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ECOSYSTEMS

Effects of Animal Husbandry on Secondary Production and Trophic Efficiency at a Regional Scale

J. Gonzalo N. Irisarri,* Martín Oesterheld, Rodolfo A. Golluscio,
and José M. Paruelo

IFEVA-Faculty of Agronomy, University of Buenos Aires-CONICET, Av. San Martín 4453, C.P:1417 Buenos Aires, Argentina

ABSTRACT

Agricultural systems are expected to have higher net secondary production (NSP) than natural systems as a result of higher trophic efficiency and lower interannual variability. These differences, however, have not been quantified across regional gradients. We compiled a dataset of herbivore biomass, consumption, NSP, annual precipitation, and aboveground net primary production (ANPP) for extensive livestock farms across a wide precipitation gradient in Argentina. We compared these data with worldwide published studies of natural systems. In a double-logarithmic scale, NSP of agricultural systems increased with ANPP from semiarid to subhumid systems and decreased from subhumid to humid systems, a response that contrasted with the linear positive increase of natural systems. Compared to natural systems dominated by homeotherms, E_{troph} (NSP:ANPP) in agricultural systems in semiarid areas was 8 times higher, due to a 2 times higher E_{consump} (Consumption:ANPP) and a 4 times higher E_{prod} (NSP:Consumption). In subhumid areas, E_{troph} was 46 times higher, due to a 13.7 times higher E_{consump} and a 3.3 times higher E_{prod}. In humid areas, E_{troph} was 5 times higher, due to a 2.5 times higher E_{consump} and a 2 times higher E_{prod}. The interannual variation of herbivore biomass, a major determinant of NSP, was 60 % lower in agricultural than in natural systems dominated by homeotherms, and was decoupled from the variability of precipitation. Agricultural systems reach higher NSP by (1) diverting a major proportion of ANPP from the detritus to the grazing chain, (2) converting more efficiently consumption into NSP, and (3) stabilizing herbivore biomass across years.

Key words: aboveground net primary production; herbivores; poikilotherm; homeotherm; interannual variation; consumption.

INTRODUCTION

Land use by humans has shaped Earth's landscape and changed natural biogeochemical processes, competing in magnitude and extension with natural effects (Vitousek and others 1997). Grazing by domestic herbivores is one of the most extensive land uses (Vitousek and others 1986). Aboveground net primary production (ANPP) is the major determinant of livestock carrying capacity and net secondary production (NSP). In fact, 70 % of the energy required by livestock to reach market is provided by rangeland ANPP (Holechek and others 1989). Animal husbandry in rangelands includes water provision, disease and predator control, pastoral practices, and the introduction of exotic herbivores. As a consequence of these practices,

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**Corresponding author; e-mail:* irisarri@agro.uba.ar

agricultural systems are expected to have consistently higher NSP than natural systems as a result of higher trophic efficiency and lower interannual variability. These impacts, however, have not been quantified across regional gradients.

Different herbivore attributes have been correlated with ANPP for natural systems and only partially for agricultural systems. In natural systems, herbivore biomass (Coe and others 1976; East 1984; McNaughton and others 1989; Fritz and Duncan 1994; Frank and others 1998) and consumption (McNaughton and others 1989; Cebrian 1999, 2004) increase exponentially across ANPP gradients, whereas NSP (McNaughton and others 1989) increases linearly. In agricultural systems of South America, herbivore biomass also increased exponentially with ANPP (Oesterheld and others 1992), but herbivore biomass per unit of ANPP was 6 times higher than in natural ecosystems (Oesterheld and others 1992), except for some natural systems with high soil fertility (Fritz and Duncan 1994). However, the consumption-ANPP and the NSP–ANPP patterns of agricultural systems have not been established. The most parsimonious hypothesis is that agricultural consumption should increase exponentially and NSP should increase linearly with ANPP, as in natural systems, but with higher levels of consumption and NSP per unit of ANPP, as suggested by the herbivore biomass pattern.

If agricultural systems have higher consumption and NSP per unit of ANPP than natural systems, their trophic efficiency, E_{troph}, must also be higher. E_{troph} has two major components: E_{consump} represents the consumption efficiency, the proportion of ANPP consumed by herbivores; and E_{prod} represents the production efficiency, the proportion of consumption transformed into NSP (Lindeman 1942; Kozlovsky 1968; Chapin 2011). The impact of animal husbandry on these ecosystem-level efficiencies has not been quantified across regional gradients. E_{troph} should be higher in agricultural systems than in natural homeotherm-dominated systems because of higher E_{consump} and E_{prod}. As stated above, E_{consump} should be higher because agricultural systems have 6 times more biomass at a similar ANPP level (Oesterheld and others 1992), and E_{prod} should be higher because agricultural systems have more digestible forage and implement sanitary management that decreases respiration costs. As a consequence, agricultural systems should produce more herbivore energy per unit of consumed forage energy. E_{troph} and its two components have never been quantified across a wide resource gradient in agricultural systems.

