetic correlation coefficient: Year 0 = 0.75, Year 4 = 0.83. Dashed lines show the trajectory of each plot over the years.

attributed almost exclusively to capybara foraging activity. Because the indirect effects of predators on vegetation depend, in part, on the impacts that herbivores have on plants, our results suggest that if the reintroduction of jaguars in Iberá reduces the number of capybaras and/or modifies their behavior, it will trigger a trophic cascade affecting plant communities in Iberá.

4.1 | Effects of Herbivory on Vegetation Structure, Biomass, and Plant Diversity

As predicted, the exclusion of capybaras increased vegetation height and aboveground plant biomass, which reduced the availability of light for other species (Borer et al. 2014). This shift allowed taller species, such as *Andropogon lateralis*, to dominate over shorter stoloniferous grasses like *A. compressus* and forbs. Consequently, species diversity decreased, and the composition changed primarily due to a reduction in the abundance of common species and an increase in the dominance of a few. Similar effects of capybara on vegetation were reported by Mata (2021) in a different area of INP, as well as in other herbivore exclusion experiments conducted in different environments (Ejrnæs et al. 2024; Koerner et al. 2018; Rysiak et al. 2021). These findings suggest that the absence of capybara herbivory facilitated the dominance of certain species in the exclosures, changing the structure and composition of plant communities.

Excluding herbivory resulted in different trajectories within the exclosures regarding plant species composition and abundance

over time. All foraging areas selected for the experiment were structurally similar at the beginning of the experiment and could be grouped based on the relative abundance of species into two initial communities dominated by species of the genus *Axonopus*, a component of the capybara diet (Quintana et al. 1994). Suppressing herbivory led to a change in diversity and floristic composition, facilitating the emergence of novel plant communities.

After 4 years of grazing exclusion, exclosures were grouped into three communities. One was dominated by *Andropogon lateralis*, another by *Trichanthecium schwackeanum* and *A. fissifolius* in similar proportions, and the third maintained the initial dominance of *A. compressus* along with a few control plots. Most control plots were grouped into a community dominated by *A. fissifolius*. Herbivory by capybaras makes potentially dominant and palatable species, such as *Andropogon lateralis*, remain in low abundance in their grazing lawns. These results suggest that the absence or decrease in grazing pressure may allow the emergence of new communities within the foraging areas currently dominated by *A. compressus* and *A. fissifolius*, modifying the heterogeneity of the vegetation at the landscape level (Monk and Schmitz 2022; Trepel et al. 2024). The results will depend on where and how intensively capybaras will be able to forage under predation pressure and the initial plant community.

The impact of large herbivores on plant diversity partly depends on the type, scale, and frequency of the disturbance they produce on vegetation and the productivity of the area (Kondoh 2001). Other factors, such as the history of herbivory of the site (Milchunas et al. 1988) and especially whether dominant plants are palatable or not to herbivores (Koerner et al. 2018), may determine the effect of herbivory on plant diversity. The type of herbivore is also a crucial determinant of their effects on vegetation, with large grazers and bulk feeders usually promoting plant diversity as a result of their non-selective feeding and their large-scale ranging patterns that determine the scale of their disturbances (Lundgren et al. 2024; Trepel et al. 2024). Given the high density and biomass of capybaras at Iberá (Avila 2017), and since it is the only large (by Neotropical standards) non-selective native grazer (Mata et al. 2024), their small-scale experimental effects on vegetation reported here are likely to be amplified at a landscape or ecosystem level.

4.2 | Potential Effects of Jaguar Reintroduction on Plant Communities

Jaguars have been absent from Iberá for 70–80 years (Zamboni et al. 2018). Preliminary data from the first four reintroduced jaguars in 2021–2022 show that 63% of their kills are capybaras (Welschen et al. 2022). Thus, the return of the jaguars to Iberá could result in a trophic cascade with multiple effects on vegetation, at least in areas used by capybaras for foraging.

