THE EFFECT OF WOODY PLANT ENCROACHMENT ON LIVESTOCK PRODUCTION: A COMPARISON OF NORTH AND SOUTH AMERICA

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Classification: BIOLOGICAL SCIENCES/Sustainability

Keywords: woody-plant encroachment, land-cover change, livestock production, global change, food production, N and S American rangelands, net primary productivity

Abstract

A large fraction of the world grasslands and savannas are undergoing a rapid shift from herbaceous to woody-plant dominance. This land-cover change is expected to lead to a loss in livestock production, but the impacts of woody-plant encroachment on this crucial ecosystem service have not been assessed. We evaluated how tree cover has affected livestock production at large scales in rangelands of contrasting socio-economic characteristics in the U.S. and Argentina. Our models indicated that in areas of high productivity, a 1% increase in tree cover resulted in a reduction in livestock production ranging from 0.6 to 1.6 reproductive cows per km^2. Mean livestock production in the U.S. is 27 Rc km^{-2}, so a 1% increase in tree cover results in 2.5% decrease in mean livestock production. This effect is large considering that woody-plant cover is increasing at 0.5-2% per year. On the contrary, in areas of low productivity, increased tree cover had a positive effect on livestock production. Our results also show that ecological factors account for a larger fraction of livestock production variability in Argentinean than in U.S. rangelands. Differences in the relative importance of ecological versus non-ecological drivers of livestock production in Argentina and the U.S. suggest that the valuation of ecosystem services between these two rangelands might be different. Current management strategies in Argentina are likely designed to maximize livestock production whereas land managers in the U.S. may be optimizing multiple ecosystem services, including conservation or recreation, alongside livestock production.

Significance Statement

Grasslands all over the world are undergoing a rapid shift from a regime dominated by herbaceous plants to one dominated by woody plants, a phenomenon known as woody-plant encroachment. The impact of this global phenomenon on livestock production, the main ecosystem service provided by grasslands, remains largely unexplored. We quantified, for the first time, the impact of woody-plant encroachment on livestock production at a large scale, finding a reduction of between 0.6 and 1.6 reproductive cows per km^2 for each 1% increase in tree cover. By comparing the largest rangelands of the Americas (U.S. and Argentina), we also showed how the impact of woody-plant encroachment is mediated by social-economic factors. Our manuscript represents a significant advance in our understanding of grasslands as complex social-ecological systems.

Introduction

Grasslands, shrublands, and savannas, collectively ‘rangelands’, constitute ca. 50% of the Earth’s land surface (1). Although characterized by low yet highly variable annual rainfall, these areas provide 30-35% of terrestrial net primary productivity (2), contain >30% of the world’s human population, and support the majority of the world’s livestock production (3, 4). Besides livestock production, rangelands also provide a variety of other ecosystem services, including fiber production, carbon sequestration, maintenance of the genetic library (conservation), and recreation (5).

One of the most striking land-cover changes in rangelands worldwide over the past 150 years has been the proliferation of trees and shrubs at the expense of perennial grasses (6). In the U.S., non-forest lands undergoing woody-plant encroachment are now estimated to cover up to 335 million ha, i.e. 40% of the coterminous U.S., (7) and the increase in woody cover ranges from 0.5 to 2% per year (8). The causes of this vegetation change are debated and the main potential drivers include intensification of livestock grazing, changes in climate and fire regimes, the introduction of non-native woody species, and declines (natural and human-induced) in the abundance of browsing animals (9-12). Historical increases in atmospheric nitrogen deposition and atmospheric carbon dioxide concentration have also been suggested to play a role (10, 11).

Woody-plant encroachment has long been of concern to a broad range of stakeholders, from pastoralists to ranchers, because of the expected negative impact on livestock production (13). In response, brush management has been widely used to reduce the cover of encroaching woody-vegetation on both public and private lands. For example, the U.S. Natural Resources Conservation Service spent $127M in brush management programs in the period 2005-2009, implemented on more than 1 million ha of rangeland (14). Despite claims about impact of woody-plant encroachment on livestock production and the large amounts of federal, state, and private spending on brush management, the impact of woody-plant encroachment on livestock production has seldom been quantified (15). Here, our objectives are i) to quantify how woody-plant encroachment affects livestock production at large spatial scales, and ii) to assess how this impact is modified under different ecological and social-economic conditions.