The impact of animal husbandry on the interannual variation of ecosystem processes has received less attention than the impact on mean values. The effects of animal husbandry on the stability of NSP can be seen in two ways. First, it is possible to compare the interannual variation of NSP between agricultural and natural systems. Second, it is possible to compare the interannual variation of NSP in agricultural and natural systems in relation to the variation of a control factor, for example precipitation. In rangelands, the relative interannual variation of precipitation decreases across gradients of mean annual precipitation (Paruelo and Lauenroth 1998). As far as we know, no study has yet compared the relative interannual variation of NSP in agricultural and natural systems, and its relation with the relative interannual variation of a control factor, such as precipitation. We expect that animal husbandry will reduce the interannual variation in NSP caused by the variation of precipitation.

In Argentina, cow–calf operation systems and sheep production takes place almost exclusively on native rangelands and nonirrigated cultivated pastures (Soriano 1983, 1992). Rangelands and cultivated pastures expand across a wide precipitation gradient, from semiarid to humid, and different types of ecosystems, including grass and shrub steppes, prairies, and subtropical savannas (Soriano 1983, 1992). This precipitation gradient provides the opportunity to assess the impact of animal husbandry on (1) the relationship between consumption and ANPP, and NSP and ANPP across a regional gradient; (2) the trophic efficiency and its components; and (3) the interannual variability of herbivore biomass, a major determinant of NSP, in relation to the variability of precipitation.

METHODS

Overview

For the first objective, we described and compared the consumption-ANPP and the NSP–ANPP relationships of agricultural and natural systems across a precipitation gradient. Consumption and NSP data for agricultural systems were gathered and compiled at the farm level for this study, whereas data for natural systems came from the literature. For the second objective, we quantified E_{troph} as NSP:ANPP. To estimate E_{consump} and E_{prod}, we estimated herbivore consumption from our own herbivore biomass dataset at the farm level for agricultural systems and from the literature for natural systems. Finally, for the third objective, we studied temporal series from our own compilation of farm-level herbivore biomass data for agricultural systems and from the literature for natural systems.

Data Sources

For agricultural systems, we gathered livestock biomass, NSP, and mean annual precipitation data from 113 Argentinean farms. This compilation included rangelands dominated by ruminant herbivores, cattle and sheep, and encompassed a wide precipitation gradient from 282 to 1,600 mm. The farms were arranged into 24 groups (Table 1). The first three groups were composed of a large farm each (50,000–170,000 ha) located in the Patagonian semiarid steppe, with wool and lamb production as the main activity. The other 21 groups were composed of smaller farms (230–18,000 ha) located on semiarid, subhumid grassland, and humid savanna areas, with cow–calf operation as the main activity in which grasslands are the main forage source (Viglizzo and others 2001). Each of these 21 groups corresponded to an interaction unit of a national consortium of farmers (CREA, http://www.aacrea.org.ar). The main objective of the consortium is to achieve profitable and sustainable enterprises by exchanging experiences and testing technologies. Farms within each interaction unit share similar ecological conditions and management. All farms share the general idea of providing rest periods within the growing season through rotational grazing (Golluscio and others 1998b; Jacobo and others 2006).

ANPP was estimated from a generalized linear relationship between ANPP and mean annual precipitation across a wide gradient of precipitation (Sala and others 1988) which is similar to other gradients in the world (Sala and others 2012), an approach also used by (Oesterheld and others 1992). Consumption was estimated as 3 % of herbivore biomass per day (McNaughton and others 1989; Oesterheld and others 1992; Cebrian 1999). NSP was calculated as the annual livestock and wool sales of each farm. This approach would overestimate or underestimate NSP if farmers sold their stock or withheld production, respectively. To evaluate this potential error, we performed a regression between livestock biomass and time. A significant trend would indicate that either stock selling or withholding was biasing the estimation of NSP. We only observed a positive significant ($P < 0.05$) trend in one group of farms, and the influence of that trend (4.14 kg/ha year) was minor compared to the total NSP estimated from annual sales (173.5 kg/ha year). Thus, we concluded that annual sales were a good estimator of NSP in this context.

For natural systems, we used consumption, NSP, and ANPP data compiled by McNaughton and others (1989, 1991), which served for the two first objectives. These compilations provided worldwide data from tundra to tropical forests, included systems dominated by homeotherm (56 % of the cases) or poikilotherm (invertebrates, 44 % of the cases) herbivores, and encompassed a wide precipitation gradient. They represent the most complete compilation of these variables for natural systems and have been used in other key studies (Cyr and Pace 1993; Cebrian 1999; Cebrian 2004). We assume that this worldwide data may be used as a reference of natural herbivory for our study region. McNaughton and others (1993) analyzed the patterns of natural herbivory in South American grasslands and savannas and concluded that herbivory by ants, the dominant herbivores, was comparable to herbivory by large mammals in similar ecosystems in Africa, which largely contributed to the database compiled by McNaughton and others (1989, 1991). For the third objective, we gathered temporal series of species or community-level herbivore biomass, a major determinant of NSP, of natural systems dominated by homeotherms, and precipitation from several references (Table 2). The selection of the natural systems was based on three criteria: the selected herbivore species were dominant, the temporal series was longer than a decade, and annual precipitation data were available for the same period.

