



# Livestock exclusion reduces the temporal stability of grassland productivity regardless of eutrophication

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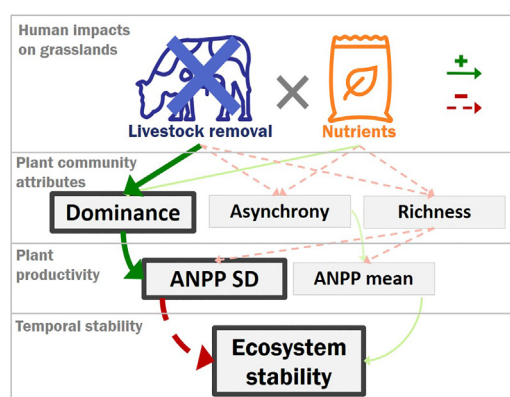
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## HIGHLIGHTS

- Livestock removal reduced grassland's stability (1/CV) by rising plant dominance.
- Livestock removal decreased the temporal asynchrony of plant species abundances.
- Livestock removal also increased the standard deviation of plant productivity.
- Nutrients reduced species richness and asynchrony but did not affect stability.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

### Article history:

Received 6 October 2021

Received in revised form 22 December 2021

Accepted 23 December 2021

Available online 2 January 2022

Editor: Elena Paoletti

### Keywords:

Aboveground net primary productivity (ANPP)

Effective species richness

Species asynchrony

Species dominance

Inter-annual variability

Flooding Pampa grassland

## ABSTRACT

Changes in livestock loads and eutrophication associated with human activities can modify the stability of grassland's aboveground net primary productivity (ANPP), by modifying the mean ( $\mu$ ) and/or standard deviation ( $\sigma$ ) of ANPP. The changes in attributes of the plant community (i.e., species richness, species asynchrony, dominance) might in turn explain the ecosystem temporal (inter-annual) stability of grassland production. Here, we evaluated the interactive effects of changes in livestock loads and chronic nutrient addition on the temporal stability of ANPP (estimated as  $\mu/\sigma$ ) in temperate grasslands. We also assessed the role of different attributes of the plant community on ecosystem stability. We carried out a factorial experiment of domestic livestock exclusion and nutrient addition ( $10 \text{ g} \cdot \text{m}^{-2} \cdot \text{year}^{-1}$  of nitrogen, phosphorus, and potassium;  $n = 6$  blocks) during five consecutive years in a natural grassland devoted to cattle production (Flooding Pampa, Argentina). Domestic livestock exclusion reduced ANPP stability by 65%, regardless of nutrient load, mainly by the increase of ANPP standard deviation. This reduction in ANPP stability after livestock exclusion was associated mostly with higher plant species dominance and also with reductions in plant effective richness and in the asynchrony of grassland's species. Despite not finding direct negative effects of eutrophication on ANPP stability, chronic nutrient addition decreased effective species richness and asynchrony, which may translate into reductions in ANPP stability in the future. Our findings highlight that the presence of livestock maintains the temporal stability of ANPP mainly by lowering the dominance of the plant community. However, increases in nutrient loads in grasslands devoted to livestock production may threaten grassland's stability.

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## 1. Introduction

Human well-being depends on the constant supply of ecosystem services by natural grasslands, such as carbon storage and forage production (Sala et al., 2017), but land-use changes and elevated nutrient deposition threaten the rate and stability of ecosystem processes (Modernel et al., 2016; Petz et al., 2014; Tamburini et al., 2016). In particular, temporal stability is the property of ecosystems to remain in the same state over time (e.g., to show low inter-annual variability) in response to environmental fluctuations and/or human perturbations (Ives and Carpenter, 2007). Facing global change, the stability of the aboveground net primary productivity (ANPP) is critical for the reliability of the ecosystem services that mostly depend on this important process (Albrich et al., 2018; Montoya et al., 2019). Grasslands harbor a high diversity of terrestrial species and provide many essential ecosystem services (Sala et al., 2017), but are threatened globally because wild herbivores were replaced by domestic livestock (Ripple et al., 2015; Thornton, 2010) and elevated nutrient deposition produces eutrophication (Galloway et al., 2008; Smil, 2000).

Temporal stability, also called “invariability”, can be estimated as the ratio between temporal mean ( $\mu$ ) and standard deviation of the mean ( $\sigma$ ), the inverse of the coefficient of variation ( $1/CV = \mu/\sigma$ ; Loreau, 2010; Tilman et al., 2014). Therefore, ecosystem stability is promoted when ANPP mean increases and/or when standard deviation decreases (Tilman, 1999; Tilman et al., 2006). Livestock grazing and soil eutrophication can differentially modify the mean and standard deviation of ANPP, with uncertain interactive consequences on its stability. In addition to these direct drivers of ANPP stability, plant species number and abundance are usually modified by these anthropogenic drivers and could mediate the stability responses of grassland ecosystems subjected to eutrophication (Hautier et al., 2014; Ives and Carpenter, 2007). Grazing by domestic livestock is the most extensive form of land use (Ellis and Ramankutty, 2008), but its combined effects with eutrophication in grasslands devoted to cattle production has not been assessed yet. The few studies that manipulated livestock and nutrient loads have assessed the stability of the structure of the plant community (i.e., diversity, standing biomass; Beck et al., 2015; Liu et al., 2021), but have not accounted for ANPP stability.

