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Spatial and temporal variation of human appropriation of net primary production in the Rio de la Plata grasslands

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ABSTRACT

Latin America, and particularly, the Rio de la Plata Grasslands (RPG), are one of the regions with the highest rates of land use change worldwide. These changes drastically alter ecosystems energy flows, affecting biodiversity, atmospheric composition, and the ecosystem capacity to provide services. In this work we evaluated the impact of these changes on Net Primary Production (NPP), one of the most important and integrative ecosystem attributes, through the calculation of Human Appropriation of NPP (HANPP), a very complete indicator of human impact on ecosystems. Our results provide a comprehensive and fine grained description of HANPP patterns over an entire biogeographical region for two periods that encompass a strong agricultural intensification process. We used medium resolution land use maps and NPP estimates from sub-national level agricultural statistics and remotely sensed data modeling. Results show that the human impact on the energy flow in RPG ecosystems reached very high levels compared to other regions of the world. The average appropriation of was 42% of the potential vegetation NPP in 2001/2002 and it increased 4.5% during the last years due to an intense land use changes. Most of the HANPP was explained by harvest rather than by land use changes, mainly in the last period due to crops yield increase and the expansion of double crop system as a common agronomic practice. High HANPP values found were associated to a set of environmental impacts that affect ecosystems sustainability and their ability to provide ecosystem services.

1. Introduction

Net Primary Productivity (NPP) (rate of biomass accumulation per unit area) is one of the most important and integrative ecosystem attributes since it determines the amount of energy available for subsequent trophic levels (Lindeman, 1942; Odum, 1971). Increase in world population and consumption has led to land use intensification with increases in both, cultivated area and crop productivity per unit area. Crops and pastures cover 38% of the world's free ice surface (Ramankutty et al., 2008; Monfreda et al., 2008). At the same time, crop yields have increased in recent years (Foley et al., 2011; Zhang and Zhang, 2016). While cultivated areas increased around 12% over the last 40 years, agricultural production more than doubled in the same period, mainly through fertilization, irrigation, high-yielding varieties and mechanization (Foley et al., 2007).

The Human Appropriation of Net Primary Production (HANPP) concept incorporates both aspects of agricultural intensification, increases in cultivated area and increases in crop yield. HANPP quantifies the portion of ecosystems NPP used directly or indirectly by humans (Vitousek et al., 1986), and it reflects the changes in available energy for the trophic web (Field, 2001). Additionally, several works have shown the relationship between HANPP and biodiversity (Wright, 1990; Haberl, 1997; Haberl et al., 2004), changes in atmospheric composition (DeFries et al., 1999; Schimel, 2000) water cycles (Gerten et al., 2005), or the provision of ecosystem services (Daily, 1997; Millennium Ecosystem Assessment, 2005). The central role on energy flow and its linkage with other ecosystem processes make HANPP a comprehensive indicator of human impact on ecosystems.

Although research on HANPP has a relatively short history, several studies have quantified it on a global (Wright, 1990; Rojstaczer et al., 2001; Imhoff et al., 2004; Haberl et al., 2007; Krausmann et al., 2013; Zhou et al., 2018), continental (Gingrich et al., 2015; Plutzar et al.,

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2016); national (Kastner, 2009; Schwarzlmüller, 2009; Fetzel et al., 2014; Niedertscheider et al., 2014; Chen et al., 2015; Saikku & Mattila, 2017; Zhang et al., 2018) or local scales (O'Neill et al., 2007; Andersen et al., 2015; Marull et al., 2018); from a set of definitions related to the ones originally proposed by Vitousek et al. (1986). As far as we know there are no regional works that calculates HANPP for a whole biome.

The Río de la Plata Grasslands (RPG) are one of largest areas of natural temperate sub-humid grasslands in the world (Soriano, 1991; Paruelo et al., 2007). They occupy more than 70×10^6 ha in southern South America, including the Pampas in Argentina and the Campos in Uruguay and southern Brazil. The RPG are one of the world's most fertile areas, most of which are suitable for agriculture and have been subjected in recent years to one of the highest rates of land use change in the world (Graesser et al., 2015; Volante et al., 2015; Baeza, 2016).

In this article we evaluated land use change impacts on energy flow in the RPGs using HANPP as a comprehensive indicator. We calculated the HANPP for the entire RPG region and its changes over time, in a period of intense land use changes. Calculations were based on land cover maps and NPP estimates derived from sub-national level agricultural statistics and modeling of remotely sensed data. We specifically addressed the following questions: How did ecosystems carbon gains vary in response to land use changes?, how did carbon gains changed over time?, how much of the C fixed in the RPG was appropriated by humans? and, how does the HANPP vary in time and space?

2. Materials and methods

2.1. Area and period studied

The study area corresponded to the RPG (Soriano,1991). In a previous work we mapped 7 land use/land cover (LULC) categories: Perennial Forage Resources (PFR), Winter Crops (WC), Summer Crops (SC) Double Crops (DC), Afforested areas and native Forests (A&F), Water and Urban, at annual intervals from 2000/2001 to 2013/2014 (Baeza, 2016). The last two categories were superimposed on all final maps, so they did not vary over time. In this article we used maps of 2 growing seasons 2001/2002 and 2012/2013 (Fig. 1). For more details on the characteristics of the study area and the maps used, see Appendix A.

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.isprsjprs.2018.07.014.

2.2. Definition and calculation of HANPP

Human Appropriation of Net Primary Productivity (HANPP) was defined in this work, as proposed by Wright (1990), Haberl (1997), Haberl et al. (2007), Krausmann et al. (2013) y Haberl et al. (2014), as the sum of the harvested Net Primary Production (NPP) and the differences in NPP due to land use changes. HANPP result from the difference between the NPP in the absence of human influence (NPP of potential vegetation: NPP_0) and the NPP of the actual vegetation

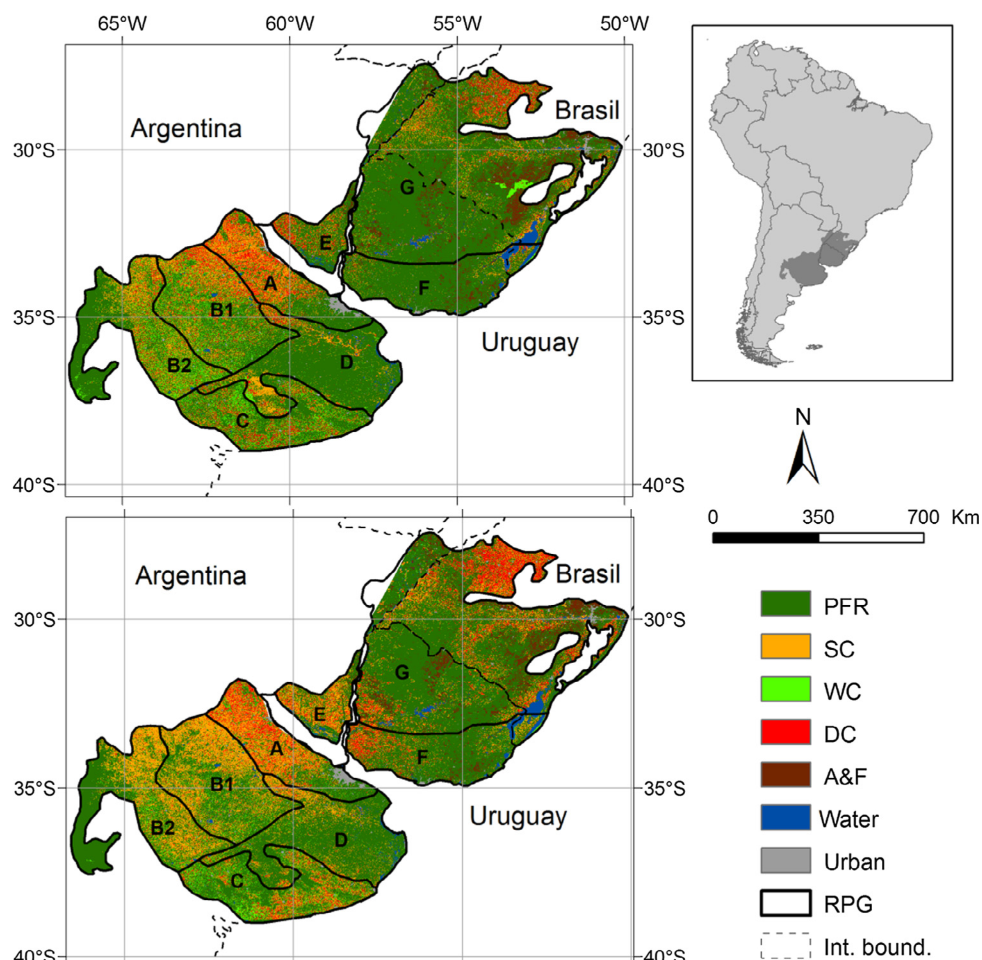

Fig. 1. Land use/land cover maps for Rio de la Plata Grasslands (RPG). Top: 2001/2002. Bottom: 2012/2013. Letters denotes different sub-regions of Rio de la Plata Grasslands. (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Southern Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos.PFR: Perennial Forage Resources; SC: Summer Crops; WC: Winter Crops; DC: Double Crops; A&F: Afforested areas and native Forests. Int. bound: International boundaries.

