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Research Article

Keywords: biodiversity, bottom-up control, invasive forage grasses, nutrient addition, Pampa grassland, plant community structure, tall fescue, top-down control

Posted Date: September 5th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-7389210/v1>

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Version of Record: A version of this preprint was published at Biological Invasions on February 20th, 2026. See the published version at <https://doi.org/10.1007/s10530-026-03785-8>.

Tall fescue invasion fostered by grazing exclusion and nutrient addition in a temperate grassland

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Abstract

Forage species that escape from rangelands can invade natural grasslands, altering their composition and functioning. Native plants and wild herbivores may limit exotic species, whereas domestic herbivores and nutrient enrichment often favour invasion in the short term. However, the long-term interplay of top-down (herbivores) and bottom-up (nutrients) forces in controlling forage invasions remains uncertain. We evaluated how cattle grazing exclusion and nutrient addition influenced the invasion of *Festuca arundinacea* (tall fescue) in the Flooding Pampa (Argentina). Using three manipulative experiments spanning almost 30 years (1989–2016), we studied (i) the effect of cattle exclusion on species composition after invasion and (ii) how exclusion combined with nutrient enrichment (NPK) affected tall fescue, plant groups, and diversity. Tall fescue first appeared in 1995, when cattle exclusion still promoted native grasses. By 2016, it dominated cattle exclosures (>80% cover) but remained scarce in grazed areas (<5%). Nutrient addition with exclusion increased tall fescue size and competitiveness, reducing native cover and richness. Declines in richness reflected both a direct negative effect of nutrients and the indirect effect of tall fescue expansion facilitated by cattle absence. In sum, cattle exclusion shifted from favoring native grasses to enabling invasive forage dominance, especially under nutrient enrichment. Long-term interactions between grazing and resources strongly shape invasion outcomes. Facing increasing forage invasions limited nutrient inputs and domestic grazing might sustain native plant communities.

Key words: biodiversity, bottom-up control, invasive forage grasses, nutrient addition, Pampa grassland, plant community structure, tall fescue, top-down control

INTRODUCTION

In natural ecosystems, plant diversity is increasingly threatened by the invasion of exotic species, a process influenced by increasing nutrient deposition and livestock pressure (Godfree et al. 2017; Komatsu et al. 2019; Scasta et al. 2015). It is well established that both cattle herbivory (top-down control) and soil resources (bottom-up control) shape plant community structure, affecting the relative abundance of native and exotic species in grasslands (Asner et al. 2004; Huston; 2004; McGranahan et al. 2012; Morgan & Lunt; 1999). However, the introduction of exotic species with novel traits may alter plant community responses to traditional management practices, such as grazing regime and fertilization. Forage grasses, selected to withstand grazing and thrive under nutrient enrichment, tend to outcompete native species in fertilized pastures (Driscoll et al. 2014; Godfree et al. 2017). Apart from pastures, these species may invade natural grasslands, potentially disrupting native plant communities and ecosystem dynamics (Scasta et al. 2015; Tognetti & Chaneton; 2015; Monroe et al. 2016). The extent of forage grass invasions is often underestimated due to the limitations of short-term, localized surveys (Hoekstra et al. 2005; Hulme et al. 2013) and the scarcity of long-term descriptive and experimental studies (Strayer 2012; Strayer et al. 2006). There is a clear knowledge gap in the long-term drivers of forage grasses invasion in natural grasslands. This knowledge is fundamental to develop management strategies that promote native plant diversity in modern grassland landscapes.

The effects of herbivory and nutrient on exotic plant species invasion in natural grasslands are strongly context- dependent (Allen et al. 2021; Parker et al. 2006; Seabloom et al. 2015; Price et al. 2023). On the one hand, cattle grazing can either promote or limit plant invasion depending on their consumption preferences for native and exotic species (Donlan et al. 2003; Gross et al. 2015; Nackley et al. 2017; Parker et al. 2006). For instance, domestic grazing reduces plant invasion when animals prefer exotic species over natives (Nackley et al. 2017), while their preference for native species weakens the biotic resistance and foster plant invasion (Chaneton et al. 2002). On the other hand, an increase in resource availability can trigger invasion (Davis et al. 2000; Tognetti & Chaneton 2015). This may occur because of competitive balance, but also because the responses of native and exotic plant species to nutrients would change herbivore preferences (Seabloom et al.

2015). When exotic species are preferred by herbivores, grazing may throw back nutrient addition effects (Campana & Yahdjian 2021). For example, nitrogen addition promoted native richness by intensifying grazing on the exotic love grass in an Australian dry grassland (Firn et al. 2010). While some studies explored the interplay of grazing and nutrient addition in plant communities with native and exotic species (Seabloom et al. 2015), few lasted long enough to unveil how the long-term invasion process impact plant community composition.

Community responses to grazing exclusion and nutrient addition are often mediated by the composition of plant functional groups in the local flora (Chaneton et al. 2002; Firn et al. 2013; Maire et al. 2012; Olff & Ritchie 1998). These groups can influence both short-term responses and long-term successional trajectories, especially under the pressure of exotic species that introduce novel traits into the system (Strayer et al. 2006). For instance, native warm-season grasses have been shown to resist exotic annuals in Flooding Pampa grasslands (Longo et al. 2013; Perelman et al. 2007). However, when disturbances reduce biotic resistance —e.g., via grazing or nutrient enrichment— invasions by exotic forbs or annual grasses can occur (Chaneton et al. 1988; Corbin & D’Antonio 2004). Despite these insights, it remains unclear how grazing and fertilization interact with the functional structure of native plant communities in the long term, particularly under the sustained invasion of forage perennial grasses.