Changes in the plant community may impact ecosystem temporal stability of grasslands (Ives and Carpenter, 2007). Effective richness, the number of species equally abundant in the community (Jost, 2006), may promote stability through different pathways: (1) effective plant richness may increase ANPP mean (Cottingham et al., 2001; Tilman et al., 2014); (2) if species respond idiosyncratically to environmental fluctuations, richness may promote stability by the reduction in ANPP standard deviation because the statistical average of the fluctuations of species abundances increases with the number of species in the community (Doak et al., 1998; Schindler et al., 2015); and (3) effective plant richness may be positively associated with species asynchrony (i.e., the negative covariance of species abundances over time; Loreau and de Mazancourt, 2008). Species may respond asynchronously to environmental fluctuations if they differ in their response and effect traits (de Bello et al., 2021), thus compensating each other and reducing ANPP variability (Muraina et al., 2021; Zhang et al., 2016) and/or increasing ANPP mean through niche complementary effects (Yan et al., 2021). In addition to these mechanisms, species dominance, or low evenness in plant communities, may also promote stability if there is constancy (Grman et al., 2010; Polley et al., 2007; Sasaki and Lauenroth, 2011) or asynchrony (Valencia et al., 2020) in the abundance of the dominant species, thus lowering ANPP standard deviation. Also, if dominants are highly productive, stability is promoted by the increase in ANPP mean (Avolio et al., 2019; Hillebrand et al., 2008). However, if dominant species are susceptible to environmental fluctuations, the stability of productivity would decrease by the raise in ANPP standard deviation of dominant species abundances (Ma et al., 2020; Zelikova et al., 2014). Knowing how these different attributes of plant communities modulate ANPP stability will facilitate the connection between ecosystem temporal reliability and the observed changes in grasslands' diversity by livestock grazing and nutrient enrichment.

Human activities in grasslands involve changes in livestock grazing and soil nutrient loads, which may modify the temporal stability of ecosystem functioning directly or through changes in the plant community (Hautier et al., 2015; Valencia et al., 2020; Worm and Duffy, 2003). On the one hand, nutrient enrichment may decrease ecosystem stability through the reduction of plant diversity (Harpole et al., 2016) and of species asynchrony (Hautier et al., 2014; Liu et al., 2019; Zhang et al., 2016) that promote the standard deviation of ANPP mean (Hautier et al., 2015). Also, increase nutrients usually promotes the abundance of dominant “competitive” plant species (Ma et al., 2020; Song et al., 2019). On the other hand, livestock may increase ecosystem stability if they reduce plant dominance and/or promote species richness and/or asynchrony (Beck et al., 2015; Koerner et al., 2018; Mortensen et al., 2018). Additionally, plant consumption by grazers may increase the mean and/or decrease the variability of ANPP (Charles et al., 2017; Kohli et al., 2019), with direct impacts on the level of provision of ecosystem services (Carnus et al., 2014). Despite its importance for management and conservation (Bailey et al., 2019), the simultaneous impact of livestock grazing and nutrient enrichment on the stability of the productivity of temperate grasslands remains to be tested. Understanding the effects of human perturbations on ANPP mean, standard deviation, and stability is needed for the long-term reliability on the level and interannual variability of ecosystem services provided by grasslands (Carnus et al., 2014).

Flooding Pampa grasslands and the forage they provide are the principal support of extensive livestock production in Argentina (Viglizzo et al., 2011). Nonetheless, this activity threatens this poorly conserved region (Nanni et al., 2020) because livestock grazing (Chaneton et al., 2002) and nutrient enrichment (Molina et al., 2021) affect plant diversity and composition. These grasslands comprise a diverse species-mix of cool- and warm-season forbs, legumes, and C3 and C4 graminoids (Perelman et al., 2001). In addition, tall fescue (*Schedonorus arundinaceus* Schreb.), an invasive perennial C3 forage grass, has spread over the region in the last decades mainly in absence of livestock (Scheneiter et al., 2016). The combination of diverse plant life-forms with different moments of peak abundance (Perelman et al., 2007) offers an excellent natural framework to evaluate the relative importance of effective species richness, temporal asynchrony, and dominance as mechanisms that modulate the impact of livestock on ANPP stability in a nutrient-enriched scenario.

The objectives of this study were to evaluate: (1) the interactive effects of livestock loads and nutrient enrichment on the inter-annual stability of ANPP through changes in ANPP mean and standard deviation; (2) the role of plant community attributes (i.e., effective richness, asynchrony, dominance) modulating ANPP stability responses in a temperate grassland of the Flooding Pampa, Argentina. We hypothesized that (1) livestock exclusion and eutrophication individually reduce the stability of ANPP by decreasing plant species asynchrony, effective richness, and increasing dominance; (2) the absence of livestock intensifies the negative effect of eutrophication on ANPP stability because the expected loss of species asynchrony, decrease in effective richness, and increase in dominance caused by nutrient enrichment is not compensated by livestock grazing.

