



Assessing nutrient enrichment and grazing rest effects on grass establishment: implications for exotic and native species

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Abstract

Anthropogenic activities have altered resource availability and disturbance regimes, to reduce the richness of native plant species and favoring the invasion of exotic species in grasslands. Therefore, it is crucial to understand the factors that control the establishment and expansion of exotic plants, as well as the limitations for the reestablishment of native species. The objective of this study was to experimentally evaluate in the field whether grazing rest, fertilization, and interactions with established vegetation modulate the spontaneous recruitment of exotic and native grasses, and whether these factors modify the interactions between established vegetation and seedlings. This experiment had a split-plot factorial design with 5 replicates in randomized complete blocks. After two years of grazing exclusion with cages, nutrient addition, and continuous removal of exotic and native groups, the total number and dry weight of newly established seedlings were measured. Fertilization and grazing rest were found to modulate the establishment of both exotic and native grass seedlings, while no significant changes were observed in the competitive situation. The number of exotic grass seedlings increased by 79% with grazing rest and by 149% with nutrient addition, while the establishment of natives was halved with grazing rest. In conclusion, both grazing rest and fertilization significantly impacted the establishment of native and exotic grasses in a short period. The results of this study provide evidence of a key process, establishment, and could help design management plans for temperate grasslands to prevent the invasion of exotic forage grasses and maintain the recruitment of native grasses.

Keywords Fertilization · Grazing · Plant interactions · Plant invasions · Seedlings · Temperate grasslands

Introduction

Anthropogenic activities have altered natural grasslands by changing resource availability, disturbance regimes, and the local and regional species pool (Estes et al. 2011; Steffen et al. 2015). Air pollution and fertilizer use have raised global and local nutrient levels (Elser et al. 2007; Borer and Stevens 2022). Additionally, the introduction of exotic forage plants to enhance livestock productivity has led to the dispersal of numerous exotic species outside those managed areas into natural grasslands (Driscoll et al.

2014; Godfree et al. 2017). These introduced species often outcompete native plants, resulting in reduced biodiversity (Godfree et al. 2017; O'Reilly-Nugent et al. 2020). Given that introduced species were selected for their nutritional quality and ability to thrive in fertilized pastures (Driscoll et al. 2014; Godfree et al. 2017), an increase in local nutrient levels, would favor the growth and dominance of invasive species over native ones in grasslands (Driscoll et al. 2014; Seabloom et al. 2015). However, their consumption by herbivores can potentially limit their spread (Gruner et al. 2008; van der Waal et al. 2016), leading to opposing effects of herbivores and nutrients on invasion dynamics. Therefore, it is crucial to understand what factors influence the establishment and expansion of exotic plants as well as the limitations associated with re-establishing native species in natural and semi-natural grasslands.

The loss of biodiversity has led to increased interest in understanding the factors that influence the vulnerability of local plant communities to invasive exotic species (Levine and D'Antonio 1999; Davis et al. 2000; Zavaleta and Hulvey

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2004; Chase et al. 2020). Research has revealed that the absence of certain species or functional groups, characterized by life form, origin, and seasonality, can reduce resistance to invasion (Hooper et al. 2005; Cardinale et al. 2006). Typically, dominant functional groups are better adapted to prevailing environmental conditions, leaving fewer resources available for less abundant species or potential invaders (Davis et al. 2000; Fargione and Tilman 2005; Hooper and Dukes 2010). Consequently, the loss of functional groups can create opportunities for invasion, especially if the exotic species share niche characteristics with the absent group or species (Seabloom et al. 2003; Walker et al. 1999; Esch et al. 2019). However, the loss of a functional group with complementary niche traits could also facilitate invasion success (Li et al. 2019). For instance, native and exotic species may only partially overlap in their phenological niches but coincide during critical stages of establishment, thereby influencing the population growth of both groups (Perelman et al. 2001). Therefore, evaluating the establishment stage is crucial, as seedlings are more vulnerable to environmental conditions and competition than adult plants (Turnbull et al. 2000).

