Potential long-term impacts of livestock introduction on carbon and nitrogen cycling in grasslands of Southern South America

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Abstract

Empirical evidence based on grazing exclusion at the scale of years to decades shows that grazing modifies carbon (C) and nitrogen (N) cycling. However, long-term effects at the scale of centuries are less known, yet highly relevant to understand local and global impacts of grazing. Additionally, most studies have focused on the isolated response of C and N, with little understanding of their interactions. Using CENTURY, a process-based biogeochemical model, we analyzed the impacts of 370 years of livestock grazing (i.e. long term, from early European colonization to present) in 11 sites across the *Río de la Plata* grasslands and compared them with those resulting from two decades of grazing (i.e. mid-term, typical exclosure experiment). In the long term, livestock grazing primarily altered the N cycle through faster N returns to the soil via urine and dung, which were offset by uninterrupted N outputs by volatilization and leaching. As a result, soil organic N decreased by $-880 \, \text{kg ha}^{-1}$ or -19%. Higher N outputs (mainly as NH_3) opened the N cycle, potentially decreasing N_2O and NO_x emissions and increasing N depositions over the region. These greater outputs of N constrained C accumulation in soils, reducing soil organic C by $-21\,200 \, \text{kg ha}^{-1}$ (-22%, a reduction of $-1.5 \, \text{Pg}$ of C for the whole region) and net primary production by $-2192 \, \text{kg ha}^{-1} \, \text{yr}^{-1}$ (-24%). Mid-term simulations showed that the effects of livestock introduction in a decadal time scale were substantially different both in magnitude and direction from long-term responses. Long-term results were not substantially affected when atmospheric CO_2 content, species composition and fire regime were changed within plausible ranges, but highlighted fire-grazing interactions as a major constraint of long-term C and N dynamics in these grasslands.

Keywords: ammonium, atmospheric chemistry, fire, grazing, plant production, soil organic matter, species composition, temporal scales

Received 3 November 2005; and accepted 23 December 2005

Introduction

Grasslands are one of the most modified biomes on Earth, as a large portion of them has been replaced by crop fields or subject to livestock grazing. Grasslands occupy nearly 50% of the earth surface (Menke & Bradford, 1992) and may currently support grazing pressures 10 times higher than those experienced in their wild stage before livestock introduction (Oesterheld *et al.*, 1992). Structurally, grazing alters the diversity of different taxa (Milchunas & Lauenroth, 1993;

Bradgett & Wardle, 2003) and the size of carbon (C) and nutrient pools (Milchunas *et al.*, 1988; Milchunas & Lauenroth, 1989). Functionally, grazing alters the exchange of matter and energy (i.e. productivity, nutrient losses and evapotranspiration) (Milchunas & Lauenroth, 1993; Oesterheld *et al.*, 1999) and the internal cycling of nutrients (i.e. mineralization, nitrification and uptake) (McNaughton *et al.*, 1997; Le Roux *et al.*, 2003).

Ecosystem responses to grazing have different time scales, from minutes to centuries (Brown & Allen, 1989). Short-term effects (within a growing season) are mostly associated to physiological plant responses and have been widely studied (Ferraro & Oesterheld, 2002). Mid-

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term impacts, from years to decades, are usually associated to ecological responses (i.e. changes in species composition and biogeochemical cycles) and have been often evaluated by comparing grazed areas and adjacent exclosures (Milchunas & Lauenroth, 1993; Chaneton & Lavado, 1996; Altesor *et al.*, 1998; Altesor *et al.*, in press). Long-term effects, from centuries to millennia, may involve profound changes in soil properties and regional biogeochemical cycles. These changes, can only be explored by paleoecological observations or modeling, and as a result are less understood and often erroneously inferred from mid-term information, because short-, mid- and long-term responses to grazing are not necessarily similar (Hyvönen *et al.*, 1998).

Soil organic carbon (SOC) and net primary production (NPP), key attributes of grassland C cycle and energy flux, are profoundly altered by mid- and long-term grazing. NPP is a major determinant of SOC and, conversely, SOC may determine NPP both in the mid- and in the long-term through its link with nutrient pools (Jenkinson *et al.*, 1999). The recalcitrant forms of C compounds in grasslands soils are an effective way for C sequestration (Lal, 2004). Resource allocation between above- and belowground organs, and the vertical distribution of belowground biomass are the main determinants of SOC distribution in the profile (Jobbagy & Jackson, 2000). Mid-term grazing alters both resource allocation and root distribution in depth (Doll & Deregibus, 1986; McNaughton *et al.*, 1998; Pucheta *et al.*, 2004) and may either increase or decrease SOC (Milchunas & Lauenroth, 1993; Lavado *et al.*, 1995; Chaneton & Lavado, 1996; Bertol *et al.*, 1998; Conant & Paustian, 2002). The effects of grazing on NPP or aboveground primary production (ANPP) are, in general, negative (Milchunas & Lauenroth, 1993; Oesterheld *et al.*, 1999), although several studies show positive effects (Frank & McNaughton, 1993; Altesor *et al.*, 2005).

Grazing alters Nitrogen (N) cycling in ecosystems and such changes may constrain C accumulation in soils. N emissions and leaching by livestock, principally from urine patches, have been broadly documented (Whitehead & Raistrick, 1993; Frank & Zhang, 1997), but their long-term consequences on ecosystem C and N pools have been rarely analyzed. N emission from dung and urine are mainly in the form of NH_3 (mostly from urine) and only a little portion of N_2O and NO_x is emitted (Zheng *et al.*, 2002). Thus, grazing may alter N fluxes to the atmosphere and change the amount of the chemical forms released. Higher N losses may impose an additional constrain to C accumulation in soils because the C/N ratio of SOM in grasslands does not change rapidly (especially in the more recalcitrant and stable pools), thus the lack of C or N could limit organic matter formation increasing losses of the other elements (Neff *et al.*, 2002).

Herbivore impacts on ecosystems can be modified by other co-occurring factors. For example, fire regime, anthropogenic N depositions, climate change, atmospheric CO_2 concentration and species changes affect ecosystem responses to grazing (Oesterheld *et al.*, 1999; Allard *et al.*, 2003; Throop *et al.*, 2004). Some of these factors are associated to grazing (i.e. species change and fire regime), whereas others are independent (i.e. atmospheric CO_2 concentration, temperature rise, anthropogenic N depositions) and result from human activities. Assessing the influence of these potentially interacting factors on long-term grazing dynamics is a critical point to understand herbivore impacts on ecosystems.

The objective of this article was to evaluate, using CENTURY, a process-based biogeochemical model, the impact of grazing by domestic herbivores since their introduction by Europeans to the present in 11 sites distributed across the main environmental gradient of the *Río de la Plata* grasslands (RPG) in southern South America. Our specific objectives were to: (1) parameterize and evaluate the model for the region; (2) analyze the changes occurred on C and N cycles after the introduction of domestic herbivores; (3) explore the mechanisms by which grazing changed ecosystem C and N cycling; (4) compare mid-term vs. long-term effects, and finally (5) perform a sensitivity analysis including changes in species composition, fire regime and atmospheric CO_2 concentration.

Materials and methods

Site description and history

The RPG occupy over 70 million ha in South America, including Uruguay, central-east Argentina and southern Brazil (Fig. 1). Livestock production is one of the main economical activities and has important social and cultural implications (Soriano, 1992). Mean annual precipitation ranges between 400 mm in the SW and 1600 mm in the NE, and mean annual temperature varies from 10 °C to 20 °C (Soriano, 1992). Rangelands cover more than half of the region and grain crops replaced more than one-third of the original grasslands (Hall *et al.*, 1992). A small fraction of the RPG have been afforested with *Eucalyptus* and *Pinus* species (INDEC, 1988; MGAP, 1999). For the last 10 000 years, soils developed under prairie vegetation (Hall *et al.*, 1992; Soriano, 1992). Trees were almost absent in the Pampas subregion and were restricted to riparian areas and some isolated rocky soils in the Campos subregion (Fig. 1) (Soriano, 1992). The first European settlers introduced domestic herbivores (cattle, horses and
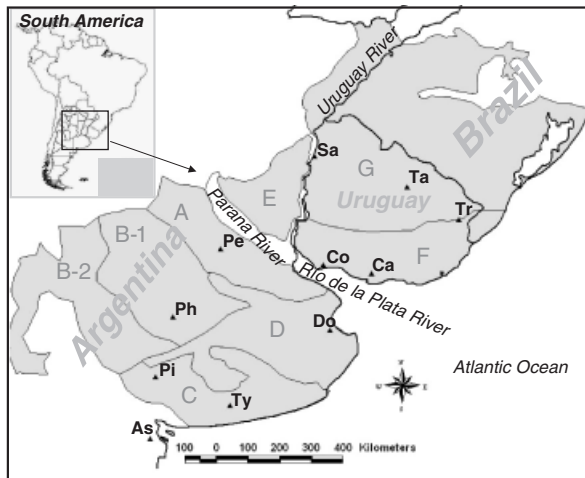
Fig. 1 Map of the *Río de la Plata* grasslands and their subregions, showing our study sites: rolling pampa (a); inland pampa (b) with two divisions, 1 – flat pampa and 2 – west pampa; southern pampa (c); flooding pampa (d); mesopotamic pampa (e); southern campos (f) and north campos (g) (Soriano, 1992).

sheep) in the mid-1500s, but their density became significant by 1600 (Soriano, 1992). Livestock density rapidly increased and became stable by 1900, once all land was fenced, at high stocking rates (currently ranging 178–302 kg ha^{-1}), consuming from 30% to 60% of annual ANPP (Oesterheld *et al.*, 1998).

