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Grazers and fires: Their role in shaping the structure and functioning of the Río de la Plata Grasslands

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Abstract. The Río de la Plata Grasslands (RPG) are one of the largest areas of open ecosystems (grasslands, shrublands and savannas) in the world. Historically, these systems have experienced, and continue to experience, an enormous loss of natural habitats. Moreover, their importance has been largely invisible in comparison to forested systems. The remaining area of open ecosystems in the RPG region varies according to the source from 38 to 58% of the original area. Open Ecosystems (OE) are a special case of agroecosystems because they can combine the supply of both provisioning and regulating and supporting ecosystem services (ES). Preserving the provision of ES in these natural habitats depends, in part, on understanding the role of the two main disturbances operating in them: grazing and fire. Although these two disturbances are natural components of OE, both are manipulated by humans. In this paper we reviewed the role played by fire and grazing in the structure and functioning of the RPG starting from the late Pleistocene and Holocene, and summarizing current evidence on the effects of fire and grazing on vegetation, fauna and biogeochemical processes. The evidence indicates that among agricultural activities, direct grazing systems in OE have the lowest environmental footprint. At the same time are the key for habitat preservation and ES supply. Overall, the OE of the RPG still represent a high proportion of the area, are capable of covering 2.5% of the world's population needs of high quality protein and, at the same time, guarding the regulation of key processes.

[Keywords: disturbances, grasslands, ecosystem services, environmental footprint]

Resumen. Herbívoros y fuegos: Su rol en la configuración de la estructura y el funcionamiento de los pastizales del Río de la Plata. Los Pastizales del Río de la Plata (PRP) son una de las áreas más extensas de ecosistemas abiertos (pastizales, arbustales y sabanas) del mundo. Históricamente, estos sistemas han experimentado, y lo siguen haciendo, una enorme pérdida de hábitats naturales. Más aun, en buena medida, su importancia ha sido invisibilizada frente a sistemas boscosos. El área remanente de ecosistemas abiertos (EA) varía según las fuentes del 38 al 58% del área original. Los EA son agroecosistemas particulares porque pueden combinar el suministro tanto de servicios ecosistémicos (SE) de provisión como de regulación y soporte. La maximización del suministro de SE en estos hábitats naturales depende, en parte, de comprender el papel de las dos principales perturbaciones que operan en ellos: el pastoreo y el fuego. Aunque estas dos perturbaciones son componentes naturales de los EA, son manipuladas por prácticas humanas. En este artículo revisamos el papel del pastoreo y el fuego en la estructura y el funcionamiento del PRP, partiendo de su papel durante el final del Pleistoceno y el Holoceno, y resumiendo evidencias de los efectos actuales del pastoreo y el fuego sobre la vegetación, la fauna y los procesos biogeoquímicos. Las evidencias muestran que los sistemas ganaderos en EA tienen, en dimensiones claves de la huella ambiental tales como la preservación de hábitats y la oferta de SE, el menor impacto entre las actividades agropecuarias. Los valores estimados de producción de carne equivalente en los EA representan una alta proporción de la producción total de la región, un volumen de producción capaz de cubrir el consumo de un 2.5% de la población mundial.

[Palabras clave: perturbaciones, pastizales, servicios ecosistémicos, huella ambiental]

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Introduction

Grasslands, savannas and shrublands are grassy or Open Ecosystems (OE) (Bond 2019) occurring in a wide range of mean annual precipitation, from 200 to 1500 mm, and temperature, from 0 to 30 °C (Lauenroth 1979). Their main physiognomic characteristics include, among other features, a relatively continuous herbaceous layer with or without scattered woody components. Temperate and subtropical subhumid grasslands and savannas are one of the most threatened biomes of the world (Hoekstra et al. 2005). The vast plains that once dominated central parts of Eurasia and North America, eastern parts of Africa and the southeastern end of South America have been profoundly altered by agricultural expansion. Surprisingly, such changes have acquired less popular visibility than those occurring in, for example, wetlands or forest (Overbeck et al. 2015). The low attention that OE receive becomes clear when the area devoted to conservation is considered. Hoekstra et al. (2005) calculated a Conservation Risk Index (CRI) and temperate grasslands, savannas and shrublands ranked first. Moreover, these ecosystems are also threatened by worldwide initiatives of massive afforestation (Bastin et al. 2019) to deal with global changes issues, neglecting the importance of OE in biodiversity conservation, C sequestration and ecosystem services in general.

Grazing, droughts and fire are key factors in shaping these OE (Oesterheld et al. 1999; Gibson 2009). Year-to-year changes, and even larger-scale trends in climatic variables, affect water availability, a major driving force of the structure and function of OE (Sala et al. 1988; Lauenroth and Sala 1992; Oesterheld et al. 1992; Paruelo and Lauenroth 1996, 1998; Paruelo et al. 1998; Paruelo et al. 1999). Grazing and fires are two paradigmatic disturbances in OE and a major pathway to release fixed C back to the atmosphere (Gibson 2009; Chapin 2002) by combustion, respiration, and methane emissions. Grazing is a complex syndrome that involves biomass removal, selectivity, trampling, defecation, and urination (Mikola et al. 2009; Lezama and Paruelo 2016). The combined effects of these components of grazing determine changes in physiognomy (i.e., Sala et al. 1996; Altesor et al. 2019; Ferreira et al. 2020), soil properties (i.e., Milchunas and Lauenroth 1993; Taboada and Lavado 1988) and ecosystem functioning (Rusch and Oesterheld 1997; Altesor et al. 2005). The frequency and intensity of fires determine a pattern of biomass removal, nutrient volatilization and ash deposition, which affect the whole ecosystem (Daubenmire 1968; Vogl 1974; Hulbert 1988; Hobbs et al. 1991; Bond and Keeley 2005; Veldman et al. 2015; Buisson et al. 2019).

The Río de la Plata Grasslands (RPG) region occupy the vast and continuous plains of central-eastern Argentina, Uruguay and southern Brazil that surround the Río de la Plata estuary and its major tributaries. This region covers about 853000 km^2 and corresponds to one of the most diverse, largest and least transformed grassland area in the world, despite the important land cover transformation that they experienced (Oyarzabal et al. 2020). Soriano (1992) defined nine subregions within the whole region (Figure 1): the Northern and Southern Campos and seven units within the Pampa: Mesopotamic, Rolling, Flat Inland, West Inland, Southern, Fluvial and Flooding Pampa. The RPG covers a range of average annual temperature from 20 °C in the north to 13 °C in the south and an annual rainfall from 1500 mm in the northeast to 400 mm in the southwest (Paruelo et al. 2007). C_3 and C_4 grasses are the co-dominant life forms, with a low cover of trees and shrubs. Other physiognomic types, such as meadows, savannas, shrublands and forests, occupy a relatively small area and become abundant in particular environments (Boldrini 1997; Overbeck et al. 2007; Perelman et al. 2001, 2017; Batista et al. 2014; Oyarzabal et al. 2018; Lezama et al. 2019). Forests are mainly restricted to riparian corridors along the large Paraná and Uruguay rivers, and their tributary streams to rocky hills and ravines, and to azonal soils formed on top of shell debris deposits (Lewis and Collantes 1973; Cabrera et al. 1976; León et al. 1979; Morello et al. 2012; Brazeiro et al. 2020). An abundant regional literature summarizes the biotic and abiotic characteristics of this biome (Vervoost 1967; Soriano 1992; Paruelo et al. 2005; Pillar et al. 2009; Perelman et al. 2001, 2017; Oyarzabal et al. 2020).

Several studies described the changes in land cover across the whole region and the spatial heterogeneity of the transformation (i.e., Hall et al. 1992; Guerschman et al. 2003; Baldi et al. 2006; Baldi and Paruelo 2008; Baeza et al. 2014; Baeza and Paruelo 2020, and recently MapBiomas initiatives). Changes are mainly associated with the substitution of permanent grazing lands with cash crops or tree plantation expansion (Vega et al. 2009). At least three cartographic products show the present distribution of grazing lands in the whole region (Figure 1) (Baeza and Paruelo 2020; Copernicus Global Land Cover [Buchhorn et al. 2020], MapBiomas Pampa and Atlantic Forest Trinational initiatives [Souza et al. 2020; Vallejos et al. 2021; Milkovic et al. 2021]). From these three independent sources, it is clear that the current area of remnant OE is controversial. The sources of this controversy are associated with the classification protocols used to construct each one of the three maps (data sources, classification techniques, etc.), the conceptual resolution of the estimates, and the quality of 'ground-truth' data may also jeopardize the estimates. Moreover, the actual definition of 'natural' grasslands is controversial (Allen et al. 2011). Old sowed pastures, intersowed grasslands or old fields may be included or not as 'natural grasslands' depending on the criteria used. The estimates of remnant OE ranged from 328739 km^2 (MapBiomas project) to 498987 km^2 (Baeza and Paruelo 2020) (a 38% and 58% of the estimated original area, respectively). In this article we used an ensemble of the three sources presented in Figure 1. We considered an area as grassy OE if it was classified as such by at least two sources (Figure 1).