The establishment of native and exotic grasses' functional groups, influencing their competitive interactions (Chesson and Huntly 1997; Chesson 2000; Borer et al. 2014), is affected by grazing and fertilization. The competitive abilities of these groups may depend on trade-offs in their growth and survival abilities in response to herbivores (Chesson and Huntly 1997). In grazed grasslands, native and exotic species may coexist if the exotic species, despite being strong competitors, are also susceptible to herbivores. However, the exclusion of herbivores could favor alien species, leading to the competitive exclusion of native species, even without complete niche overlap (Chesson 2000; MacDougall et al. 2009). Furthermore, increased nutrient levels can alter competitive relationships by promoting exotic species biomass production (Shea and Chesson 2002; Elser et al. 2007; Stevens et al. 2018) and intensifying competition for light within the community (Borer et al. 2014). Experimentally removing functional groups, fertilization and herbivore exclusion experiments could reveal how competition with exotics, disturbances, or multiple factors affect native species diversity (Heard and Sax 2013; Seabloom et al. 2015).

The native grasslands of the flooding Pampa have not escaped global transformations. These ecosystems provide the main forage resource in the region, with increased inputs to improve their nutritional conditions and livestock production (Cid et al. 2011). Introduced as winter forages in sown pastures, exotic grasses like *Lolium multiflorum*, *Gaudinia fragilis*, and *Festuca arundinacea* have become naturalized in the natural Pampas grasslands (Cabrera and Añón Suárez 1963; Scheneiter et al. 2016). While it is known that these exotic species can dominate certain communities and reduce plant diversity (Chaneton et al. 2002; Tognetti et al. 2010),

the underlying mechanisms remain unclear. However, management practices like fertilization and grazing are thought to play a role in altering the competitive balance between species and promoting or limiting their invasion (Longo et al. 2013).

In these grasslands the growing seasons of the native summer and exotic winter grasses do not overlap, however, the recruitment of one functional group could be affected by the other one (Perelman et al. 2007). The persistence of exotic annual species in these grasslands has been shown to be highly dependent on seedling recruitment during fall, a period that overlaps with the active growth of native summer grasses (Oosterheld and Sala 1990; Deregibus et al. 1994; Jacobo et al. 2006). Therefore, it has been suggested that a well-developed canopy of native grasses would interfere with the recruitment of exotics, resulting in a decrease in their cover and diversity (Perelman et al. 2007). Longo et al. (2013) found that removing native summer grasses led to a substantial increase in the biomass of winter-spring exotics, with the magnitude of this effect depending on the functional group of the removed species. Although there is a subtle overlap between native and exotic grasses in late spring (Perelman et al. 2007), the impact of exotic winter grasses on the establishment of native summer grasses at the end of spring remains unexplored. The mechanisms underlying these interactions in the context of nutrient inputs and livestock grazing are not well understood, which hampers the development of effective strategies for the restoration of native species.

The aim of this study was to assess the effects of livestock grazing exclusion and fertilization on the establishment of native and exotic grasses, as well as the potential modifications of interspecific interactions between established vegetation and seedlings. To achieve this, we conducted a selective removal experiment of functional groups. Specifically, we tested three hypotheses: (1) Livestock grazing limits the growth of exotic grasses and the establishment of their seedlings. Exotic grasses typically tend to have higher growth rates and are preferred by livestock, leading to higher consumption compared to native grasses. Native grasses, however, have developed strategies, such as creeping or tougher leaves, to resist grazing (Chaneton 2006; Galeano 2016). Consequently, grazing can directly hinder the establishment of exotic seedlings through consumption, and/or indirectly facilitate the establishment of native seedlings by reducing the asymmetric competition imposed by adult exotic grasses. (2) Fertilization favors the establishment of exotic grass seedlings more than that of native grasses and also intensifies the asymmetric competition exerted by adult exotic grasses on native grass seedlings. This is because exotic species generally have a greater capacity to capitalize on the increase in resource levels and increase their growth compared to

native species (Seabloom et al. 2015). (3) The asymmetric competition exerted by adult grasses limits the establishment of seedlings, whether native or exotic, due to temporal overlap during critical moments of the establishment (Perelman et al. 2007).