Data Analysis

For the first objective, we analyzed the consumption-ANPP and the NSP–ANPP relationships of agricultural systems by means of regression techniques of the log-transformed variables, and compared it with the corresponding relationship for natural systems found in the literature (McNaughton and others 1991):

$$\log \mathrm{NSP} = b \times \log \mathrm{ANPP} + \log a \tag{1}$$

These are power-law functions:

$$\mathrm{NSP} = \mathrm{ANPP}^{b} \times a \tag{2}$$

b greater than 1 indicates a more than proportional increase in NSP with a unit changes in ANPP, whereas b greater than 0 and lower than 1 indicates a less than proportional increase in NSP with a unit change in ANPP. When $b = 1$, the response of NSP is linear. We explored three techniques to fit data:

Table 1. Groups of Farms Analyzed as Agricultural Systems

Farm group	Number of farms	LAT	LON	Vegetation type	Productive activity	ANPP (kJ/m^2 year)	HB (kJ/m^2)	NSP (kJ/m^2 year)
Chubut—Languineo	1	43° 29′S	70° 48′W	Steppe	Wool and lamb	3,527	23	12
Chubut—Cushamen	1	42° 24′S	71° 04′W	Steppe	Wool and lamb	2,309	15	9
R. Negro—Pilcaniyeu	1	41° 07′S	70° 43′W	Steppe	Wool and lamb	2,545	19	10
B. Aires—C. Pringles	4	37° 59′S	61° 18′W	Grassland	Cow calf	8,866	354	124
B. Aires—B. Juarez	4	37° 40′S	59° 48′W	Grassland	Cow calf	10,416	264	78
B. Aires—Laprida	4	37° 32′S	60° 47′W	Grassland	Cow calf	10,424	445	191
B. Aires—C. Suarez	4	37° 27′S	61° 54′W	Grassland	Cow calf	6,885	160	51
La Pampa—Utracán	4	37° 22′S	64° 36′W	Grassland	Cow calf	6,624	75	25
B. Aires—G. Lamadrid	9	37° 14′S	61° 15′W	Grassland	Cow calf	8,202	417	196
B. Aires—Ayacucho	7	37° 08′S	58° 28′W	Grassland	Cow calf	7,610	406	171
B. Aires—G. Madariaga	6	36° 59′S	57° 08′W	Grassland	Cow calf	8,852	339	137
B. Aires—Maipú	6	36° 51′S	57° 52′W	Grassland	Cow calf	8,043	359	153
B. Aires—Rauch	5	36° 46′S	59° 05′W	Grassland	Cow calf	8,866	360	144
La Pampa—Lovontué	3	36° 28′S	65° 19′W	Grassland	Cow calf	5,075	123	53
B. Aires—Tapalqué	7	36° 21′S	60° 01′W	Grassland	Cow calf	7,697	358	133
B. Aires—Tapalqué	4	36° 21′S	60° 01′W	Grassland	Cow calf	7,697	359	156
B. Aires—Las Flores	4	36° 00′S	59° 5′W	Grassland	Cow calf	9,323	396	168
B. Aires—R. Pérez	7	35° 25′S	59° 19′W	Grassland	Cow calf	10,126	352	168
B. Aires—25 de Mayo	4	35° 25′S	60° 10′W	Grassland	Cow calf	10,926	521	221
Corrientes—C. Cuatiá	6	29° 47′S	58° 03′W	Savanna	Cow calf	14,759	258	77
Corrientes—Mercedes	6	29° 11′S	58° 04′W	Savanna	Cow calf	14,070	259	75
Corrientes—G. Alvear	6	29° 03′S	56° 32′W	Grassland	Cow calf	17,434	161	43
Corrientes—S. Roque	6	28° 57′S	58° 34′W	Grassland	Cow calf	15,853	236	62
Formosa—M. S. F. de Laishi	4	26° 14′S	58° 37′W	Savanna	Cow calf	10,344	161	40

Each group received a name that combines the province and the county most closely related to that group. ANPP = aboveground net primary production; HB = herbivore biomass; NSP = net secondary production. The groups are listed from South to North.