The main economic activity on the remnant grasslands, savannas and shrublands (OE) of the RPG is cattle and sheep ranching (Oyarzabal et al. 2020). Livestock production has been strongly questioned from an environmental perspective. Probably the FAO´s document 'Livestock's long shadow' from 2006 started the controversy on the negative effects of livestock farming on the environment, but a series of articles and books have further elaborated on this issue (i.e., Oppenlander 2013 for the general public and Garibaldi et al. 2018 in an academic context). The concerns are linked, in general, to three aspects: trophic efficiency of grain-feed production in confined

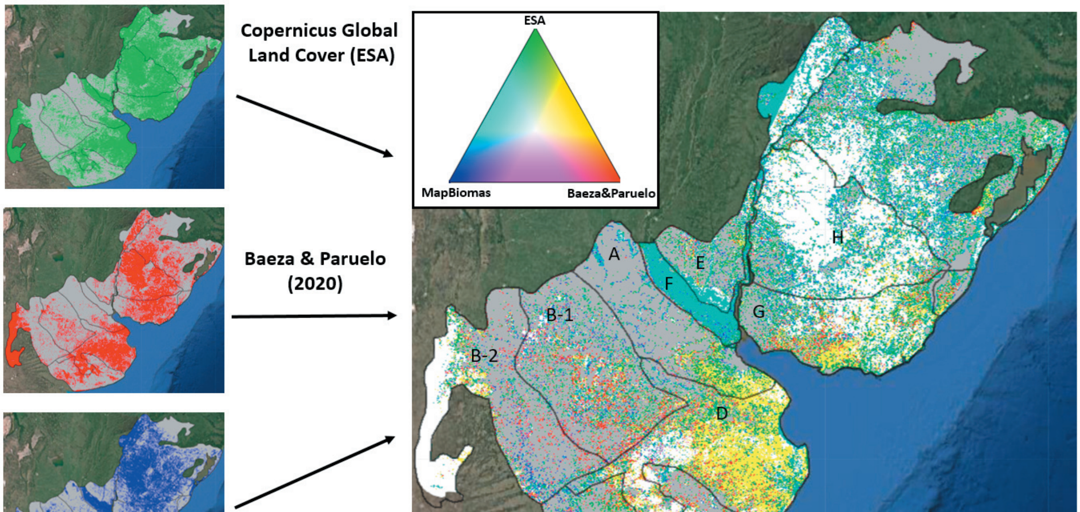

Figure 1. Maps of the distribution of Open Ecosystems (OE) (grasslands, savannas, shrublands and wetlands) in the Río de la Plata Grasslands (RPG) region, according to three sources highlighted in green, red and blue, respectively: a) Copernicus Global Land Cover (ESA) (Buchhorn et al. 2020), b) Baeza and Paruelo (2020), and c) MapBiomas Project (pampa.mapbiomas.org/initiatives). The map on the right shows a combination of the three sources, highlighting in magenta, yellow, cyan and white the coincidence of at least two sources, while in gray land cover types other than Open Ecosystems are indicated. On top of the maps are outlined the subregions according to Soriano (1992). A: Rolling Pampa, B-1: Flat Inland Pampa, B-2: West Inland Pampa, C: Southern Pampa, D: Flooding Pampa, E: Mesopotamic Pampa, F: Fluvial Pampa, G: Southern Campos, H: Northern Campos.

Figura 1. Mapas de la distribución de Ecosistemas Abiertos (EA) (pastizales, sabanas, matorrales y humedales) en la región de los Pastizales del Río de la Plata (PRP), según tres fuentes resaltadas en verde, rojo y azul, respectivamente: a) Copernicus Global Land Cover (ESA) (Buchhorn et al.2020), b) Baeza y Paruelo (2020), y c) Proyecto MapBiomas (pampa.mapbiomas.org/initiatives). El mapa de la derecha muestra una combinación de las tres fuentes, destacando en magenta, amarillo, cian y blanco la coincidencia de al menos dos fuentes, mientras que en gris se indican tipos de cobertura terrestre distintos de los ecosistemas abiertos. Sobre los mapas se indican las subregiones según Soriano (1992). A: Pampa Ondulada, B-1: Pampa Interior Plana, B-2: Pampa Interior Oeste, C: Pampa Austral, D: Pampa Deprimida, E: Pampa Mesopotámica, F: Pampa Fluvial, G: Campos del Sur, H: Campos del Norte.

systems, the destruction of natural habitats (mainly forests) and biodiversity losses and the impact on ecosystem services supply, particularly on biodiversity and greenhouse gases (GHG) emissions.

Open Ecosystems (OE) are a special kind of agroecosystems because they may combine the supply of both provisioning (i.e., meat and wool) and regulating and supporting ecosystem services (ES) (i.e., C sequestration, water supply, biodiversity conservation). Maximizing ES supply on these natural habitats depends, in part, on understanding the role of the two main disturbances that operate on them: grazing and fire. Though these two disturbances are natural components of OE, both are manipulated by humans. In this article we reviewed the role of fire and grazing on the structure and functioning of the RPG. We first present a synthetic review of the importance of both disturbances over the end of Pleistocene and the Holocene. Then, the evidence of the current effects of fire and grazing on vegetation, fauna and biogeochemical processes is presented. Finally, we evaluate the potential for meat production in native grasslands, shrublands and savannas of the RPG and two estimates of the environmental footprint of ranching in OE.

The evolution of the grass-dominated vegetation and the influence of large herbivores and fire

At present, grass-dominated vegetation characterizes the RPG, which has been an important natural asset for the economy of the region since the introduction of livestock by Europeans. These ecosystems present a long evolutionary history of herbivory by large grazers that existed throughout South America (MacFadden 2005; Strömberg 2011). Data from plant silica (phytoliths) in sediment cores collected in Patagonia indicate that grass-dominated vegetation developed under the influence of large grazers about 18 million years before present (BP) (Strömberg et al. 2013), and possibly since about 8 million years BP in the RPG (Strömberg 2011). The now extinct megafauna of large herbivores included species such as *Equus neogeus*, *Toxodon platensis* and *Notiomastodon platensis*, which presented C_4 plants in their diets, as inferred by carbon isotopes, a clear indication that they were grazers (MacFadden 2005; Morosi and Ubilla 2019; Domingo et al. 2020; Omena et al. 2020).

Large herbivores became extinct in South America by the end of the Pleistocene and the beginning of the Holocene (Prado et al. 2015), and the extinction process was likely human-driven (Prates and Pérez 2021). The time window of ca. 10 thousand years without grazing by large herbivores until the introduction of domestic livestock was not enough, in evolutionary terms, for substantially changing the regional pool of grassland species, as shown by pollen and phytolith evidence (e.g., Iriarte 2006; Behling and Pillar 2007).

Further, by the end of the Pleistocene, fire frequency increased in some regions of the RPG (Behling et al. 2005), likely due to the change from cold and dry to warm and humid climatic conditions, which increased primary production, and to the direct fire ignition by humans. In addition, the lack of large grazers may have been an important factor for this change of fire frequency. Thus, without grazing, fire may have played the role of herbivory (Bond and Keeley 2005) by maintaining in humid ecosystems an analogous selective pressure towards traits that are also adapted to grazing, such as fast regrowth after biomass loss (Díaz et al. 2007). Nevertheless, the remaining populations of grazers likely concentrated nearby landscape positions with available drinking water, such as ponds and river margins (Oesterheld et al. 1992, 1999). In those areas, the evolution under grazing led also to plants presenting a prostrate habit (e.g., McNaughton 1984). This evolutionary long-term dynamics of plants under grazing —and possibly under fire— was embedded into the dynamics of the climate during the Quaternary. The RPG, which at present is characterized by a strong NE-SW precipitation gradient (from ca. 1500 mm in southern Brazil to 400 mm in the West Pampa in Argentina) has undergone climatic shifts during the late Pleistocene and the Holocene, when species from the north have expanded their distribution towards the south and vice-versa (Tonni et al. 1999; Quattrocchio et al. 2008). This has been reflected in the vegetation (Iriarte 2006; Behling and Pillar 2007) and in the soils (Quattrocchio et al. 2008). These climatic changes explain the 'aeolian deposits interbedded with paleosols' that are observed in the Pampa (Iriondo 1999). At present, species richness is related to this climatic gradient, with higher diversity towards the NE, where the climate is warmer, and the precipitation regime is less seasonal (Perelman et al. 2017; Bergamin et al. 2022).