By investigating these hypotheses, we aim to gain insights into the complex dynamics of interspecific interactions and the factors influencing native and exotic grass establishment in order to enhance our understanding of grassland restoration and management.

Methods

Study site

The study was conducted in a natural grassland located approximately 40 km from the city of Pila, Buenos Aires Province (Estancia "Las Chilcas," 36°30' S, 58°30' W). The topography is extremely flat, which favors recurrent flooding, especially between autumn and spring, and there are usually intense droughts in the summer (Lavado and Taboada 1987). The grassland has not been plowed or fertilized, and it is grazed by cattle at a mean stocking rate of 0.55–1 cows/ha/year (Chaneton et al. 2002). The current plant community is composed of winter (C3) and summer (mostly C4) grasses and low-growing herbaceous dicotyledons (Perelman et al. 2001; Rusch and Oesterheld 1997; Chaneton et al. 2002). Regionally, the aboveground biomass relative to the total annual biomass is composed of: 56% warm-season native grasses (17 spp), 25% cool-season exotic grasses (8 spp), 12% cool-season native grasses (21 spp), 4.5% exotic dicotyledons (15 spp), and 2.5% native dicotyledons (33 spp) (Longo et al. 2013). Cool-season grasses have their maximum aboveground production from late spring to early summer, while warm-season grasses have their maximum production from late summer to early autumn (Sala et al. 1981). In the study site, the group of exotic grasses is mainly represented by *Lolium multiflorum* and *Gaudinia fragilis* (annuals), and *Festuca arundinacea* (perennial), all of which grow during winter. The group of native grasses is mainly composed of *Panicum gouinii* E. Fourn, *Paspalidium paludivagum* (Hitchc. and Chase) Parodi, *Leersia hexandra* Swartz, *Paspalum dilatatum* Poir, *Setaria geniculata* (Lam.) Beauv., and *Stenotaphrum secundatum* (Walt.) Kuntze, all of which are perennials and grow during summer (Longo et al. 2013; Chaneton 2006). Many of the summer native grasses are resistant to both grazing and prolonged flooding (Rusch and Oesterheld 1997; Chaneton et al. 2002). At the local scale, winter native grasses are poorly represented in the grassland (Chaneton et al. 2002).

Study design

We set up a field experiment focused on selectively removing certain species. Our primary objective was to evaluate the consequences of livestock grazing exclusion through the use of wire mesh cages and nutrient addition via fertilization on the dynamics of native and exotic grass species, as well as their ecological interactions. Following two years of treatment implementation, we assessed the influence of grazing exclusion and fertilization on the establishment of both native and exotic grasses. This experiment has a split-plot factorial design with five replications in randomized complete blocks. Each block consists of four main plots of 1 m² (total = 20 plots) arranged 10–20 m apart, with grazing exclusion and fertilization factors crossed (Fig. 1a). For this purpose, half of the plots in each block were protected from grazing by 1.5 × 1.5 m metal cages fixed to the ground. The microclimatic conditions were not modified by the mesh of the cage. Nutrient addition was carried out by the application of NPK fertilizers at a rate equivalent to 10 g m² of each element (nitrogen –N–, phosphorus –P–, and potassium –K–), applied three times a year in May, September, and December. N was applied as urea, P as triple superphosphate, and K as potassium sulfate. In each application, 35.5 g m² of sand was added to increase the volume of fertilizer and thus, its application was more homogeneous in each plot. Plots that were not fertilized received the same amount of sand as the other treatments. Then, the 4 treatments at the main plot level resulted from the combination of the two levels of each factor. Grazing exclusion (with or without cages) and fertilization (with or without NPK). Control plots were those representing the natural conditions in the field (without cages, without NPK) (Fig. 1a). In turn, each main plot was subdivided into three subplots of 0.50 × 0.50 m in which treatments of selective removal of different groups of grasses were applied (Fig. 1b). The subplots with the treatments of removal of one of the two dominant groups (native grasses or exotic grasses) vs. the subplot with the treatment where both groups were removed, were used to evaluate the interactions between natives and exotics. The removal of grasses was manually performed periodically, during the two years prior to the measurement moment. For both groups, the establishment was evaluated at critical moments of species emergence (Longo et al. 2013).