The invasion of forage grasses poses a major threat to biodiversity in temperate grasslands, one of the least protected biomes globally (Hoekstra et al. 2005; Paruelo et al. 2022). *Festuca arundinacea* Schreb. (“tall fescue”; Gibson 2009) is a highly productive forage species that has invaded grasslands across multiple continents (Scasta et al. 2015; Monroe et al. 2016). Tall fescue exhibits rapid growth (Maire et al. 2012; Scheneiter & Améndola 2012), reduces native species richness (Cully et al. 2003; McGranahan et al. 2012), and hinders grassland restoration (Tognetti & Chaneton 2012; Molina et al. 2021). Although absent from initial floristic surveys of the Flooding Pampa (León et al. 1979; Sala et al. 1986), this species is now frequent along roadsides and abandoned fields (Tognetti et al. 2010), suggesting a rapid and ongoing regional expansion (Scheneiter et al. 2016). In addition to its ecological impact, tall fescue can negatively affect livestock health due to the presence of endophytic fungi (Gundel et al. 2009), undermining its value as a forage

resource. In this context, it becomes crucial to investigate whether grazing exclusion and soil nutrient enrichment promote or suppress its spread to design management actions that prevent further degradation.

Here, we evaluated the long-term (~30 years) effects of cattle grazing exclusion and their interaction with nutrient addition on the invasion of tall fescue in a native grassland of South America (Flooding Pampa, Argentina). We also associated tall fescue invasion with changes in plant community structure and species richness during early-, mid-, and late-stages of invasion. We used vegetation data from three consecutive experiments spanning ~30 years in the same experimental site (1989-2016), which provides a real long-term description of the patterns and process of forage species invasion. We hypothesized that (H1) during early invasion stages (1989-2004), there is a low incidence of cattle grazing on tall fescue abundance due to low invader frequency (Levine et al. 2004). Then (H2) during mid and advanced invasion stages (2003-2016), tall fescue outcompetes native grasses and dominates the plant community, but only in the absence of big herbivores (Gross et al. 2015; Parker et al. 2006). The presence of cattle grazing controls tall fescue spread, and (H3) overcomes positive nutrient effect on the invader (top-down > bottom-up control (Chesson & Kuang 2008; Campana & Yahdjian 2021)).

MATERIALS AND METHODS

Study system

We combined three studies conducted in a natural grassland of the Pampa Region (South America) in the Pila County, Buenos Aires province, Argentina (36°16' S, 58°15' W; 15 m.a.s.l.). The site, never ploughed, sown or fertilized, has been grazed at 0.5 cattle units ha⁻¹ for nearly 100 years. Precipitation peaks in spring and autumn, with a mean annual rainfall during 1979-2016 of 983 mm/yr (inter-annual SD = 177 mm; 1980-2016). Annual rainfall has not shown any significant temporal trends during this period (Supplementary Fig. S1.a). Mean monthly temperatures range between 8.2 °C in July and 21.8 °C in January. Soils are Natraquolls with 3.1% organic matter and varying salinity (Rubio et al. 2019).

Plant communities are mesophytic prairies, with a rich mix of perennial cool- and warm-season native grasses and forbs (Perelman et al. 2001; Longo et al. 2013). Apart from the perennial grass tall fescue, exotic species are mainly annual cool-season grasses and forbs (Chaneton et al. 2002). We identified five main plant functional groups according to plant life form, phenology, and origin: native warm-season grasses, native cool-season grasses, native forbs, exotic annual grasses, and exotic forbs. These plant functional types have been studied for their contribution to community primary productivity, responses to disturbances, and invasion process (Longo et al. 2013; Rusch & Oosterheld 1997; Sala et al. 1986). Importantly, perennial exotic grasses as tall fescue were not considered in previous works (but see Molina et al. 2021; Silvano et al. 2025).

Experimental design and data collection

To study the long-term effects of cattle exclusion and its interaction with nutrient addition on tall fescue invasion, we analysed data from three consecutive experiments conducted in the same experimental site (Fig. S1). Experiments spanned early (1989-2004), mid (2003-2016) and late (2012-2016) tall fescue invasion stages. The response variables were assessed with similar methodologies in the three experiments established in the same community stands, thus their results are comparable (Sala et al. 1986; Chaneton et al. 2002; Longo et al. 2013; Molina et al. 2021).

Experiment 1. Grazing exclusion during 1989-2004. To evaluate the impact of cattle exclusion on community composition and tall fescue abundance during its early invasion stage, we analysed data from a grazing exclusion experiment (Chaneton et al. 1988; 2002; Fig S1). The experiment comprised two 0.1 ha permanent plots located in opposing positions inside a 4-ha grazing enclosure and in the adjacent grazed area. Every summer from 1989 to 2002 (in January, peak of plant richness), plant-basal cover was measured using four 5 m long linear transects placed randomly in each plot. The distance between samples in grazed and ungrazed plots ranged from 100 to 250 m and samples within a given plot were at least 20 m apart (Chaneton et al. 2002). The contacts of each species with the transect line were summed and transformed to percentage cover.