Table 2. Data Sources for Herbivore Biomass and Annual Precipitation Temporal Series in Natural Systems

Site	LAT	LON	*n* (years)	Density source	Species	Body mass (kg)	Body mass source
Hirta, UK	57° 48′N	008° 34′W	52	(1)	*Ovis aries*	31	(4)
Isle Royal, USA	48° 00′N	089° 02′W	49	(1)	*Alces alce*	367	(5)
Tshokwane Kruger national park, SouthAfrica	23° 37′S	031° 33′E	11	(1)	*Tragelaphus strepsiceros*	301	(6)
Pretorious Kope Kruger national park, South Africa	23° 47′S	031° 34′E	11	(1)	*Tragelaphus strepsiceros*	301	(6)
Rum island, Scotland	57° 00′N	006° 19′W	70	(1)	*Cervus elaphus*	$65_F/91_M$	(1)
Serengeti, Tanzania	02° 09′S	034° 41′E	14	(2)	*Connochaetes gnou*	200	(6)
Yellowstone national park, USA	44° 37′N	110° 31′W	51	(1)	*Cervus canadensis*	250	(1)
Ram mountain, Canada	51° 58′N	115° 15′W	27	(1)	*Ovis canadensis*	72	(1)
Sheep River, Canada	49°54′N	114° 02′W	20	(1)	*Ovis canadensis*	72	(1)
Kruger national park, South Africa	23° 40′S	031° 34′E	24–29	(3)	*Giraffa camelopardalis*	1,555	(7)
					Taurotragus oryx	650	(7)
					Syncerus caffer	550	(7)
					Tragelaphus strepsiceros or *imberbis*	301	(6)
					Hippotragus equinus	262	(7)
					Hippotragus niger	230	(7)
					Connochaetes gnou	200	(6)
					Damaliscus lunatus	140	(6)
					Phacochoerus africanus	90	(6)
					Kobus ellipsiprymnus	90	(6)
					Aepyceros melampus	57	(7)

Because most records counted individuals, we multiplied the yearly counts by average adult biomass reported in previous studies. For one site, Rum Island, counts were discriminated by gender, and so was biomass. We estimated herbivore biomass at the community level. We searched average adult body mass of species with counts, and multiplied counts by body mass and added species biomass to estimate community herbivore biomass. (1) = Owen-Smith and Marshal (2010); (2) = Mduma and others (1999), (3) = Ogutu and Owen-Smith (2005); (4) = Robinson and other (2006); (5) = Jordan and other (1971); (6) = Wilson and Reeder (2005); (7) = Pettorelli and other (2009); (8) = Owen-Smith and Mills (2006).

two forms of linear regression, simple and polynomial of second degree, and a nonlinear method, piecewise regression, which finds a natural breakpoint, and adjusts linear regressions to the two segments of data thus formed (Dorronsoro and others 2002). We chose the most parsimonious model based on two statistical criteria: the lowest AIC value and the highest adjusted R^2. In order to have all variables in energy units, we transformed kg of fresh weight into kJ using a conversion factor of 9,900 kJ/kg of fresh weight (Coughenour and others 1985). A factor of 36,919 kJ/kg was used to transform wool mass into energy (Burton and Reid 1969). ANPP dry matter (DM) was transformed into energy as 16,760 kJ/kg DM (Golley 1968).

For the second objective (trophic efficiency and its components), we used the models fitted for the previous objective to generate models of trophic efficiency (E_{troph} = NSP:ANPP), consumption efficiency (E_{consump} = consumption:ANPP), and production efficiency (E_{prod} = NSP:consumption) across the ANPP gradient.

For the third objective, effects of animal husbandry on the interannual variability of herbivore biomass, a major determinant of NSP, we performed linear regressions between the interannual coefficient of variation (CV) of herbivore biomass and the interannual CV of precipitation for both agricultural and natural systems.

RESULTS

For agricultural systems, the relationship between consumption or NSP and ANPP depended on ANPP. For ANPP below 4,962 kg DM/ha year (3.92 in the log ANPP scale), consumption and NSP increased with ANPP, whereas for ANPP above this threshold they decreased (Figure 1; Table 3). All slopes were significantly higher than |1|, except for the negative relation between consumption and ANPP, which was not different from 1. A significantly higher slope than |1| indicates that a unit change in ANPP was followed by a more than proportional change in consumption or NSP, whereas a slope equal to 1 indicates a proportional change (Table 3). The piecewise method performed better than any of the two forms of linear regression (simple linear regression: $R^2 = 0.38$, AIC = 18.9 for NSP and $R^2 = 0.58$, AIC = 11.9 for consumption; polynomial linear regression: $R^2 = 0.66$, AIC = 5.2 for NSP and $R^2 = 0.82$, AIC = −6.9 for consumption). Both the polynomial and the piecewise methods supported a two-phase pattern. For natural systems, consumption increased more than proportionally with ANPP for systems dominated by homeotherms, but there was no pattern for systems dominated by poikilotherms (Figure 1; Table 3). For the two groups of natural systems, NSP proportionally increased with ANPP across the whole gradient with a slope not different from 1 (Figure 1; Table 3).