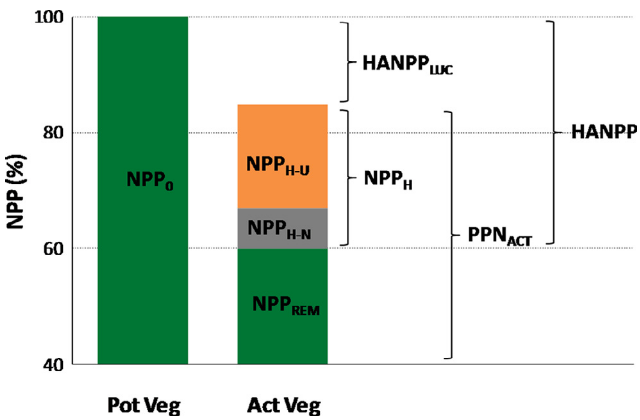

Fig. 2. Components involved in Human Appropriation of Net Primary Productivity (HANPP) calculation. NPP_0: NPP of potential vegetation (Pot Veg); NPP_{ACT}: NPP of the current vegetation; NPP_{REM}: NPP of current vegetation remaining after harvest; NPP_H: harvested NPP; NPP_{H-U}: harvested NPP used by humans as agricultural products (grain, wood, meat, etc.); NPP_{H-N}: harvested NPP not used (Crop residues, underground biomass); $HANPP_{LUC}$: HANPP due to land use changes.
Adapted from Haberl et al. (2014).

remaining after harvest (NPP_{REM}). NPP_{REM} was calculated as the NPP of the current vegetation (NPP_{ACT}) minus the harvested NPP (NPP_H), directly appropriated by humans as agricultural products (grain, wood, meat, etc.) or destroyed during harvest (see below) (Fig. 2).

$$HANPP = NPP_0 - NPP_{REM} = NPP_0 - (NPP_{ACT} - NPP_H)$$

The difference between NPP_0 and NPP_{ACT} represents HANPP due to land use changes ($HANPP_{LUC}$), so HANPP can also be formulated as:

$$HANPP = NPP_H + HANPP_{LUC}$$

This approach requires the calculation of three components: NPP_0, NPP_{ACT} and NPP_H. The calculations were based on two data sets. First, the area covered by each LULC category (in each period considered) and, second, spatial explicit NPP estimates. Depending on the LULC category, NPP estimates were based on official agricultural statistics, or modeled from time series of satellite images.

2.2.1. Spatial resolution of the analysis and data used

The spatial resolution of the analysis corresponded to a 9.3 × 9.3 km cell grid constructed from the geometric structure and the original projection of MODIS images used to generate LULC maps (a total of 8983 cells). Each MODIS pixel has a spatial resolution of 250 × 250 m (approximately 231 × 231 m in our latitude) and each cell of the grid contains exactly 1600 MODIS pixels (40 × 40 pixels) (aprox. 8586 ha). For each of LULC categories (PFR, WC, SC, DC, A&F) we calculated Aboveground NPP (ANPP), Belowground NPP (BNPP), total NPP (NPP) and harvested NPP (NPP_H). The productivities used in HANPP calculations (NPP_{ACT}, NPP_H, NPP_{REM}) were calculated as the average productivity of each class (in $KgDM\,ha^{-1}\,year^{-1}$), weighted by its surface inside each grid cell. Water and Urban categories were excluded from the analysis.

HANPP and their different components for each considered period were compared using repeated measures analysis of variance (ANOVA). Since generally the compared data did not have variance homogeneity, we also included the results of the nonparametric equivalent test (Friedman test). Statistical analyses were performed with STATISTICA 8.0. (Statsoft, Inc. Tulsa, OK, US).

2.2.2. NPP of the current vegetation (NPP_{ACT})

NPP_{ACT} was estimated independently for agriculture (NPP_{ACT-AG}, decomposed in turn in NPP_{ACT} of winter crops, summer crops and double crop), Perennial Forage Resources ($NPP_{ACT-PFR}$), and Afforested areas and Forests ($NPP_{ACT-A\&F}$); according to:

$$NPP_{ACT} = \sum_i NPP_{ACTi} * P_{Ci}$$

where NPP_{ACTi} is the NPP_{ACT} of each LULC category and P_{Ci} is its proportion in each grid cell.

2.2.2.1. Agricultural NPP_{ACT} (NPP_{ACT-AG}). NPP_{ACT} for agricultural categories (SC, WC, DC) was calculated from the estimated yield of the main crops as reported by official agencies of each country at the smallest administrative unit for which information was available (Fig. 2, Appendix B) and for the closest time period to the date of the LULC maps. We used 862 administrative units covering the entire study area (194 municipalities in Brazil, 163 departments in Argentina and 505 census units in Uruguay).

NPP of each crop was calculated from three years average yield, corrected for grain moisture content, by applying two fixed coefficients per crop: Harvest index and below ground biomass/total biomass ratio (Lobell et al., 2002; Hicke et al., 2004; Guerschman, 2005). Harvest index is the ratio of crop harvest to total aboveground biomass of the specific crop type (Donald and Hamblin, 1976; Verón et al., 2002). To estimate total NPP from ANPP we used a belowground/total biomass ratio (Prince et al., 2001). For details in agricultural NPP_{ACT} calculation see Appendix B.

Average NPP (and ANPP or BNPP) of SC and WC categories in each administrative unit were calculated as the weighted average of different crops productivity, according to the area planted with each one and grouped by their growth cycle. In this way, sown areas of different crops reported by official statistics were used exclusively to calculate SC and WC average productivity in each administrative unit and period, while the surfaces used in calculations come from LULC maps. For the DC category, average NPP of each administrative unit was calculated by summing up the average WC NPP and 71% of the average SC NPP, accounting for yield reduction when more than one crop per year is performed (Caviglia et al., 2011).

2.2.2.2. Perennial Forage Resources NPP_{ACT} ($NPP_{ACT-PFR}$). The NPP of PFR (including native grasslands and sowed pastures) was estimated from Normalized Difference Vegetation Index (NDVI) time series provides by MODIS sensor (product MOD13Q1 "Vegetation Indices 16-Day L3 Global 250 m" obtained through the Land Processes Distributed Active Archive Center: EOS Data Gateway) and Monteith́s model (Monteith, 1972). Monteith́s model states that ANPP is equivalent to the total amount of photosynthetically active radiation absorbed by canopy (APAR) multiplied by a radiation-use efficiency coefficient according to following equation:

$$ANPP = APAR * RUE = PAR * fPAR * RUE$$

where APAR is the total amount of photosynthetically active radiation absorbed by green vegetation ($MJ\,m^{-2}\,day^{-1}$), PAR is the incident photosynthetically active radiation ($MJ\,m^{-2}\,day^{-1}$), fPAR is the fraction of that radiation intercepted by green vegetation and RUE, the energy conversion coefficient of absorbed radiation into above-ground biomass ($gDM\,MJ^{-1}$). PAR is measured by meteorological stations and fPAR is positively related to spectral indices derived from the reflectance in the red and infrared portion of the electromagnetic spectrum, such NDVI (Rouse et al., 1974; Sellers et al., 1992, Di Bella et al., 2004; Flanagan et al., 2015; Verrelst et al., 2015). RUE varies between zones, mainly due to vegetation type (species composition, structure and photosynthetic metabolism) and, within the same zone, according to environmental conditions, mainly temperature and available water (Bradford et al., 2005, Piñeiro et al., 2006).