Experiment 2. Grazing exclusion during 2003-2016. To evaluate grazing exclusion effects on tall fescue biomass during a mid to late invasion stage, we used six 1000 m² enclosures installed in

December 2003 (Fig. S1). Each enclosure was paired spatially with an adjacent grazed area, forming six blocks that allowed for direct comparison between grazed and ungrazed conditions (Longo et al. 2013). In late summer (March) of 2003, 2004, 2005, 2007, 2012 and 2016 we harvested peak biomass in each plot using one 0.2×1.0 m frame. All rooted plants were cut to 1 cm, sorted by species, and dried at 62°C until stable weight (see Longo et al. 2013). We estimated species richness as the total number of species rooted within each frame. Biomass in the grazed areas was not harvested in 2007.

Experiment 3. *Grazing exclusion combined with nutrient addition during 2012-2016.* To evaluate the interactive effects of long-term cattle exclusion and nutrient addition on tall fescue expansion, we established a full factorial experiment of grazing exclusion and fertilization in December 2012. In each of the six blocks described for Exp. 2, we delimited four plots of 5 x 5 m, two inside and two outside each enclosure. Plots were separated by at least 10 m from each other and randomly assigned to control or fertilized treatments (10 g·m⁻²·yr⁻¹ of Nitrogen, Phosphorous and Potassium + micronutrients following the Nutrient-Network protocol; Borer et al. 2014). In summer between 2012 and 2016 (December and March), we estimated aerial cover of all plant species rooted in one 1 x 1 m quadrat to the nearest 5% using a modified Daubenmire method (Borer et al. 2014). Plant species were grouped into five functional groups (see above) and richness was assessed as the total number of species rooted in the quadrat. In March 2016, we evaluated tall fescue population structure by counting and measuring the basal diameter of all tall fescue individuals along two 2 m transects in each plot. Each tiller separated by more than 2 cm from each other was considered an independent individual (i.e *genet*; Rolhauser et al. 2007).

Statistical analyses

Tall Fescue Invasion

To describe changes in tall fescue abundance inside and outside exclosures between 1989 and 2004, we used descriptive statistics (Chaneton et al. 1988), separating early (1989–1992) and late (2001–2004) periods (Fig. S1). Additionally, we modeled tall fescue biomass from 2003 to 2016 as a function of time × grazing using a blocked factorial design and linear mixed-effects models (*lme* function in the nlme package; Pinheiro & Bates 2000), with blocks (n = 6) treated as random factors

to account for repeated measures. In the last year of the experiment, we analyzed population structure (plants·m⁻¹, plant size, and basal cover) as a function of grazing exclusion × nutrient addition and performed multiple comparisons using Tukey test.

Changes in community structure

To assess the effects of cattle exclusion on plant community composition from 1989 to 2004, we conducted a PERMANOVA and non-metric multidimensional scaling (NMDS) using Bray–Curtis dissimilarity with 1000 permutations (*adonis* function in *vegan*; Oksanen, 2017). We focused on the variance explained by time and grazing in the Year × Species matrix for grazed and ungrazed transects and visualized plant cover dynamics in the ordination space. We tracked the abundance of tall fescue and other species in grazed and ungrazed plots using *metaMDS* and *envfit* functions in *vegan* (Oksanen 2017).

For the period 2012–2016, we evaluated the effects of grazing exclusion and nutrient addition on functional group cover using mixed-effects models. We modeled the values of plant functional group cover, which were averaged between December and March to reduce intra-annual variability (Molina et al. 2023), as a function of grazing exclusion × nutrient addition × time. Blocks and fertilization nested within grazing were the random effect factors to account for the split-plot and repeated measures design (Zuur et al. 2009). In the final year, we tested the effects of grazing exclusion × nutrient addition and applied Tukey test for comparisons.

Changes in species richness

We analyzed total, native, and exotic species richness between 2003 and 2016 using a mixed-effects model with time × grazing as fixed effects, and blocks (n = 6) as random factors for repeated measures. For the 2012–2016 period, we modeled richness as a function of grazing exclusion × nutrient addition × time, following the same random structure. In the final year, we evaluated treatment effects (grazing exclusion × nutrient addition) and applied Tukey test for multiple comparisons. Finally, we used structural equation modeling (SEM) to assess the direct and indirect effects of grazing exclusion and nutrient addition on total plant species richness, considering tall

fescue and functional group cover as mediators (*sem.fit* function in piecewiseSEM; Lefcheck 2016). The SEM accounted for spatial and temporal random structure (split-plot design with repeated measures; Lefcheck 2016). We started with a saturated model including all possible paths and simplified it based on AICc and modification indices (Grace 2006; see Appendix SF2). The model used data from 2014 to 2016, excluding 2012–2013 to minimize early treatment transients. All statistical analyses were conducted in R version 4.2.2 (R Core Team 2022). When appropriate, we incorporated covariance structures (e.g., corAR1) and variance heterogeneity (e.g., varIdent) to improve model fit based on AIC criteria (Pinheiro & Bates 2000; Zuur et al. 2009).

RESULTS

Tall fescue invasion

Tall fescue was first registered on the site in 1995, and it was barely recorded until 2004. Between 2003 and 2016, tall fescue biomass increased annually at a higher rate in ungrazed than in grazed areas ($27.4 \pm 6.81 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ and $1.14 \pm 4.83 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ungrazed than in grazed respectively; Grazing Exclusion x Time: $P < 0.01$; Supplementary Table S1). By 2016, tall fescue accounted for 45% of total live biomass inside exclosures and less than 5% in grazed areas (Fig. 1a). Total fescue live biomass was $347 \text{ g} \cdot \text{m}^{-2}$ inside exclosures (inter annual SD = $208 \text{ g} \cdot \text{m}^{-2}$) and $245 \text{ g} \cdot \text{m}^{-2}$ in grazed plots (inter annual SD = $155 \text{ g} \cdot \text{m}^{-2}$); standing dead biomass was also significantly ($p < 0.01$) higher inside the exclosures (Table S1).