Data analysis

After two years of selectively removing functional groups and following the last removal in 2018, we measured the establishment of new seedlings based on two response variables, number and dry weight. The number of seedlings provides an idea of population density, while dry weight is a measure of growth (Maestre et al. 2005); both variables are measures of

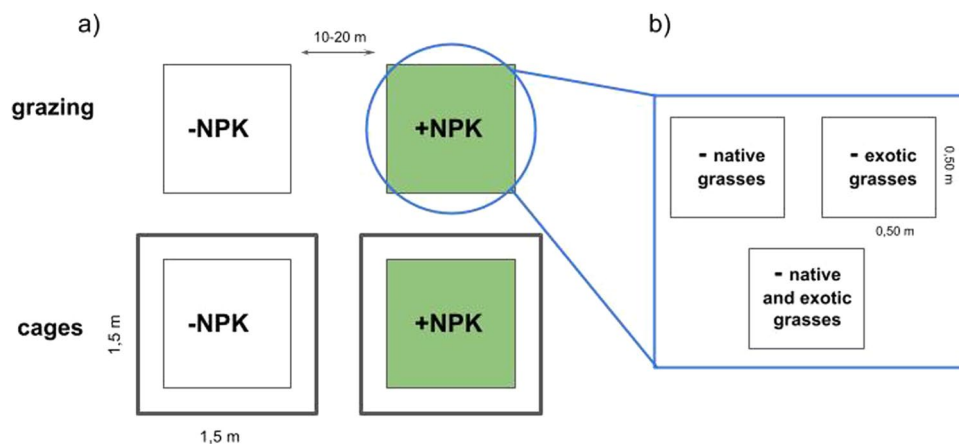


Fig. 1 Scheme of the main plots (a) and subplots (b) comprising a block. Plots surrounded by bold lines represent wire mesh cages that exclude livestock grazing, while those not surrounded represent grazed plots. Green shaded plots represent fertilized plots with NPK, while non-shaded plots represent unfertilized plots (-NPK). Furthermore, each plot is divided into subplots with 3 removal treat-

ments. Each subplot has a competition treatment resulting from the selective removal of functional groups: i) competition with winter exotic grasses through prior and sustained removal of summer native grasses, ii) competition with summer native grasses through prior and sustained removal of winter exotic grasses, and iii) without competition: through sustained removal of both groups of grasses

establishment. To measure the number of established individuals, we first sorted the harvested seedlings from each sub-plot by species and functional group (native or exotic grass) and then counted them. We then dried the seedlings at 60 °C for 48 h and weighed them to obtain the bulk seedling weight (g) for each group (native vs exotic) per sampled plot area.

To evaluate whether establishment was modulated by fertilization, grazing exclusion, and/or competition with previously established vegetation, we used generalized linear and mixed models with a negative binomial distribution for the number of seedlings, and linear mixed models with a normal distribution for biomass (Inchausti 2023). The fixed effects were the grazing exclusion, fertilization, and removal factors (each with two levels for each group of species). For the random effect, we respected the hierarchy of divided plots with the block as the main effect, which has the grazing exclusion and fertilization at a higher level and removal at a lower level (Næs et al. 2007). We also tested whether variables such as incident light percentage, bare soil coverage, litter, and other functional groups covaried with the number and weight of seedlings. However, we discarded covariates that were not significant. Finally, we selected models with the lowest Akaike information criterion (AIC) value (Zuur et al. 2010). All statistical analyses were performed in R (R version 3.6.3, R Core Team 2018), with the Infostat interface (Di Rienzo et al. 2020).