Century description and site-specific data

We used the process-based biogeochemical model CEN-TURY (Parton *et al.*, 1987; CENTURY 5.3 version, www.nrel.colostate.edu/projects/century5/) to perform our analysis for eleven sites across the RPG (Fig. 1). The model operates for a variety of land covers (grasslands, crops, forests and savannas) and simulates C, N, water, phosphorus and sulfur dynamics (Parton *et al.*, 1993; Parton & Rasmussen, 1994). SOM is divided into three different pools: active, slow and passive (recalcitrant organic matter), with turnover times of 1–5, 20–40 and 100–1000 years, respectively. Surface microbial activity is simulated and litter is divided into belowground and surface pools, as well as into structural and metabolic components (Parton *et al.*, 1987). Soil fluxes are controlled by environmental variables (temperature, water and texture) and by lignin/N and C/N ratios. Above- and belowground plant production is controlled by water, nutrient and shading factors. CENTURY may simulate different episodic events such as fire, fertilizations, grazing, plowing or irrigation. In our work we did not simulate phosphorus or sulfur limitations. Data needed to run the model were ob-

tained from local agencies and published literature (see Supplementary Material 1 for details).

Model setup and simulation experiments

Model parameterization and evaluation. For model parameterization, we used published and unpublished local data, leaving default values if no information was available (see Supplementary Material 2 for details and references). We evaluated CENTURY's performance by comparing simulation outputs, after parameterization, against measured SOC and ANPP data, not used in the parameterization process (Table 1). As local and regional experiments suggest that several years of cultivation decrease soil C by 20–30% (Burke *et al.*, 1989; Andriulo *et al.*, 1999; Fabrizzi *et al.*, 2003), SOC data for sites with agricultural history were corrected by increasing current values by 25% (Table 1). ANPP data were available for only seven sites, generally including several years of measurements (Table 1). Because of the scarce ANPP data available, we also compared CENTURY ANPP with results of some empirical models that relate grassland ANPP to precipitation (Sala *et al.*, 1988; McNaughton *et al.*, 1993). Comparisons were made by regressing observed vs. predicted values, and testing slope and intercept deviation from the 1 : 1 relationship (H$_0$: slope = 1, intercept = 0). Total errors between predicted and observed values were separated into different sources calculating Theil's partial inequality coefficients (*U*) (Smith & Rose, 1995; Paruelo *et al.*, 1998).

General patterns of the long-term effects of domestic herbivores on ecosystem structure and functioning. We simulated 8000 years of grazing by native herbivores followed by 370 years of grazing by domestic herbivores, a simulation we will hereafter call 'baseline simulation'. The first 8000 years served to stabilize SOM pools at each site and provided a reference to contrast with the following 370 years. This simulation had the following assumptions (see Supplementary Material 2 for details):

(i) stable vegetation structure and species composition during the simulation period;
(ii) native herbivore grazing during soil stabilization and domestic herbivore grazing at increasing stocking rates from 1600 through 1970 with logistic growth;
(iii) no direct short-term effect of grazing on ANPP or root/shoot partitioning (grazing affected these

Table 1 Sites descriptions

Code	Ta Tacuarembo	Tr Treinta y tres	Sa Salto	Co Colonia	Ca Canelones	Pe Pergamino	Ph Pehuajo	Do Dolores	Ty Tres Arroyos	Pi Pigüé	As H. Ascasubi
Weather station name											
Lat	−32.11	−33.08	−31.25	−34.37	−34.62	−33.91	−35.85	−36.21	−38.38	−37.6	−39.33
Long	−55.29	−53.8	−57.87	−57.66	−56.3	−60.35	−61.9	−57.44	−60.29	−62.4	−62.55
MAT* (°C)	17.3	16.8	18.5	16.7	16.5	16.3	15.8	15.2	14.5	13.8	15.1
MAP* (mm)	1403	1323	1268	1115	1087	965	945	915	809	793	464
MAPadj.† (mm)	959	1323	760	775	902	917	945	915	650	793	464
RAD* (MJ m⁻² yr⁻¹)	7264	6917	7537	6625	7318	6223	5548	6369	5293	5366	6698
ANPP‡ (g m⁻² yr⁻¹)	400		389	422	602	840		399			240
SOC§ (g m⁻²)	3408	5908	11040	3961	6353	4284	6826	4142	5980	4978	1373
SOC¶ Est. (g m⁻²)	3408	7877	11040	5281	8471	8000	9101	4142	7973	6637	1831
%C₄/%C₃‖	100/0	75/25	50/50	75/25	75/25	50/50	50/50	75/25	75/25	75/25	0/100
Dominant soil type**	Typic Hapludalfs	Typic Argialbolls	Lithic Hapludoll	Typic Hapludoll	Typic Argiudolls	Typic Argiudolls	Thapto argic Hapludolls	Aquic Argiudolls	Shallow Typic Argiudolls	Shallow Typic Argiudolls	Typic Natrargides
Current land use††	Rangelands	Agriculture (rice)	Rangelands/ Agriculture	Rangelands/ Agriculture	Dairy	Agriculture	Agriculture/ Rangelands	Rangelands	Agriculture (winter crops)	Agriculture (winter crops)	Agriculture/ Rangelands

*Mean annual temperature, mean annual precipitation, and mean annual solar radiation from INIA in Uruguay (www.inia.org.uy) and from INTA (www.inta.gov.ar) in Argentina.

†Mean annual precipitation minus runoff and deep discharge, estimated as the balance between daily precipitations and soil reservoirs minus potential evapotranspiration.

‡Above ground net primary production reported by Olmos (1994) for Ta; Berreta (1998) for Sa; Formoso (1994) for Co; Altesor *et al.* (2005) for Ca; Oesterheld and León (1987) for Pg, Sala *et al.* (1981) and Semmartin and Oesterheld (2001) for Do; Distel and Fernandez (1986) for As.

§Soil organic carbon contents as surveyed by MGAP (1979), INTA-SAGYP (1990), by year 1970.

¶Estimated soil organic carbon contents before crops introduction (25% reduction by cropping). See text for details.

‖Species Composition in percentage of C₄ and C₃ species, estimated from Paruelo *et al.* (1998) and Perelman *et al.* (2001).

**Dominant soil types as reported by MGAP (1979) and INTA-SAGYP (1990).

††Current land uses as reported by INDEC (1988) and MGAP (1994).

variables via other mechanisms as discussed in Supplementary Material 2);

(iv) constant N deposition through time, but variable among sites in direct relationship with annual precipitation;

(v) N returns in urine and dung set to 70% of consumed N;

(vi) C respired by livestock estimated as the inverse of the digestibility of consumed biomass, which varied according to the C_4/C_3 ratio of each site (see Supplementary Material 2 for details);

(vii) constant atmospheric CO_2 concentration ($\sim$300 ppm);

(viii) no fire events either before or after herbivore introduction;

(ix) constant climate (present conditions based on records of approximately the last 60 years).

We performed several analyses from this baseline simulation. We related N and C pools and fluxes, and also estimated N openness, which reflects the importance of N inputs to ecosystem in the N cycle, by two approaches: (a) dividing the amount of N inputs (or outputs) by the amount stored in the ecosystem pools (Austin & Vitousek, 1998), and (b) dividing the N inputs by the N flow. The last approach avoids considering the large passive N pools, but requires selecting a variable that represents N flow. Gross mineralization + N excretion in urine were considered a good indicator of ecosystem N flow, because they comprise all N that is available for plant and microbial growth. We also related SOC and NPP changes after domestic herbivore introduction with mean temperature, solar radiation, precipitation, soil texture, SOC contents, ANPP and % of consumption across sites.