Between 2013 and 2016, nutrient addition increased tall fescue cover in cattle-grazed and exclusion areas (Fig. 1b, Nutrients x Time: $P < 0.01$; Table S2). By 2016, tall fescue reached 100% cover in fertilized enclosure plots, whereas the cover was nearly 10% and 5% in grazed plots with and without nutrients added, respectively (Fig. 1b).

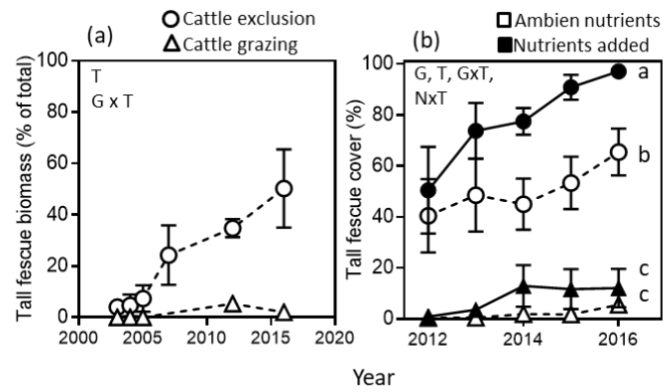


Fig. 1. Changes in tall fescue relative biomass (a) and cover (b) in the experimental plots. Uppercase letters in each panel indicate significant terms in mixed effects models (G: grazing, N: nutrient addition and T: time; see Supplementary Tables S1-2). Lowercase letters indicate *post-hoc* differences in the last year.

229

230 The structure of tall fescue populations differed among treatments, with more and bigger
 231 individuals under cattle exclusion (Fig. 2, Table S3). Density and diameter of tall fescue individuals
 232 were lowest under grazing (Fig. 2a-b), whereas nutrients increased the size of tall fescue individuals
 233 by 4.5 cm·pl⁻¹ inside enclosures (Grazing x Nutrients: P=0.017; Fig. 2b). Overall, cattle grazing
 234 exclusion and fertilization independently increased tall fescue basal cover (Fig. 2c).

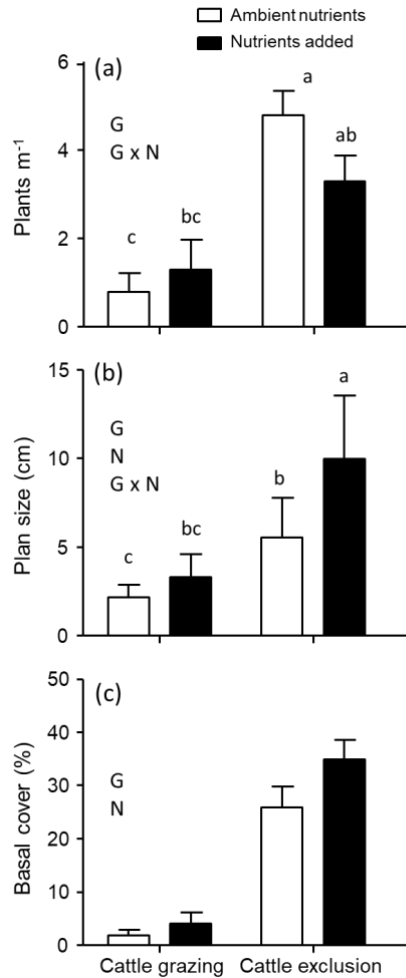


Fig. 2. Tall fescue population structure in 2016: (a) plant density; (b) plant size; (c) plant basal cover of tall fescue individuals. Uppercase letters indicate significant terms in mixed effects models (G: grazing; N: nutrient addition; see Table S3). Lowercase letters indicate *post-hoc* differences at $P < 0.05$ after Tukey test.

Community structure

For the period 1989-2004, grazing exclusion was more important than time in affecting plant community composition (Fig. 3; PERMANOVA: Grazing exclusion $R^2=0.36$, $P < 0.001$; Time $R^2=0.19$, $P < 0.001$; GxT $R^2=0.05$, $P=0.021$). Ordination distinguished grazing vs. enclosure along the first axis and time along the second (Fig. 3a). Tall fescue was correlated with time in the community ordination ($r = 0.27$, $P < 0.005$; Fig. 3b).

Importantly, there was a change in the effect of grazing exclusion with time on plant community composition (GxT: $P=0.021$; Fig 3). During the early 1990s, enclosures comprised mostly cool and warm-season native grass species (i.e., *Nassella philipii*, *Danthonia montevidensis*, *Bothriochloa laguroides*, *Steinchisma hians*; lower-right quadrants in Fig. 3, Table S4). Winter

native grasses cover was three times higher in exclosures (mean $\pm$ S.E = 5.34 $\pm$ 1.07 vs. 18.65 $\pm$ 2.7 % for grazing and exclosure areas, respectively), whereas native summer grasses and forb cover was higher in grazed areas (Table S4). Since the year 2000, exclosures comprised tall fescue and warm-season native grasses (e.g. *Paspalidum paludivagum*, *Leersia hexandra*, upper-right in Fig. 3). The cover of native warm-season grasses decreased from 34% to 19% whereas tall fescue increased ten times (0.24 to 2.2 %) with cattle exclusion (Table S4). Plant richness was ~40% lower inside the exclosure (Table S4).