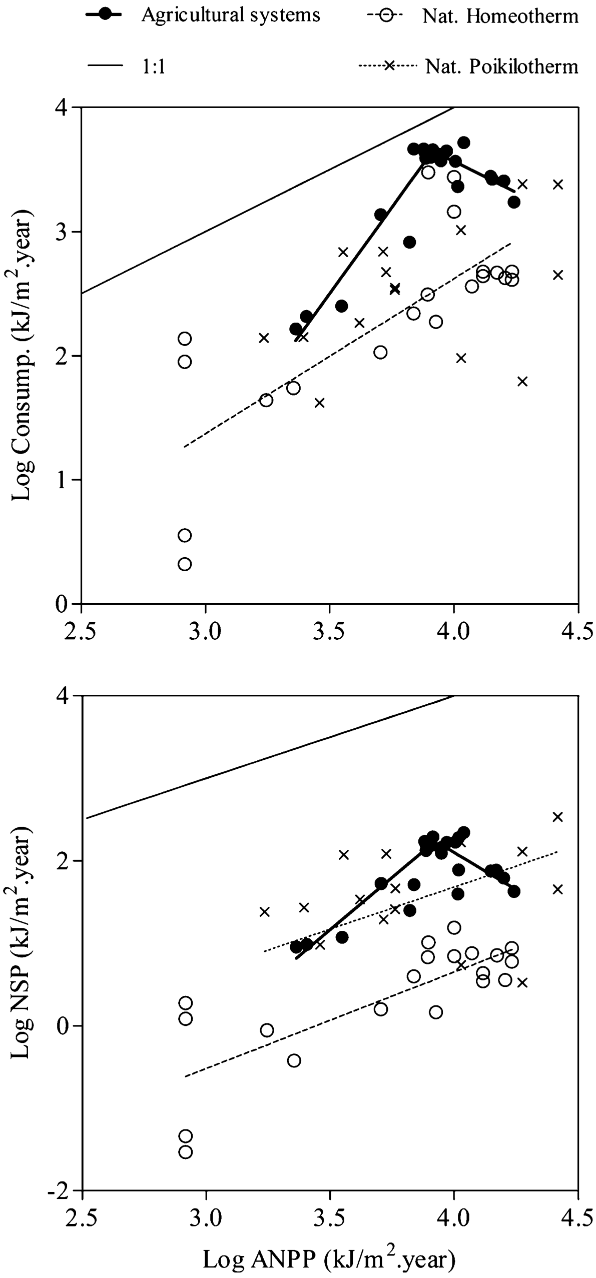

Figure 1. Relationship between consumption and ANPP, and NSP and ANPP. Logarithms are on a decimal base. Data for natural systems are from McNaughton and others (1989, 1991). For systems dominated by poikilotherm herbivores, there was no significant model for the consumption-ANPP pattern (*Consumption* mean = 633 KJ/m^2 year ± 193 SE; $n = 16$).

Table 3. Regression Models Between log Consumption (Consump.) or log NSP and log ANPP

System	Model	*P* value	Adj. R^2	*n*
Agricultural systems ($<$4,962 kg DM/ha year)	$\log \text{NSP} = 2.53 \log \text{ANPP} - 7.69$	<0.0001	0.83	13
	$\log \text{Consump} = 2.77 \log \text{ANPP} - 7.20$	<0.0001	0.90	
Agricultural systems ($>$4,962 kg DM/ha year)	$\log \text{NSP} = -1.80 \log \text{ANPP} + 9.30$	<0.007	0.53	11
	$\log \text{Consump} = -1.00 \log \text{ANPP} + 7.60$	<0.005	0.60	
Natural homeotherm	$\log \text{NSP} = 1.17 \log \text{ANPP} - 4.03$	<0.001	0.62	20
	$\log \text{Consump} = 1.25 \log \text{ANPP} - 2.38$	<0.001	0.57	
Natural poikilotherm	$\log \text{NSP} = 1.02 \log \text{ANPP} - 2.40$	0.004	0.45	16
	Nonsignificant model	–	–	

For agricultural systems three types of models were fitted (piecewise, curvilinear, and linear). For the piecewise regression technique, the breaking point represents 3.92 ANPP log (kJ/m^2 year). Models for natural systems were obtained from McNaughton and other (1991).

According to the fitted models, considering the original, nontransformed values, consumption was larger in agricultural than in natural systems, 2–14 times for homeotherms and up to 7 times for poikilotherms (Figure 1). NSP for agricultural systems was between 5 and 46 times above the natural systems dominated by homeotherms, and 4 times above natural systems dominated by poikilotherms only at intermediate ANPP values (Figure 1).