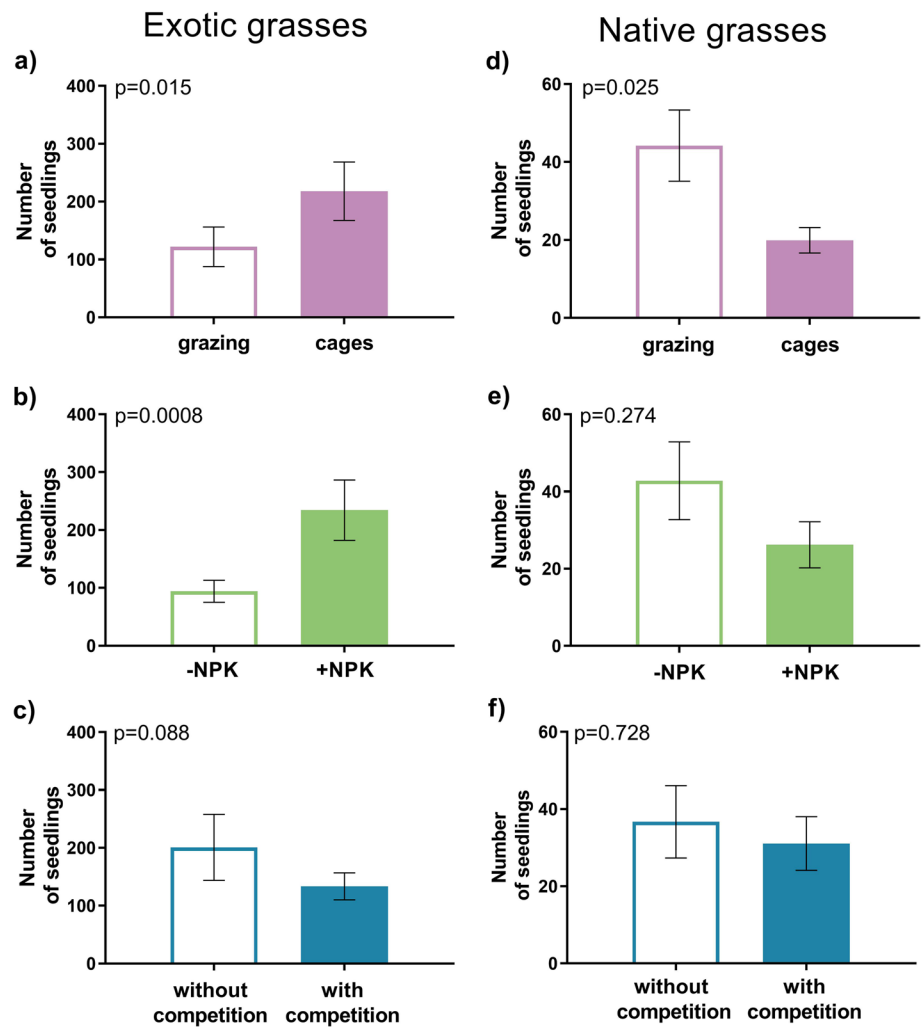
Results

Number of established seedlings

The grazing exclusion and fertilization positively affected the establishment of exotic grasses. The number of exotic grass seedlings increased 79% in caged plots compared to grazed plots (Fig. 2a, Grazing exclusion, $p = 0.015$, Table S1). Also, exotic grasses increased 149% more in fertilized plots compared to unfertilized plots (Fig. 2b, Fertilization, $p = 0.0008$, Table S1). The number of exotic seedlings established in plots where native grasses were removed tended to increase compared to plots without the removal of native grasses (Fig. 2c, Removal, $p = 0.088$, Table S1).