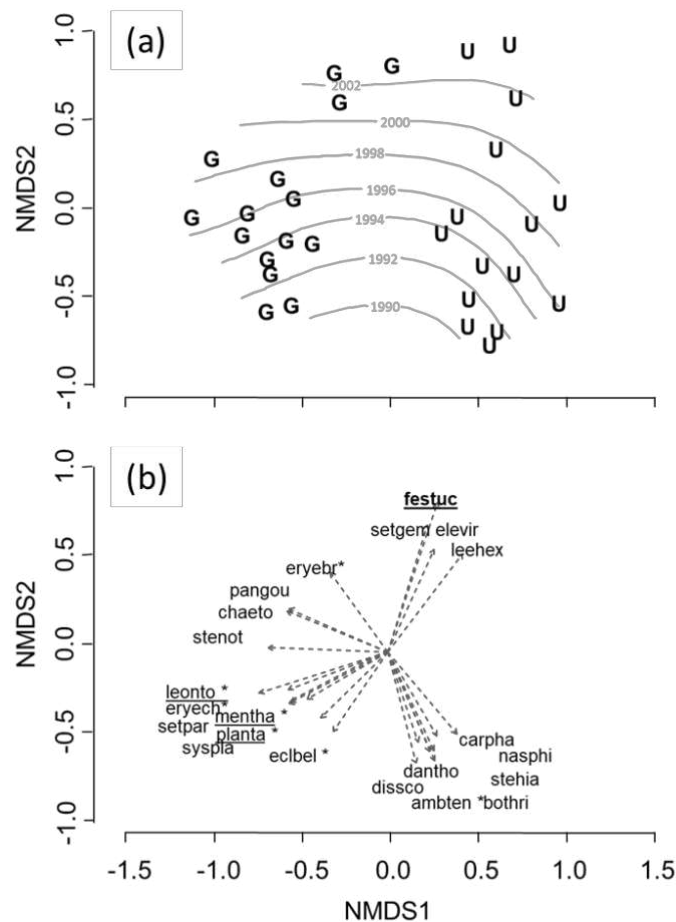


Fig. 3. Non-metrical multidimensional scaling of 1989–2004 grassland plant community composition (stress=0.145). a) Position of the grazed (G) and ungrazed (U) plots in the ordination space. Grey lines are year-isoclines, associated with NMDS2 axis. b) Trends in species abundance along time in ordination space. Exotic species are underlined; forbs are shown with *. Acronyms: festuc: *Festuca arundinacea*; elevir: *Eleocharis viridans*; leehex: *Leersia hexandra*; disco: *Distycklis scoparia*; setpar: *Setaria parviflora*; syspla: *Sysirinchium platensis*; dantho: *Danthonia montevidense*; bothri: *Bothriochloa laguroides*; stehia: *Steinchisma hians*; nasphi: *Nassella philipii*; carpha: *Carex phalaroides*; stenot: *Stenotaphrum secundatum*; chaeto: *Chaetotropis elongate*; pangou: *Panicum gouini*; setgem: *Setaria geminata*; eryech (*); *Eryngium echinatum*; eryebr (*): *E. ebracteatum*; leonto (*); *Leonthodon taraxacoides*; mentha (*): *Mentha pullegium*; planta (*): *Plantago lanceolata*; eclbel (*): *Echlypta belillioides*; ambten (*): *Ambrosia tenuifolia*.

Between 2012-2016, grazing exclusion and nutrient addition affected the abundance of native and exotic plant functional groups (Fig. 4, Table S2; for tall fescue see Fig. 1). Among natives, the cover of species warm-season grasses decreased with grazing exclusion, especially under nutrient addition (Fig. 4a; Grazing x Nutrient x Time $P=0.044$; Table S2; lower-case letters in Fig. 4a). Native winter grasses decreased with time independently of nutrient addition (Fig. 4b), whereas native forbs decreased more in the ungrazed fertilized plots (Fig. 4c, Table S2). Contrarily, grazing exacerbated the positive effect of nutrient addition on exotic annual grasses and forbs (Fig. 4d-e, Table S2), and during the last year, annual grasses doubled, and forbs tripled their cover in the grazed and fertilized plots compared with other treatments.