The last 500 years of the RPG were characterized by increased human influence. First, livestock reinstated grazing as a disturbance throughout the area and reached an average density six times greater than the density of large natural grazers in comparable ecosystems of the world (León et al. 1984; Soriano 1992; Oesterheld et al. 1992). Thus, livestock grazing was a novel disturbance at a very short-time scale, which led some authors to assign these grasslands a short evolutionary history of grazing. However, as seen above, in a broader framework, these 10 thousand years may be seen as a brief interruption of a several million-year coevolution with large grazers.

During the 20th century, crops spread in the most favorable subregions and coexisted with livestock in the same farms within a rotation between sown pastures and crops (Hall et al. 1992). Native OE were restricted, in general, to habitats with limited conditions for cropping. In the late 20th century and over the course of the current century, technological and global market changes further facilitated the expansion of crops to marginal soils and the lengthening of the crop phase in the rotation.

Effects of grazing and fire on the structure and functioning of the RPG

<u>Effects on vegetation structure</u>. Several studies in the RPG have evidenced profound consequences of grazing on vegetation structure, with the magnitude of its impact being greater as habitat productivity increases (Lezama et al. 2014) (Figure 2). Grazing induces changes in species composition by replacing the dominant tall grasses with prostrate warm-season species (Facelli et al. 1989; Rodríguez et al. 2003; Altesor et al. 2005, 2006; Ferreira et al. 2020). This leads to a strong change in the vertical distribution of leaves, which concentrate their biomass in the first centimeters above the ground (Sala et al. 1986; Altesor et al. 2006; Ferreira et al. 2020). Grazing also exerts a positive effect on species richness (Rusch and Oesterheld 1997; Altesor et al. 2006; Lezama et al. 2014; Ferreira et al. 2020), particularly of graminoids and forbs (Lezama et al. 2014). In the Flooding Pampa, species richness increases mainly through the addition of exotic cool-season forbs (Facelli et al. 1989; Rush and Oesterheld 1997), differently from what occurs in the Uruguayan Campos, where no impact of grazing on the number of exotics has been observed, probably related to the relative importance of prostrate C_4 grasses in this region (Altesor et al. 2006; Bresciano et al. 2014). Unlike richness, forb and graminoid cover lack a consistent grazing response. It is likely that the functionally heterogeneous composition of these groups, which includes both grazing-intolerant and resistant growth forms, leads to variable responses to grazing, depending largely on local factors (e.g.,

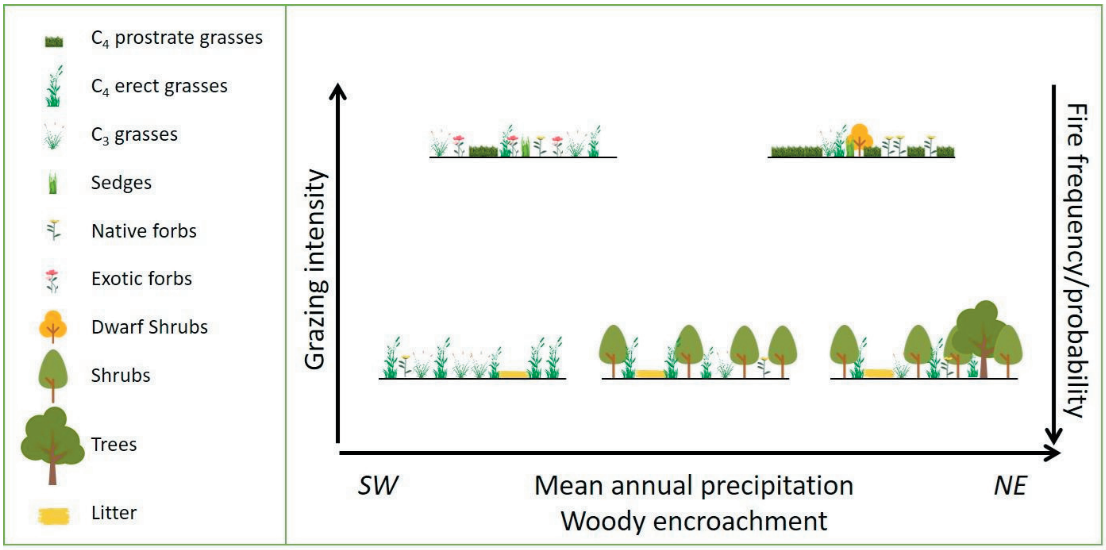

Figure 2. Schemes of the physiognomy of different Open Ecosystems (OE) across a gradient of grazing (Y axis left), fire (Y axis right) and geographic (X axis) in the RPG.

Figura 2. Esquemas de la fisonomía de diferentes Ecosistemas Abiertos (EA) a lo largo de gradientes de pastoreo (eje Y izquierdo), fuego (eje Y derecho) y geográfico (eje X) en los PRP.

management) and environmental stochasticity (Rodriguez et al. 2003; Lezama et al. 2014). At larger scales, grazing reduces the spatial heterogeneity or β diversity (Chaneton and Faceli 1991; Chaneton et al. 2002; Lezama et al. 2014).

A particular pattern observed as a response to grazing in the RPG is the decrease in the richness and cover of shrubs (Altesor et al. 2006; Lezama et al. 2014; Ferreira et al. 2020). Despite the apparent homogeneity in grazing response patterns in the RPG, there are climatic, topographic and edaphic differences that interact with disturbances and lead to the emergence of different patterns. In areas with the presence of boundaries between forests and grasslands (e.g., the Mesopotamic Pampa [Biganzoli et al. 2009; Chaneton et al. 2012], southern Brazil [Muller et al. 2012; Overbeck et al. 2016] and eastern Uruguay [Altesor et al. 2006; Gallego et al. 2020]), it has been observed that grazing and/or fire suppression increases shrub and tree species cover, either native or exotic (Figure 2).

In the RPG, prescribed fires are common in areas dominated by tussock grasses. As documented in many OE, fire and grazing importance is negatively correlated (Karp et al. 2021). Fire spreads fueled by standing dead biomass of the tussocks and temporarily reduces its coverage and height (Laterra et al. 1998; Overbeck et al. 2005; Overbeck and Pfadenhauer 2007; Beal-Neves et al. 2020; López-Mársico et al. 2021). Soon after fire, the tussocks begin to produce fresh green leaves, which are attractive and consumed by livestock (Laterra et al. 1998; Laterra et al. 2003; López-Mársico et al. 2021). Also, fire generates bare soil spaces that are quickly occupied by a large number of species found in the regional species pool, but poorly represented before fire (Laterra et al. 1998; Overbeck et al. 2005; Fidelis et al. 2012; Beal-Neves et al. 2020; Cuello et al. 2020; López-Mársico et al. 2021), such as rosette forbs (Overbeck and Pfadenhauer 2007; Fidelis et al 2012). Specifically in the Flooding Pampa, fire promotes the invasion of exotic species (Laterra 1997; Juan et al. 2000; Laterra et al. 2003). Accordingly, fire increases spatial heterogeneity that results in higher plant species richness (Overbeck et al. 2005; Beal-Neves et al. 2020; López-Mársico et al. 2021) or, occasionally, in equal numbers (Fidelis et al. 2012). As time since the fire increases, or when it is suppressed, standing dead biomass of the dominant tussock grasses accumulates and prevents the establishment of many less competitive herbaceous species.

Effects on fauna. It has been proposed that disturbances in grasslands, such as grazing and fire, create a shifting mosaic of patch types that differ in plant community composition and structure, translating into greater diversity at higher trophic levels (Fuhlendorf et al. 2006). Birds have been one of the most studied taxa in the RPG. Most bird species use grasslands for nesting and foraging. In addition, several species are long-distance migrants that use grasslands for wintering or breeding (Aspiroz et al. 2012). Spatial heterogeneity of vegetation enhances diversity of birds, as some species are either restricted to short (Isacch and Martínez 2003; Aldabe et al. 2019) or tall grasslands (Isacch and Cardoni 2011), while many others make broader use of both grassland types (Aspiroz et al. 2012). Accordingly, it has been proposed that heterogeneous grazing and fire management optimizes conservation of grassland birds (Develey et al. 2008; Isacch and Cardoni 2011; Jakobosky et al. 2017; Beal-Neves et al. 2020).