We developed a general framework in which livestock production depends on net primary production, woody-plant cover, and other non-biological determinants. Net primary production sets the total amount of biomass and energy that is available to herbivores (16). The most common view on woody-plant encroachment is that encroachment diverts herbaceous productivity, on which cattle feed, to unpalatable woody-plant productivity, thus reducing potential energy intake (17-19). Thus overall, primary production and woody-plant encroachment jointly determine the livestock carrying capacity of an ecosystem.

In natural ecosystems from forests to deserts, there is a tight correlation among primary productivity and secondary productivity and animal biomass (16). Social and economic factors determine how close current livestock stocking is to the carrying capacity of the site, which is determined by NPP. Oesterheld et al. (20) assessed the relationship between net primary productivity and livestock production in managed rangelands in Argentina, where management focuses on food production, and found that the link between primary and secondary productivity was even tighter than in natural ecosystems. Management practices such as providing water and minerals, regulating animal distribution, and reducing parasitism, predation and diseases, resulted in stocking rates that were closely associated with net primary productivity.

We expect that in advanced industrial societies, where the production of goods (e.g., food by means of agriculture and ranching) plays a secondary role in the economy (21), landscapes will be managed to maximize multiple ecosystem services, and thus livestock production might be less driven by ecological drivers. Ecological factors, including net primary productivity and woody-plant cover, determine potential stocking rate but actual stocking rate is modulated by manager's decisions (22). In some cases, land managers overstock rangelands leading to degradation and desertification (23) while in other cases managers understock. The latter results from pursuing optimization of multiple ecosystem services of which food production is only one. Rangelands managed for multiple purposes and ecosystem services (24) seek provisioning of food, fiber, firewood, carbon sequestration, conservation or recreation.

Our hypotheses are i) that overall livestock production decreases with woody-plant encroachment, ii) the effect of woody-plant encroachment on livestock production is modulated by NPP, with a larger negative impact of woody-plant encroachment in those areas with higher net primary productivity, and iii) the role of ecological drivers (net primary productivity and tree cover) on livestock production is larger in regions where the demand for ecosystem services is concentrated exclusively on food production.

The scarcity of studies attempting to quantify the impact of woody-plant encroachment on livestock production reflects the enormous difficulties of addressing this issue by means of conventional field approaches. An experimental approach necessitates monitoring the change in livestock production in a number of locations during the encroachment process, a process that might take decades (11). Our approach has been to explore how current rangeland livestock production varies at a regional scale along sites with different net primary productivity and woody cover. We thus assessed the consequences of the process of woody-plant encroachment by evaluating the relationship between tree-cover and livestock production at a given point in time across multiple locations. This approach of swapping time for space has been used to predict future trajectories of species in an ecological succession (25), and more recently, the expected change of organisms ranging from microbes (26) to trees (27) under a changing climate. We are aware of the limitations of the approach mostly associated with the existence of lags that result in different models through space and time (28). Given the limitations of alternative options and the urgency of the problem, we consider our approach to be promising.

To test our hypotheses, we collected information about woody-plant cover and primary productivity from remote sensing sources and about livestock production from agricultural census data. Woody-plant encroachment occurs when there is an increase in the abundance of trees or shrubs. The type of woody component depends on mean annual precipitation with arid systems being invaded by shrubs and mesic ecosystems being invaded by trees. In our study areas, the transition between shrub and tree domains occurs approximately at 600 mm of annual precipitation (Fig S2). In the present work, we focused on encroachment of trees (i.e., areas >600 mm) because current remote sensing tools assess tree cover with accuracy, but they do not adequately estimate shrub cover (29) and thus our approach is not feasible in shrublands. We aggregated data at the county level and combined remote sensing and census data in a model that yields estimates of the impact of woody-plant cover on livestock production at large scales. To account for the effects of socio-economic factors, we quantified the impact of tree cover on livestock production in two regions of the world that have extraordinary environmental similarity but have contrasting socio-economic characteristics (30, 31). The two regions are the U.S. Central Grassland Region and the Argentinean Central Grassland. Both share similar temperature and precipitation gradients, yielding vegetation types that are remarkably similar (31) (Fig. 1). These environmental similarities contrast with large socio-economic differences in the rural sector, and specifically regarding livestock production (Supplementary Information, Fig. S1). During the last decades in the U.S., there has been a reduction of people making a living from agriculture (40% reduction since 80s) and a negative trend in the number of cattle in the region (22% reduction since the 70s). At present, a large proportion of stakeholders in the U.S. are not full-time ranchers but maintain livestock production as a source of secondary income or for cultural or recreational reasons (USDA economic service; www.ers.usda.gov). In Argentina, although the relative importance of ranching has decreased due to the expansion of crop products, especially soybean, the reduction in the number of cattle has been much smaller (4% reduction since the 70s, Fig. S1); and beef is still the agricultural commodity with the largest output value (28% of the total agricultural production 2005-2007) (32). As a result, we expected stocking rates in Argentina to be closer to the NPP-derived carrying capacity of the system, and thus more tightly driven by ecological factors, than in the U.S. (20).