We used three years average of quality filter-NDVI-MODIS time series for each analyzed period. NDVI values were transformed to fPAR values by a linear interpolation (Ruimy et al., 1994) regionally parameterized (Baeza et al., 2010). PAR and RUE values were taken from

Paruelo et al. (2010) and capture internal differences of different RPG sub regions. Belowground NPP of PFR was estimated from biomass partition coefficients in a similar way to than for agricultural crops (see Appendix B for details).

Calculations were performed for a random sample of 1000 pixels classified as PFR in each RPG sub region and each analyzed period. Final NPP values were assigned to grid cells. When two or more pixels were in the same grid cell we assign to the cell the average value. For grid cells without any selected pixel, the value of the nearest grid cell was.

2.2.2.3. Afforested areas and forests NPP_{ACT} ($NPP_{ACT\text{-}A\&F}$). $NPP_{ACT\text{-}A\&F}$ calculations were performed in the same way as for $NPP_{ACT\text{-}PFR}$, estimating it from NDVI time series and Monteitĥs model. As in the previous case, 1000 pixels per RPG sub-region and period were random selected to perform NPP calculations. For each selected A&F pixel, APAR values were calculated using the same images, corrections, time intervals and PAR values than those used for PFR. RUE values for afforested areas and forests were taken from literature. For afforested areas we used the RUE value (0.79 gDM MJ^{-1}) proposed by Vassallo et al. (2012). For forests we used the RUE value proposed by Jarvis & Leverenz (1983) and compiled by Ruimy et al. (1994) for a warm-temperate evergreen forest (0.30 gDM MJ^{-1}). Because the LULC maps used did not discriminate between afforested areas and native forests, the proportion of each class was taken from official statistics. Similarly to previous section, BNPP was estimated from published biomass partition coefficients. We used belowground to aboveground biomass ratio (Root/Shoot ratio: R/S) proposed by Jackson et al. (1996) for temperate forests around the world (R/S = 0.23). A fully and detailed description of methods used to calculate the different PPN_{ACT} components can be found in Appendix B.

2.2.3. Harvested NPP (PPN_H)

Human-harvested NPP (NPP_H) was calculated according to the definition proposed by Haberl et al. (2007), which includes both the appropriate biomass as agricultural products (grain, wood, meat, etc.) and the biomass destroyed during harvest. Thus, all aerial plants residues and belowground biomass of agricultural (SC, WC, DC) and A&F categories are included in this calculation. In PFR, despite biomass "harvested" by herbivores, plants remains alive and therefore its belowground biomass is not computed as harvested. Under this definition, for SC, WC, DC and A&F, NPP_H is equal to NPP. Livestock NPP_H in PFR ($NPP_{H\text{-}PFR}$) was calculated as a fixed proportion of $ANPP_{PFR}$ using the biomass harvest index by domestic herbivores developed by Oesterheld et al. (1992) and Golluscio et al. (1998), and a forage digestibility of 65% (Guerschman, 2005).

NPP harvested but not appropriated as agricultural product was also quantified because it constitutes a very important return flow of carbon to ecosystems. This harvested but not appropriated biomass is not available to herbivores but mostly returns to ecosystems and is available for decomposers. This return flow was calculated as the difference between the total NPP_H minus the NPP_H used by humans as direct agricultural products ($NPP_{H\text{-}U}$).$NPP_{H\text{-}U}$ is also defined by its three components: agricultural, livestock and forestry. In the agricultural component $NPP_{H\text{-}U}$ represents NPP directly appropriate as grain and is calculated, as explained above, from crop yields corrected by the moisture content. In the case of PFR, $NPP_{H\text{-}U}$ is the ANPP consumed and assimilated by cattle. For A&F, $NPP_{H\text{-}U}$, (i.e. harvested wood for pulpwood, solid wood , etc.), was estimated following the approach used by Harberl et al. (2007), as a constant proportion of the ANPP of native forests and afforested areas. As in NPP_{ACT}, used and unused NPP_H were calculated for each period from a 3 years average, in order to avoid the effect of years with unusually high or low productivities. For details in NPP_H calculations see Appendix B.

2.2.4. Potential vegetation NPP (NPP_0)

The NPP of potential vegetation (NPP that would exist in the absence of human land use: NPP_0) is usually estimated from vegetation models of varying complexity, ranging from empirical relationships between NPP and climate, to dynamic ecophysiological models. In this work NPP_0 was assumed equal to NPP_{PFR} (as proposed by Guerschman (2005). Most of the PFR corresponded to native grasslands, the original

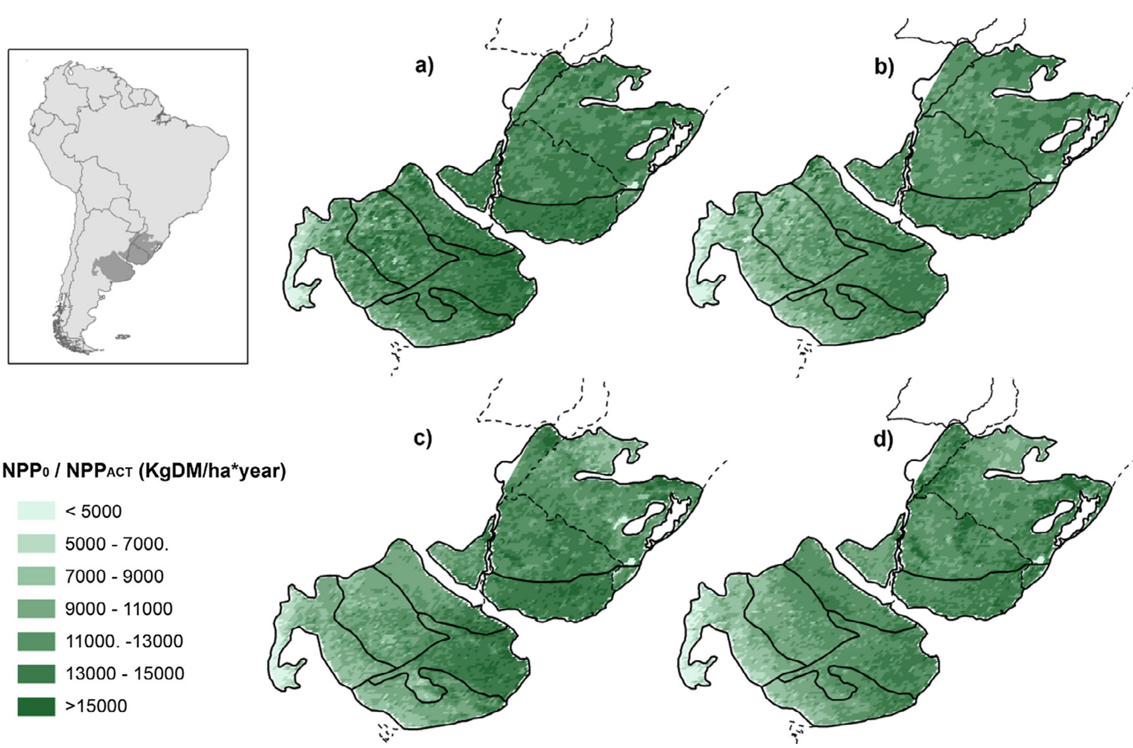

Fig. 3. Potential vegetation NPP (NPP_0) for 2001/2002 (a) and 2012/2013 (b); and current vegetation NPP (NPP_{ACT}) for 2001/2002 (c) y 2012/2013 (d) in Rio de la Plata Grasslands.

vegetation type of the whole region. Grazing by domestic herbivores did not have consistent effects on NPP on these grasslands (Oesterheld et al., 1999; Rusch and Oesterheld, 1997; Altesor et al. 2005).