The above-mentioned patterns had major consequences on E_{troph} and its components across the ANPP gradient (Figure 2). In the semiarid end of the gradient, trophic efficiency (E_{troph} = NSP:ANPP) was 8 times higher in agricultural than in natural systems dominated by homeotherms, due to a 2 times higher consumption efficiency (E_{consump} = Consumption:ANPP), and a 4 times higher production efficiency (E_{prod} = NSP:Consumption). In the middle part of the gradient—subhumid areas—E_{troph} was 46 times higher, due to a 13.7 times higher E_{consump} and a 3.3 times higher E_{prod}. In the humid end of the gradient, E_{troph} was 5 times higher, due to a 2.5 times higher E_{consump}, and a two times higher E_{prod}. Compared to systems dominated by poikilotherms, agricultural systems had lower E_{troph} in semiarid and humid areas and 4 times higher E_{troph} in subhumid areas (Figure 2).

Interannual variability of herbivore biomass, a major determinant of NSP, was 60 % lower in agricultural systems (Figure 3, mean = 0.11 ± 0.05 SE; $n = 24$) than in natural systems (Figure 3, mean = 0.28 ± 0.10 SE; $n = 10$). The interannual variability of herbivore biomass was not related to the interannual variability of annual precipitation (Figure 3). As indicated by the position of the data points above or below the equality line of Figure 3, most sites had a lower herbivore biomass CV than precipitation CV.

DISCUSSION

Human impact largely modified general patterns previously known for natural systems. The two phases of the log Consump–log ANPP and log NSP–log ANPP relationships for agricultural systems may reflect a variable limitation of consumption and NSP across the precipitation gradient. The positive phase may reflect more than a simple limitation by forage production. It may also reflect the stronger limitation imposed by higher seasonality and lower forage quality at the lower end of the gradient. ANPP is concentrated in early spring in the semiarid Patagonia (Paruelo and others 2004; Fabricante and others 2009), and more evenly distributed through the seasons in the subhumid Flooding Pampa (Semmartin and others 2007). Besides, forage digestibility is lower (37–68 %, Somlo and others 1985) at the lowest end of the ANPP gradient than at the middle (47–77 %, Hidalgo and others 1998). Forage digestibility changes are a consequence of changes in the proportion of plant functional types across the ANPP gradient (Paruelo and others 1998; Epstein and others 2002). At the lowest end of the ANPP gradient, in the semiarid Patagonian steppes, low-digestibility C_3 grasses and xerophytic shrubs are dominant (León and others 1998; Epstein and others 2002), whereas at intermediate ANPP values, in the Flooding Pampa grasslands, mesophytic, higher-digestibility C_3 and C_4 grass species and forbs are dominant (Paruelo and others 1998; Perelman and others 2001; Epstein and others 2002). In this positive phase, a unit change of ANPP represented a more than proportional change in consumption, a pattern shared with natural systems dominated by homeotherms; and in NSP, a pattern that contrasts with the linear response of natural systems dominated by homeotherms.