Grazing effects mechanisms. We performed a factorial simulation experiment to explore the mechanisms by which grazing affected ecosystem functioning and structure. We modified the amount of C respired by livestock and the rate of N return in urine and faeces to simulate a complete C or N return to the soil after herbivore consumption. We evaluated the relative effect of suppressing C, N and C&N outputs associated to livestock upon the whole ecosystem C and N cycles. The treatments included were the conditions of the baseline simulation and the turn off of herbivore output fluxes of C (C-off), N (N-off) and C&N (CN-off). Although, these simulations correspond to essentially impossible situations in the real world, they are valuable tools to explore the mechanism of grazing effects observed in the baseline simulation.
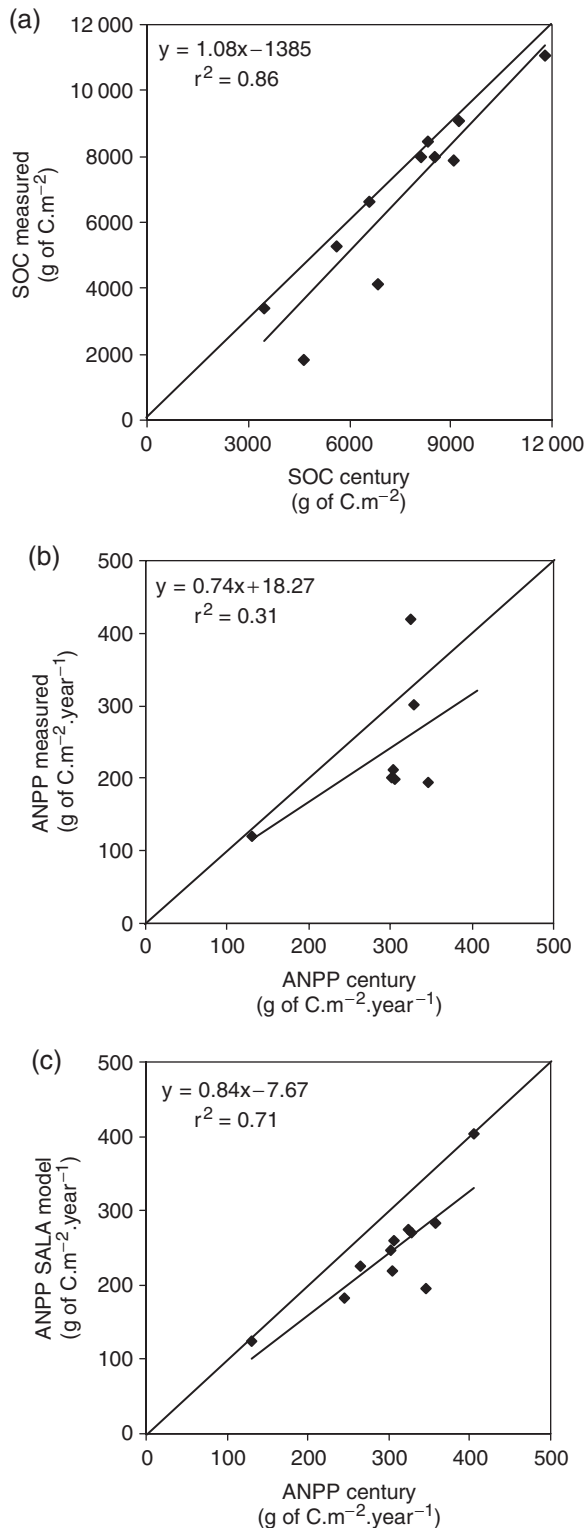
Mid-term vs. long-term grazing effects. We performed a set of simulations focusing on mid-term effects of grazing (20 years). We generated steady-state conditions under native herbivore grazing and then simulated the introduction of livestock at present stocking rates. These simulations reflect the effects of high stocking rates on C and N cycles at the time scale most often analyzed by empirical studies that compare contrasting grazing regimes, such as grazed vs. ungrazed.

Sensitivity analyses. Sensitivity analyses were carried out to evaluate some of the general assumptions used in the baseline simulation (structure and species composition, fire regime and atmospheric CO_2 concentration). Based on the literature (see Supplementary Material 3), we performed three new sets of simulations and compared their results with the baseline simulation. First, we increased the proportion of C_3 species by 25% at each site during soil stabilization (except at H. Ascasubi site that already had 100% of C_3 species), and then shifted to current species composition (see Supplementary Material 3 for details). Second, we assumed that the RPG evolved under an intense fire regime during the soil stabilization stage (Pillar & Quadros, 1997, see Supplementary Material 3 for details), and then we established three possible fire scenarios immediately after herbivore introduction. In the first scenario (fire 1), fire continued at high frequencies (every 8 years) and intensities (see Supplementary Material 3 for fire intensity parameters), in the second scenario (fire 2), fire intensity gradually decreased while frequency was maintained constant, and in the third scenario (fire 3), fires were suppressed. Third, we simulated a gradual increase of CO_2 from 280 ppm in 1800 to 370 ppm in 2000 (see Supplementary Material 3).

Results

Model parameterization and evaluation

The model acceptably reproduced the regional patterns of SOC (Fig. 2a), but yielded a poorer representation of aboveground net primary production (ANPP) (Fig. 2c). The regression between measured and estimated values of SOC had a high r^2, and its slope and intercept did not differed from 1 and 0, respectively (Table 2). However, Theil's coefficients indicated that 40% of the unexplained variance was due to deviations in the intercept (see U_{bias} in Table 2), suggesting that CENTURY slightly overestimated SOC. For ANPP, the lack of field data restricted the comparison between modeled vs. observed values to only seven sites. CENTURY overestimated ANPP values for most of the sites. The scatter plot of predicted vs. observed values showed a low

(a)

$y = 1.08x - 1385$
$r^2 = 0.86$

SOC measured (g of C.m^{-2})

SOC century (g of C.m^{-2})

(b)

$y = 0.74x + 18.27$
$r^2 = 0.31$

ANPP measured (g of C.m^{-2}.year^{-1})

ANPP century (g of C.m^{-2}.year^{-1})

(c)

$y = 0.84x - 7.67$
$r^2 = 0.71$

ANPP SALA model (g of C.m^{-2}.year^{-1})

ANPP century (g of C.m^{-2}.year^{-1})

Fig. 2 CENTURY outputs vs. measured or independently estimated values of soil organic carbon (SOC) (a), and aboveground net primary production (ANPP) (c, d). SOC values are for the first 20 cm of depth.

Table 2 Match between CENTURY-predicted values and independent reference estimates

	SOC observed	ANPP observed	ANPP Sala
P values			
H_o: $a = 0$	0.259	0.887	0.892
H_o: $b = 1$	0.592	0.592	0.377
Theils's partial inequality coefficients			
U_{bias}	0.37	0.38	0.69
U_{slope}	0.02	0.04	0.03
U_{error}	0.61	0.58	0.28

P values for slope and intercept drift from the 1 : 1 relationship ($a = 0$, $b = 1$) are indicated. Partition of error into Theils's partial inequality coefficients (U) are reported for each test. Soil organic carbon (SOC) observed refers to model predictions vs. independent measures of SOC, aboveground net primary production (ANPP) observed refers to model predictions vs. independent measures of ANPP, ANPP Sala refers to model predictions vs. ANPP predicted by Sala *et al.* (1988) model based on mean annual precipitation.

variation in CENTURY estimates, with most of the estimates close to 350 g C m^{-2} yr^{-1} (Fig. 2c). CENTURY estimates agreed better with estimates derived from empirical models and local precipitation and soil data (for Sala *et al.*, 1988, see Fig. 2d; for McNaughton *et al.*, 1993, $n = 11$, $r^2 = 0.75$, $P < 0.01$), than with reported field ANPP values. However, CENTURY also overestimated ANPP compared with these models and almost 70% of the unexplained variance was due to biases between models (see Fig. 2d and Table 2 for Sala's empirical model).

General patterns of the long-term effects of domestic herbivores on ecosystem structure and functioning. After 370 years of grazing, domestic herbivores reduced the size of C pools and NPP at all sites. The largest reductions took place in the slow SOC pool (Fig. 3a). Relative reductions of total organic C ranged from 15% to 30% among sites. Absolute reductions varied between 15 and 40 t C ha^{-1}. NPP (C input) decreased after 370 years of grazing, but ecosystem respiration (C output) decreased more. SOM and litter respiration (C outputs) decreased, and herbivore respiration increases were not enough to compensate this decline (Fig. 3b). Consequently, both C inputs and outputs decreased after grazing and were, by year 1970, almost at steady state as before livestock introduction. However, much less C (24.6%) and energy was flowing through the ecosystem.