3. Results

3.1. Net Primary production of potential vegetation (NPN_0)

Total NPP_0 (the NPP that would exist in the absence of human disturbances, assuming that the entire study area was covered by native grasslands) in the RPG was higher ($F_{(1,\ 8965)} = 5124$, $p < 0.001$; $X^2_{(1,\ 8965)} = 3388$, $p < 0.001$) in 2001/2002, where it reached 9.70×10^{11} kgDM year^{-1}, than in 2012/2013, where it reached 8.68×10^{11} kgDM year^{-1} (approximately 100 TgDM year^{-1} less), with average values for grid cells of 12930 and 11563 kgDM ha^{-1} year^{-1} for 2001/2002 and 2012/2013 respectively. This temporal pattern, with lower values during 2012/2013, occurred in all RPG sub regions ($p < 0.001$, data not shown). Overall NPP_0 increased from Southwest to Northeast with a similar pattern in both periods. Average NPP_0 was maximum in the Southern Campos (14180 and 13108 kgDM ha^{-1} year^{-1}, for 2001/2002 and 2012/2013 respectively) and minimum in West Inland Pampa, in both periods (10198 and 8148 kgDM ha^{-1} year^{-1}, for 2001/2002 and 2012/2013 respectively) (Fig. 3a and b).

3.2. Net Primary production of actual vegetation (NPP_{ACT})

Actual NPP was slightly lower ($F_{(1,\ 8965)} = 161$, $p < 0.001$; $X^2_{(1,\ 8965)} = 288$, $p < 0.001$) in 2001/2002 than 2012/2013, reaching 8.79×10^{11} and 8.63×10^{11} kgDM year^{-1} for the entire RPG region, with average values of 11716 and 11511 kgDM ha^{-1} year^{-1}, respectively. Unlike NPP_0, there was no clear Southwest-Northeast gradient in NPP_{ACT} and its regional patterns was more associated to LULC differences. Again, maximum average values occurred in the Southern Campos (13858 and 13004 kgDM ha^{-1} year^{-1}, 2001/2002 and 2012/2013 respectively) and minimums in the West Inland Pampa (8508 and 7637 kgDM ha^{-1} year^{-1}, for 2001/2002 and 2012/2013 respectively) (Fig. 3c and d).

Different land uses contributed differentially to NPP_{ACT}. Fig. 4 shows the relative contribution of different LULC categories to NPP_{ACT} in both periods, for the whole region (a) and for each RPG sub region (b). Considering the whole region, the NPP_{ACT} provided by Perennial Forage Resource (PFR) was always greater than that provided by the other land covers, representing 76% in 2001/2002 and 63% in 2012/2013. Differences in NPP_{ACT} between two periods is mainly explained by the growth of crop contribution, which increased from 19.2% in 2001/2002 to 31.4% in 2012/2013, while $NPP_{ACT\text{-}A\&F}$ contribution remained relatively constant (4.8% and 5.5%, respectively) (Fig. 4a). This pattern of higher contribution of PFR to NPP_{ACT} occurred in all RPG sub regions, except for the Rolling and Flat Inland Pampas during 2012/2013, where the contribution to NPP_{ACT} by crops ($NPP_{ACT\text{-}AG}$) was greater. In all sub regions, the contribution of crops to NPP_{ACT} increased between the periods studied. The highest increase in absolute terms occurred in the Mesopotamic Pampa, where it rose from 20.9% of NPP_{ACT} in 2001/2002 to 48.2% in 2012/2013. Minimum increases in absolute terms occurred in the Flooding Pampa, where the contribution of crops went from 11.4 to 18.2% of NPP_{ACT} (Fig. 4b). In relative terms, largest increase occurred in Southern Campos, where crops contribution increased by 186% (7.2% and 20.5% of NPP_{ACT} in 2001/2002 and 2012/2013 respectively). Lowest relative increase occurred in the Inland Pampas where crops contribution to NPP_{ACT} grew 26.7 and 30.3% respectively. This increase in agricultural NPP resulted not only from areal expansion (Fig. 1), but also to yield increases (Table 1).

3.3. Human appropriation of NPP

Human Appropriation of Net Primary Production (HANPP) in RPG decreased more than 2.5 TgDM (2.75×10^9 kgDM) in the period between the two dates analyzed (4.05×10^{11} kgDM in 2001/2002 and 4.02×10^{11} kgDM in 2012/2013). Such decrease was mainly driven by a 10% decrease in NPP_0 and relatively stable NPP_{ACT} values (see above). This implied that HANPP explained by land use changes ($HANPP_{LUC}$) was very low during 2012/2013 (only 0.5% of NPP_0) (Fig. 5, Table 2). The decrease in HANPP due to a decrease in NPP_0 was offset by increase in harvested NPP (NPP_H), which increased from 3.13×10^{11} kgDM year^{-1} in 2001/2002 to 3.98×10^{11} kgDM year^{-1} in 2012/2013 (32,3–45.8% of NPP_0).

Despite decreasing in absolute terms, in relative terms HANPP was higher ($F_{(1,\ 8965)} = 944$, $p < 0.001$; $X^2_{(1,\ 8965)} = 1006$, $p < 0.001$) in 2012/2013 when it reached 46.5% of the NPP_0, 4.5% more than 2001/2002. In 2001/2002 $HANPP_{LUC}$ represented 22.6% of total AHPPN, while NPP_H accounted for 77.4%. This means that land use changes implied a NPP decrease in RPG around 9.4%. In 2012/2013 HANPP was explained almost exclusively by harvest (99.5% of the total AHPPN), since $HANPP_{LUC}$ was minimal as a consequence of NPP_0 decrease (Fig. 5, Table 2).

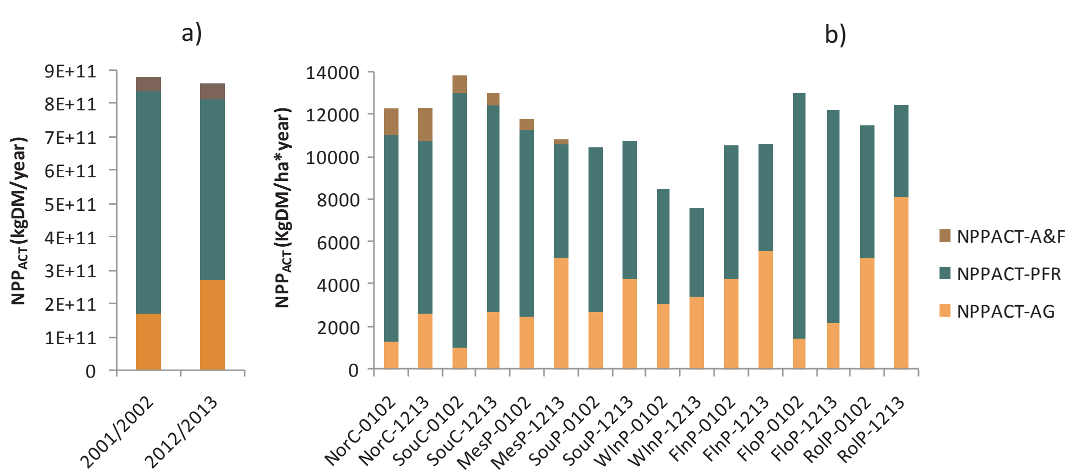

Fig. 4. Contribution of each category, in each period, to NPP of current vegetation (NPP_{ACT}) for entire RPG region (a) and average values for each sub region (b). A&F: Afforested areas and Forests; PFR: Perennial Forage Resources; AG: Agricultural categories (summer, winter and double crops). NorC: Northern Campos; SouC: Southern Campos; MesP: Mesopotamic Pampa; SouP: Southern Pampa; WInP: West Inland Pampa; FInP: Flat Inland Pampa; FloP: Flooding Pampa; RolP: Rolling Pampa.

Table 1
Average NPP (KgDM/ha*year) for each LULC, each RPG sub region and each analyzed period. NorC: Northern Campos; SouC: Southern Campos; MesP: Mesopotamic Pampa; SouP: Southern Pampa; WInP: West Inland Pampa; FInP: Flat Inland Pampa; FloP: Flooding Pampa; RolP: Rolling Pampa. PFR: Perennial Forage Resources; SC: summer crop; WC: winter crop; DC: double crop; A&F: Afforested areas and Forest. The NPP values for each sub region and LULC category were statistically different between periods ($p < 0.01$) except for SC and A&F in the Mesopotamic Pampa (repeated measures ANOVA and Friedman test).