Compared to the number of seedlings of exotic grasses, the establishment of native grass seedlings was significantly lower throughout the experiment, differing by an order of magnitude. In plots where grazing occurred, the total number of native grass seedlings doubled in comparison to the plots that were left ungrazed (Fig. 2d, Grazing exclusion, $p = 0.025$, Table S2). Seven out of the nine native species recorded increased in grazed sites (Table S3), although not statistically tested due to

Fig. 2 Number of seedlings of exotic (**a**, **b**, and **c**) and native (**d**, **e**, and **f**) grasses in 0.25 m² plots. **a** and **d**) Sites with and without grazing exclusion cage ($n=20$). **b** and **e**) Sites with and without fertilization with NPK ($n=20$). **c** and **f**) Sites with and without removal of the other functional group ($n=20$). The bars represent the mean number of seedlings, \pm standard error, with an α of 0.05



potential data sparsity at the species level. Prostrate perennial grasses, *Paspalidium paludivagum* and *Stenotaphrum secundatum*, exhibited the highest number of seedling establishments in the grazed sites. Neither fertilization nor removal of exotic winter grasses significantly affected the number of established native seedlings (Fig. 2e, f, Table S2).

Under grazing exclusion, the values of photosynthetically active radiation (PAR %) decreased compared to grazing. The decrease was even more significant when fertilized, with an 88% reduction in PAR relative to grazed areas without fertilization (Table S4). Soil moisture measured through time domain reflectometry (TDR) was 24% lower in sites with grazing exclusion compared to grazed sites, and 15% lower in fertilized sites compared to unfertilized sites (Table S4).

Dry weight of established seedlings.

The dry weight of exotic grass seedlings varied with grazing exclusion and fertilization (Fig. 3, GxF $p=0.028$, Table S1).

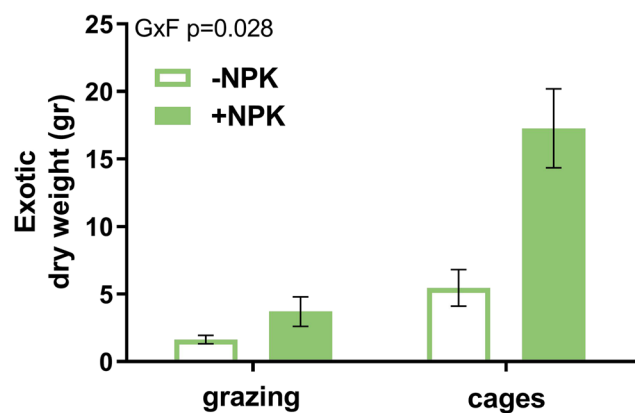


Fig. 3 Effect of grazing exclusion and fertilization on the dry weight of winter exotic grasses ($n=10$). Unfilled green represents unfertilized sites, and filled green represents fertilized sites with NPK. The bars represent the mean dry weight of seedlings \pm standard error, with an α of 0.05. "G" denotes grazing exclusion, and "F" denotes fertilization

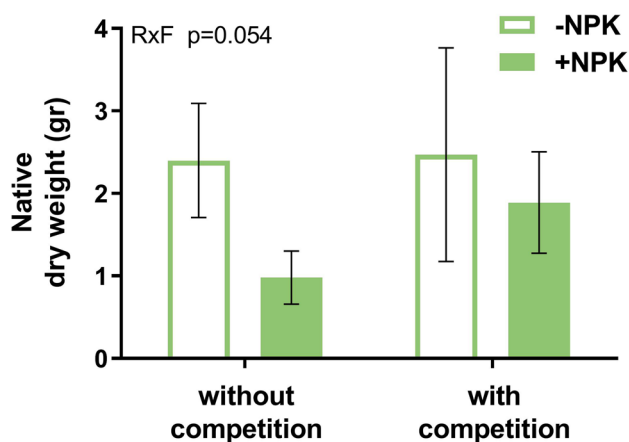


Fig. 4 Effect of fertilization and removal of exotic grasses on the dry weight of native grasses ($n=10$). Unfilled green represents unfertilized sites, and filled green represents fertilized sites with NPK. The bars represent the mean dry weight of seedlings \pm standard error, with an α of 0.05. "F" denotes fertilization, and "R" denotes removal