Livestock grazing also reduced all N pools. Like with C, the largest reductions occurred in the slow SOM pool (Fig. 4a). Relative reductions of total
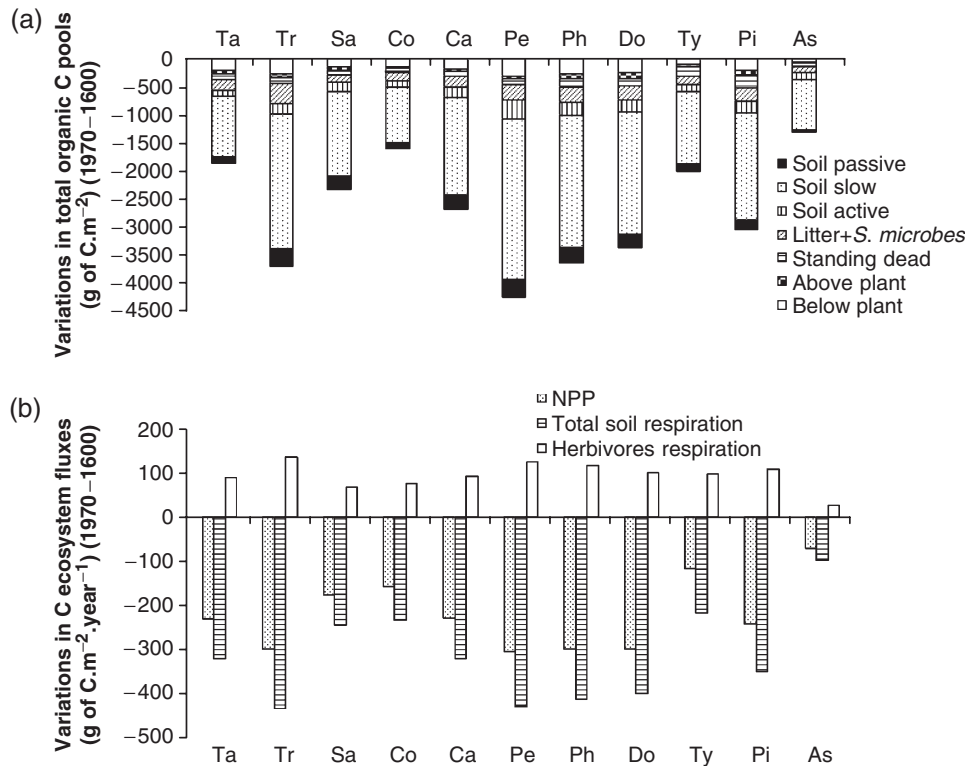
Fig. 3 Variations in ecosystem carbon (C) pools (a) and fluxes (b) after 370 years of domestic herbivores grazing for each site analyzed (see Table 1 for sites descriptions). Differences are computed between year 1970 and 1600. Panel (a) shows C variations for each ecosystem pool. Panel (b) shows variations in C inputs (net primary production) and outputs (respiration). Total soil respiration includes all soil C respired from decomposing organic matter and surface litter.

organic N in the ecosystem were similar among sites and ranged from 12% to 28%. Absolute reductions were important, with a maximum of 1.8 t N ha^{-1} at Pergamino (25% of total N contents) and occurred mainly in the soil, as in the case of C. Both proportion and magnitude of grazing-induced soil organic nitrogen (SON) reductions were correlated with SOC reductions ($r > 0.93$, $n = 11$, $P < 0.01$).

Reductions in SON were associated to changes in total N outputs and shifts in the source of N outputs. After 370 years of domestic grazing, N outputs were still greater than inputs (1.1 vs. 0.72 g N m^{-2} yr^{-1}, respectively), suggesting that the N cycle did not reach a steady state (Fig. 4b). The sources of N outputs changed drastically between 1600 and 1970. The contribution of herbivore-derived outputs increased from 0.041 g m^{-2} yr^{-1} (6% of total outputs) to 0.71 g m^{-2} yr^{-1} (63% of total outputs), while outputs from soil and vegetation were reduced from 0.67 g m^{-2} yr^{-1} (94% of total outputs) to 0.38 g m^{-2} yr^{-1} (only 37% of total outputs) (in average for all sites, see variations in output fluxes for each site in Fig. 4b).

Herbivore consumption, excretion, respiration and N output fluxes increased immediately after livestock

introduction and remained at high values thereafter, increasing the openness of the N cycle (Fig. 5). A greater portion of NPP was respired by herbivores after livestock introduction (increasing from 0.8% to 16%), reducing C availability to soil biota and then decreasing soil respiration by 35%. This 'bypass' could have promoted the reduction of soil C pools, but, as shown below, N dynamics was the main driver of SOC reductions. N excretion from herbivores increased, but plant N detritus flux to the soil and gross N mineralization decreased in higher magnitudes (Fig. 5). Consequently, herbivores slowed down N circulation and N uptake by plants at all sites. Although N recycling (in terms of gN m^{-2} yr^{-1} that are reused) was reduced after grazing, N turnover of the different soil pools before and after livestock introduction were similar (active pool = 1.77 and 1.76 years, slow pool = 27.6 and 27.9 years and passive pool = 1235 and 1226 years, mean for all sites). Thus, the reductions in N recycling were associated with declines of the SON pools rather than with a lower rate of decomposition per unit of SON. The reduction of N recycling by herbivores turned the ecosystem more dependent on external N sources. As Odum (1969)
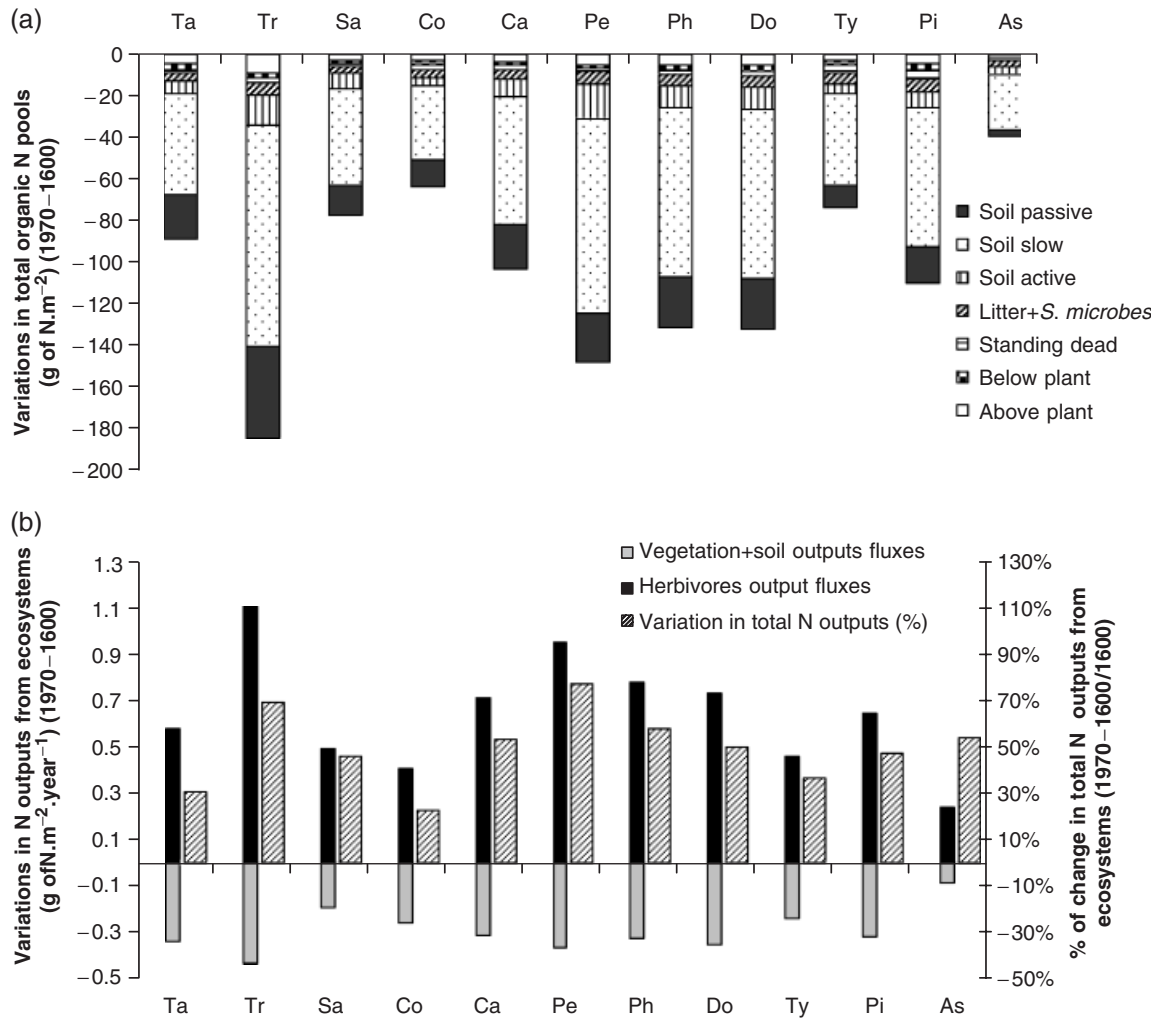
(a)

(b)

Fig. 4 Variations in ecosystem nitrogen (N) pools (a) and fluxes (b) after 370 years of domestic herbivores grazing for each site analyzed (see Table 1 for sites descriptions). Differences ere computed between year 1970 and 1600. Panel (a) shows N variations for each ecosystem pool. Panel (b) shows variations in N outputs from ecosystems. N inputs to ecosystems are considered constant. Vegetation + soil outputs includes all N releases from soil during denitrification and nitrification, N leaching and N losses during vegetation senescence. Herbivores N outputs include all losses from urine and dung patches.

hypothesized, disturbance (in our case domestic herbivores introduction) increases the openness of biogeochemical cycles, particularly for N. Grazing increased N openness measured as the N input/N storage ratio from 0.14% to 0.18%, whereas based on the N input/N flux ratio, it increased N openness from 1.7% to 2.7% (gross N mineralization + N excretion in urine varied from 41.2 to $26.6 \, \text{g m}^{-2} \, \text{yr}^{-1}$). Both ratios suggest that atmospheric N deposition became gradually and increasingly important in the N budget of grazed systems.