Conversely, it seems that disturbances negatively affect the presence of non-flying small mammals (such as rodents and marsupials), which have more restricted mobility than birds. Pedó et al. (2010) found that species richness and abundance of small mammals more than tripled inside protected areas, compared to grazed or periodically burned grasslands of southern Brazil. Similarly, Luza et al. (2018) found that three rodent species, that are among the most abundant species in the South Brazilian grasslands, preferentially occupy paddocks subjected to moderate or low grazing intensities.

Information about the effect of disturbances on invertebrate diversity is scarce and seems to be group-specific. An increase in resource quantity (i.e., plant biomass) or quality (i.e., plant diversity) as well as a greater complexity in vegetation architecture may lead to an increase in the richness and abundance of arthropods (Evans et al. 2015). A study in southern Brazil showed that high-taxa richness and abundance of vegetation-dwelling arthropods increased under deferred grazing or grazing exclusion, while epigeic arthropod communities did not respond to grazing management (Ferreira et al. 2020). Also, it has been observed that certain communities of below-ground biota, such as mites (Altesor et al. 2006) and earthworms

(Zerbino et al. 2006), show striking differences in species composition when grazed/ungrazed plots are compared. On the other hand, given the low intensity and rapid spreading of grass-fueled fires, arthropod communities would not be greatly affected by this disturbance. Although individual mortality by heating may instantly reduce populations, spider (Podgaiski et al. 2013) and grasshopper (Ferrando et al. 2016) communities recover promptly from small-scale fires through fast recolonization from unburned patches, tracking changes in vegetation. After one year since the fire, communities from burned sites were indistinguishable from unburned ones. Also, fire favors the growth and reproduction of several low competitive plant species, which in turn may also benefit species from other trophic levels, like pollinators (da Silva et al. 2021), extrafloral nectaries-visiting ants (da Silva et al. 2020) or thrips (Podgaiski et al. 2018).

Effects on primary production. Average aboveground net primary production (ANPP) over the whole region, based on remotely sensed estimates, was 5090 $kg.ha^{-1}.year^{-1}$ (p10: 2912 $kg.ha^{-1}.year^{-1}$ and p90: 6495 $kg.ha^{-1}.year^{-1}$, STD: 1445 $kg.ha^{-1}.year^{-1}$). More than 75% of the variation in average ANPP of the herbaceous layer of OE can be accounted for by their mean annual precipitation (McNaughton 1985; Sala et al. 1988a; McNaughton et al. 1993; Paruelo et al. 1999). This pattern was also observed in the RPG region, despite the limited range of mean annual precipitation studied (Paruelo et al. 2010; Durante et al. 2017). However, at the local scale, landscape and soil characteristics modulate the vegetation response to rainfall (Sala et al. 1988; Lane et al. 1998).

On top of these abiotic factors, primary production is affected by the disturbance regime. Grazing increases or decreases ANPP when compared to non-grazed nearby areas, but the relative effect was in general, no larger than 50% and showed no relationship with mean annual precipitation (Oesterheld et al. 1999). In the RPG, only two studies specifically addressed the effect of grazing on ANPP, with contrasting results. In the Flooding Pampa, grazing reduced ANPP (Rusch and Oesterheld 1997), while in the Campos region, increased it (Altesor et al. 2005), compared to an adjacent exclosure. The intra-regional differences indicate that the effect of grazing on primary production is difficult to generalize, as it can be mediated by different components of the vegetation (e.g., species composition/diversity or canopy structure) or the grazing regime (e.g., stock density or defoliation frequency and intensity). Four studies addressed the effect of grazing on belowground net primary production in the RPG (Doll and Deregibus 1986; Soriano 1992; López-Mársico et al. 2015, 2016). Generally, grazing promoted an increase in root production, reaching a maximum in spring or summer.

The synthesis from Oesterheld et al. (1999) showed that for OE worldwide, the effects of fire on productivity were relatively larger than the effects of grazing and showed a significant pattern along the precipitation gradient. Both positive and negative effects of fire on productivity appear to be more intense than the effects of grazing. The effect of fire on productivity was positively associated with mean annual precipitation, showing that the increases in productivity in burned areas are larger in the wet portion of gradient, which include a substantial portion of the Campos of the RPG. The local evidence on the effect of fire on primary production is scarce. Laterra et al. (1998) indicated that fire effects on tall grasslands of the Flooding Pampa showed no clear patterns. The effects ranged from nil to a 50% increase (Hidalgo and Laterra 1993, 1995). Prescribed fires are used as a management tool in some areas of the RPG to control shrubs or tall tussock grasses (Laterra et al. 1998; Overbeck et al. 2007; López-Mársico et al. 2021). A study conducted in the eastern Uruguayan grasslands using NDVI (Normalized Difference Vegetation Index), a spectral index closely related to primary production, showed that after a reduction of biomass due to fire, NDVI experience a rapid recovery (72±37 days) and values of burned sites can even exceed those of adjacent non-burned sites (Bruzzone et al. 2018; Bruzzone 2019).

Effects on biogeochemical cycles. Grazing and fire both have the fundamental effect of opening biogeochemical cycles in ecosystems. Fire consumes biomass and releases large amounts of inorganic or simple organic compounds, increasing the exchange of nutrients with the atmosphere and the surrounding ecosystems (Bond and Keeley 2005). Therefore, large amounts of nutrients are usually lost from burned ecosystems, although nutrient availability also increases, potentially increasing some processes such as C gains (Oesterheld et al. 1999; Harris et al. 2007). Grazing, on the other hand, though not as fast as fire, also consumes biomass and releases inorganic nutrients and easily decomposable feces, accelerating nutrient cycles (Bond and Keeley 2005). The concentration of nutrients in urine and dung patches also increases nutrient losses from ecosystems (Piñeiro et al. 2006). Large herbivores concentrate nutrients over the landscape due to their behavior patterns (affected by water availability and sleeping sites), favoring volatilization and leaching of inorganic compounds (Chapin et al. 2002; Pastor et al. 2006).

Soil organic matter (SOM) is the main reservoir of nutrients and C in most grasslands (Parton et al. 1993). SOM may store energy that equals more than 10 years of grassland's primary production and large stocks of nutrients and carbon (Paruelo et al. 2010). Grazing can change soil structure, function and its capacity to store SOM, and then, C stocks. Energy stored in SOM fuels soil microorganisms that make nutrients available for plants and maintains biogeochemical cycles (Chapin et al. 2002). Changes in SOM would influence soil physical properties and intermediate ES supply (nutrient retention and mineralization, water holding capacity, soil biodiversity, etc.). SOM is a key structural aspect in determining, regulating and supporting ES (Paruelo and Vallejos 2013). Grazing and fire affect SOM by altering either carbon inputs or outputs to the soil. Such inputs and outputs are in turn affected, directly or indirectly, by changes in the nitrogen cycle (Piñeiro et al. 2009; Piñeiro et al. 2010). OE soils contain large stocks of carbon that remain sequestered when grazed by domestic herbivores, but are vulnerable to being released to the atmosphere as CO_2 under alternate uses (Caride et al. 2012). Sequestration of C in SOM is considered one of main CO_2 capture strategies (Chabbi et al. 2017). OE store more C in mineral-associated organic matter (MAOM), which is more persistent but has a higher nitrogen demand and saturates (Cotrufo et al. 2019). The C/N ratio of the MAOM fraction is lower than in the Particulate Organic Matter (POM) fraction, consequently C accumulation in the MAOM fraction is necessarily accompanied by large nitrogen storages. MAOM is mainly retained by N adsorption to clays and therefore, clay slots may become saturated at high MAOM contents (Six et al. 2002).

Nitrogen plays a central role in controlling carbon inputs and outputs from SOM because it controls simultaneously primary production, plant carbon allocation and SOM stabilization in the mineral associated organic matter (MAOM), the main SOM fraction in grasslands (Piñeiro et al. 2010; Lavalle et al. 2020) (Figure 3). Increasing N inputs (i.e., by overseeding legumes to increase biological N fixation) has been proposed as an alternative to increase C sequestration in grasslands soils (Figure 3). However, empirical data shows that SOM may increase or decrease with more legumes depending on grazing management (Bondaruk et al. 2020).