## 2. Methods

### 2.1. Study area

The experiment was conducted in ‘Las Chilcas’ ranch, 40 km south of Pila, Buenos Aires province, Argentina (36°16' S, 58°15' W; 15 m.a.s.l.). The regional climate is temperate sub-humid. Annual temperature range is 9.2 °C in July and 21.2 °C in January. Long-term mean annual precipitation was 926 mm/year (1950–2018), and during the study (2014–2018) the mean annual precipitation was close to average (1000.6 ± 194.2 mm/year; mean ± SD; CV: 19%; see Supplementary Fig. S1). Soils are typical Natraquoll, with 3.1% organic matter and limited water infiltration (Lavado and Taboada, 1987). The grassland type corresponds to humid mesophytic meadows of the central Flooding Pampa (Perelman et al., 2001). Grazed grasslands are dominated by native C4 grasses

(e.g., *Stenotaphrum secundatum*, *Panicum gouinii*, *Paspalidium paludivagum*, *Paspalum dilatatum*), non-native C3 grasses (*Gaudinia fragilis*, *Lolium multiflorum*), legumes (*Lotus glaber*), and non-legume forbs (e.g., *Mentha pulegium*). Sites without livestock are dominated by an invasive C3 perennial grass (tall fescue, *Schedonorus arundinaceus*).

The site was never ploughed or fertilized. The paddock (~1000 ha, without internal divisions) has been grazed with heifers, mothers, and calves at 0.5 cattle units.ha<sup>-1</sup> for nearly 100 years. This is considered a normal stocking rate for this region, and this specific paddock has no signs of grassland degradation (*personal observation*; Rodríguez and Jacobo, 2012). Livestock consume 31% of ANPP, on average (Campana, 2020). Grassland management involves summer grazing through late fall, and livestock resting in winter and spring. Small herbivores (e.g., *Lepus europaeus*, *Akodon azarae*, *Oryzomys flavescens*, among others) are also present in the area, but their impact on plant productivity and species composition inside enclosures was negligible compared with livestock effects (*personal observation*).

## 2.2. Experimental design

We established a factorial experiment of livestock grazing exclusion and fertilization in a split-plot design. The fertilization experiment started in March 2013 and it was replicated in plots in six paired grazed areas and 20 × 50 m enclosures (blocks) established in 2004 and located at least 100 m apart from each other. Thus, fertilization started nine years after the beginning of the enclosure treatment. At each block, we delimited four 25 m<sup>2</sup> plots, two of which were located inside the enclosures and the other two in the area with livestock grazing. In each grazing and enclosure area (i.e., main plot factor) we randomly assigned plots to the nutrient addition level (i.e., sub-plots), unfertilized or fertilized with NPK + micronutrients. Fertilization consisted of the addition of N, P, and K (10 g.m<sup>-2</sup>.year<sup>-1</sup> each), following the Nutrient Network experimental protocol (Borer et al., 2014). Nutrients were applied in granulated formulations of urea (N), triple superphosphate (P), and potassium sulphate (K) three times a year, in May, September, and December. During the first experimental year (2013) a mix of micronutrients, including Fe, S, Mg, Mn, Cu, Zn, B, and Mo, was also applied with NPK fertilizer (Borer et al., 2014).

## 2.3. Data collection and calculations

We calculated ANPP temporal stability for each plot as:

$$\text{Temporal stability} = \mu/\sigma \quad (1)$$

where  $\mu$  is the temporal mean of ANPP and  $\sigma$  is its standard deviation (Tilman et al., 2006) over the experimental period. We measured growing season aboveground net primary productivity (ANPP) from the third (2016) to the fifth (2018) experimental year to evaluate the stability of ANPP after transitory changes resulting from the first years of treatment application. ANPP was estimated as the positive differences between final (March) minus initial (November of the previous year) growing season biomass, considering live, standing dead, and litter compartments (Campana and Yahdjian, 2021). In spring (November), we harvested aboveground plant biomass within one 0.2 × 0.5 m frame in each plot. Simultaneously, we installed mesh movable cages (60 cm long × 30 cm wide × 45 cm high) in the grazed (fertilized and unfertilized) plots in order to temporarily exclude livestock grazing (Oesterheld and McNaughton, 2000). At the end of the growing season (March), we removed the cages and harvested plant biomass inside and outside cages and in the enclosure plots within one 0.2 × 0.5 m frame. Samples were separated, dried at 62 °C for 72 h, and weighed to the close 0.01 g. One cage was lost during 2016, resulting in 5 replicates that year.

We calculated three attributes of the plant community to characterize its diversity and dynamics. To calculate them, we measured aerial cover of each species rooted in one permanent 1 × 1 m<sup>2</sup> quadrat inside each

plot, to the nearest 5%, using a modified Daubemaire method (Borer et al., 2014). Aerial plant cover was measured in mid Spring and late Summer (November and March, respectively) in order to capture the peak abundance of cool- and warm-season species (Perelman et al., 2007). We selected the maximum value per species at each sampling date to estimate year-round plant community composition (Molina et al., 2021).

Then, we estimated plant species asynchrony as:

$$\text{Asynchrony} = 1 - \frac{\sigma^2}{\left(\sum_{i=1}^S \sigma_i\right)^2} \quad (2)$$

where  $\sigma^2$  is the temporal variance of total cover in each plot,  $\sigma_i$  is the temporal standard deviation of species “i” cover in a plot with S species over the three-year period (Loreau and de Mazancourt, 2008). This metric can have values between zero (perfect temporal correspondence between plant species abundance) and one (perfect asynchrony, species respond independently to environmental fluctuations). We used the *synchrony* function (‘codyn’ package, Hallett et al., 2016) to calculate synchrony metrics in R (R Core Team, 2018). With plant species cover, we also estimated effective species richness, the number of species equally abundant in the community, as the exponential of Shannon-Wiener index (Jost, 2006):

$$\text{Effective richness} = e^{-\sum_{i=1}^S p_i \cdot \ln p_i} \quad (3)$$

where  $p_i$  = proportion of total plant cover for species “i” and S = total number of plant species per plot. This metric is less sensitive to the presence of rare species than species richness and it has the advantage that can be partitioned into species richness and evenness, the two components of diversity (Jost, 2006). Finally, we estimated the dominance of the plant community with the Berger-Parker Index, the cover proportion ( $p_i$ ) of the most abundant species in each plot (Berger and Parker, 1970):

$$\text{Berger-Parker} = p_{i, \max} \quad (4)$$

This dominance index provides a simple and easily interpretable measure of dominance and it has the advantage of being mathematically independent of richness. Effective richness and Berger-Parker dominance were calculated from 2016 to 2018 and then averaged, to obtain one value per plot.