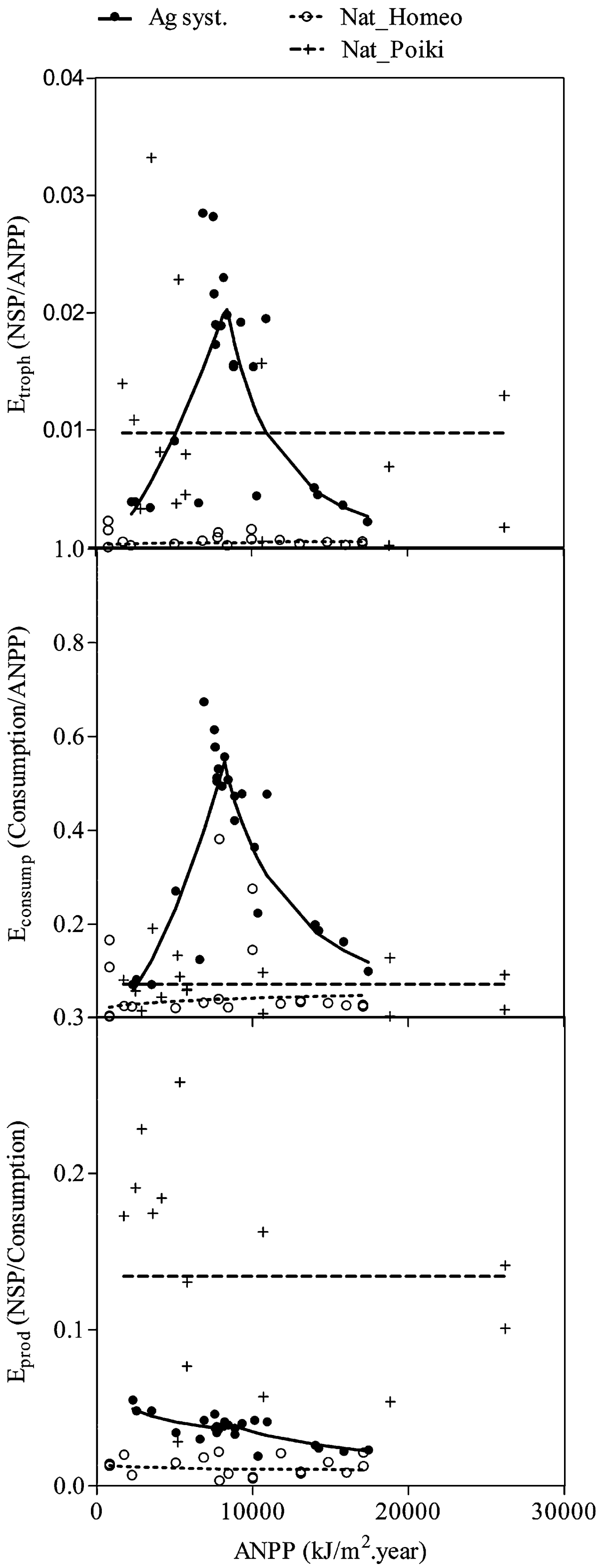

Figure 2. Efficiencies for agricultural and natural systems dominated by homeotherm or poikilotherm herbivores. The *lines* represent the efficiencies based on the models of Figure 1 and Table 3. *Dots* represent the observed efficiencies. Data for natural systems are from McNaughton and others (1989, 1991).

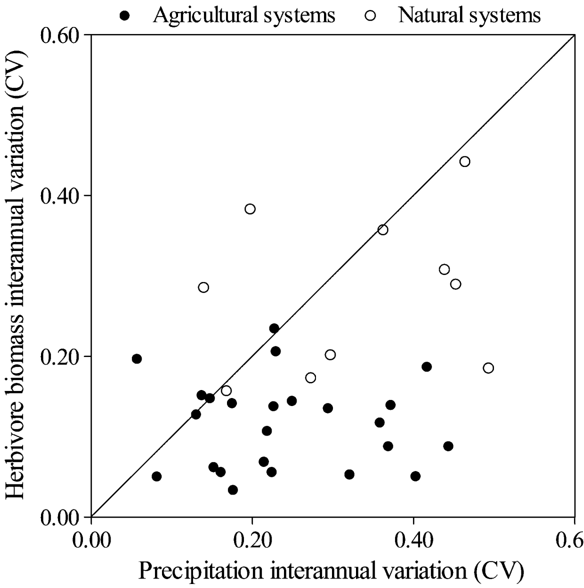

Figure 3. Relationship between the interannual variation (CV) of herbivore biomass, a surrogate of NSP, and the interannual variation of precipitation (CV), for agricultural and natural systems dominated by homoetherms. Data for natural systems were gathered from several references (Table 2). The *solid line* represents the 1:1 relation. Each *point* represents a single site with at least 4 years of herbivore biomass and annual precipitation data.

The negative phase may be a consequence of the interaction of two factors, the limitation imposed by forage quality and the homogenization of herbivore type through management. Forage digestibility decreases with ANPP (45–60 %, Avila and others 2012). At the highest end of the ANPP gradient, in the Campos grasslands and savannas, the landscape is dominated by low-digestibility subtropical C_4 grass species (Paruelo and others 1998; Epstein and others 2002) which limits herbivore consumption. Regarding the homogenization of herbivore type, the negative phase may be attributed to the maintenance of cattle (ruminant homeotherms) as the main herbivore type across the subhumid–humid gradient. In contrast, natural humid systems with high ANPP are dominated by nonruminant herbivores (Olff and Ritchie 2002). In this type of area, with fiber content above 65 % (Treydte and others 2007), consumption is 60 % lower in ruminants than in nonruminant herbivores (Meyer and others 2010). The negative phase suggests that the amount of energy usable for primary consumers decreases toward the subtropical areas.

The patterns of variation of NSP and consumption we just discussed differ from the variation of herbivore biomass in agricultural systems (Oesterheld and others 1992) and NSP in natural systems (McNaughton and others 1989), which increased linearly with ANPP in a log–log scale. Although the linear log–log fit of herbivore biomass in agricultural systems properly represented the variation across a wide gradient of ANPP (Oesterheld and others 1992), closer inspection of the data suggests a leveling off of herbivore biomass around the same values of ANPP that split the two phases of our NSP and consumption gradient. Thus, at high ANPP levels, herbivore biomass of agricultural systems did not increase with ANPP (Oesterheld and others 1992) and NSP decreased (Figure 1). In contrast, biomass and NSP of natural systems increased across the entire gradient, although with lower values (McNaughton and others 1989). This pattern of agricultural systems at the high end of the productivity gradient may be a consequence of (1) declining usable energy because of forage quality limitations, as indicated above, and (2) the lower reproductive efficiency of subtropical cow–calf operation systems, whose calving age is at least 1.5 years later than in temperate systems, largely due to breed characteristics (Lemka and others 1973).