Results and Discussion

In both the U.S. and Argentina, livestock production shows a W to E gradient of increasing reproductive density. The maximum value in the U.S. is 66 reproductive cows (Rc) per km^2 in the eastern part of the region. In Argentina, this gradient is more apparent than in the U.S., reaching maximum values of 43 Rc km^{-2} (Fig. 2). This directional gradient is the same for NPP and tree cover gradients in both regions, following mean annual precipitation gradients (Fig. 1).

In accordance with our first hypothesis, woody-plant encroachment in both rangelands had a negative impact on livestock production. An increase of 1% in tree cover resulted in an overall decrease in livestock production ranging from 0.6 to 1.6 Rc km^{-2} (Fig. 3, Table 1). In the U.S., an increase in tree cover of 1% decreased livestock production by 0.57 Rc km^{-2}. Mean livestock production in the U.S. is 27 Rc km^{-2}, so a 1% increase in tree cover results in 2.5% decrease in mean livestock production of the region. In NPP units, a 1% increase in tree cover had the same impact on livestock production as an NPP decrease of 41 g C m^{-2} y^{-1}. The magnitude of the impact can be gauged when taking into account that, in North America, the increase of woody cover ranges from 0.5 to 2% per year (8).

As in our second hypothesis, in Argentina, a significant interaction between NPP and tree cover as drivers of livestock production exists, although we did not find this interaction when evaluating the U.S. data (Fig. 3, Table 1). At high productivity values (900 g C m^{-2} y^{-1}), an increase of 1% tree cover decreased livestock production by 1.6 Rc km^{-2}, relative to livestock production ranging between 1 and 43 Rc km^{-2}. However, at productivity values of less than 365 g C m^{-2} y^{-1}, tree cover enhanced livestock production. In low productivity (300 g C m^{-2} y^{-1}) areas in Argentina, an increase in tree cover of 1% increased livestock production by 0.24 Rc km^{-2}. This result contradicts current understanding of the impact of woody-plant encroachment, which is thought to have a negative impact on livestock production (6, 17-19, 33). Note that the lower limit of NPP in our study area in the U.S. occurs above 365 g C m^{-2} y^{-1}, obscuring a possible positive effect of tree cover on livestock production at low productivity values. Potential explanations of this positive effect of woody-plant encroachment on livestock production at low productivity values may be found in factors other than the amount of food available for livestock production. For example, most of the areas of low productivity in our study area are associated with low precipitation and high temperature (Fig. 1). In these areas, tree cover might provide shelter and shade or overall near-ground temperatures, decreasing animal respiration costs (34) .

Our results showed that the effect of NPP and tree cover on productivity was larger in Argentina than in the U.S. (R^2= 50% and 24% respectively, Table 1), indicating a strong difference between the two study areas in the importance of the drivers of livestock production. This aligns with our third hypothesis, that the role of ecological drivers (net primary productivity and tree cover) on livestock production would be larger in regions where the demand for ecosystem services is concentrated exclusively on food production. The effect of tree cover on livestock production relative to the effect of net primary productivity on livestock productivity was similar in the two study regions, with the explanatory power of NPP being five times larger than that of tree cover (U.S.: $R^2_{NPP} =$ 20% and $R^2_{TC} =$ 4%; Argentina: $R^2_{NPP} =$ 42% and $R^2_{TC} =$ 8%, being R^2_{NPP} and R^2_{TC} the percentage of variance accounted for by net primary productivity and tree cover) (Fig. 4). The similarity in the relative importance of NPP and tree cover indicates that, despite the difference in socio-economic differences, the underlying ecological mechanisms driving livestock production are similar.