Livestock introduction increased the C/N ratios of all ecosystem pools and changed the proportion of the active, slow and passive SOM fractions, suggesting that N-limited organic matter accumulation more than C

(Table 3). The relative contribution of the slow fraction to total SOC decreased from 54% to 46%, whereas the contribution of the passive fraction increased from 39% to 47%. It is important to highlight that the behavior of C/N ratios and SOC fractions produced a counterintuitive result: whereas the C/N ratio of all ecosystem pools increased after grazing, the C/N ratio of the total soil and ecosystem decreased (Table 3). This paradoxical result is due to the variation in the proportion of each fraction and its mathematical causes and importance have been already highlighted (Piñeiro *et al.*, in press).

Regionally, the reductions in SOC and NPP associated to livestock introduction were marginally correlated ($r = 0.49$ $P = 0.12$, $N = 11$), and their
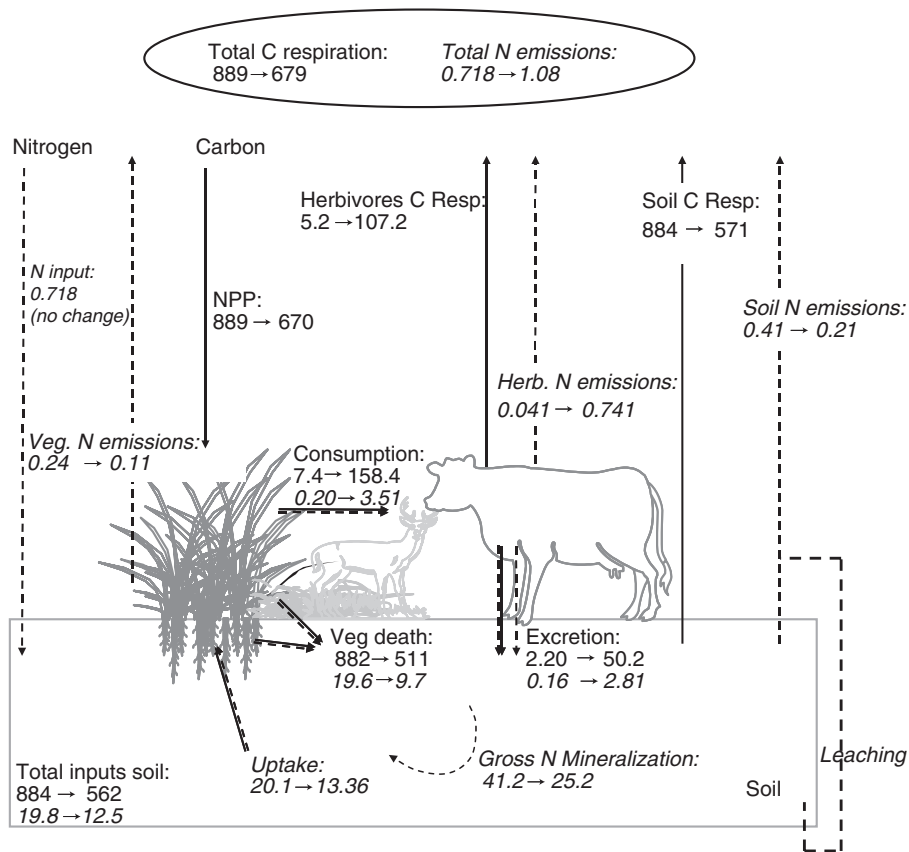
Fig. 5 Ecosystem carbon (C) and nitrogen (N) fluxes before and after 370 years of domestic grazing ($g\,m^{-2}\,yr^{-1}$), average for all study sites. Values in regular font are for C and values in italics are for N. Values indicate flux magnitude before (left side of the arrow) and after livestock introduction (right side of the arrow). Pool sizes are shown in Table 2.

Table 3 C and N content ($g\,m^{-2}$), and C/N ratios in different ecosystem pools before (year 1600) and after domestic herbivore introduction (year 1970)

Variable	Carbon		Nitrogen		C/N		
	1600	1970	1600	1970	1600	1970	Difference
Above plant	126	70	4	2	33.2	38.4	5.1
Below plant	1003	802	15	11	65.0	72.2	7.2
Total plant live	1129	872	19	13	58.7	67.4	8.7
Standing dead	189	74	3	1	56.3	66.0	9.8
Litter and surface microbes	485	277	10	5	50.4	55.5	5.1
Total nonsoil	1804	1223	32	19	56.0	64.2	8.2
Soil active	701	516	25	17	28.2	31.0	2.8
Soil slow	5429	3697	168	107	32.3	34.6	2.2
Soil passive	3951	3754	273	254	14.5	14.8	0.3
Total soil	10 082	7967	465	377	21.7	21.1	−0.5
Total organic	11 886	9190	498	396	23.9	23.2	−0.7

Values are averages for all sites.

variation among sites was explained by different factors. Soils with higher silt content and rainfall had high SOC reductions, whereas soils with high sand content had the lowest ones (Table 4). NPP changes were only associated with NPP levels before grazing (more negative changes in sites with higher NPP) (Table 4).

Grazing effects mechanisms. Simulations suppressing either herbivore respiration (C-off), N outputs (N-off) or both (CN-off) showed, that in the model, the

Table 4 Association of site attributes to soil organic carbon (SOC) and net primary production (NPP) changes following grazing introduction

Variable	SOC changes	Variable	NPP changes
Silt %	−0.76*	NPP 1600	−0.85*
MAP adj.*	−0.60*	NPP 1970	−0.64*
Sand %	+ 0.54*	SOC 1600	−0.31 ns
SOC 1600[†]	−0.37 ns	MAT	−0.28 ns
MAT*	−0.30 ns	Silt %	−0.25 ns
NPP 1600[†]	−0.29 ns	Sand %	+ 0.23 ns

The correlation coefficient (r) and its significance are shown for the 6 attributes with higher r.
*See Table 1 for definition.
[†]NPP (or SOC) 1600 (or 1970), represent the amount simulated by the model in that year.

reduction of both C and N pools after 370 years of grazing were driven by the higher N outputs promoted by livestock. When N output fluxes from herbivores (volatilization and leaching from urine and dung patches) were turned off in the model (N-off scenario), N pools increased after 370 years of grazing (Table 5a), in contrast with the baseline simulation. Total N increase was 17.3 g N m^{-2}, which represented an increase of 3.3% (mean for all sites). The largest N increases occurred in the soil (4.4%; Table 5a). Total organic C stocks did not increase under this scenario, but C reductions in ecosystem pools were notably lower or absent. The impact of turning off C output fluxes (respiration) from domestic herbivores (C-off scenario) had much less impact on C storage than suppressing N outputs driven by livestock. Only when both C and N outputs from herbivores were turned off in the model (CN-off scenario), did grazing increased the stocks of C and N.

As for C stocks, N outputs promoted by livestock also accounted for the reductions in C uptake (NPP) and C

Table 5 Changes in C and N pools (a) and fluxes (b) under different scenarios of C and N outputs from livestock

	C before livestock introduction	Carbon variations (1970–1600) under different scenarios				N before livestock introduction	Nitrogen variations (1970–1600) under different scenarios			
		Baseline simulation	N-off	C-off	CN-off		Baseline simulation	N-off	C-off	CN-off
(a) Pools (g m^{-2})										
Plant live	1129	−257	87	−344	19	19	−6.3	0.3	−7.8	−0.9
Standing dead	189	−116	−85	−128	−93	3.3	−2.3	−1.7	−2.4	−1.8
Litter and surface M. org	485	−208	−56	−63	141	9.6	−4.6	−1.8	−3.3	0.1
Total nonsoil	1804	−581	−55	−535	67	32	−13.2	−3.1	−13.5	−2.6
Soil active	701	−185	40	−210	8	24	−8.2	2.1	−8.9	1.2
Soil slow	5429	−1732	−197	−1416	292	167	−61.0	10.3	−57.7	13.1
Soil passive	3951	−197	−4	−193	18	272	−19.0	8.1	−20.8	5.7
Total soil	10 082	−2115	−161	−1819	318	465	−88.2	20.5	−87.4	20.0
Total organic	11 886	−2696	−216	−2353	384	497	−101.4	17.3	−100.9	17.4
(b) Fluxes (g m^{-2} yr^{-1})										
NPP/N uptake	889	−219	71	−295	3	20.1	−6.8	0.9	−8.4	−0.6
Herbivore consumption	7.4	151	222	151	207	0.203	3.3	5.5	3.4	5.1
Vegetation N emissions						0.249	−0.1	−0.1	−0.2	−0.1
Soil respiration/N emissions	884	−313	−63	−286	1	0.418	−0.2	−0.01	−0.2	0.00
Herb. respiration/N emissions	5.2	103	151	0	0	0.041	0.7	0.0	0.7	0.0
Total respiration/N emissions	889	−210	88	−286	1	0.718	0.4	−0.1	0.4	−0.1
Herbivore excretions	2.20	48	71	151	207	0.162	2.6	5.5	2.7	5.1
Plant death	882	−371	−151	−446	−204	19.6	−9.9	−4.4	−11.6	−5.6
Total C or N entering the soil	884	−322	−80	−295	3	20.6	−6.6	1.7	−8.2	0.2
Gross N mineralization						41.2	−16.0	0.7	−13.3	2.2