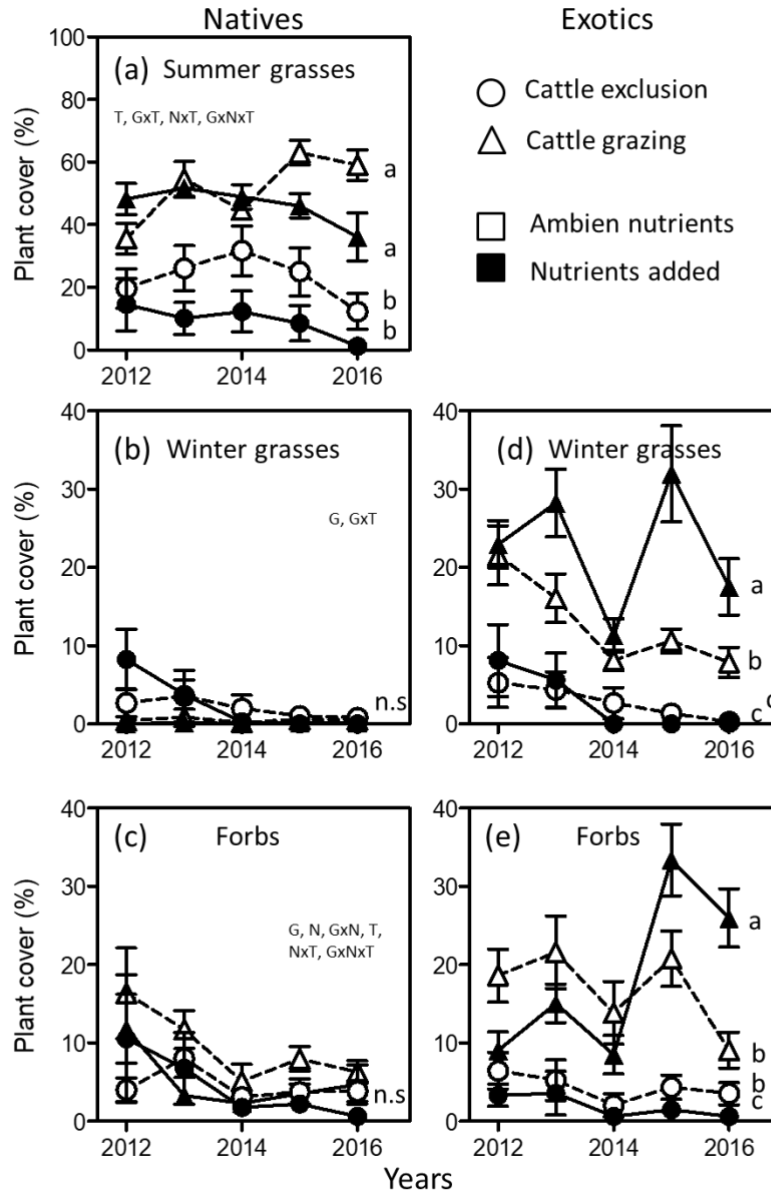


Fig. 4. Changes in the cover of native (left panels) and exotic (right panels) plant functional groups in the grazing exclusion x nutrient addition experiment (Experiment 3) during 2012-2016. a) native summer grasses; b) native winter grasses; c) native forbs; d) exotic annual grasses; e) exotic forbs. Year 2012 corresponds to pre-fertilization conditions. Uppercase letters indicate significant terms in the mixed effects models (G: grazing; N: nutrient addition; T: time; see Table S2). Lower-case letters indicate *post-hoc* differences at $P < 0.05$ after Tukey test for the last experimental year. Notice the differences in the y-scale. There were no exotic summer grasses in the region during this period.

262

263 *Species richness*

264 Between 2003-2016, total plant species richness decreased, especially inside exclosures (Grazing x
 265 Time: $P < 0.05$; Fig. 5a, Table S1). This decrease was steeper for the richness of native than exotic
 266 species (Table S1). Total richness and tall fescue biomass were negatively correlated (Pearson's $r =$

-0.526; $P < 0.01$). Between 2012-2016, cattle grazing exclusion reduced total plant species richness (Fig. 5b, Grazing: $P = 0.04$), and the negative effect of nutrient addition on plant richness increased with time (Nutrients x Time: $P = 0.04$). By the end of the experiment, excluding grazers and fertilization reduced plant richness by 11 and 6 species m^{-2} , respectively (Grazing: $P = 0.003$; Nutrients, $P = 0.003$; GxN: $P = 0.386$).

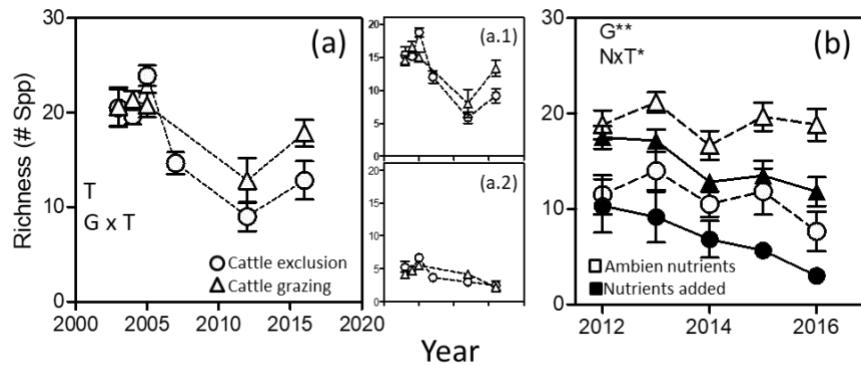


Fig. 5. Changes in plant species richness in grazing exclusion during 2003-2016 (a) and the grazing exclusion x nutrient addition experiment (b). (a.1) Native plant species richness; (a.2) exotic plant species richness. Upper case letters in each panel indicate significant terms in mixed effects models (G: grazing, and T: time; see Supplementary Table S2). In (b), year 2012 corresponds to pre-fertilization experiment. Upper case letters indicate significant terms in the mixed effects models (G: grazing; N: nutrient addition; T: time; see Supplementary Table S1).

For the period 2013-2016, direct and indirect effects of grazing exclusion and nutrient addition explained 83% of the variance in tall fescue cover and in plant richness (Fisher's $C = 1.01$, $df = 4$, $P < 0.908$; Fig. 6; Table S5-6). Grazing exclusion, alone and combined with nutrient addition, increased tall fescue cover (Fig. 6, Table S5-6), which negatively affected the abundance of the other functional groups and total plant species richness (coef. = -0.85, $P < 0.006$; Table S5). Nutrient addition increased the cover of exotic forbs and grasses. There was a direct, negative effect of nutrient addition on species richness (coef. = -0.65). Finally, all native plant functional groups were negatively affected by tall fescue cover, whereas only native forbs exerted a positive effect on plant richness (coef. = 0.18, Tables S5-6).