Both grazing and fire reduce the amount of carbon inputs to the soil, due to biomass consumption, potentially decreasing SOM stocks. Heavily and frequently burned areas and overgrazing undoubtedly decrease SOM stocks, but moderate grazing and infrequent burning have shown variable results (Abdalla et al. 2018). Several works report both increases, decreases or unchanged SOM stocks under contrasting grazing conditions and fire regimes across temperature and precipitation gradients, suggesting that grazing and fire influence the factors that control SOM accumulation in complex ways (Piñeiro et al. 2010). Clearly a major control of the magnitude of SOM increases or decreases is associated with the C saturation level of the soil in each particular condition (Stewart et al. 2007). As shown in previous sections, grazing and fire impacts on both below and aboveground primary production by modifying C inputs (Figure 3). Grazing may increase root allocation in some environments and therefore increase SOM stocks (because of higher SOM formation efficiency of roots), particularly in the particulate organic matter fraction (POM) (Piñeiro et al. 2010). Such changes may derive from the effect of disturbance on species and plant functional type composition (Figure 3). Disturbance would also impact on soil respiration directly affecting SOM accumulation (Figure 3).

Environmental footprint of livestock ranching in the RPG

The environmental footprint of agricultural activities is directly linked to its impact on biodiversity and ES supply. Previous sections on the effect of grazing and fire management on vegetation structure and fauna stressed the importance of disturbances on maintaining or even increasing plant and animal biodiversity. Both disturbances play, then, a critical role in determining the supply of ES.

Sala and Paruelo (1997) summarized the potential contribution of grassland areas to

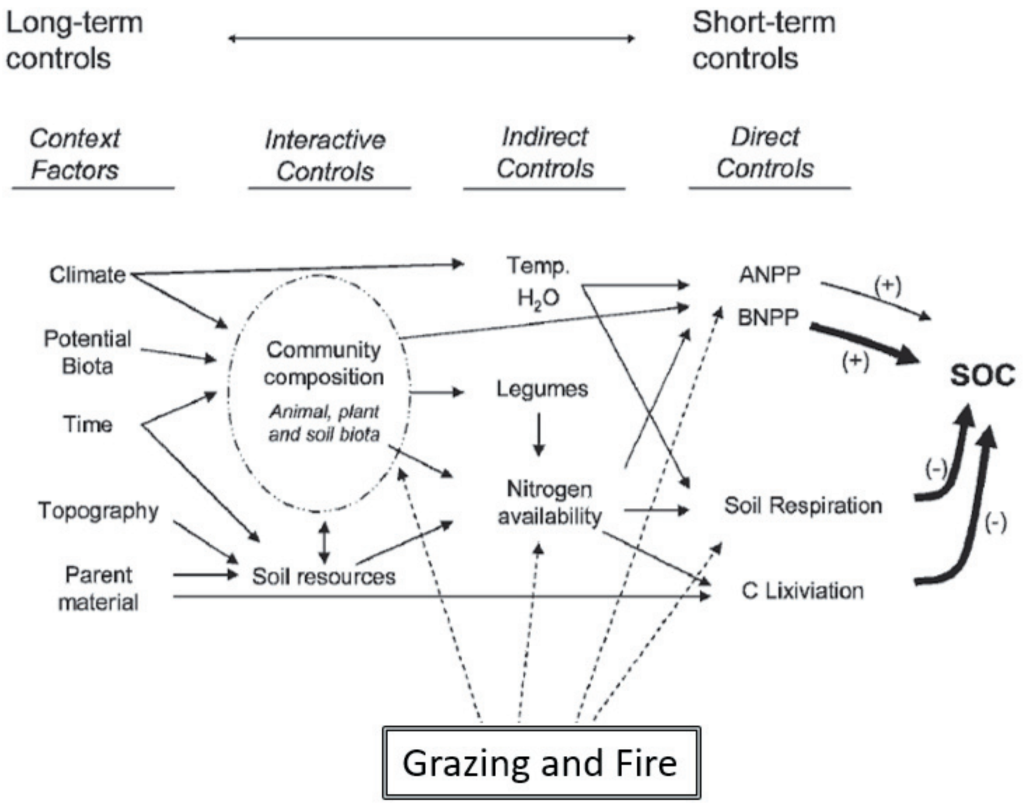

Figure 3. Soil organic carbon (SOC) controls at different temporal scales. Dashed lines show which controls are affected by grazing and fire. ANPP is aboveground net primary production and BNPP is belowground net primary production. Modified from Piñeiro et al. (2010).

Figura 3. Controles del carbono orgánico del suelo (COS) a diferentes escalas temporales. Las líneas discontinuas muestran qué controles se ven afectados por el pastoreo y el fuego. ANPP (PPNA, por sus siglas en español) es la producción primaria neta aérea y BNPP (PPNS, por sus siglas en español) es la producción primaria neta subterránea. Modificado de Piñeiro et al. (2010).

the supply of ES. The referred article focused on services whose value is not reflected in the market (atmospheric gases regulation, genetic library, soil conservation and climate regulation). As in a foundational article on the subject (Costanza et al. 1997), the focus was on monetizing the contribution of rangelands to the supply of these services. The economic valuation of ES has been controversial (i.e., Silvertown [2015]) and it was perceived as 'commoditization' of nature. The development of integrative conceptual frameworks that connect ecosystem structure and functioning with ecosystem services and benefits to the society (the 'cascade model', Haines-Young and Potschin [2010]) helps developing alternatives to quantify the supply of ES and to integrate them into decision making processes (Paruelo and Laterra 2019; Staiano et al. 2021). The contribution of OE is particularly important because it includes both provisioning (meat, wool, water supply) and regulating services (pollination, C sequestration, hydrologic regulation) (Yahdjian et al. 2015). Moreover, Yahdjian et al. (2015) strongly emphasized the importance of considering not only the supply of ES but also the demand. Clearly, the society qualitatively modified the demand of ES in OE. Supporting and regulating ES and the conservation of natural habitats became critical in defining the environmental footprint of systems that focus on provisioning ES such as meat or wool. In fact, documenting the impact of the production systems on regulating ES, its environmental footprint, is crucial to access to some markets (Kehoe et al. 2020).

The previous sections documented the effect of grazing and fire, often associated with ranching activities, on several structural and functional aspects of OE. Such effects, in many cases, determine a higher supply of regulating ES compared to other land uses and even to the absence of grazing (Gallego et al. 2020). Empirical studies all over the RPG documented that grasslands, regardless of the grazing and fire regime, accumulate more soil organic C and emit less N_2O than most of the other land covers in the region (Mazzilli 2015; Della Chiesa et al. 2019). Two metrics provided synoptic estimates of the environmental footprint of agricultural activities over the RPG: the Human Appropriation of Net Primary Production (HANPP) (Baeza and Paruelo 2018) and the Ecosystem Service Supply Index (ESSI) (Paruelo et al. 2016).

Human appropriation of net primary production (HANPP)

HANPP results from the difference between the NPP in the absence of human influence (NPP of potential vegetation: NPP_0) (e.g., the native grasslands) and the NPP of the actual vegetation (e.g., a grassland, a pasture, an annual crop or a tree plantation) remaining after harvest (NPP_{REM}). NPP_{REM} was calculated as the NPP of the current vegetation (NPP_{ACT}) minus the harvested NPP (NPP_H), directly appropriated by humans as agricultural products (grain, wood, meat, etc.) or destroyed during harvest.

$$HANPP = NPP_0 - NPP_{REM} = NPP_0 - (NPP_{ACT} - NPP_H) \qquad \text{(Equation 1)}$$

The complement of HANPP quantifies the energy available for ecosystem processes which, in turn, are responsible for regulating ES supply. HANPP in the RPG ecosystems, considering all land uses, increased from 41.8% to 46.4% from 2001/2002 to 2012/2013 (Baeza and Paruelo 2018). Appropriation surpassed the 70–80% of NPP_0 in agricultural and