If jaguars reduce capybara density and/or modify their behavior and habitat use patterns (Avila et al. 2022), grazing levels are expected to change according to capybaras´ abundance and predation risk, leading to new equilibria in plant diversity values and vertical structure within patches (Koerner et al. 2018; Kondoh 2001). These new equilibria are likely to be dynamic, with an initial phase primarily driven by reductions in capybara abundance due to increased predation and prey naivety (Avila et al. 2022). Over the longer term, as prey naivety diminishes, behaviorally mediated effects are expected to become more pronounced (Avila et al. 2022). As a result, several effects on vegetation and ecosystem processes are expected. First, since capybaras avoid predation attempts by seeking refuge in deep rivers and lagoons (Avila et al. 2022; Herrera and Macdonald 1989), areas far from the water will be less used or abandoned and grazing pressure on them will be reduced or disappear. In these areas, a process similar to that simulated by experimental exclusion is expected, where an increase in vertical vegetation structure and aboveground biomass could lead to changes in species composition and a reduction in plant diversity due to the increased dominance of a few species. Second, in areas near water (low predation risk), grazing pressure could remain the same or increase, keeping the aerial biomass and vertical structure of plants low in those intensively foraged areas. Third, changes in vegetation could benefit other species, such as grassland birds like the endangered Strange-tailed Tyrant *Alectrurus risora* (Azpiroz et al. 2012; Browne et al. 2023) and the capuchino seedeaters *Sporophila* sp. (Turbek et al. 2021), by providing nesting habitat. Finally, several ecosystem processes may be restored, such as nutrient cycling, by creating nutrient hotspots when herbivores concentrate activity in safe habitats, and nutrient subsidies when they migrate daily between safe and risky habitats (Monk and Schmitz 2022). Other changes in ecosystem processes as a result of changes in capybara abundance and behavior include spatial shifts in carbon sequestration patterns by photosynthesizing plants (Wilmers and Schmitz 2016), and in fire regimes by altering the distribution of fuel properties (amount, structure, and condition of vegetation) (Foster et al. 2020). This last process is of paramount importance due to the recurrence of wildfires of gigantic proportions in Iberá National Park that may jeopardize the ongoing rewilding initiative (Di Bitetti et al. 2022).

The capybara is the last surviving large grazer in the Iberá ecosystem (Mata et al. 2024). The shift in the spatial and temporal scale of its effects on vegetation under heavy predation pressure by jaguars will determine the net effects of rewilding on vegetation. Overall, jaguars might enhance landscape heterogeneity. In the absence of predation risk, capybaras generate ample grazing lawns and open areas of short-height vegetation at different distances from water bodies, surrounded by taller grasslands. These open and relatively homogeneous areas constitute an important proportion of the Iberá landscape. The return of the top predator to this ecosystem could reinforce heterogeneity at the landscape scale by creating a different pattern of grazing pressure, resulting in different plant communities that vary in their diversity, species composition, vegetation height, and biomass accumulation. Conversely, the areas abandoned by capybaras would generate homogeneous areas similar to the taller grasslands surrounding them, at least in terms of vertical structure. Biodiversity in each of these patches will be determined by the level of grazing, system productivity, and species palatability (Koerner et al. 2018; Kondoh 2001). At the landscape level, this would give rise to a mosaic of habitats with structural

characteristics different from the current ones in the absence of the top predator.

5 | Conclusions

The results of the exclusion experiment indicate that capybaras markedly affect the vegetation, underscoring their role in shaping plant communities. Excluding capybaras leads to shifts in aboveground vegetation biomass and structure, and species composition, highlighting the importance of herbivory in maintaining ecosystem heterogeneity and setting the stage for a potential trophic cascade triggered by the return of jaguars to the Iberá Wetlands. If restored, such a mechanism could lead to profound changes in plant community structure and function, potentially affecting threatened grassland birds, nutrient cycling, carbon sequestration, and fire regimes. Establishing this experimental baseline of capybara impacts on vegetation is essential for further understanding the important role of herbivores in shaping ecosystems and the significance of rewilding as a conservation strategy.

Author Contributions

Ana Belen Avila: conceptualization, methodology, formal analysis, investigation, writing – original draft, writing – review and editing, funding acquisition. **María Jose Corriale:** conceptualization, methodology, formal analysis, writing – review and editing. **Debora Di Francescantonio:** conceptualization, methodology, formal analysis, writing – review and editing. **Pablo Ignacio Picca:** investigation, data curation, writing – review and editing. **Emiliano Donadio:** conceptualization, methodology, writing – review and editing, funding acquisition. **Mario Santiago Di Bitetti:** conceptualization, writing – review and editing. **Agustín Paviolo:** conceptualization, methodology, project administration. **Carlos De Angelo:** conceptualization, methodology, writing – original draft, writing – review and editing, funding acquisition, project administration.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data can be downloaded at http://hdl.handle.net/11336/254762.

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Supporting Information

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