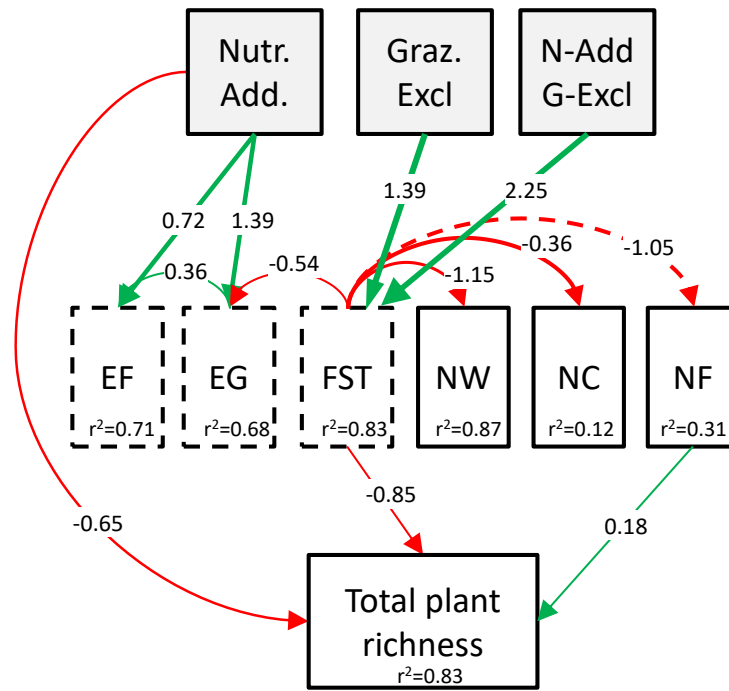


Fig. 6. Structural equation model for the effects of grazing exclusion (Graz. Excl.) and nutrient addition (Nutr. Add.) on total plant species richness through the cover plan functional groups (exotic grasses (EG), exotic forbs (EF), tall fescue (FST), native warm-season grasses (NW), native cool-season grasses (NC), and native forbs (NF)). Green are positive and red are negative standardized coefficients and arrow widths indicate their relative strength. Central boxes with dotted and solid lines represent exotic and native plant cover, respectively. Curved lines indicate correlation ($\leftrightarrow$) and straight arrows regressions ($\rightarrow$) paths.

DISCUSSION

Our long-term study clearly links how changes in land use, associated with alterations of cattle grazing regimes and in soil nutrients, can drastically alter the effects of herbivore exclusion on plant communities, ultimately favouring the invasion of the exotic forage grass *Festuca arundinacea*. . Over three decades, cattle exclusion shifted from promoting native grass species and reducing the cover of annual exotic forbs, to fostering the dominance of a highly competitive perennial species. This effect was amplified by nutrient addition, which further increased the invader's abundance while reducing the cover of other native functional groups and total species richness. Although nutrient addition had a direct negative effect on richness, much of this decline was explained by the increase of tall fescue under cattle exclusion. These findings challenge the traditional view that grazing exclusion is an effective conservation strategy for controlling plant invasion and maintaining biodiversity in temperate grasslands.

Our results contrast with earlier work at the same site, where short-term cattle exclusion increased native grasses and reduced exotic species (Sala et al. 1986; Chaneton et al. 1988, 2002; Rush & Oosterheld, 1997). They also challenge the prevailing expectation that removing native or domestic herbivores generally benefits native species (Parker et al. 2006). This discrepancy arises because short- and long-term dynamics differ; early in the invasion, native species were not strongly affected, but over time, grazing exclusion allowed *tall fescue* to competitively displace native grasses and forbs. Such temporal shifts reflect cumulative processes, where local plant–plant and plant–animal interactions interact with regional drivers—such as changes in the species pool and land-use legacies—to alter successional trajectories (MacDougall & Turkington, 2005; Seastedt & Pyšek, 2011). At the regional scale, *tall fescue* now dominates roadsides over more than 200,000 km² in central Argentina (Scheneiter et al. 2016), indicating a strong dispersal source that can feed local invasions. Our experiments reveal how reduced herbivory, combined with nutrient enrichment, facilitates the establishment and dominance of this widespread invader. This outcome can only become apparent through long-term monitoring, which captures shifts in the regional species pool and their cascading effects on local community composition (Levine et al. 2004; Shea & Chesson, 2002; Strayer et al. 2006).

Exotic domestic grazers can promote exotic plant invasion (Parker et al. 2006; Perelman et al. 2007), but our results suggest that they limit exotic forage grass invasion in the long-term. Compared to grazed conditions, cattle exclusion increased the size and density of tall fescue individuals, enhancing its competitive ability and progressively displacing native grasses and forbs (tall fescue size and basal cover correlation with its biomass: $r=0.78$ and $r=0.77$, respectively; $P<0.01$, $n=24$). Thus, an increase in tall fescue biomass may strengthen competitive hierarchies and eventually outcompete native grasses when it is out of the control of cattle herbivory (Graff et al. 2020; Silvano et al. 2025). Under certain circumstances, trade-offs between herbivory susceptibility and the strength of plant-plant competitive interactions can be similar for native and exotic species (Gross et al. 2015). However, these may change if exotic plant species fill winter productivity gaps left by native grasses thus being more consumed by livestock, as is the case for exotic forage species in the Pampas (Gibson 2009; Perelman et al. 2007). Our work supports the idea that when exotic

species occupy early (i.e., ruderals) and late (i.e., competitive dominants) successional niches (Martinez et al. 2015), the disturbance-succession management may no longer be suitable for the recovery of native plant species in rangelands (Briske 2017). In turn, this change in grazing exclusion effect on native and exotic species poses a challenge for conservation strategies in productive natural grasslands.