Differences in the relative importance of ecological vs. non-ecological (social) drivers on livestock production in Argentina and the U.S. suggest that the value of the various ecosystem services provided by rangelands may be different in these two regions. Rangelands produce a variety of ecosystem services including food and fiber production, carbon sequestration, maintenance of the genetic library (conservation), and recreation (5). Current management strategies in Argentina are likely to be designed to maximize a single ecosystem service (livestock production). On the contrary, land managers in the U.S. appear to be optimizing multiple ecosystem services, including conservation or recreation alongside livestock production. Therefore, it is important to measure the effects of woody-plant encroachment on the entire portfolio of ecosystem services that are provided by rangelands. Most changes in ecosystem services due to woody-plant encroachment remain unclear and have been identified only in a qualitative fashion (but see (33)). Future quantitative studies taking into account multiple ecosystems services are needed in order to assist in decision making whether to implement or not brush management actions. Livestock production is currently one of the most important ecosystem service provided by rangelands but the development trajectory highlighted by the differences between Argentina and the U.S. point out that other ecosystem services will likely become increasingly important as economies undergo a transition from the production of goods to the provision of services.

Our study demonstrates that livestock production is part of an integrated socio-ecological system where ecological and social-economic drivers interact along gradients of climate and economic development (22). In high productivity regions, woody-plant cover negatively affects livestock production mainly through reductions in forage availability. The negative effect of woody plants on forage availability is overwhelmed in low productivity regions by the positive effects of woody cover that may be linked to the amelioration temperature, a possible linkage that requires examination. As economic development increases the demand for ecosystem services from rangelands becomes more diversified. In least developed regions, food and fiber dominate the demand for ecosystem services. On the contrary, in developed regions there are multiple demands from rangelands beyond food production that include conservation, carbon sequestration, water supply and recreation. As development increases and demand diversifies the importance of ecological drivers decreases while that of social-economic factors increases. The future of woody-plant encroachment and its consequences on ecosystem services will be modulated by changing climate and social and economic conditions.

Methods Summary

Study areas

We modeled the impact of woody plant encroachment on livestock production at a county resolution for both U.S. and Argentinean rangelands (Fig. 1). Both areas share a similar latitudinal temperature gradient and a longitudinal precipitation gradient, with precipitation increasing from W to E. These similar climatic patterns yield vegetation types that are remarkably similar (31). These similarities contrast with large social-economic differences (see Introduction and Figure S1), which make them a perfect study system to address the impact of woody-plant encroachment on livestock production at a regional scale and the variation of this impact between different socio-economic regions.

The U.S. and Argentinean rangelands constitute, together with the Brazilian Cerrado, the two main rangelands of the Americas (35). Here, we used rangelands in a very broad sense; our two study areas comprise the transition between the desert and the forest biomes. We defined our study areas in the U.S. and Argentina as those encompassing the prairie, savanna, and temperate and subtropical desert and steppes divisions and regimen mountain divisions, according to Bailey's ecoregions (1). Within those areas, we excluded those counties with mean annual precipitation values below 600 mm, thus focusing on the tree dominion (Fig S2) and excluding woody cover due to shrubs. The resulting areas in the U.S. and Argentina had the same precipitation lower limit (600mm) but differed in their upper limit (U.S.=1260 mm, Argentina= 2270 mm). In order to make the analysis of both areas fully comparable we limited the upper precipitation limit of Argentina to that of the U.S. (i.e., 1260 mm). Taking into account also those counties excluded due to low representation of non-crop lands (see below), the resulting number of sampling units (i.e., counties in the U.S., departments in Argentina) was 242 for the U.S. and 125 for Argentina.

Livestock production data

Data on livestock production were obtained from the USDA Census Database (www.agcensus.usda.gov) and Argentinean Food and Agriculture Administration (SENASA; http://www.senasa.gov.ar) (Fig. 2). In both cases, we used the last available livestock data (2007 for the U.S., and 2010 for Argentina). We focused on cattle, which is the main livestock type in both areas. For comparability, we used the number of reproductive animals, a metric present in both data bases. This metric corresponded to the class 'Cows incl. calves' in the USDA Census data and to the class 'Cows' in the SENASA database (range: 1.5-66.4 and 0.5-43.2 animals per km^2 for the U.S. and Argentina respectively). In the U.S. we subtracted the number of cows on feedlots, also available in the U.S. Census Database, from the total number of cows.