In the C-off scenario all C consumed by livestock was returned to the soil as dung (no herbivore respiration). In the N-off scenario all N consumed by livestock was returned to the soil in dung and urine, and in the CN-off scenario all C and N consumed by herbivores were returned to the soil. Values are averages of all sites. The second and seventh column of the table show C and N pools and fluxes before domestic herbivores introduction. The rest of the columns show the differences between 1970 and 1600 of C and N pools and fluxes after 370 years of grazing under different scenarios.
NPP, net primary production.

flow through the ecosystem after livestock introduction. Productivity and C flow are limited by N in these ecosystems, because the more positive values of C change (that symbolize positive effects of grazing on C fluxes) were obtained under the N-off scenario (Table 5b). Under this scenario, annual NPP increased $71 \, g \, C \, m^{-2}$, a large change compared with the reduction occurred after 370 years of domestic grazing in the baseline simulation ($-219 \, g \, C \, m^{-2}$). Herbivore consumption and excretion of C and N increased markedly after livestock introduction in all simulations, whereas the flux from the vegetation to the soil of both elements decreased. The balance among these fluxes led to a reduction of total C and N inputs to the soil after domestic grazing in all scenarios except in the CN-off scenario, where soil inputs were similar to the pristine situation with native grazers. Noticeably, in the C-off situation, C inputs to soil did not change much compared with the baseline simulation ($589–562 \, g \, C \, m^{-2} \, yr^{-1}$, respectively). However, when N outputs by herbivores were removed (N-off scenario), C inputs to the soil were much larger than in the baseline simulation ($804–562 \, g \, C \, m^{-2} \, yr^{-1}$, respectively). This suggests that C flow to the soil is strongly limited by N availability and hence, in the long term, it is affected by N outputs induced by herbivores. Soil N and C outputs were reduced after grazing because of the lower mineralization and the reduction of the SOM pools (Table 5a). Only in the CN-off scenario, when both respiration and N outputs by herbivores were suppressed, soil output fluxes were similar to the quantities achieved by year 1600 under native herbivores (at very low densities). As in the baseline simulation C balance was near equilibrium after 370 years of domestic grazing at all scenarios (see Table 5b). On the other hand, N inputs and outputs were not balanced and net losses of N were obtained in the baseline simulation and in the C-off scenario, whereas in the N-off and CN-off scenarios ecosystems were raising their N stocks after 370 years of grazing.

Mid-term vs. long-term grazing effects. Mid-term consequences (1–20 years) of introducing livestock at high stoking rates differed significantly from the long-term effects shown before. Mid-term simulations of livestock grazing at current stocking rates suggested increased N returns via urine and dung by $40.2 \, kg \, ha^{-1} \, month^{-1}$ (2564%), that overcompensated lower N outputs via volatilization and leaching accounting $9.2 \, kg \, ha^{-1} \, month^{-1}$ (127%), promoting a transient increase of soil inorganic N content of $11.8 \, kg \, ha^{-1}$ (51%), average for all sites. In the model, less productive sites (H. Ascasubi, Dolores, Tacuarembó, Tres Arroyos, Pigüé, Colonia; Table 1)

responded to higher inorganic N availability raising plant N uptake and NPP as well as SOC and SON storage in labile soil fractions during the first years after livestock introduction (Fig. 6b), in contrast to more productive sites (Canelones, Pergamino, Treinta y Tres, Salto and Pehuajo), where this ecosystem attributes remained unchanged or decreased slightly (Fig. 6a).

Considering all sites together, the initial N content of the slow turnover SON pool was the variable that best explained the mid-term variations in NPP, active SOC and slow SOC (the two soil pools that supply nutrients at this time scale) ($r^2_{adj} = 0.64$, 0.69 and 0.77; respectively) (Fig. 7). At sites with high levels of N in the slow SON, livestock grazing diminished NPP and the active SOC pool, whereas at sites with low or intermediate levels of N the opposite happened in the first years after livestock introduction (Fig. 7a and b). The slow SOC pool decreased after domestic herbivore introduction, but reductions were larger in sites with greater initial N contents in the slow SON pool (Fig. 7c). Our model suggests that mid-term responses to grazing differed from long-term effects, varied among sites and were shaped by N stocks in the slow SON pool, that reflects the mid-term availability of N and the productivity of the sites (because N contents in the slow SON fraction are correlated with NPP, $r = 0.72$, $P < 0.01$, $n = 11$).

Sensitivity analyses. The sensitivity analysis showed that our modeled results were not substantially affected after changing our initial assumptions on fire frequency, species composition and atmospheric CO_2 content. However, these analyses revealed important interactions between fire and grazing which may have large influences on C and N dynamics in these grasslands. Table 6 shows SOC and NPP values before and after 370 years of grazing under different fire, atmospheric CO_2 and species compositions scenarios. In the Fire 1, 2 and 3 scenarios, SOM pools were stabilized (running 8000 years) under high fire frequencies, with no influences of charcoal in SOC accumulation. Under this scenario, NPP and SOC pools by year 1600 were lower than values obtained in the baseline simulation. In the Fire 1 scenario, where intense and frequent fires were simulated both before and after livestock introduction, grazing effects did not differ much from those in the baseline simulation, which assumed no fires at all. Fire 2 scenario represents the more plausible scenario for the region, with high fire frequencies and intensities before domestic herbivore introduction and a gradual decrease since then. In this situation livestock effects did not differ much from the baseline simulation, but
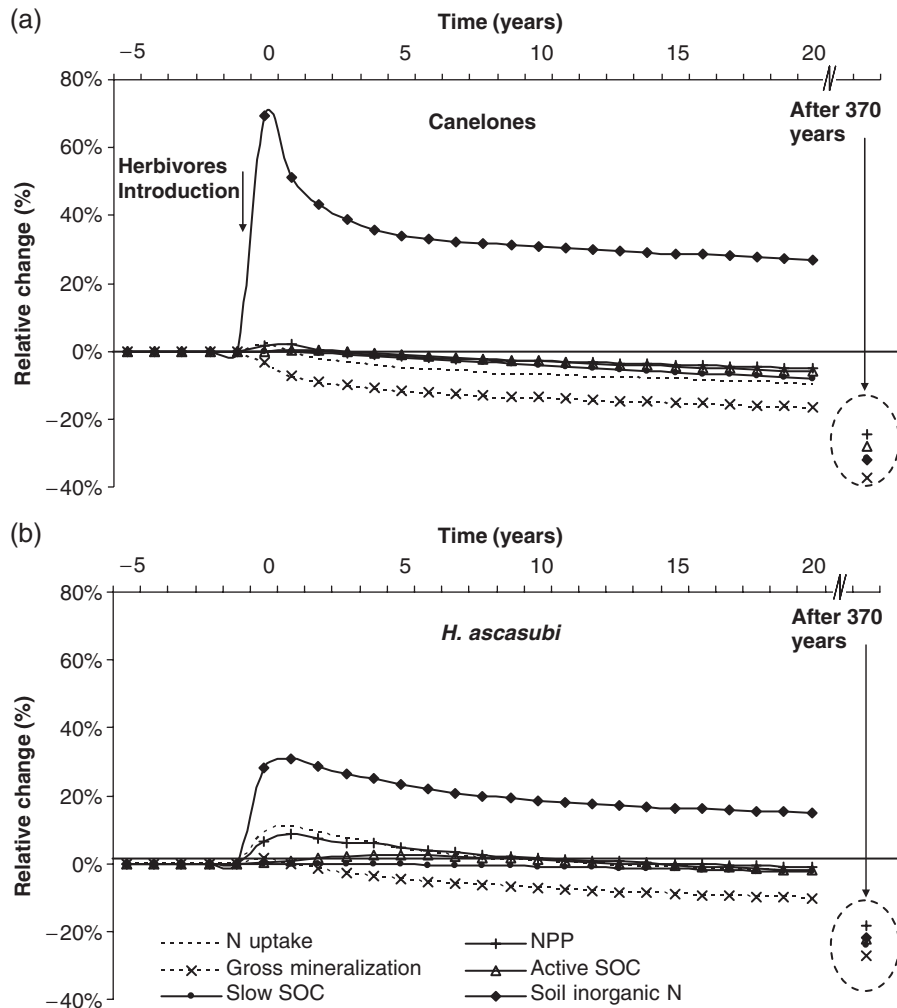
Fig. 6 Mid-term ecosystem variations in key ecosystem variables after domestic herbivores introduction, at two contrasting sites across the studied gradient analyzed. Domestic herbivores at high stocking rates were introduced at year 0. Trajectories at Canelones represent those observed in other sites with high fertility soils (Pergamino, Treinta y Tres, Salto and Pehuajo) whereas trajectories at Ascasubi represent those of sites with low fertility soils (Dolores, Tacuarembo, Tres Aroyos, Pigue and Colonia).