The weight of exotic grasses was 10 times greater in caged and NPK plots, compared to grazed and non-fertilized sites. On the other hand, the weight of exotic grasses did not vary with the removal of native grasses (Removal, $p=0.512$, Table S1).

The biomass of native grass seedlings tended to decrease in the absence of exotic grasses and in fertilized sites, although this effect was marginal (Fig. 4, FxR, $p=0.054$). Unlike the number of seedlings, the weight of the native grasses did not vary with grazing exclusion (Grazing exclusion, $p=0.812$, Table S2).

Discussion

The exclusion of grazing had opposing effects on the establishment of exotic and native grass seedlings. On the one hand, grazing exclusion using wire mesh cages resulted in the increased establishment of exotic grasses. Livestock generally prefers exotic forage grasses over native ones, leading to their higher consumption (Chaneton 2006; Galeano 2016), which supports our hypothesis that grazing restricts the establishment of exotic grass seedlings. Despite studies spanning over two decades indicating that grazing exclusion was traditionally used to recover native cover in Pampa grassland communities (Chaneton and Facelli 1991) and in other grasslands around the world (Seabloom et al. 2015), recent evidence stresses the increasing invasion of forage grasses in long-term grazing exclosures (see Graff et al. 2020; Molina et al. 2021). Considering the increasing dispersal of human-improved forage species in natural grasslands (Driscoll et al. 2014; Godfree et al. 2017), the exclusion of grazing as a management approach may have detrimental

effects on biodiversity (Li et al. 2017). Removal of grazing could allow highly competitive species adapted to grazing pressure to gain an advantage, out-competing native species for vital resources such as sunlight, water, and nutrients (Borer et al. 2014; O'Reilly-Nugent et al. 2020). Furthermore, the historical association of many invasive grassland plants with intensive human agriculture and grazing suggests the influence of selective breeding programs, which have played a role in their effective colonization and proliferation (Seabloom et al. 2015). These invasive plants, with their historical connections to human activities, pose additional challenges to the management and restoration efforts to promote native vegetation in grassland communities.

On the other hand, grazing rest resulted in a decrease in the establishment of all native grass seedlings. The native species that established greater abundance in grazed sites were summer grasses, which have grazing evasion strategies and are characterized by their low-growing, small-leaved, and prostrate growth (Bonomo 2013; Galeano 2016). Within this functional group, *Paspalidium paludivagum* and *Stenotaphrum secundatum* exhibited the highest number of seedling establishments in the grazed sites. Although competition with adult exotic grasses did not explain the decrease in native seedlings, the presence of cages had an indirect effect by increasing the height of the canopy and limiting light availability. Grazing exclosures tend to create a taller vegetation structure, which can restrict the establishment of species with shorter structures by limiting their access to light (Dorrough et al. 2007; Borer et al. 2014; Price et al. 2022). Moreover, it is important to consider that the short-term effects of grazing exclusion may differ from the long-term outcomes. Recent studies indicate that long-term exclosures promote taller vegetation structures compared to grazed sites, suggesting that changes in species composition play a significant role in shaping vegetation patterns (Connell et al. 2018; Porensky et al. 2020). These observations emphasize the need to assess the long-term implications of grazing exclusion on native grassland communities, highlighting the necessity of maintaining some level of grazing in the system to resist invasion and preserve ecosystem integrity in the long term (Porensky et al. 2020).