Exotic species may capitalize the increase in soil resources (Davis et al. 2000; Huston, 2004; Tognetti & Chaneton, 2015), but their interactive outcome combined with herbivory has been less clear (Li et al. 2022). We observed that nutrient addition amplified cattle exclusion increases on tall fescue, but also exotic annual grasses and forbs augmented with nutrient addition under grazing conditions (e.g., grasses: *Lolium multiflorum*, *Gaudinia fragilis*; forbs: *Lotus spp.*; Longo et al. 2013). This agrees with previous evidence showing differential responses to nutrient availability of native and exotic plant functional groups under different disturbance regimes (Tognetti & Chaneton, 2015; Seabloom et al. 2015). Grazers may equalize competitive interactions between native and exotic plants (MacDougall et al. 2009), but the control attained by herbivores on the invader (i.e., predators reducing fitness differences; top-down control) can compensate for or overcome the positive effect of nutrient addition (i.e., resources enhancing fitness differences; bottom-up control; Chesson & Kuang 2008). We found that under grazing conditions, the positive effect of nutrient addition on tall fescue has not overcome the negative effect of grazing. Herbivores can consume more plant biomass on fertilized plots and increase grazing pressure on exotic species (Firn et al. 2010, but see Borer et al. 2021), exacerbating nutrient effects against exotic species (Campana & Yahdjian 2021). Importantly, this reinforces that interactive top-down and bottom-up mechanisms regulate community structure and plant species invasion in natural grasslands.

Nutrient addition reduced species richness through both direct and indirect pathways. Indirectly, fertilization increased *tall fescue* dominance in ungrazed plots, likely reducing light availability and other resources for native species (Molina et al. 2021; Campana et al. 2022; Eskelian et al. 2022). Directly, nutrient enrichment may have removed competitive trade-offs that help maintain coexistence in these communities (Harpole et al. 2016). In our study, nutrient and grazing effects on richness were largely independent, with no evidence that herbivores offset nutrient-driven

declines in species richness (Borer et al. 2014; Molina et al. 2021). However, nutrients and grazing interacted in shaping the abundance of native and exotic functional groups, suggesting that community structure and diversity respond to different ecological scales and mechanisms. This decoupling highlights a challenging conservation scenario in which nutrient deposition simultaneously promotes invasion and erodes native diversity (Seabloom et al. 2015).

Excluding cattle grazing was ineffective for native species recovery, stressing novel processes involved in the persistence and abundance of native and exotic species (Firn et al. 2013; Funk et al. 2008; Lunt et al. 2007). Cattle removal may be considered a conservation strategy to reduce the abundance of exotic annual grasses and forbs under some scenarios (Chaneton et al. 2002; Donlan et al. 2003). However, our long-term monitoring evidenced that a formerly plausible management action may now jeopardize native plant species richness by promoting the invasion of highly competitive perennial forage species. In Pampa grasslands, native warm-season grasses are more important than native cool-season grasses (Longo et al. 2013; Perelman et al. 2007), which results in the fact that most invaders are cool-season annual species (Chaneton et al. 2002; Perelman et al. 2007; Wolkovich and Cleland 2011). Instead of excluding grazing, overlapping grazers' forage demand with the susceptible period for exotic plant species might be a criterion to managing grasslands while limiting invasion (Firn et al. 2013; Perelman et al. 2007). Thus, invaded sites can be grazed or hayed in specific periods during the year under an adaptive management framework (Bakker et al. 2017; Lunt et al. 2007).

In conclusion, complementary experiments lasting three decades showed that cattle grazing exclusion followed by increases in soil nutrients fostered tall fescue invasion, reduced the abundance of native grasses and forbs, and declined plant species richness. Long term monitoring permitted to observe a shift in the effect of grazing on exotic plants and to understand the factors controlling the expansion and impacts of a hazardous forage species in natural grasslands. Apart from warning about the use of exotic plant species as forage for domestic grazers due to their long-lasting negative effect on grasslands (Driscoll et al. 2014), our study stresses the importance that domestic grazers may have as a management player for modern landscapes (Pillar & Overbeck 2025). For rangelands to persist

as reserves of grassland biodiversity, new management strategies should balance native over exotic forage resources as part of productive schemes.

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Statements & Declarations

Funding

This work was funded by Agencia Nacional de Promoción Científica y Tecnológica (PICT-2014-1109 to PMT), Universidad de Buenos Aires (UBACyT-2014-2017-20020130100695BA, UBACyT-2014-2017-20020130100423BA) and CONICET (PIP-112-2015-0100709).

Competing Interests

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

Author Contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by all authors and coordinated by PMT. The first draft of the manuscript was written by PMT and all authors commented on previous versions of the manuscript. All authors read and approved of the final manuscript. Dr.

Enrique Chaneton, deceased in 2019, participated in early stages of this study.

Acknowledgements

Dedicated to the memory of Profs. Rolando León and Enrique Chaneton, who dedicated their lives to the study of these grasslands. We thank to the Bordeu family and rangers from Estancia “Las Chilcas” and to Marina Omacini, Cecilia Molina, Celeste Silvosio, and Caterina Cimolai who helped in the field. Dr. Martin Oesterheld suggested valuable comments.

Data Availability Statement

All the authors agree to upload the original datasets to a repository with DOI or permanent URL. Meanwhile, datasets are available from the corresponding author.

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