Environmental data

Net primary productivity, tree cover, and land uses per county were quantified by using Moderate-resolution Imaging Spectroradiometer (MODIS) products (Fig. 2). All environmental variables were characterized by the mean annual values of the year of the livestock data (2007 for the U.S., and 2010 for Argentina) and the four previous years. The value of the Net primary productivity was assessed using the Photosynthesis and Net Primary Productivity algorithm MOD17A3 (36). Here, production is determined by first computing a daily net photosynthesis value which is then composited over an 8-day interval of observations over a year, to produce a net primary productivity measure. Tree cover was assessed by means of MODIS Vegetation Continuous Fields product MOD44B (29). This product represents Earth's terrestrial surface as a proportion of three surface cover components: percent tree cover, percent non-tree cover, and percent bare ground. Land uses were assessed by the MODIS product MCD12Q1 (37). This land-use remote sensing data allowed us to exclude crops and urban areas in our analysis, and thus to obtain a more accurate measure of the net primary productivity available for livestock consumption per county. Additionally, in order to remove those counties with low sampling size, we also excluded from our analyses those counties with less than 1000 km^2 or 25% of rangelands.

Mean annual precipitation values were obtained from Earth observations and climatic models. Specifically, annual precipitation values for the study periods in Argentina were obtained from the Tropical Measuring Mission (TRMM; www.trmm.gsfc.nasa.gov) at a 0.25° resolution. In the U.S., annual climatic data at a 2.5' resolution were obtained from the PRISM Climate Group (Oregon State University; www.prism.oregonstate.edu).

Hypotheses testing

Our first two hypotheses describe the impact of net primary productivity and tree cover on livestock production and were tested by means of the model $LP = \beta_0 + \beta_1*NPP + \beta_2*TC + \beta_3*NPP*TC$, where LP is livestock production, NPP is net primary productivity and TC is tree cover. The sign and significance of β_2 and β_3 in the models fitted for the two study areas (U.S. and Argentinean rangelands) tested first and second hypotheses.

The third hypothesis, that states that the role of ecological drivers (net primary productivity and tree cover) on woody-plant encroachment on livestock production would be larger in regions where the demand for ecosystem services is concentrated exclusively on food production, was tested by means of examining model results in the U.S. and Argentinean rangelands separately. In particular, we examined the explained variance of the model in each country. The relative explanatory power of NPP and tree cover was assessed by means of a variance partitioning analysis (38, 39), which allowed us to break down the total explained variance in four fractions: pure effects of NPP, pure effects of TC (i.e., variance exclusively explained by NPP or TC), join effect of NPP and TC (i.e., variance explained simultaneously by NPP and TC) and the effect of the synergistic interaction between the two drivers (variance explained by NPP*TC).

The model $LP = \beta_0 + \beta_1 * NPP + \beta_2 * TC + \beta_3 * NPP * TC$ was fitted with three candidate sets of variables describing NPP and TC considering one, three or five years of previous information: a) variables describing NPP and TC values for the year of census (2007 for the US and 2010 for Argentina), b) variables describing the average NPP and TC values of the year of the census and the two previous years and c) the average NPP and TC values of the year of the census and the four previous years. For both the U.S. and Argentina, the three candidate set of variables yielded very similar patterns, although the models with largest values of explained variance, and thus those presented here, were those with independent variables describing NPP and TC the year before the livestock census data.

Acknowledgements

This work has been supported by the National Academies Keck Futures Initiative award 025512 (NAKFI), and by NSF DEB 09-17668 and DEB 1235828. K. Havstad, S. Archer and G. Ruyle, E. Jobággy and C. Rueda provided valuable suggestions during the development of the project. F. Maestre kindly reviewed a previous draft of the manuscript. X. Li and Y. Zhang (Environmental Remote Sensing and Geoinformatics Lab, Global Institute of Sustainability, ASU) assisted with the processing of MODIS data.

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Table 1. Models assessing the effect of ecological drivers (net primary productivity and tree cover) on livestock production in the U.S. and Argentinean rangelands. R^2 = % of explained variance. N.s. = non-significant effect (not included in the final model).