	PFR		SC		WC		DC		A&F	
	01/02	12/13	01/02	12/13	01/02	12/13	01/02	12/13	01/02	12/13
NorC	12973	12097	10946	11353	3671	5753	9175	13814	13374	14588
SouC	14172	13096	10567	10909	4388	7305	9454	15051	14446	13965
MesP	13631	12286	8623	8466	3387	6821	7875	12832	9986	10046
SouP	12522	11149	5706	6162	6284	10701	8790	15076		
WInP	10198	8148	8479	7412	4471	5182	8760	10444		
FInP	12607	10321	9553	10500	5624	8074	10327	15529		
FloP	14179	12688	8251	8588	5243	10168	9361	16266		
RolP	13609	11988	9468	11060	5159	8489	9971	16341		
Mean	12897	11398	8875	9056	4724	7715	9106	14145	12602	12866

3.3.1. Human appropriation of PPN due to land use change

Average HANPP due to land use changes ($HANPP_{LUC}$) was much higher ($F_{(1,\ 8965)} = 3549$, $p < 0.001$; $X^2_{(1,\ 8965)} = 2017$, $p < 0.001$) during 2001/2002 when reached 1214 kgDM ha^{-1} year^{-1}, than in 2012/2013 (54 kgDM ha^{-1} year^{-1}). This pattern varies among RPG sub regions and periods and responds to the relative variation of NPP_0 and NPP_{ACT}. For example, negative $HANPP_{LUC}$ values were associated with low NPP_0 values and/or high NPP_{ACT} values due to land use changes to highly productive land covers (Afforested areas, Double crop, maize or rice crops with high yields) (Fig. 6). During 2001/2002, average $HANPP_{LUC}$ per RPG sub region was always positive, with maximum values in the Rolling Pampa (2094 kgDM ha^{-1} year^{-1}) and minimums in the Southern Campos (322 kgDM ha^{-1} year^{-1}). In general, during 2001/2002, $HANPP_{LUC}$ values were much higher in the Pampas (somewhat less in Flooding Pampas) than in the Campos. During 2012/2013 average $HANPP_{LUC}$ values were generally low (excluding the Mesopotamic Pampa), and were negative in the Northern Campos, West Inland Pampa and Rolling Pampa. Maximum average $HANPP_{LUC}$ during 2012/2013 occurred in the Mesopotamic Pampa (1421 kgDM ha^{-1} year^{-1}) and minimum in the Rolling Pampa (-479 kgDM ha^{-1} year^{-1}) (Figs. 6 and 7)

3.3.2. Human appropriation of NPP due to harvest

The HANPP due to harvest (NPP_H) varied regionally with high values associated with the large agricultural foci. Maximum average values occurred in the Rolling Pampa in both periods (6236 and 8770 kgDM ha^{-1} year^{-1}, for 2001/2002 and 2012/2013 respectively), while minimum values occurred in the Flooding Pampa (3348 and 3729 kgDM ha^{-1} year^{-1}, for 2001/2002 and 2012/2013 respectively)

Table 2
Energy flows related to Human appropriation of NPP for the entire RPG region expressed in absolute values and as percentage of NPP of potential vegetation (NPP_0) for 2001/2002 and 2012/2013 periods. NPP_{ACT}: NPP of current vegetation for Perennial Forage Resources (PFR), Agricultural categories (AG) and Afforested areas and Forest (A&F); and for the sum of the three categories ($NPP_{ACT\text{-}Total}$); $HANPP_{LUC}$: Human appropriation of NPP due to land use changes; NPP_H (for PFR, AG, A&F and the sum of them); Total HANPP: sum of $HANPP_{LUC}$ and NPP_H; Return: energy return to ecosystems as biomass harvested or destroyed but not used.

	2001/2002		2012/2013	
	kgDM/year	%	kgDM/year	%
NPP_0	9.70×10^{11}	100	8.68×10^{11}	100
NPP_{ACT_PFR}	6.68×10^{11}	68.8	5.44×10^{11}	62.7
NPP_{ACT_AG}	1.69×10^{11}	17.4	2.71×10^{11}	31.3
$NPP_{ACT\_A\&F}$	0.42×10^{11}	4.3	0.47×10^{11}	5.5
NPP_{ACT_Total}	8.79×10^{11}	90.6	8.63×10^{11}	99.5
$HANPP_{LUC}$	0.92×10^{11}	9.4	0.05×10^{11}	0.5
$NPP_{H\text{-}PFR}$	1.03×10^{11}	10.6	0.79×10^{11}	9.1
$NPP_{H\text{-}AG}$	1.69×10^{11}	17.4	2.71×10^{11}	31.3
$NPP_{H\text{-}A\&F}$	0.42×10^{11}	4.3	0.47×10^{11}	5.5
$NPP_{H\text{-}Total}$	3.13×10^{11}	32.3	3.98×10^{11}	45.8
NPP_{REM}	5.65×10^{11}	58.2	4.65×10^{11}	53.6
Total HANPP	4.05×10^{11}	41.8	4.02×10^{11}	46.4
Return	0.91×10^{11}	9.4	2.11×10^{11}	24.4

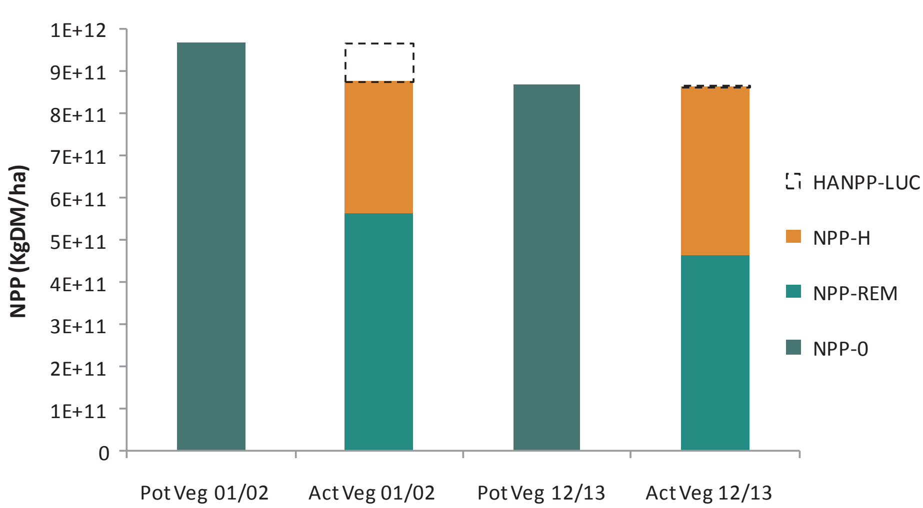

Fig. 5. Human appropriation of NPP and its different components for RPG region in 2001/2002 and 2012/2013. Pot Veg: potential vegetation; Act Veg: current vegetation, $HANPP_{LUC}$: Human appropriation of NPP due to land use changes; NPP_H: Appropriate NPP at harvest; NPP_{REM}: NPP remaining in the ecosystem, NPP_0: NPP of potential vegetation.

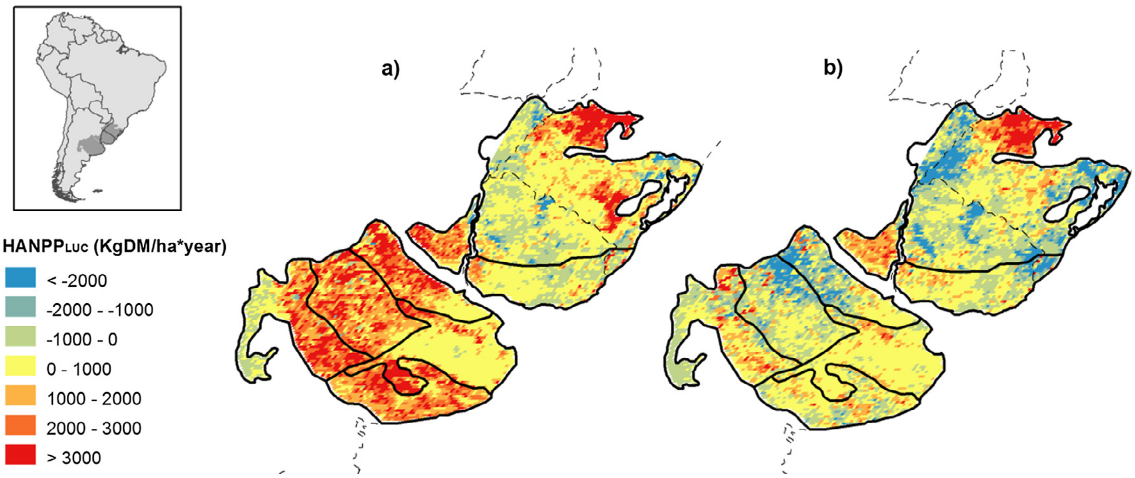

Fig. 6. Human appropriation of NPP due to land use change ($HANPP_{LUC}$) in RPG for 2001/2002 (a) and 2012/2013 (b).