## 2.4. Statistical analyses

To analyze the effects of livestock exclusion and fertilization on temporal stability of ANPP, its components ( $\mu$  and  $\sigma$ ), and plant community attributes (species asynchrony, effective richness, dominance), we used mixed-effect models (*lme* function in ‘nlme’ package, (Pinheiro et al., 2017; Zuur et al., 2009) with R (R Core Team, 2018). The fixed factors were livestock exclusion, fertilization, and their interaction, while random structures included blocks ( $n = 6$ ) and plots nested within blocks to account for the split-plot design. Stability, standard deviation of ANPP, and species dominance were log<sub>10</sub>-transformed to accomplish distributional assumptions. Residuals were normally distributed (Shapiro-Wilk test). Variance heterogeneity was modeled when necessary (*varIdent*; Pinheiro et al., 2017). When interactions were significant ( $P < 0.05$ ), we performed Tukey’s post hoc comparisons.

We complemented three approaches to assess the role of the plant community modulating ANPP temporal stability. First, we performed simple regressions (individual tests) of ANPP stability and plant species asynchrony, effective richness, and dominance (fixed effects). Random structures included blocks ( $n = 6$ ) and plots nested within blocks (*lme* function in ‘nlme’ package; Pinheiro et al., 2017). ANPP stability was log<sub>10</sub>-transformed in all models. We modeled variance heterogeneity when necessary (*varIdent*; Pinheiro et al., 2017). We evaluated the fit of the models through residual exploration (Crawley, 2013), and added a quadratic term when this change improved model’s AIC (Zuur et al., 2009).

Second, we used a multi-model approach to evaluate the relative importance of each attribute of the plant community on ANPP stability. ANPP stability was  $\log_{10}$ -transformed, whereas species asynchrony, effective richness, and dominance were standardized (Z-scores; Burnham and Anderson, 2002). For multi-model selection we used *dredge* function ('MuMIn' package; Barton, 2019) and selected the models with lower AICc (small-sample-corrected Akaike information criterion). To evaluate the relative importance of each variable of the plant community to explained ANPP stability, we also estimated the sum of weights of all models in which each variable was included (*importance* function, 'MuMIn' package; Barton, 2019).

Finally, to weigh direct and indirect paths by which livestock exclusion and fertilization modify ANPP stability by changes on ANPP mean and standard deviation, we performed a structural equation model (SEM; *psem* function in 'piecewiseSEM' package; Lefcheck, 2016). As effective species richness and dominance were highly correlated (Pearson =  $-0.94$ ,  $P < 0.0001$ , see Supplementary Table S1), we performed separate models in which we included effective richness or dominance (see Supplementary Fig. S2). SEMs accounted for the random structure of the experimental design (split-plot design; Lefcheck, 2016). We initially depicted all theoretically relevant paths for the data (directed acyclic graph; see Supplementary Fig. S2, Table S2), and trimmed models eliminating non-significant paths (d-separation test; Lefcheck, 2016). The final models have the lowest AICs and non-significant  $P$ -values, which indicate non-detectable differences between the observed and predicted data (Lefcheck, 2016). As SEMs with effective richness or dominance similarly explained ANPP stability ( $R^2 = 0.85$ ), we opted for the SEM including dominance because this variable better explained ANPP stability in single and multi-model regressions.

### 3. Results

Excluding livestock reduced the temporal stability of growing season ANPP by 65% in relation to the grazed grassland, regardless of nutrient addition (Fig. 1a, see Supplementary Table S3). Stability reduction was mainly explained by a 97% increase in growing season ANPP standard deviation ( $P = 0.07$ ; Fig. 1b), as there were no significant changes in ANPP mean after livestock exclusion ( $P > 0.10$ , Fig. 1c). Although fertilization

did not affect stability, it increased both the mean ( $P = 0.02$ ) and the standard deviation ( $P = 0.05$ ) of ANPP by 33% and 40%, respectively (Fig. 1b-c).

ANPP stability was associated with different attributes of the plant community, which in turn were modified by livestock and nutrient loads (Fig. 2, see Supplementary Table S4). First, stability showed a unimodal association with species asynchrony ( $P = 0.07$ ), being lower at intermediate levels of asynchrony (Fig. 2a). Species asynchrony decreased by 13% with livestock exclusion showing a similar effect with nutrient addition, but when both factors were combined species asynchrony was reduced by 55% (see Supplementary Fig. S3a). Second, stability was positively associated with effective plant richness ( $P = 0.04$ ; Fig. 2b), which decreased by 69% with livestock exclusion and by 40% with nutrient addition (see Supplementary Fig. S3b). Finally, stability was negatively associated with plant community dominance ( $P = 0.01$ ; Fig. 2c). Dominance significantly increased when livestock was excluded ( $P = 0.006$ ), but by 124% without nutrient addition and by 205% with fertilization (E x N:  $P = 0.07$ ; see Supplementary Fig. S3c).