E_{troph} was larger in agricultural than in natural systems dominated by homeotherms due to different increments of production and consumption efficiencies across the gradient. In semiarid areas, it was mainly associated with a larger E_{prod}. This larger E_{prod} may be related to disease control on livestock, higher forage digestibility, higher digestive capacity of domestic herbivores, and the type of secondary production, that is, wool or meat. Disease control may decrease respiration losses associated with mouth and foot disease or internal parasites or increase reproductive efficiency which can be largely affected by brucellosis (abortion fever). Fourichon (1999) and Bennett (2003) described up to 70 % NSP losses associated with disease in dairy production and cow–calf operation systems, respectively. In both cases, the comparison was made between farms that had sanitary plans and those that only used sanitary assistance in case of the presence of a disease. Regarding forage quality, at both ends of the ANPP gradient, agricultural systems are sustained largely on low-quality native steppes and grasslands (Golluscio and others 1998a; Viglizzo and others 2011). In the subhumid area, there is a larger proportion of cultivated pastures along with native grasslands (Viglizzo and others 2011), but both resources have similar forage quality (Hidalgo and Cauhépé 2009). Regarding interspecific differences, Schaefer (1978) and Koch (1995) compared E_{prod} of *Bos taurus* and *Bison bison*, and concluded that it was similar. Finally, regarding the type of secondary production, E_{prod} reached its maximum within semiarid Patagonia where wool production was the main secondary product, suggesting that the appropriated product by humans may represent a major influence when regional gradients are evaluated.

In subhumid areas, the larger E_{troph} of agricultural systems was mainly associated with a larger E_{consump}. This larger E_{consump} may be related to three factors: E_{consump} decreases with travel distance to drinking water points (Bailey 1996) which are more available in current agricultural systems than in pre-Europeans times (Tapia 2005); fencing and animal movements allow regulation of consumption through the control of the occupancy period, frequency, and instantaneous stocking rate (Heitschmidt and Stuth 1991); control of predators increases the available time for consumption. The first two factors are influenced by the degree of subdivision of farms into paddocks, which, in agreement with our results, is more intense in the subhumid Pampas than in semiarid Patagonia or in humid Campos and agrees with our finding that the higher impact of animal husbandry on E_{consump} was more important in the subhumid portion of the gradient. Predators are much more under control in the subhumid and humid portions of the gradient than in the semiarid portion (Kissling and others 2009).

We focus our comparison on the trophic transference of energy. If nonrenewable energies are taking into account, that is fossil fuels, the global efficiency of agricultural systems must decrease with the use of that type of energy source (for example, fertilizers or pesticides). Natural systems in protected areas also demand nonrenewable energies, that is rangers' surveillance, perimeter fence maintenance, policy implementation such as invasive species removal, and its global efficiency should also decrease.

Animal husbandry more than halved the interannual variation of herbivore biomass, indicating that management ‘‘buffers’’ the system. The lower interannual variation of agricultural systems suggests that the addition of drinking water points, which secures a critical resource in dry years, and sanitary plans, which increase the accumulation of new herbivore biomass, not only increased the proportion of ANPP transformed into NSP, but also stabilized it. For example, Chamaillé-Jammes (2007) observed that the interannual variation of elephant density decreased with the incorporation of drinking water points within the landscape of a savanna area in South Africa. The agricultural systems encompassed in our study are based on direct utilization of rangeland areas and nonirrigated pastures. The success of these systems is associated with strategies to mitigate seasonal fluctuations in forage, through forage transference practices, and vegetation changes, through rotational grazing and without use of external feeding (Jacobo and others 2006). Both strategies depend on the existence of fences. A consequence of the lower variability of herbivore biomass in agricultural systems is that in years of very low ANPP, a higher percent consumption of ANPP occurs, whereas in years with high ANPP managers cannot exploit the forage surplus. This in turn may decrease long-term mean ANPP as suggested by simulation models (Piñeiro and others 2006).

We expected a positive relationship between CV of herbivore biomass and CV of precipitation because the variability of precipitation should be related with the variability of ANPP, the major energy source for herbivores (Paruelo and Lauenroth 1998; Fang 2001). However, some regional studies showed a lack of relationship between the CV of ANPP and the CV of precipitation (Knapp and Smith 2001), indicating that input variability is not simply related with output variability. Additionally, the lack of relationship may result from the temporal resolution of the analysis.

In conclusion, we identify three major ways in which animal husbandry reaches high NSP. First, the pattern of agricultural systems showed two phases, while in natural systems, the relationship was linear (for NSP) and positive. At similar levels of ANPP, agricultural systems had higher consumption and NSP when compared to their natural counterpart, homeotherm-dominated systems. Second, the major consequence of the abovementioned patterns was that E_{troph} of agricultural systems was much higher than E_{troph} of natural homeotherm-dominated systems, and higher than poikilotherm-dominated systems in subhumid areas. The difference of E_{troph} was largely accounted for by E_{prod} in semiarid areas, by E_{consump} in subhumid areas, and by both E_{prod} and E_{consump} in humid areas. Finally, animal husbandry strongly reduced NSP interannual variation, which was decoupled from the variability of precipitation across the regional gradient.

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