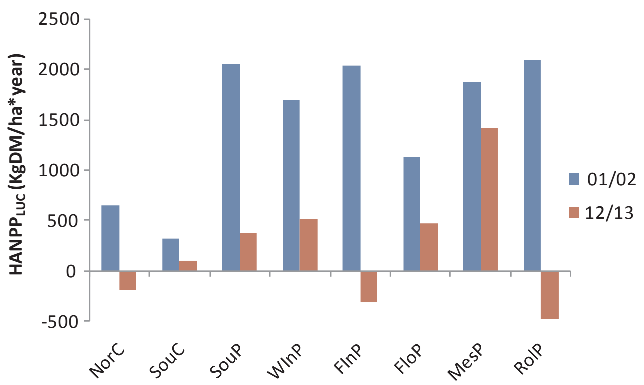

Fig. 7. Average Human Appropriation of NPP due to land use change ($HANPP_{LUC}$) for RPG sub regions in 2001/2002 and 2012/2013. NorC: Northern Campos; SouC: Southern Campos; SouP: Southern Pampa; WInP: West Inland Pampa; FInP: Flat Inland Pampa; MesP: FloP: Flooding Pampa; Mesopotamian Pampa; RolP: Rolling Pampa.

(Fig. 8).

NPP_H increases were mainly located in large agricultural foci and were related both to an increase of the sown/afforested area and to an increase in productivity associated with higher yields and the expansion of the area devoted to DC (Fig. 8c). Largest increases occurred on both sides of the Uruguay River (Mesopotamic Pampa, West of Southern Campos and southwest of Northern Campos), the northwestern half of the Rolling Pampa, east of the Southern Pampa, north of the Northern Campos, some sectors of the Inland Pampa (Flat and West) and northwest of the Northern Campos (the Brazilian side of the Argentina-Brazil border). Average NPP_H was always higher ($F_{(1,\ 8965)} = 2671$, $p < 0.001$; $X^2_{(1,\ 8965)} = 1596$, $p < 0.001$) during 2012/2103, with maximum differences in the Rolling Pampa, showing an increase of 2534 kgDM ha^{-1} $year^{-1}$, and minimum differences in the West Inland Pampa, with an increase of 172 kgDM ha^{-1} $year^{-1}$. NPP_H decreases occurred in areas dominated by PFR in both periods and were associated with high NPP in 2001/2002.

The increase in the relative importance of NPP_H implies an increase in the NPP appropriated by humans but not used (agricultural residues, belowground biomass, etc.), which mostly remain in the ecosystem, but is exclusively available for detritivorous. This return flow reached 0.91×10^{11} Kg DM $year^{-1}$ during 2001/2002 and 2.11×10^{11} KgDM $year^{-1}$ during 2012/2013 (Table 2).

3.3.3. Total Human appropriation of NPP

Total HANPP, resulting from sum of land use change ($HANPP_{LUC}$) and harvest (NPP_H) appropriation, was always positive (in both periods and for the whole region), with values ranging from 209 to 16963 kgDM ha^{-1} $year^{-1}$, during 2001/2002, and between 185 and 15528 kgDM ha^{-1} $year^{-1}$ during 2012/2013. In relative terms, HANPP values ranged from 6.6% to 100% of the NPP_0 in 2001/2002 and between 6.3% and 100% in 2012/2013. This implies that human activity generated net carbon losses in the whole region, despite the high yields of some agricultural and tree crops. Maximum average values for the different RPG sub regions occurred in the Rolling Pampa, reaching 8338 and 8291 kgDM ha^{-1} $year^{-1}$ for 2001/2002 and 2012/2013 respectively. Minimum average values occurred in Southern Campos during 2001/2002 (4070 kgDM ha^{-1} $year^{-1}$) and in Flooding Pampa during 2012/2013 (4199 kgDM ha^{-1} $year^{-1}$).

Fig. 9 shows HANPP spatial variation in both periods, expressed as a percentage of NPP_0. These variations were mostly associated with those of NPP_H (the most important component of total HANPP), so their spatial patterns were similar, mainly during 2012/2013 when the relative importance of $HANPP_{LUC}$ was minimal. Similarly, HANPP differences between the two periods mainly reflect what happened with NPP_H. Extremely low values in HANPP differences recorded in southwest of Flooding Pampa and west of Northern Campos may be the consequence of cartographic errors in the 2001/2002 LULC map.

4. Discussion

We documented the human impact on the energy flow over the Rio de la Plata grasslands both in terms of the relative importance of different components of the human appropriation of the NPP and in the amount of NPP remaining in the systems. Previous estimates described patterns of HANPP at the scale of countries provided global figures. Our study went a step further providing a comprehensive and fine grained description of HANPP patterns over an entire biogeographycal region.

In contrast to other works, our HANPP estimates were based on medium resolution LULC maps (250x250m), for a large area (ca. 82.5 million Ha) and for two periods that encompass a strong agricultural intensification process. In addition, calculations were based on agricultural statistics at sub national level (departments, municipalities, census units) and NPP derived from a solid model based on remotely sensed data. This gives to calculations a high level of detail. Previous studies on HANPP were exclusively based on sub national agricultural statistics (Guerschman, 2005), use medium resolution LULC maps and national or regional agricultural statistics (Haberl et al., 2007; Krausmann et al., 2013), or did not consider LULC maps to describe the spatial patterns (Musel, 2009; Kastner, 2009; Gingrich et al., 2015; Saikku & Mattila, 2017).

Our results showed the large proportion of NPP necessary to meet a

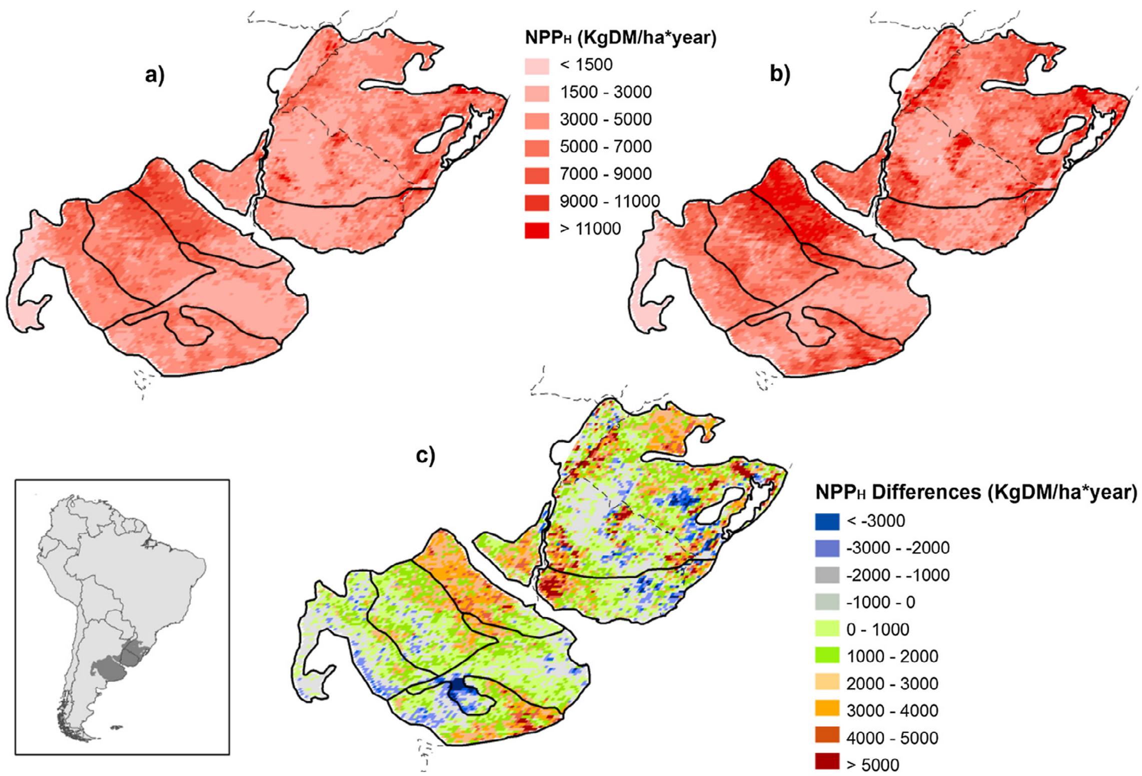

Fig. 8. Human appropriation of NPP by harvest (NPP_H) for 2001/2002 (a), 2012/2013 (b) and differences between two periods (2012/2013–2001/2002) (c).