Among all attributes of the plant community, plant species dominance was the variable that best explained ANPP stability (see Supplementary Table S5). Dominance was the most important predictor to explain stability by its own, as its individual model showed a higher weight and lower AICc compared with the other plant community attributes. Dominance also had the highest sum of weights considering all the possible models where each community variable was included (see Supplementary Table S5). The second most important attribute of plant community to predict stability after dominance was the effective species richness and finally the asynchrony.

Excluding livestock under a nutrient-enriched environment explained 85% of the variance on ANPP stability via changes in species asynchrony and dominance (Fig. 3, see Supplementary Table S6). Interestingly, nutrient enrichment in the grazed grassland directly increased ANPP mean without changes in species asynchrony or dominance. Livestock exclusion, alone and under a nutrient enriched condition, reduced plant species asynchrony and increased species dominance (Fig. 3). In sum, treatments explained more than 80% of the changes in species asynchrony and dominance of the plant community ( $R^2$  values of 0.85 and 0.81, respectively). There were positive associations of species asynchrony with ANPP mean and of plant dominance with ANPP standard deviation, showing parallel lines of action on

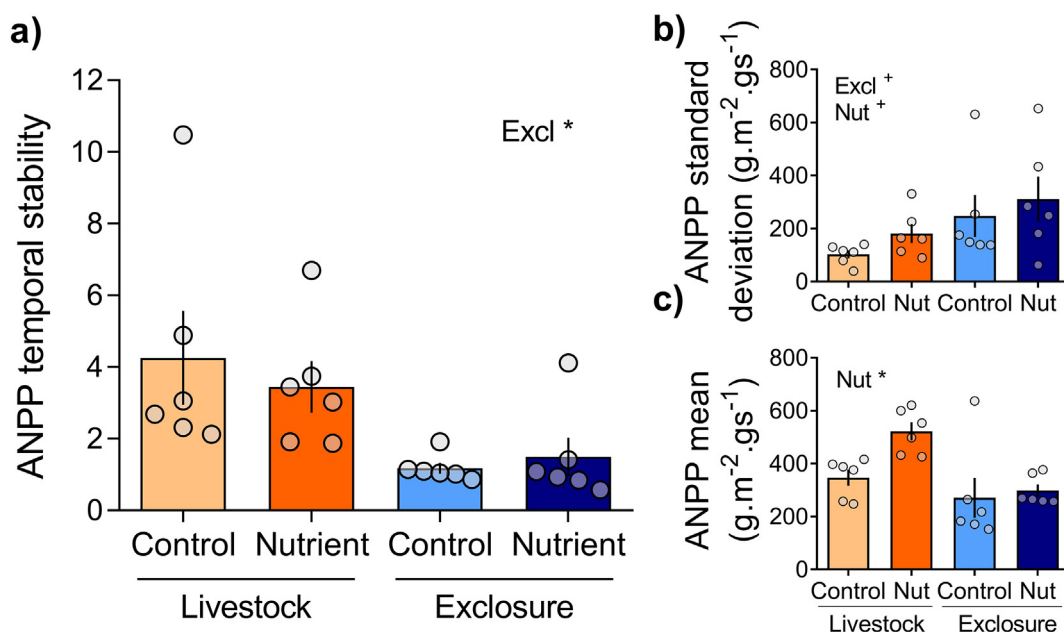


Fig. 1. Effect of livestock exclusion (Excl), nutrient addition (Nut), and their interaction (Excl x Nut) on growing season (gs) ANPP a) temporal stability (estimated as  $\mu/\sigma$ ; unitless), b) standard deviation ( $\sigma$ ;  $\text{g.m}^{-2}.\text{gs}^{-1}$ ), and c) mean ( $\mu$ ;  $\text{g.m}^{-2}.\text{gs}^{-1}$ ). Bars are mean values  $\pm$  SE and points are individual values;  $n = 6$ . +  $P < 0.1$ , \*  $P < 0.05$ .