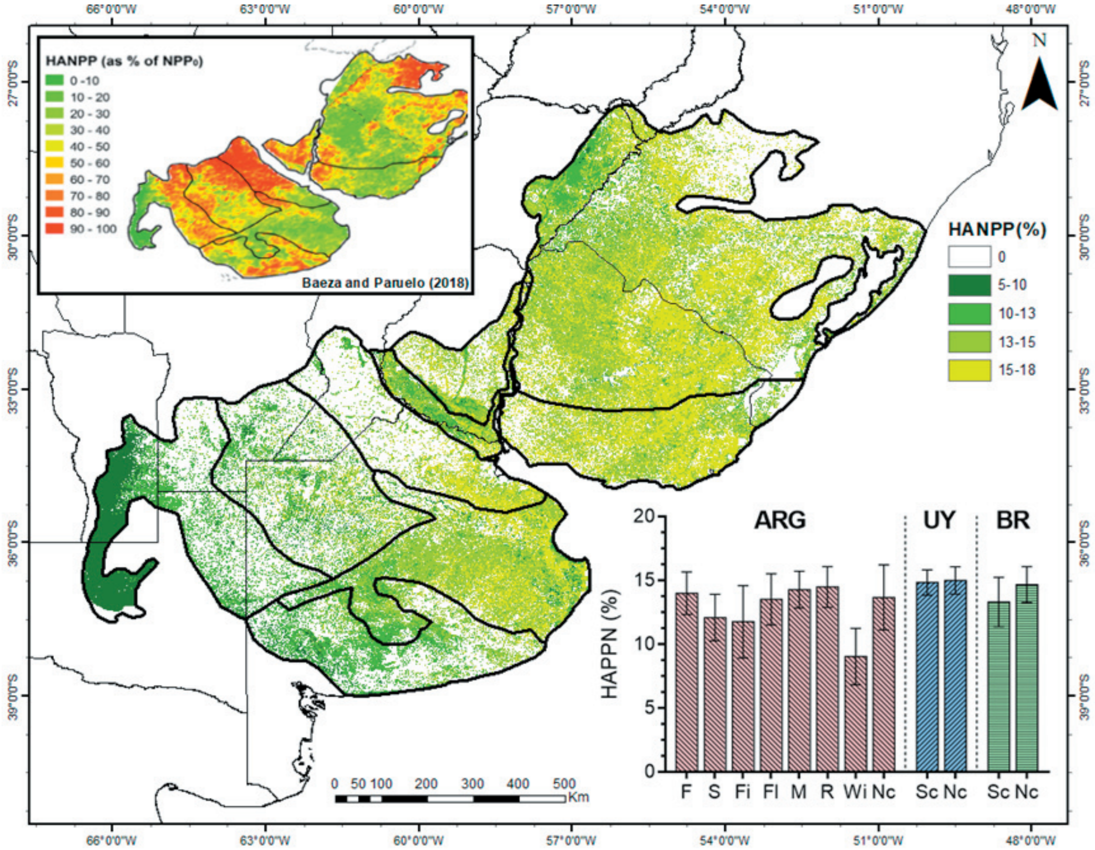

Figure 4. Mean Human Appropriation of Net Primary Production (HANPP) on the ensemble remnant Open Ecosystem (OE) of the Río de la Plata Grasslands (RPG) for the period 2001-2019, calculated according to Baeza and Paruelo (2018). The inserted map in the upper left corner shows the original map of Baeza and Paruelo (2018) including all land covers. The graph in the bottom right corner shows the mean HANPP (%) of OE areas per subregion and country. The lines on the bars indicate the standard deviation. F: Flooding Pampa, S: Southern Pampa, Fi: Flat Inland Pampa, Fl: Fluvial Pampa, M: Mesopotamic Pampa, R: Rolling Pampa, Wi: West Inland Pampa, Nc: Northern Campos, Sc: Southern Campos.

Figura 4. Apropiación Humana de la Productividad Primaria Neta (AHPPN) promedio de los Ecosistemas Abiertos (EA) remanentes del conjunto de los Pastizales del Río de la Plata (PRP) para el período 2001-2019, calculado según Baeza and Paruelo (2018). El mapa insertado en la esquina superior izquierda muestra el mapa original de Baeza y Paruelo (2018) incluyendo todas las coberturas terrestres. El gráfico de la esquina inferior derecha muestra la AHPPN promedio (%) de EA por subregión y país. Las líneas de las barras indican el desvío estándar. F: Pampa Deprimida, S: Pampa Austral, Fi: Pampa Interior Plana, Fl: Pampa Fluvial, M: Pampa Mesopotámica, R: Pampa Ondulada, Wi: Pampa Interior Oeste, Nc: Campos del Norte, Sc: Campos del Sur.

afforested areas. Using the same approach as Baeza and Paruelo (2018) (see Supplementary Material) we calculated the HAPPN for the remnant OE areas of the RPG (Figure 4). On average, the HANPP on the OE of the RPG is less than 11% and it varied from 9% (West Inland Pampa) to 15% (Northern Campos of Uruguay) (Figure 4), values substantially lower than the regional average (42%). These numbers indicate that the energy available for other trophic levels and supporting ecosystem services is substantially higher in OE than in more transformed covers.

The Ecosystem Service Supply Index (ESSI)

Paruelo et al. (2016) presented a synoptic indicator of 'bundles' supporting and regulating ES related to carbon and water dynamics, the Ecosystem Services Supply Index (ESSI). It is based on vegetation indices derived from remote sensing data, which constitute robust estimators of net primary production (NPP) (Monteith 1972; Piñeiro et al. 2006), an integrating variable of ecosystem functioning (McNaughton et al. 1989). The ESSI merges two attributes of the NDVI annual dynamics: the annual average ($NDVI_{MEAN}$, a proxy of total C gains) and the intra-annual coefficient of variation ($NDVI_{CV}$, an indicator of seasonality):

$$ESSI = NDVI_{MEAN} * (1 - NDVI_{CV})$$

Those sites where annual production is higher and more seasonally stable would have a higher ES supply.

The foundation of the ESSI is based on both the conceptual framework of the ES cascade

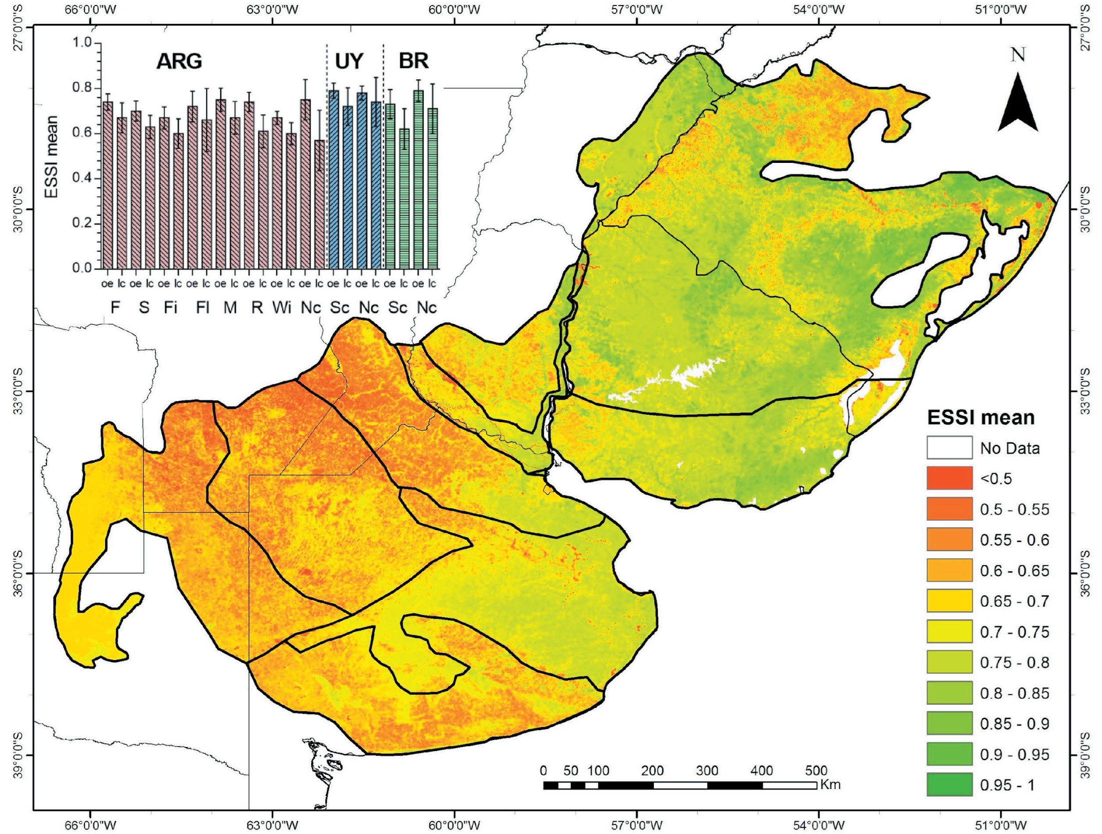

Figure 5. Mean Ecosystem Services (regulation/support) Supply Index (ESSI) on the ensemble remnant Open Ecosystems (OE) of the Río de la Plata Grasslands (RPG) for the period 2001-2019 calculated according to Paruelo et al. (2016). The graph in the upper left corner shows the mean ESSI for Open Ecosystem areas (OE) and other land covers (lc) per subregión and country. The lines on the bars indicate the standard deviation. F: Flooding Pampa, S: Southern Pampa, Fi: Flat Inland Pampa, Fl: Fluvial Pampa, M: Mesopotamic Pampa, R: Rolling Pampa, Wi: West Inland Pampa, Nc: Northern Campos, Sc: Southern Campos.