single species needs, and hence, the degree of influence that humans have on Earth's resources. More than 40% of RPG NPP is appropriate every year (and used directly or indirectly) by humans. Agriculture intensification led to an increase in HANPP, from 41.8% to 46.4% in 11 years. HANPP surpassed the 70–80% of NPP_0 in agricultural and forestry foci, mainly during the last years. Most of this increase was driven by NPP_H increases rather than by land use changes ($HANPP_{LUC}$). NPP_H increases resulted not only from an increase in cultivated area,

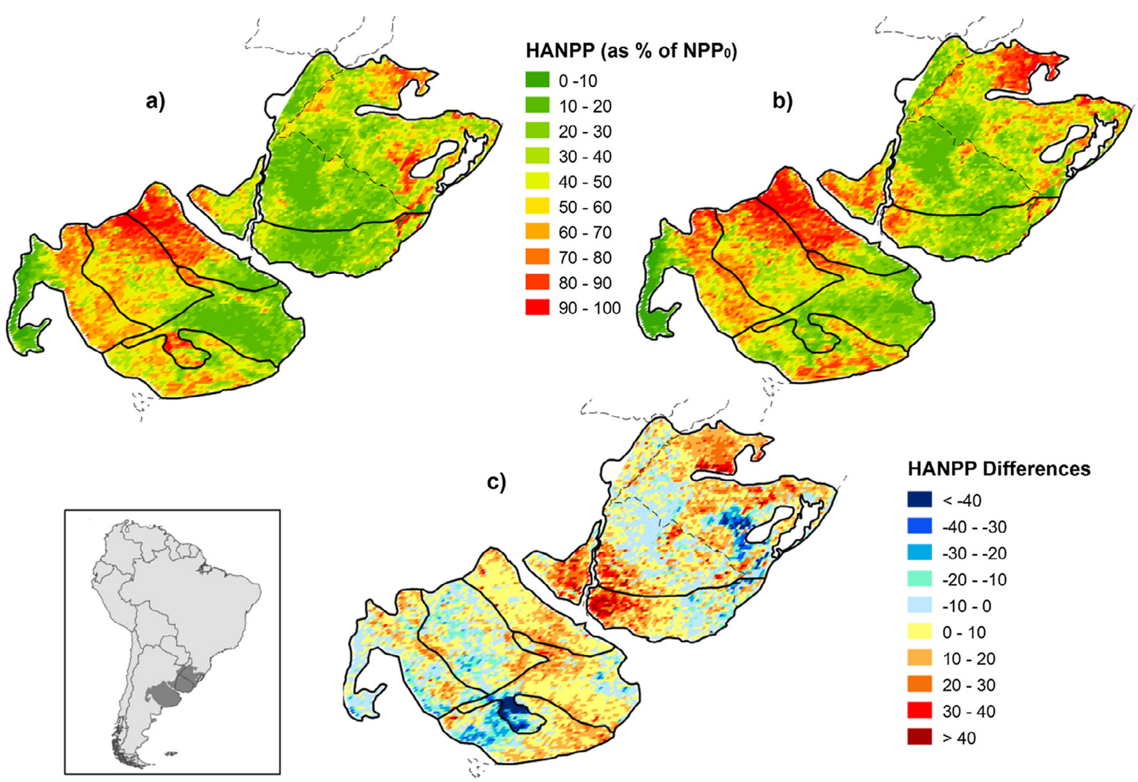

Fig. 9. Human Appropriation of NPP (HANPP) in RPG, expressed as a percentage of NPP potential vegetation (PPN_0) for 2001/2002 (a), 2012/2013 (b) and differences between two periods (2012/2013–2001/2002) (c).

but also from yields increases and to the expansion of double crop systems. This increase in the cultivated area of the RPG has been already reported in other studies (Guerschman, 2005, Baldi et al., 2006, Viglizo et al., 2011, Graesser et al., 2015; Modernel et al., 2016; Dias et al., 2016; de Oliveira et al., 2017).

The HANNP values estimated in this study were higher than those reported at global scale. For example, Vitousek et al. (1986) in his HANNP intermediate estimate, reports values of 30.7%; Rojstaczer et al. (2001), 32%; Haberl et al. (2007), 23% of $NPP_{0,}$ respectively. These results represent planet averages, and include areas with low HANPP due to low NPP (deserts, high latitudes) or sparsely populated or protected (rainforests), to regions with very high HANPP such as most of Europe, India, Southeast Asia or some portions of the United States. Maps presented in Haberl et al. (2007), show, for the RPG, HANPP values between 30 and 60% of the NPP_0 with spatial patterns similar to our results. The only regional antecedent of HANPP estimation conducted by Guerschman (2005) reports average values for Pampa region around 25% of NPP_0, ranging from 20 and 45%. The low HANPP values reported by Guerschman (2005) are due to the calculation method, which does not include the unused part of NPP_H (harvest residues and belowground biomass).

The HANPP increase found in this work is consistent with the results of Krausmann et al. (2013), the only study that analyzes the temporal trajectory of the HANPP worldwide in the last century. Krausmann et al. (2013) report that the world average HANPP went from 13% to 25% of NPP_0 during the 20th century, with maximum regional increases in Asia, Latin America and Africa. These results average values throughout Latin America, masking the high levels of HANPP in the RPG with areas of very low HANPP, such as a large part of the Amazonian rainforest or the Patagonian steppes of southern Argentina and Chile (Haberl et al., 2007).

4.1. Potential NPP of RPG

Calculated NPP_0 (and $NPP_{ACT\text{-}PFR}$) values are comparable to NPP (or ANPP) values reported in other RPG studies, using satellite imagery (Piñeiro et al., 2006; Paruelo et al., 2010; Baeza et al., 2010; Gallego et al., 2017) or biomass harvesting (Rusch and Oesterheld, 1997; Pérez and Frangi, 2000; Altesor et al., 2005; Jaurena et al., 2016). Our NPP_0 estimations in RPG are in the same order as those reported by Haberl et al. (2007) for global NPP_0, which reach 502 gC m^2 year^{-1} (or 11156 kgDM ha^{-1} year^{-1}, applying the necessary corrections); in addition, maps presented in these work shows NPP_0 values for RPG region between 600 and 800 gC m^2 year^{-1}, a similar range to those reported in our work.

NPP_0 spatial variation is linked to environmental gradients. First, it increases throughout Southwest-Northeast precipitation gradient that goes from semi-arid conditions in central Argentina to humid in southern Brazil (Soriano, 1991; Paruelo et al., 2007). This positive relationship between NPP and precipitation has been extensively documented for grasslands in the region (Guerschman et al., 2003; Paruelo et al., 2010) and the word (Lauenroth, 1979; Sala et al., 1988; McNaughton and Sala, 1993; Guo et al 2012; Knapp et al., 2015). Within this general pattern, there are portions of RPG where NPP_0 decreases due to restrictions imposed by substrate type (Sala et al., 1988), as large areas with shallow soils in different portions of the Northern Campos (Duran, 1991; Paruelo et al., 2007).

Since grasslands NPP is strongly controlled by precipitation, lower NPP_0 values in 2012/2013 were probably due to lower water availability than in 2001/2002. An analysis of cumulative rainfall in years used to make NPP_0 estimates (26/06/2000–25/06/2003 for 2001/2002 and 26/06/2011–25/06/2014 for 2012/2013), based on data from the 5 meteorological stations throughout Uruguay (INIA, agroclimatic data bank), shows that the cumulative rainfall in the period used to calculate 2012/2013 NPP estimates was, on average, 24% lower than those used for 2001/2002. Another explanation for NPP_0 decrease is the degradation of PFR over time caused by overgrazing. Texeira et al. (2015), detected significant decreasing trends in the fraction of Photosynthetically Active Intercepted Radiation by Vegetation (fPAR) in areas dominated by natural grasslands in the Northern Campos of Uruguay, through a 30-year time series analysis. This work estimated an ANPP reduction for these grasslands between 10 and 25%. More detailed analyzes are needed to determine the causes behind NPP_0 reduction.