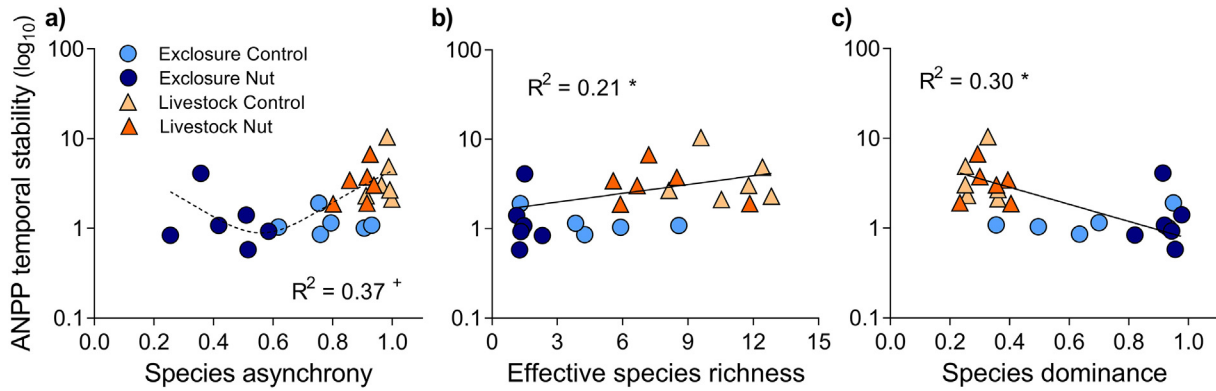


Fig. 2. Relationship between ANPP temporal stability ( $\log_{10}$ ) and attributes of the plant community: a) species asynchrony, b) effective species richness ( $e^H$ ), and c) species dominance (Berger-Parker index). Points are mean values per plot of the variables represented in the x-axis;  $n = 3$  years. The corresponding  $R^2$  is indicated on each panel. Solid lines are significant regression lines ( $P < 0.05$ ) and dotted lines show marginally significant regressions ( $P < 0.1$ ) fitted for each variable.  $^+ P < 0.1$ ,  $^* P < 0.05$ .

these two attributes of plant community. The promotion of ANPP standard deviation via changes in species dominance had a greater impact on stability (standardized estimate:  $-0.88$ ) than the effect of the ANPP mean increase via changes in species asynchrony (standardized estimate:  $0.64$ ), resulting in a net decrease of ANPP stability with livestock exclusion (Fig. 3).

#### 4. Discussion

Understanding livestock loads effects on ecosystem stability in a nutrient-enriched scenario contributes to predict long-term consequences

of human activities and help to improve grassland management. Here, we found that livestock exclusion reduced ANPP temporal stability independently of chronic nutrient enrichment (Fig. 1a). In addition, the expected negative effect of eutrophication on stability was not evident either in the absence of livestock (Fig. 1a), thus dismissing the hypothesis of an interaction between nutrients and livestock grazing in the studied time lapse. The exclusion of livestock decreased stability mainly by an increase in ANPP standard deviation, whereas nutrient addition increased both the mean and standard deviation of ANPP (Fig. 1b-c). Species dominance, which increased with livestock exclusion, explained the reduction in ANPP stability

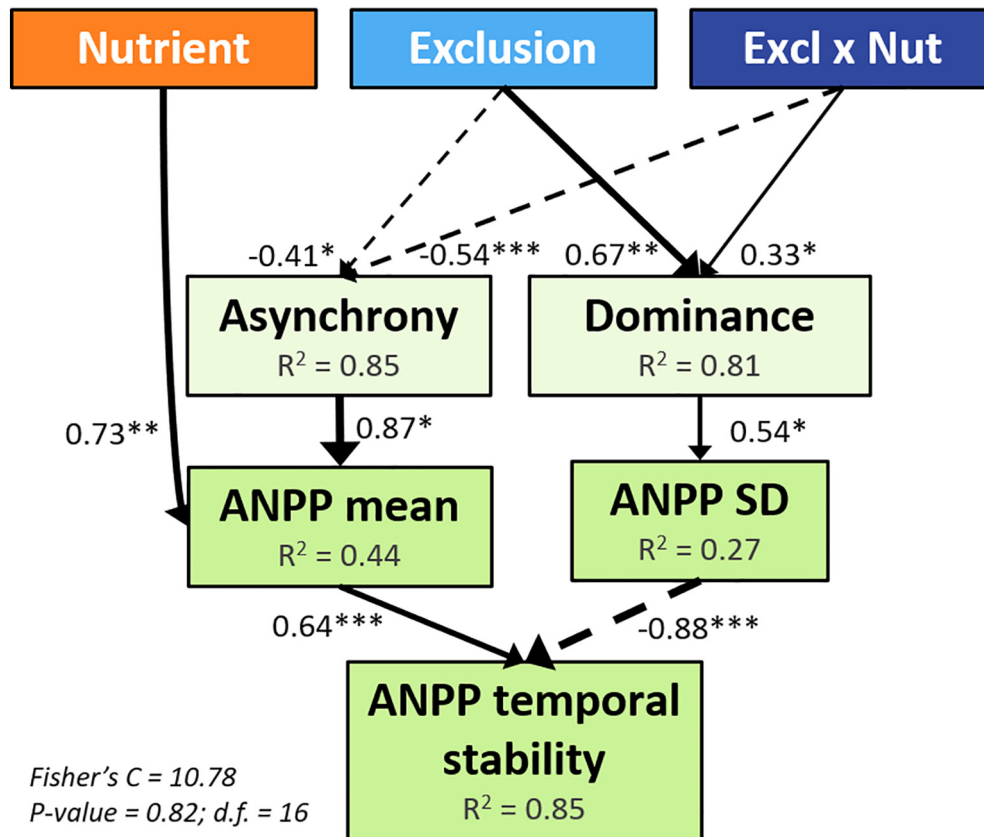


Fig. 3. Structural equation model of the effect of livestock exclusion, nutrient addition, and their interaction (Excl x Nut) on ANPP temporal stability via changes in attributes of plant community (species asynchrony and species dominance), growing season ANPP temporal mean, and ANPP standard deviation (SD;  $g \cdot m^{-2} \cdot gs^{-1}$ ). The  $R^2$  values within the boxes indicate the proportion of the variance explained by the model for each response variable. The displayed estimates are standardized path coefficients. The width of the arrows reflects the strength of the positive (solid) or negative (dashed) paths. Significance levels of path coefficients are shown as  $^*$  ( $P < 0.05$ ),  $^{**}$  ( $P < 0.01$ ), and  $^{***}$  ( $P < 0.001$ ).

through the promotion of ANPP standard deviation (Fig. 3). Species dominance was the attribute of the plant community that better explained changes in ecosystem stability (Fig. 2c). Furthermore, stability increased with effective species richness (Fig. 2b), which in turn was reduced by livestock exclusion and nutrient addition. Species asynchrony promoted stability by indirectly fostering ANPP mean (Figs. 2a, 3). Therefore, livestock exclusion overrides the impact of eutrophication on ANPP stability on this temperate grassland through the increase of species dominance of the plant community.