NPP and slow SOC pool decreases were less pronounced. Fire 3 scenario represents a more extreme and unlikely situation in which fire disappeared immediately after livestock introduction. Under this scenario livestock effects differed from the baseline situation. Although the active and slow SOC pools and NPP decreased after domestic herbivore introduction (and fire removal), the reduction was smaller than the observed in the baseline simulation. In addition, the passive SOC pool increased in opposition to the baseline situation. Thus, the substitution of fire by grazing altered the relative contribution of each SOC pool into the total SOC, changing the quality of the organic matter.

The effects of domestic herbivores on C and N cycles were slightly affected by changes in species composition and atmospheric CO_2 concentration. The species shift scenario represents the more likely situation in these grasslands after domestic herbivore introduction (see evidences in Materials and methods). Species effects were small but tended to offset herbivore effects on C biogeochemical cycles, probably because C_4 vegetation needs less N to maintain high levels of productivity (higher N use efficiency). Finally, the effects of increasing atmospheric CO_2 were relatively small compared with changes registered in the other scenarios, and the human-induced increase of atmospheric CO_2 did not enhance NPP in the model. The decrease of SOC promoted by livestock introduction was responsible for masking the positive effects of atmospheric CO_2 concentration on plant production at the entire ecosystem level.
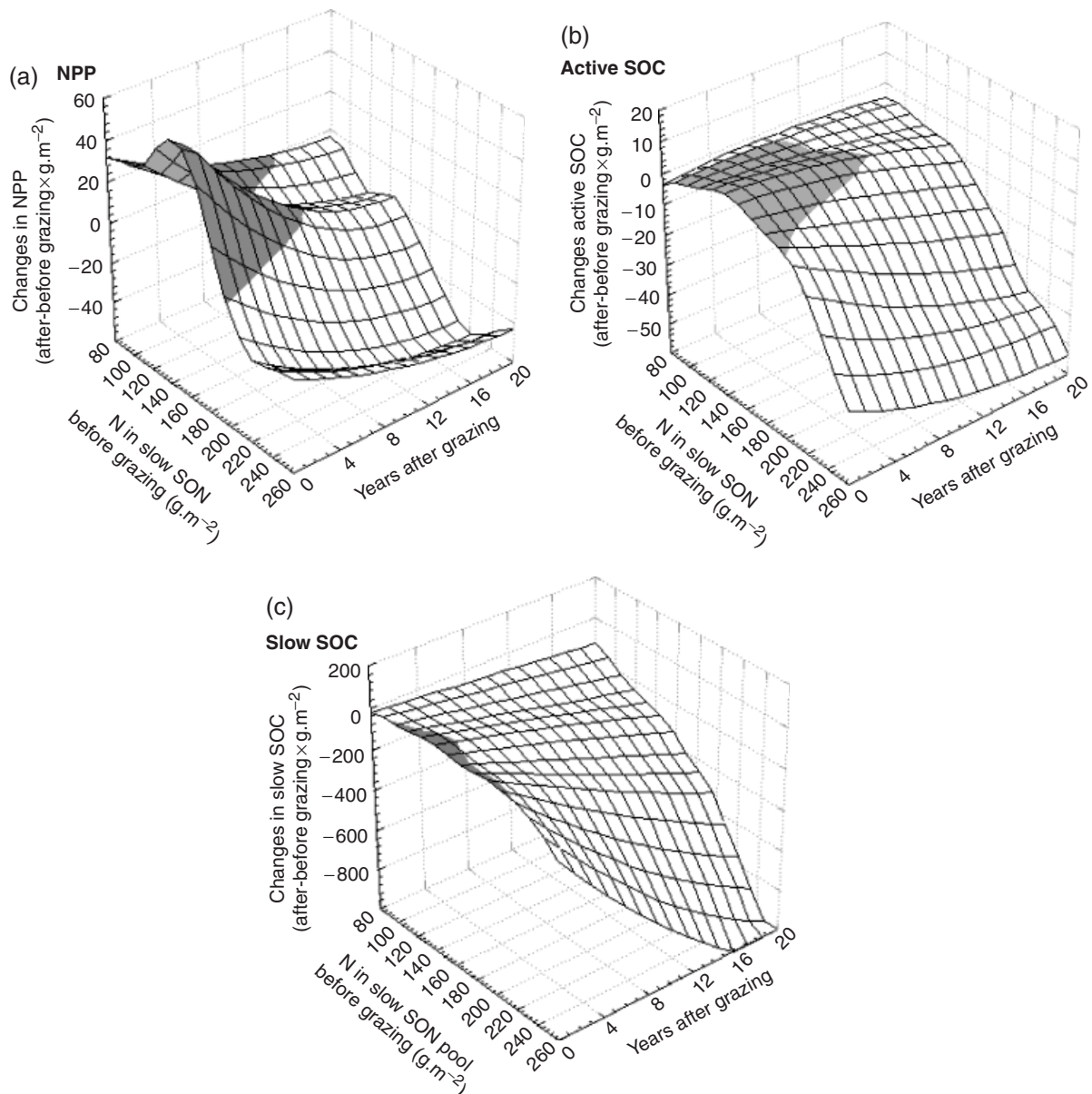
Fig. 7 3D scatter plots of mid-term changes in net primary production (NPP) (a), active soil organic carbon (SOC) turnover pool (b) and slow SOC turnover pool (c), after domestic herbivores introduction, as a function of their N content in the slow SON turnover pool before grazing and years of grazing. Domestic herbivores at high stocking rates were introduced at year 0. Adjusted r^2 of multiple regressions were, 0.64, 0.69 and 0.77 for NPP, active SOC and slow SOC, respectively. The shaded area indicates positive changes in the y-axis.

Discussion

Our simulation results suggest that herbivore N returns via urine and dung are the main biogeochemical alteration induced by grazers, although their mid- and long-term effects are opposite. Herbivore N depositions produce two main effects on N cycling: elevated N volatilization and leaching (Lovell & Jarvis, 1996; Frank & Evans, 1997), and faster N returns to the soil (Frank et al., 2000). In our simulations, at both mid- and long-term scales, higher N volatilization and leaching from urine and dung patches increased total ecosystems N outputs. Higher N outputs were compensated in the mid term by the faster N returns via urine and dung causing increased inorganic N in the soil solution in this time frame (Fig. 6). In less fertile sites, this extra N availability was capitalized by plant N uptake, NPP and/or soil N storage in SON pools (Figs 6 and 7). The mid-term faster N circulation induced by heavy grazing shown by this simulation study is in agreement with

Table 6 Carbon pools before domestic herbivore introduction (1600) and 370 years after (1970) under different scenarios of the *Rio de la Plata* Grasslands

Treatment		Base simulation	Fire 1	Fire 2	Fire 3	Species shift	CO_2
Stabilization		No fire/current species/normal CO_2	Fire high	Fire high	Fire high	Current species + 25% C_3	Normal CO_2
1600–1700		Idem	Fire high	Fire high	No fire	Current species	Normal CO_2
1700–1800		Idem	Fire high	Fire medium	No fire	Current species	Normal CO_2
1800–1900		Idem	Fire high	Fire low	No fire	Current species	Increased CO_2
1900–1970		Idem	Fire high	No fire	No fire	Current species	Increased CO_2
Active SOC (g C m^{-2})	1600	701	458	458	458	663	701
	1970	516	319	375	416	522	519
	% variation	−29%	−33%	−21%	−12%	−24%	−28%
Slow SOC (g C m^{-2})	1600	5429	3328	3328	3328	5096	5429
	1970	3697	2173	2607	2936	3616	3656
	% variation	−31%	−33%	−19%	−8%	−29%	−32%
Passive SOC (g C m^{-2})	1600	3951	2446	2446	2446	3706	3951
	1970	3754	2310	2344	2512	3599	3751
	% variation	−5%	−5%	−3%	4%	−3%	−5%
NPP (g C m^{-2} yr^{-1})	1600	889	584	581	584	865	889
	1970	670	454	510	554	673	655
	% variation	−25%	−22%	−12%	−5%	−22%	−26%

Under the *Baseline Simulation* we show the values obtained in the main simulation of the article, see Materials and methods for assumptions and details. The *fire* scenarios are different possibilities of fire progress in the region. The *species shift* scenario simulates an increase of C_3 species after livestock introduction. The *CO_2* scenario simulates human derived increases in atmospheric CO_2 content. All situations include grazing by native herbivores before 1600 and a gradual increase of grazing by domestic herbivores thereafter. Values are averages of all sites. See Materials and methods and Supplementary Material 3 for a detailed description of each scenario.