4.2. Current NPP of RPG ecosystems and their variations in space and time.

Despite intense process of land use change, net carbon intakes in the Río de la Plata Grasslands remained relatively constant, with values around 8.6–8.8 × 10^{11} kg year^{-1}. This NPP_{ACT} stability occurred in all RPG sub regions, with mean maximum differences between periods of around 10%. This is mainly due to the combined effect of increased crop contribution (both in area and yield, see above) and decrease in PFR contribution to NPP_{ACT}. As with crops, PFR contribution to NPP_{ACT} decreased both by a reduction in its area and by a lower NPP, as discussed in the previous section.

In spite of the expansion of crops, grasslands made the largest contribution to total Carbon inputs in the RPG, except in the most transformed sub-regions (the Rolling Pampa and the Flat Inland Pampa). However, crops contribution to NPP increased markedly, practically doubling, during the period analyzed.

4.3. HANPP partition between PPN_H and $HANPP_{LUC}$ and their variations over time

HANPP due to land use changes ($HANPP_{LUC}$) markedly decreases in 2012/2013, reaching negative values in some RPG sub regions. This result coincides with those of Krausmann et al. (2013), which show that $HANPP_{LUC}$ declined over time around the world, while PPN_H increased. In RPG, this pattern resulted not only to a reduction in NPP_0, but also to crop yield increases and the expansion of double cropping. In single crop systems, the fallow periods reduce the total amount of radiation intercepted by green tissues compared to natural grasslands. When crops are very productive, NPP exceeds that of original vegetation (Burke et al., 2000; Brye et al., 2002) and $HANPP_{LUC}$ becomes negative. A similar situation occurs when grasslands are replaced by tree plantations, which surpass, soon after planted, grasslands NPP (Nosetto et al., 2005; Vassallo et al., 2012). Similar results in the $HANPP_{LUC}$ have been reported by other authors for several regions of the world (Haberl et al., 2007; Plutzar et al., 2016).

4.4. HANPP relations at regional and global levels

The recorded increase in RPG HANPP contrasts with the reduction detected in other regions of the world (see, for example, Musel, 2009, Schwarzlmüller, 2009, Niedertscheider et al., 2014). This contrast in the sign of the temporal trends reveals the teleconections existing in the biosphere conceived as a system. For example, for nine European countries, Gingrich et al. (2015) report significant HANPP decreases in recent decades. This implies a decrease in the anthropogenic pressure in Europe, but not necessarily, less pressure on the global environment. From trade analysis it can be seen that this is partly due to decline in agriculture European production and import of biomass from other world regions (Gingrich et al., 2015; Kastner et al., 2014). Erb et al. (2009) maps show the RPG region as net exporter, with differences between HANPP and the portion locally consumed around 1000 and 5000 kgDM ha^{-1} year^{-1}, depending on the portion of RPG considered. Since the countries included in the RPG are major exporters of food and raw materials, a significant part of the increased pressure on these ecosystems occurs to meet the consumption needs of other parts of the world

4.5. HANPP environmental impacts

Since HANPP quantifies how humans change biomass flows, it directly describes the human impact on the available energy in the trophic web and its partition into different consumption chains. For example, energy available for herbivory trophic chains is markedly reduced due to human extraction and/or destruction of much of the biomass. Energy extracted or destroyed by harvest in the RPG represented 32.3 and 45.8% of the NPP_0 in 2001/2002 and 2012/2013 respectively. On the other hand, the energy flow form plants to decomposers (without herbivorous mediation) is noticeably increased, generally in punctual and great magnitude events, by harvested but not used biomass (belowground biomass, crop residues). This flow towards decomposers was multiplied by 2.5 in RPG in the analyzed period.

HANPP directly impact on biogeochemical cycles (Haberl et al., 2014). For example, Caride et al. (2012) reported 15% loss of soil organic carbon by agriculture for Pampean region. The high levels of HANPP found and the fact that HANPP was always positive implies that human activity generated net carbon losses in the entire region.

HANPP often involves drastic changes in vegetation cover (the replacement of perennial grasslands by annual crops or tree plantations) that impact on water dynamics, so it is also expected that HANPP is directly related to strong changes in water cycle by modifying evapotranspiration (ET). Nosetto et al. (2012) evaluated the effect land uses changes on ET in a transition zone between grasslands and xerophytic forests in the western border of the RPG finding a 41% increase in ET when grassland are afforested and a 14% decrease when grasslands are replaced by annual crops.

Since the replacement of the original vegetation by crops or tree plantations results in fragmentation (or total loss) of habitats available to other species, HANPP is also related to biodiversity loss. Potential HANPP effects on biodiversity are implicit on the origin of the concept: Vitousek et al. (1986) argued that the unequal proportion of NPP appropriated by humans contributed to species extinction. Wright (1990) includes the species-energy hypothesis (Wright, 1983) in HANPP concept. The species-energy hypothesis states that the available energy is an important factor determining large-scale biodiversity patterns. Wright (1990) uses HANPP calculations to estimate the number of extinct or endangered species and finds results that coincide with the reported values. Haberl (1997) and Haberl et al. (2004), found results coinciding with the species-energy hypothesis, reporting negative relationships between HANPP and diversity or positive relationships between HANPP and extinctions of different taxa. Our analysis design (a regular grid of approximately 10 × 10 km) would allow to analyze the relationship between HANPP and the diversity patterns of different taxa and to evaluate the species-energy hypothesis in this region.

4.6. Scope and limitations of used approach

HANPP estimates have different sources on uncertainties, some derived from the assumptions and other from the input data. Errors in the LULC maps, NPP estimates derived from both grain yields and spectral data, could affect the reported results due to error accumulation and propagation. A sensitivity analysis conducted by Rojstaczer et al. (2001) on the parameters used to estimate HANPP and its effect on the results showed that the variables that provide greater uncertainty were linked to agricultural productivity (yield and sown area) and productivity of tropical forests (secondary forest biomass, deforestation for agricultural use). In our work, agricultural productivity is calculated from three years average of agricultural statistics reported with good level of detail and LULC maps with medium resolution and good levels of accuracy (see Appendix A), so that, the contribution to the uncertainty on HANPP patterns should be minimal. In the RPG, natural forests are relatively marginal, they are located in sites with severe restrictions to agriculture and have low replacement rates. The influence of this source of uncertainty highlighted by Rojstaczer et al. (2001) should not significantly affect our results.

To minimize errors and biases on general description of the impacts of land use and its changes, on the NPP and its appropriation by humans at regional and sub regional levels we were particularly careful in avoiding: (1) spatial biases, (2) artifacts from downscaling information, and (3) the influence of particular years. In this sense, the calculations made for grid cells of approximately 10 × 10 km, with LULC maps of medium spatial resolution (250 × 250 m) and NPP estimates from NDVI-MODIS time series (250 × 250 m) or agricultural statistics to the best available resolution (administrative unit average size: approximately 90000 ha), ensured a good representation of what happened in each of the RPG sub regions, clearly capturing patterns also reported in other works. Additionally, all NPP estimates (both derived from agricultural statistics and those modeled from remote sensing) were generated as the average of 3 years, in order to minimize the effect of years with unusually high or low productivities (due to changes in climate, presence of pests, etc.).

4.7. Conclusions

By quantifying and mapping the changes produced by humans on ecosystem energy flow, AHPPN provides an estimate of land use intensity. Our regional analyses showed that humans appropriate more than 40% of the annual production of the entire Rio de la Plata Grasslands (RPG) biome, a percentage much higher than that found in other regions of the world or in global scale studies based on the same approach (Vitousek et al., 1986; Rojstaczer et al., 2001; Haberl et al., 2007). We showed that the appropriate percentage increased due to the strong process of agricultural intensification that took place in the RPG. HANPP was highest in agricultural and forestry foci where it may exceed 70–80% and it was mainly associated with increases in harvested NPP due to both the expansion of the cultivated area and the crop yields. A very important portion of RPG HANPP would satisfy the consumption needs of other parts of the planet. The HANPP due to LULC change shows that the productive potential had not been reached yet on several portions of the RPG. This would allow to increase production without diminishing ecosystems carbon gains. However, HANPP provide a partial description of the impacts of agriculture. A complementary description of how ecosystem services supply changes across the HANPP gradient is needed to support decision making.

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