The effect of livestock and nutrient loads on ecosystem stability were explained by how they differently modified ANPP mean and standard deviation (Fig. 1b-c). The increase in the standard deviation of ANPP in relation to its mean accounted for the reduction in stability in response to livestock exclusion. These results differ from a former study which did not find effects of wild herbivores removal on ecosystem stability due to the compensation of ANPP mean and standard deviation (Kohli et al., 2019). Hence, our findings support that the impact of livestock grazing on ANPP stability should not be inferred from their wild counterparts (Borer et al., 2020; Charles et al., 2017). Furthermore, eutrophication increased ANPP mean but also increased its standard deviation in a similar magnitude, therefore resulting in a null effect on stability (Fig. 1). The large effect of chronic nutrient addition on ANPP standard deviation, despite not affecting stability on our study, has been identified as an indicator of regime shifts (Carpenter and Brock, 2006). Additionally, nutrient enrichment may increase the sensitivity of ANPP to precipitation changes (Bharath et al., 2020). These evidence suggest a risky nutrient-enriched scenario for the provision of ecosystem services in temperate grasslands (Carnus et al., 2014).

The relationship between livestock loads and ecosystem stability was driven by three interrelated attributes of the plant community: species asynchrony, effective richness, and dominance (Figs. 2 and 3). Asynchrony, which was higher in the grazed grassland than inside enclosures, was positively associated with stability by increasing ANPP mean (Figs. 2a, 3). This is a novel result, as species asynchrony generally buffered temporal fluctuations of plant communities, thus lowering standard deviation (Muraina et al., 2021; Zhang et al., 2016). As asynchrony involves different responses to environmental fluctuations (de Bello et al., 2021), it is feasible that the presence in this grassland of functionally diverse plant species with different moments of peak abundance compensated each other (Perelman et al., 2007), thus increasing ANPP mean through niche complementarity (Tilman et al., 2014; Yan et al., 2021). In addition, this result suggests that these plant species overlap their response traits, which were modified by livestock, and their effect traits, which promoted ANPP (Suding et al., 2008).

The reduction in stability with livestock exclusion in our study contrasts with previous evidence showing that the absence of livestock promoted ecosystem stability while grazing intensity decreased it (Liu et al., 2021; Qin et al., 2019; Valencia et al., 2020). This discrepancy probably occurs because in those sites, livestock exclusion also increased plant richness (Liu et al., 2021; Qin et al., 2019) and species asynchrony (Valencia et al., 2020). Interestingly, the fact that there were positive associations between species richness or asynchrony and ecosystem stability in all cases, previous studies and our results, suggests a consistent stability mechanism explained by plant diversity (Hautier et al., 2014, 2015; Tilman et al., 2014; Valencia et al., 2020). The discrepancy between studies holds on the effect of grazing exclusion on plant diversity, which has already been demonstrated to be variable (Koerner et al., 2018). Despite chronic eutrophication reduced species richness and asynchrony (see Supplementary Fig. S3), these changes did not translate into a decrease in ANPP stability as expected (Hautier et al., 2014; Liu et al., 2019; Song et al., 2019; Valencia et al., 2020; Zhang et al., 2016). The slight increase in the standard deviation of the ANPP seems to be offset by the promotion of ANPP mean by nutrient enrichment (Figs. 1 and 3).

Species dominance, or low community evenness, was the attribute of the plant community that better explained the reduction in stability of grassland productivity by increasing ANPP standard deviation (Fig. 3; best model and highest sum of weights in multi-model selection, see Supplementary Table S5). ANPP stability was minimum when the plant community had higher species dominance and lower diversity, estimated by

effective plant richness, which were directly related to the absence of livestock (Fig. 2b-c). Thus, the promotion of dominance and the decline in plant diversity, as a consequence of livestock exclusion (Koerner et al., 2018), decreased ANPP stability (Beck et al., 2015; Zelikova et al., 2014). This contrast with studies that report an increase in ecosystem stability as a result of constancy in the abundance of the dominant species (Grman et al., 2010; Polley et al., 2007; Sasaki and Lauenroth, 2011). Plant dominance was positively correlated with the relative cover of *S. arundinaceae* (tall fescue; Pearson = 0.98,  $P < 0.001$ ), a non-native perennial C3 grass that has been introduced as forage and now is invading the ungrazed areas of the region (Scheneiter et al., 2016). In this grassland, sites with higher tall fescue abundance accumulated more aboveground biomass than the livestock-grazed grassland (Campana and Yahdjian, 2021), but their productivity would be more variable over time making this ecosystem prone to collapse (Carpenter and Brock, 2006). This poses a threat for the conservation of the Pampa region, as the dominance of *S. arundinaceae* in the absence of livestock not only compromises the richness of native plant communities but also affects ecosystem functioning (Spirito et al., 2014; Yahdjian et al., 2017), including grassland's stability. Thus, the identity and fluctuations of the abundance of dominant plant species (Avolio et al., 2019; Grime, 1998; Hillebrand et al., 2008; Valencia et al., 2020) controlled the stability of this grassland in the absence of livestock.