Figura 5. Índice de Oferta de Servicios Ecosistémicos (IOSE) de regulación y soporte promedio de los Ecosistemas Abiertos (EA) remanentes del conjunto de los Pastizales del Río de la Plata (PRP) para el período 2001-2019, calculado según Paruelo et al. (2016). El gráfico en la esquina superior izquierda muestra el IOSE promedio para áreas de Ecosistemas Abiertos (EA) y otras coberturas terrestres (lc) por subregión y país. Las líneas de las barras indican el desvío estándar. F: Pampa Deprimida, S: Pampa Austral, Fi: Pampa Interior Plana, Fl: Pampa Fluvial, M: Pampa Mesopotámica, R: Pampa Ondulada, Wi: Pampa Interior Oeste, Nc: Campos del Norte, Sc: Campos del Sur.

model and the ES bundles concept (Raudsepp-Hearne et al. 2010). According to this scheme, the ESSI represents an integrative index of ecosystem functioning which gives rise to the cascade. It can describe the variation in different regulating and supporting ES (some of them intermediate and others final ES) that vary together in the same direction (ES bundles). The support for using ESSI as a proxy of ES supply was originally based on its positive relationship with four ES estimated from empirical data or mechanistic models: groundwater recharge and avian richness in Dry Chaco forests and soil organic carbon (SOC) in the RPG (Paruelo et al. 2016). Two additional studies provided additional support to the use of ESSI (Weyland et al. 2019; Staiano et al. 2021). The index has been used in a variety of systems to evaluate spatial and temporal patterns of the environmental footprint of agricultural activities (Verón et al. 2018; Staiano et al. 2021; Gallego et al. 2020; Jullian et al. 2021; Camba Sans et al. 2021).

The ESSI of the natural OE of the RPG was higher than the values of transformed land covers (in average, 15% higher), except for tree plantations (Figure 5). Differences were more important in those subregions where the level of agricultural intensification was higher (i.e., the Rolling Pampa in Argentina, 22%) than in those experiencing lower levels (i.e., the Northern Campos in Uruguay, 5%). The temporal trends of ecosystem supply showed even larger differences. Less than 4% of the grasslands, savannas and shrublands of the RPG showed a significant reduction in ES supply for the period 2001-2019 (Figure 6). For the rest of the region, almost 25% of the area experienced a loss in ES supply over the

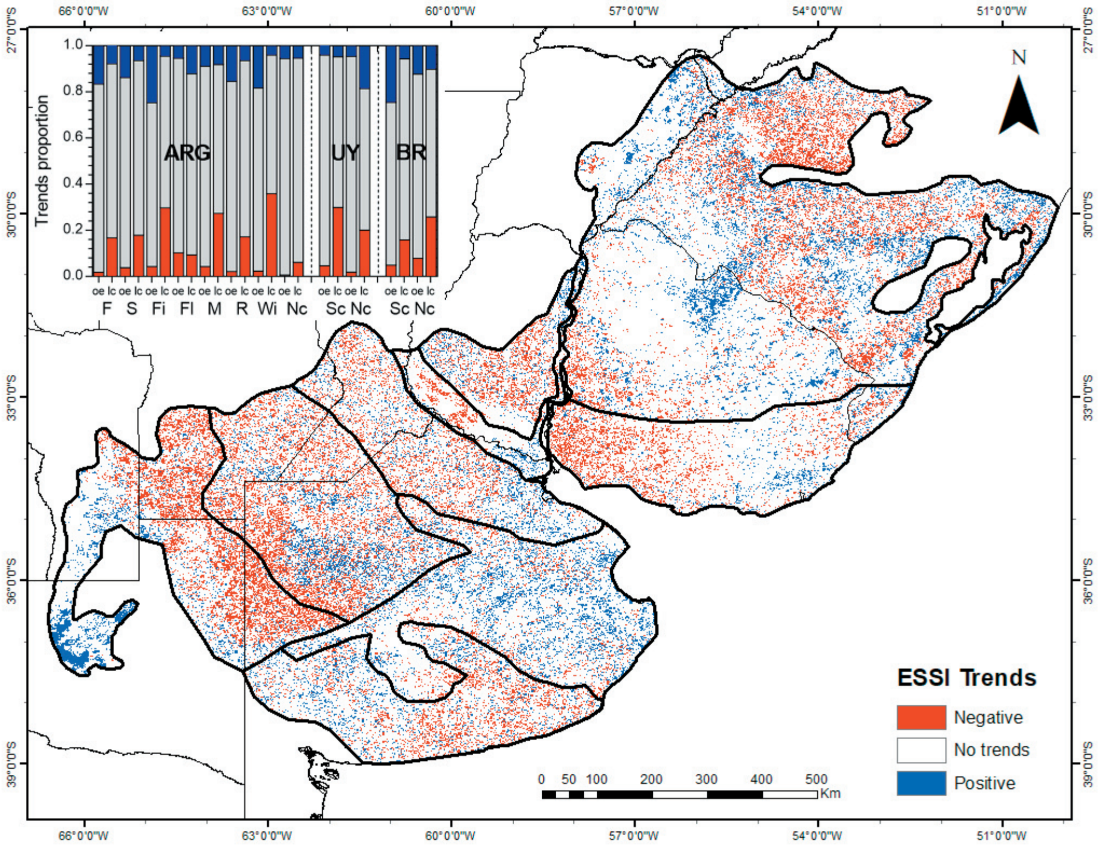

Figure 6. Trends of the Ecosystem Services Supply Index (ESSI) for the period 2001-2019, being positive (blue), negative (red) and no temporal trends (white). The graph in the upper left corner shows the proportion of the area of each subregion with significant both trends positive and negative and without trend, differentiating between Open Ecosystem areas (OE) and other land covers (lc). F: Flooding Pampa, S: Southern Pampa, Fi: Flat Inland Pampa, Fl: Fluvial Pampa, M: Mesopotamic Pampa, R: Rolling Pampa, Wi: West Inland Pampa, Nc: Northern Campos, Sc: Southern Campos.

Figura 6. Tendencias del Índice de Oferta de Servicios de los Ecosistemas (IOSE) para el período 2001-2019, siendo positivas (azul), negativas (rojo) y sin tendencias temporales (blanco). El gráfico de la esquina superior izquierda muestra la proporción del área de cada subregión con tendencias significativas, tanto positivas como negativas, y sin tendencia, diferenciando entre áreas de Ecosistemas Abiertos (EA) y otras coberturas de suelo (lc). F: Pampa Deprimida, S: Pampa Austral, Fi: Pampa Interior Plana, Fl: Pampa Fluvial, M: Pampa Mesopotámica, R: Pampa Ondulada, Wi: Pampa Interior Oeste, Nc: Campos del Norte, Sc: Campos del Sur.

last two decades. As any indicator ESSI must be used in a multidimensional diagnosis. For example, higher ESSI values for tree plantations have to be considered with the level of HANPP (Figure 4) or the proportion of habitat conservation (Figure 1).

Meat equivalent production in Open Ecosystems (OE) of the RPG

Oesterheld et al. (1992) showed that in livestock systems of South America, herbivore biomass increased exponentially with ANPP and that herbivore biomass per unit of ANPP was 6 times higher than in natural ecosystems. Over regional scales, ANPP is the major determinant of meat equivalent (meat+milk+wool) production (ME), a substantial portion of the net secondary production. Compared to natural OE dominated by homeotherms, trophic efficiency (NSP/ANPP) in managed systems is higher due to increases in production efficiency and, mainly, on consumption efficiency (Irisarri et al. 2014). Such increases in efficiency results from several management actions such as animal health care, water supply, breeding, etc. In general, livestock managed systems reach higher NSP by 1) diverting a major proportion of ANPP from the detritus to the grazing chain, 2) converting consumption more efficiently into NSP, and 3) stabilizing herbivore biomass across years.