Fertilization significantly increased the number and weight of exotic grass seedlings, while having only a marginal effect on the dry weight of native grass seedlings. Consistent with our hypothesis, the effect of fertilization on the establishment of exotic grass seedlings suggests that exotic species are generally favored by nutrient inputs. Indeed, Seabloom et al. (2015) found that nutrient addition in various grasslands worldwide leads to an increase in exotic species cover and a decrease in native species richness and cover. It has been suggested that this pattern is driven by the greater resource uptake, growth rate, and reproductive output of exotic species compared to natives (van Kleunen

et al. 2010; Duell et al. 2021). This differential response to nutrient availability between native and exotic grasses may render fertilized sites more vulnerable to exotic species invasions. While native summer grasses typically exhibit higher aboveground biomass compared to exotic winter grasses in the region (56 vs. 25%, respectively) (Longo et al. 2013), our study revealed that the establishment of exotic grass seedlings was significantly greater than that of native grass seedlings. This stark difference can be attributed to the reproductive strategy of exotic species, which generally allocate more resources to reproduction, produce a higher quantity of seeds that are better dispersed, and exhibit faster germination rates compared to native species (Ordonez et al. 2010; van Kleunen et al. 2010). In the context of this particular grassland, the limited ability of native species to recolonize from neighboring areas and their reliance on clonal growth (Longo et al. 2013; Facelli et al. 1988) could also contribute to their lower establishment rates compared to exotic grasses.

We did not find support to accept the hypotheses regarding competition, as neither the absence of grazing nor fertilization modulated the relationships between native and exotic species. This could be because competition is more important in another phase of the life cycle of grasses. Larger plants usually have higher resource requirements, which intensifies the impacts of competition, and they are also less sensitive than seedlings to large environmental changes (Le Roux et al. 2013). Thus, at the establishment stage, big changes in environmental conditions may be more important than competition in determining success (Kempel et al. 2013). Consistent with this, the results of this study show that both grazing exclusion and fertilization had a direct and large impact on seedling establishment, without mediating interactions between them. It is noteworthy to mention that grazing exclusion and fertilization reduced light and soil moisture, which could influence seedling establishment. Moreover, we have not explored whether other interactions could be relevant at this stage. For example, it has been shown that seedlings are much more sensitive than adults to soil-borne pathogens (Kardol et al. 2013; Bezemer et al. 2018), so interactions with other trophic levels could be modulating seedling establishment. While the observed effect was marginal, fertilization appeared to reduce the weight of native grasses in areas where exotic grasses had been removed. This counterintuitive pattern could not be attributed to a higher number of seedlings with lower weights, nor to the presence of other non-grass species in the plots. One plausible explanation is that, despite the frequent removal of exotic grasses during the growing season, intermittent competition might have intensified due to fertilization during the intervals between the removal of exotic grasses.

In conclusion, grazing rest as a method for restoring native grasses in grasslands does not appear to be the best management strategy since it not only limits the establishment of natives but also promotes that of exotic forage grasses. Grazing rest or removal has been one of the most recommended tools for the restoration of native plant communities in many grasslands worldwide (Firn et al. 2010). However, in the context of increasing dispersal of human-improved forage species in natural grasslands (Driscoll et al. 2014; Godfree et al. 2017) and nutrient levels, this management approach may have unfavorable effects on biodiversity. Additionally, increasing local nutrient levels considerably increased the establishment of exotic grasses. In particular, fertilization along with the absence of grazing may favor invasion by promoting the establishment of exotic plants. In combination with the higher number of propagules compared to natives, it is likely that there is a higher probability of invasion than restoration in this grassland. This study contributes to the knowledge of a crucial stage in invasion, which is establishment. However, to generate long-term management strategies, it would be necessary to evaluate whether these factors have an impact on the growth and persistence of native and exotic grasses.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11258-023-01380-8>.

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Author contributions All the authors conceived the ideas, designed the methodology, and collected and analyzed the data. All the authors contributed critically to the drafts and gave final approval for publication.

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Data Availability All data analysed in this study is available in the Supporting Information.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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