We evaluated stability over a three-year period of ANPP measurements. This is not the only study that analyzes ecosystem stability along the same time span (Hautier et al., 2014). Hautier et al. (2015) evaluated data from 12 multiyear experiments and found that there is consistency between the short- (3-year period) and long-term (4 to 28 years) mechanisms that explain ecosystem stability responses to different global change drivers. In addition, data from a coordinated experiment spanning 58 grasslands around the globe (including our study site) found consistent short- and long-term impact of grazing removal and fertilization on plant aboveground biomass (Borer et al., 2020).

Three strengths highlight the importance of our results. First, the experiment was carried out during years with variable precipitation (CV: 19%). Thus, the obtained results and the ANPP damping in the presence of livestock are realistic considering the normal climatic variability of the grassland (see Supplementary Fig. S1). Second, we started measuring ANPP stability after two years of manipulations, allowing the stabilization of the plant community response to chronic nutrient addition. We did not measure ANPP during the period of plant acclimation to fertilization, which response is more related to physiological than ecological mechanisms. Instead, we have allowed the plant community enough time to show changes in its diversity and composition (Smith et al., 2009). Finally, the livestock enclosures were established nine years before the beginning of the nutrient addition treatment. In this way, few years of nutrient enrichment did not counteract the long-lasting effect of livestock on plant diversity and ANPP stability on this grassland. As richness was highly reduced in the absence of livestock, the effect of dominance on grassland stability will depend on the stability of the most abundant species of the community (Grman et al., 2010; Polley et al., 2007; Sasaki and Lauenroth, 2011). However, we have already observed negative impacts of nutrients on plant diversity (see Supplementary Fig. S3). In the grazed grassland, where richness is higher than in the absence of livestock, it is feasible that chronic eutrophication may continue decreasing plant effective richness (Harpole et al., 2016; Molina et al., 2021; Seabloom et al., 2020), asynchrony (Song et al., 2019; Zhang et al., 2016), and/or increasing dominance over time (Ma et al., 2020; Song et al., 2019), which would further reduce ecosystem stability in a nutrient-enriched scenario (Doak et al., 1998; Hautier et al., 2014; Liu et al., 2019). Therefore, we have evidence to expect that the differences among treatments showed here will persist or, even more, will intensify as time goes by.

## 5. Conclusion

In conclusion, livestock exclusion reduced ANPP temporal stability while chronic nutrient addition did not alter ecosystem stability. The

decrease in the stability of plant productivity was mainly driven by higher species dominance, increasing ANPP standard deviation, and by lower species asynchrony, positively associated with ANPP mean, when livestock were removed. Even though eutrophication lowered species richness and asynchrony, these changes were not directly translated into reductions in ANPP stability. These results highlight the role of dominant species identity and asynchrony in modulating the stability of plant productivity in grasslands (Avolio et al., 2019; Hillebrand et al., 2008; Valencia et al., 2020). Furthermore, our findings emphasize that alterations in livestock loads and the increase in soil nutrients in grasslands, two consequences of human activities (Galloway et al., 2008; Smil, 2000; Thornton, 2010), impacted ecosystem stability and its drivers. Human well-being relies on the constant supply of ecosystem services, so knowing that moderate livestock grazing in temperate grasslands is a strategy to maintain ANPP provision over the years poses an optimistic management scenario (Bailey et al., 2019). Although we have not found direct negative effects of eutrophication on ANPP stability, chronic nutrient addition increased ANPP mean and standard deviation, with negative effects on plant diversity. The decrease in plant diversity and stability could lead to changes in other trophic levels, having consequences on the functioning of the entire ecosystem (Worm and Duffy, 2003). Therefore, rangers should be concerned about using fertilization to increase momentary ANPP as it may jeopardize the stability of the provision of diverse ecosystem services in the future (Petz et al., 2014).

### Funding sources

This study was funded by ANPCyT (PICT 2014-3026 and PICT 2019-02324), Universidad de Buenos Aires (UBACyT 2018 20020170100191BA and UBACyT 2020 20020190100212BA), and Neotropical Grassland Conservancy. SC was supported by a fellowship from CONICET.

### Data availability

The data that support this study are available via GitHub (<https://github.com/SofiaCampana/LasChilcas-ANPP.TemporalStability>).

### CRedit authorship contribution statement

**Sofía Campana:** Investigation, Funding acquisition, Formal analysis, Visualization, Writing – original draft. **Pedro M. Tognetti:** Investigation, Funding acquisition, Writing – review & editing. **Laura Yahdjian:** Investigation, Funding acquisition, Writing – review & editing, Supervision.

### Declaration of competing interest

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

### Acknowledgments

This paper is dedicated to the memory of Enrique J. Chaneton, who helped to conceive the original idea and made invaluable contributions to this work. We thank Mariana Ciavattini, Viviana Bondaruk, Pamela Graff, Cecilia Molina, and Celeste Silvano for field assistance and helpful suggestions. Bordeu family allowed us to work on their field and 'Nutrien Ag Solutions' provided the fertilizers. We thank Elizabeth Borer and Eric Seabloom for leading the Nutrient Network and for stimulating discussions. The authors have no conflict of interest to declare.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.152707>.

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