Combining the data from Irisarri et al. (2014) and Gutiérrez et al. (2020) we generated a model on the relationship between ANPP and PSN for the entire region (Figure A1, Supplementary Material). A particular feature of the fitted model indicates that a unit change in ANPP generates a more than proportional change in ME production. Because of this pattern, the conversion of ANPP dry matter into live weight decreased from more than 100 kg DM per kg of live weight, for sites below 2500 kg DM.ha^{-1}.year^{-1} of ANPP, to 80 to 60 kg of DM per kg of LW or even less than 60 kg of DM per kg of LW for sites located above 4500 kg DM.ha^{-1}.year^{-1} of ANPP (Figure A1, Supplementary Material).

Based on this model and the ensemble map of remnant OE in the RPG (see Figure 1), we estimated the production of ME on OE of the RPG. The average value per hectare was 78 kg.ha^{-1}.year^{-1}, with extreme values of 92.5 and 35.2 kg.ha^{-1}.year^{-1} for the Southern Campos of Uruguay and the West Inland Pampa, respectively. Over the whole region the total volume of ME production on OE was 3488.6x10^{3} t liveweight/year, for the ensemble map of distribution of remnant OE. These figures represent the ME production volume of the region with the lowest environmental footprint, at least based on Soil C dynamics and biodiversity conservation. The estimated values of ME production on the grassy ecosystems of the RPG represents a high proportion of the total production in the region. For the case of Uruguay the potential production of ME with minimum environmental footprint is equivalent to the total slaughtered bovines (1160 *vs.* 1173x10^{3} t liveweight/year for 2019, according to OPyPA [2020]). Assuming a per capita red meat consumption of 6.27 kg/year (data.oecd.org/agroutput/meat-consumption.htm) and a yield of 35%, the remnant OE of the RPG region may cover the current consumption of more than 195x10^{6} people, approximately a 2.5% of the world population. The people from the RPG may invite an 'asado con cuero' to half the world population based on meat with the lowest possible environmental footprint.

The contribution of Open Ecosystems (OE) to local and global sustainability

Grasslands, shrublands and savannas are under threat worldwide and particularly in South America. The proportion of the remaining grassland, shrublands and savannas area under protection is the lowest among the different terrestrial ecosystems (Jones et al. 2018). In the Argentine Pampa, the proportion is lower than 1% (Burkart 2005; Moreno et al. 2008). The grassland area under protection is even lower in Uruguay. Brazil has 1% of the RPG under strict protection and 2% more under sustainable use (Metzger et al. 2019), but legal reserves in private land could protect almost 300 thousand hectares of grassland remnants if the Brazilian legislation on native vegetation were enforced (Overbeck et al. 2015). Agricultural conversion during the first 14 years of XXI century expanded 23% (Baeza and Paruelo 2020), a value similar to the rate observed for subtropical forests (Volante et al. 2016). Moreover, two key components of these systems, grazing and fire, are often demonized, perhaps for its deleterious role in forested ecosystems. The evidence suggests that fire and grazing are critical to maintain the biodiversity at the species and landscape level and to increase the supply of ES. In areas where most of the land is privately owned, well managed ranching is the most affordable alternative to preserve natural habitats and to develop sustainable systems in environmental, social and economic terms. Grazing lands have the highest potential for soil C sequestration (Caride et al. 2012; Li et al. 2018; Baethgen et al. 2021), reduction of NO_2 emissions (Della Chiesa et al. 2019), water regulation (Nosetto et al. 2005) and biodiversity preservation (Altesor et al. 2006; Lezama et al. 2019) among the different land cover that occupied the RPG landscapes. Here, we showed that those areas have a higher supply of regulating and supporting ES than those that were transformed. Moreover, the area of OE experiencing positive trends in regulating ES supply is three times higher than that showing negative trends. The higher supply of regulating ES would be directly linked to the higher availability of energy as indicated by the lower C exports from these ecosystems.

Livestock production, the main economic activity on OE, generates, though, a major concern: enteric methane emissions (Friedlingstein et al. 2019; Clark et al. 2020). This is a highly controversial issue regarding the environmental impacts of cattle and sheep ranching. Methane emissions are, no doubt, a critical problem of livestock industry but the environmental footprint of meat production has to include other dimensions: for example, SOC balance, habitat and biodiversity preservation, regulating and supporting ES supply, and the fact that almost half of those cattle are shepherded by small farmers who live in rural areas.

For Uruguayan livestock systems producing 136 ME kg.ha^{-1}.year^{-1} (in farms including natural grasslands and 50% of sowed pastures), CH_4 emissions, in CO_2 equivalent, was estimated in 421 kg of C ha^{-1}.year^{-1} (1549 kg CO_2eq.ha^{-1}.year^{-1}) (Becoña et al. 2013). Tough it is not possible to claim for a generalized neutral C scenario (Villarino et al. 2020), field data showed that, in the RPG, grazing can increase or slightly reduce (±8%) the amount of C accumulated in the soil compared to not grazed situations for long periods of time (Piñeiro et al. 2009). Simulation studies and long-term experiments on sowed pastures also showed a high potential of C sequestration but a strong dependence of the initial values (Baetghen et al. 2021). Due to C saturation the best-preserved soils may present low or null rates of C accumulation (Cotrufo et al. 2019). However, more degraded soils, showing reduced SOC stocks, may sequester a considerable amount of C if properly managed. The C footprint of OE areas must then consider the ability of management strategies to both preserve and increase SOC stocks.

Terrer et al. (2021) show from a synthesis of CO_2 enrichment experiments from different ecosystems that soil organic carbon (SOC) can increase by approximately 5% in response to a 65% step increase in CO_2 with a strong coupling between driven changes in aboveground plant biomass and SOC. However, the coupling between plant biomass and soils is an inverse relationship opposite to that simulated by many ecosystem models (e.g., Todd-Brown et al. 2014). That is, if it accumulates in plant biomass it does not accumulate in the soil. The results highlight the potential for grassland soils to store carbon as atmospheric CO_2 levels continue to rise. An estimate of this is that C accumulation should increase by about 187 kg.ha^{-1}.year^{-1}, a figure of the same order of magnitude as those from preliminary long-term studies on SOC stocks changes in Uruguay (Bazzoni, personal communication).

The main determinant of the negative environmental impact of livestock production systems is the conversion of natural habitats (Griscom et al. 2020; Cusack et al. 2021). Preserving grasslands, savannas and woodlands would warrant lower GHG emissions and biodiversity preservation. The actual opportunity to accumulate C depends on OE management (Cusack et al. 2021), being grazing management a key factor. Abdala et al. (2018) showed that moist/warm grasslands, such as those in the RPG, have the highest potential of C sequestration under grazing. For the main plant communities of the RPG, the conservation status has a major effect on preserving functional, specific and structural diversity (Altesor et al. 2019). Specific management actions have been crafted to both maximize ME production and C accumulation and biodiversity preservation (Jaurena et al. 2021).

The Mercosur countries faced some serious challenges to add value (from both an ethical and economical perspective) to their agricultural products (see Kehoe et al. 2020). Showing the connection between OE conservation and the environmental footprint of the production is critical. The importance of preserving forest ecosystems is well established and it concentrates important resources. Grassland, shrublands and savannas conservation has not been incorporated into the conservation political agenda. For example, since 2007, Argentina has a national law to regulate deforestation (Aguiar et al. 2018) and a similar one aimed to preserve wetlands is under discussion, while in Brazil, the federal Law on Native Vegetation Protection has not been enforced to protect native grassland vegetation (ecoqua.ecologia.ufrgs.br/arquivos/Agonia_do_Pampa.pdf). Open Ecosystems (OE) conservation requires a myriad of public policies, ranging from restrictions to incentives. The regional scientific system is able to provide policy makers not only the conceptual basis, but a number of building blocks to develop such policies, including: a) management schemes of extensive livestock systems (Jaurena et al. 2020), b) monitoring systems of remnant OE areas (MapBiomas Pampa), c) grassland inventories (Perelman et al. 2001; Batista et al. 2014; Lezama et al. 2019), d) estimates of forage production and net secondary production of livestock systems (Grigera et al. 2007; Irisarri et al. 2014; Gutiérrez et al. 2020), e) indices and protocols for monitoring ES supply, environmental footprint and/or conservation status at the field level (Altesor et al. 2019; Blumetto et al. 2019) and regional level (Paruelo et al. 2016; Baeza and Paruelo 2018; Texeira et al. 2019), and f) schemes of co-innovation to connect the scientific system and the stakeholders (Albicette et al. 2017; Rugia et al. 2021).

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