SOC, soil organic carbon; NPP, net primary production.

several empirical studies (Chaneton *et al.*, 1996; Frank & Evans, 1997; McNaughton *et al.*, 1997), and contrary to others (Ritchie *et al.*, 1998; Verchot *et al.*, 2002) made in grazing exclosures that represent the opposite trajectory as simulated here. Remarkably some of these field studies, were performed in the same sites (exclosures in Yellowstone National Park) with 5 years of lag (Frank & Evans, 1997; Verchot *et al.*, 2002), and showed a shift from lower to faster N circulation as a result of grazing exclosure (assuming the reversal situation, a shift from faster to slower N circulation due to grazing). In the model, long-term faster N circulation was offset by the uninterrupted outputs of N from urine and dung under grazing, which reduced SON and overall N availability (see Fig. 6).

Observed SON reductions summed a total of 61.7 Tg of N when extrapolated to the entire RPG region. Additionally, the ratio of gross mineralization/SON (or gross mineralization/SOC) was lower after 370 years of grazing, indicating that the relative amount of N released by mineralization from SON decreased after long-term grazing. In our simulations, livestock increased long-term N recycling and availability only when N outputs from herbivore excreta were turned

off (N-off and CN-off scenarios) (Table 5), and hence gross mineralization increased after livestock introduction. From our modeling results, we can state that mid-term biogeochemical consequences of grazing are transient changes until SOC and SOM pools are again stabilized under the new grazing conditions (whether in 370 or in longer periods). Mid-term effects may reverse in longer terms, and their magnitude and sign depend on the initial fertility (N status) of the ecosystem. Thus, extrapolation from mid-term studies to longer time scales may lead to wrong conclusions.

A reduction in NPP because of long-term grazing implies less energy flowing through the ecosystems. Although the model failed to reproduce NPP values properly, the relative changes in NPP after long-term grazing should be reliable because they are derived from SOC reductions (see Table 5), which were accurately simulated by the model. Our simulations suggest that the changes in NPP and SOM occurred slowly and hence they were imperceptible for ranchers and stakeholders, in contrast to the high rate of SOM losses associated to agriculture (Andriulo *et al.*, 1999; Fabrizzi *et al.*, 2003). SOM losses have not been identified as an important dimension of land degradation in these

rangelands, probably because local mid-term experiments did not find clear differences on SOM in grazed vs. exclosured sites (Lavado *et al.*, 1995; Chaneton & Lavado, 1996). However, as shown in our simulations, SOM reductions after grazing will occur in the long term, whereas mid-term effects are variable. Total C reductions after long-term grazing were estimated on $21.5\,\mathrm{t\,ha^{-1}}$ and $1.5\,\mathrm{Pg}$ of C, for all the RPG.

CENTURY results suggest that N losses promoted by livestock are the main drivers of C losses in the soil. Our simulations performed turning off livestock N and C outputs clearly showed that N was constraining C accumulation in SOM and not vice versa. The SOM C/N ratio was an important indicator of N limitation after livestock introduction and could be used to detect changes in SOM quality in field experiments. Our modeled results support previous works that show tight linkages between N and C dynamics on ecosystems (Neff *et al.*, 2002; Baisden & Amundson, 2003), and suggest that N additions are necessary to increase C stocks at many sites (Murty *et al.*, 2002; Poulton *et al.*, 2003; Conant *et al.*, 2005). Several works in the region and elsewhere show that SOM contents increase after sowing pastures that include legumes, mainly due to biological N fixation (Drinkwater *et al.*, 1998). C sequestration in soils promoted by sown legumes could be an important management practice for mitigating herbivore-promoted N losses in the RPG. However, secondary effects of legume introduction, like N leaching to streams and groundwater (Scholefield *et al.*, 1993), increased N_2O emissions (Petersen *et al.*, 2005), or changes in vegetation structure and biodiversity (Vitousek *et al.*, 1997) should be carefully evaluated.

Model results highlighted the importance of ecosystem conditions before herbivore introduction in shaping grazing effects on grasslands. Evolutionary history of grazing controls species changes because of grazing (Milchunas *et al.*, 1988; Sala, 1988; McNaughton *et al.*, 1993). In a similar way, the historical disturbance regime can alter the biogeochemical responses of ecosystems to grazing, through their effects on the initial nutrient pools. In our simulations, the relatively low grazing pressures supported by native grasslands during soil development partially determined the reductions in SOM observed at high livestock stocking rates. However, fires are very common in grasslands subjected to low herbivore densities because large quantities of flammable biomass can accumulate (Oesterheld *et al.*, 1999). Thus, either fire or grazers would consume aboveground grass biomass (Bond & Keeley, 2005). When fires were considered during the period simulated to reach ecosystem steady-state conditions, low SOC contents were obtained (because of the elevated N emissions in fire events). As a consequence, SOC losses

because of livestock grazing diminished (Table 6). Our model suggests that the historical fire regime and the magnitude and form of the substitution of fire by grazing were the main drivers of biogeochemical changes in the RPG grasslands. In our simulations, N dynamics controlled the long-term effects of fire and grazing on SOM accumulation.

Our simulations suggest that domestic herbivore introduction could not only increase N volatilization, but also change the proportion of the chemical forms released. N emission from faeces and urine are mainly as NH_3 and only a small portion as N_2O and NO_x (Zheng *et al.*, 2002). Therefore, domestic animals are globally the main source of NH_3 emissions, greater than any other human or natural source (Bouwman *et al.*, 1997). In contrast, soil emissions of reactive N (without considering N_2) are mainly as N_2O and NO_x (Schlesinger, 1991). Consequently, the switch of N emissions from soils to domestic herbivores simulated by CENTURY, will increase NH_3 volatilization and decrease N_2O and NO_x releases to the atmosphere. These results suggest that grazing could have beneficial impacts by diminishing N_2O concentrations in the atmosphere (a greenhouse gas that also depletes stratospheric ozone), and the harmful generation of ozone by NO_x in the troposphere (Schlesinger, 1991). Additionally, since NH_3 is poorly transported in the atmosphere (Schlesinger, 1991), elevated N emissions from animal waste could significantly increase N inputs into adjacent ecosystems (Galloway & Cowling, 2002). Local measurements of NH_3 and NO_x deposition (from 7.0 to $19.7\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) (De Hein *et al.*, 1981; Morras, 1983) are higher than estimates made by global models for the region ($NH_3 = 2.0$, $NO_x = 2.0$ and $\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$) (Holland *et al.*, 1999), suggesting that models fail to correctly assess herbivore effects. A simultaneous increase in N emissions and redepositions will probably diminish the reductions in SON estimated by CENTURY, because the model considered constant N inputs. Perhaps grazing may be increasing an atmospheric pathway for N cycling that makes N cycling more open at the local scale yet still more closed at a regional scale because of regional redeposition of NH_3. However, higher abundance of N-reactive forms in the atmosphere will increase chances of N exports to adjacent regions (of land or oceans), making the N cycle more leaky. Further measurements are needed to correctly assess N emissions and depositions throughout the region and our results point to NH_3 as a key N-form to observe in this region.

Conclusions

Using a locally parameterized and evaluated version of CENTURY for the RPG, we simulated biogeochemical

changes associated to livestock introduction by European's. From our simulation we can conclude that:

- After 370 years of grazing, livestock reduced SOC contents by 22% (10.5–35.0 t C ha^{-1}, from the less to the more productive sites). These changes are similar in magnitude to those occurred in shorter periods (20–40 years) after plowing and crop sowing. SOC reductions after long-term grazing were 21.5 t ha^{-1} and summed 1.5 Pg of C, for all the RPG.

- Four centuries of domestic herbivore grazing changed N cycling in the RPG, diminishing soil N storage (by 19% or 970 kg of N ha^{-1}) and N recycling, while increasing N outputs (67%) and N cycle openness (64%). N reductions occurred mainly as a consequence of N volatilization and leaching from urine and dung patches. Livestock N emissions probably altered N depositions and N-reactive forms in the atmosphere. SON reductions extrapolated to the entire region summed a total of 61.7 Tg of N.

- The time frame of analysis is a key factor for understanding herbivore impacts on biogeochemical cycles. Most grazing experiments focus on short to mid-term consequences. We showed that long-term effects could be substantially different both in magnitude and direction from short- to mid-term responses. Hence, we should be cautious in extrapolating results from field experiments to longer terms.

- Fire frequencies and intensities interact with the grazing regime determining long-term ecosystem functioning and structure. Our results suggest that C accumulation in the soils of the RPG is mainly constrained by these two disturbances via N limitation. Evolutionary history of grazing and historical fire regimes, through their effect on the size of the C and N pools, seem to be important factors in determining the effects of domestic grazing on grasslands.

Acknowledgements

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