	U.S.		Argentina	
	Estimate	p-value	Estimate	p-value
Intercept	-40.8044	0.8424	-22.75	0.6015
NPP	0.133	<0.0001	0.09796	<0.0001
Tree cover	-0.5754	0.0005	1.1360	0.0006
NPP*Tree cover	-	n.s.	-0.003	0.0001
R^2	24.01		50.26	

Figure 1. Main environmental gradients (mean annual precipitation and mean annual temperature) in the U.S. and Argentinean rangelands. Rangelands are defined in this work as those areas encompassing the prairie, savanna, and temperate and subtropical desert, steppes and mountain divisions, according to Bailey's ecoregions (1). Within these areas our work focused on those counties with mean annual precipitation values between 600 and 1260 (see Methods Section and Fig. 2). For both areas, national (bold lines) and county (thin lines) borders are drawn. In the US state borders are also drawn (bold lines).

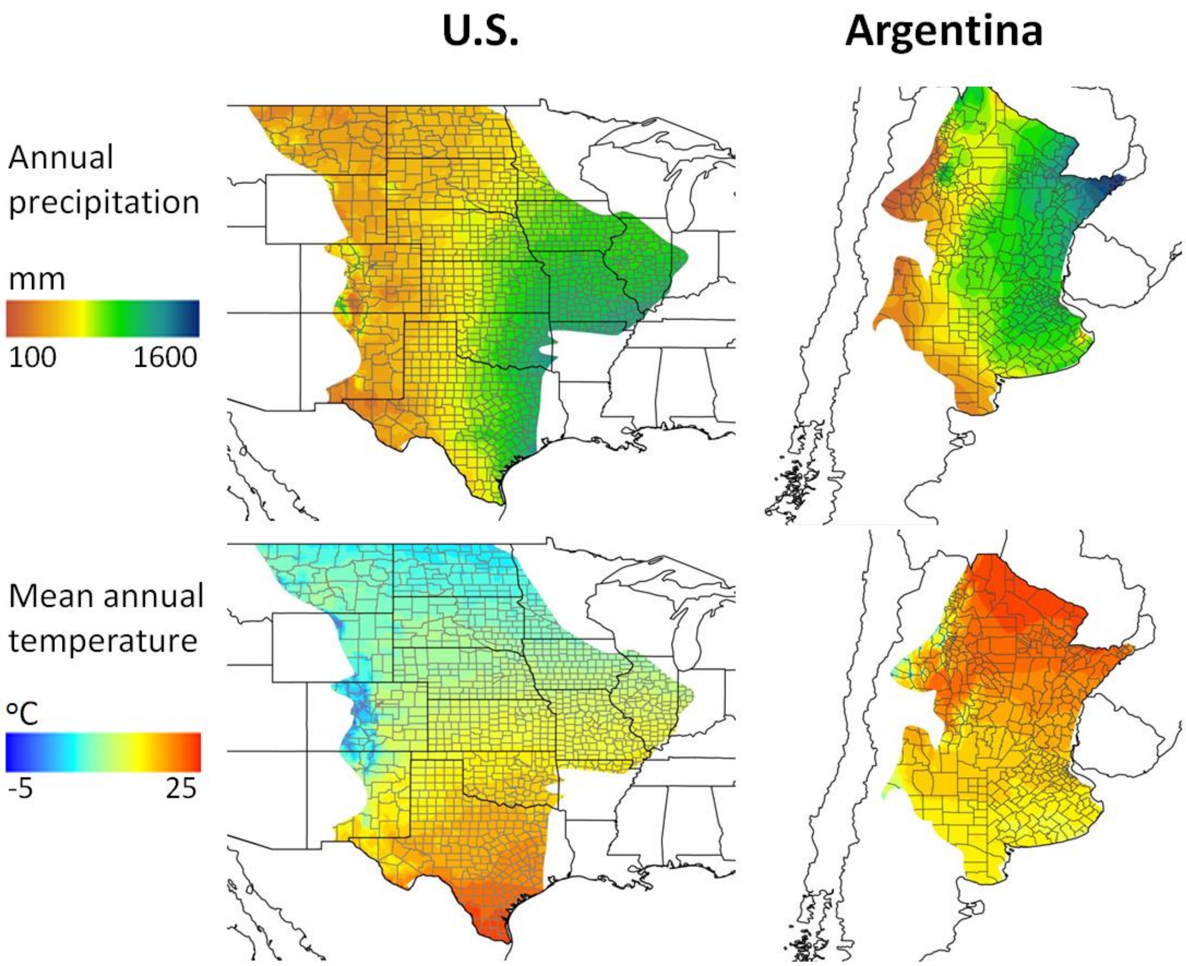


Figure 2. Livestock production, net primary productivity (NPP) and tree cover for our study counties. Rangelands not included in the analyses (in grey) are those counties with annual precipitation less than 600 mm or larger than 1260 mm (light gray) or those counties with less than 1000 km^2 in rangelands or less than 25% of their total area in rangelands (dark gray; see Methods).

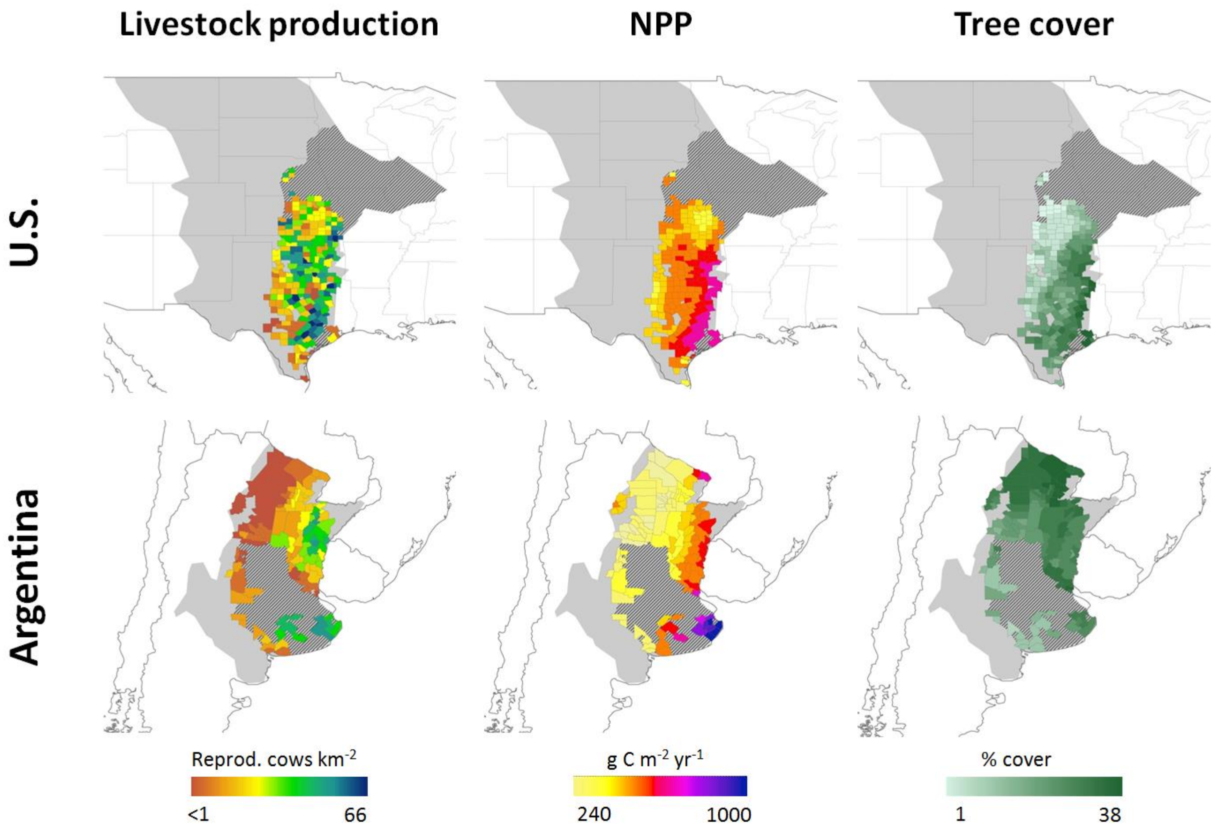


Figure 3. Response models of livestock production to net primary productivity and tree cover in the U.S. and Argentinean rangelands. Equations for response models are shown in Table 1. The red area indicates the NPP range where the impact of tree cover on livestock production is negative. The green area indicates positive effect. Rc km^{-2}= Number of reproductive cows per km^2.

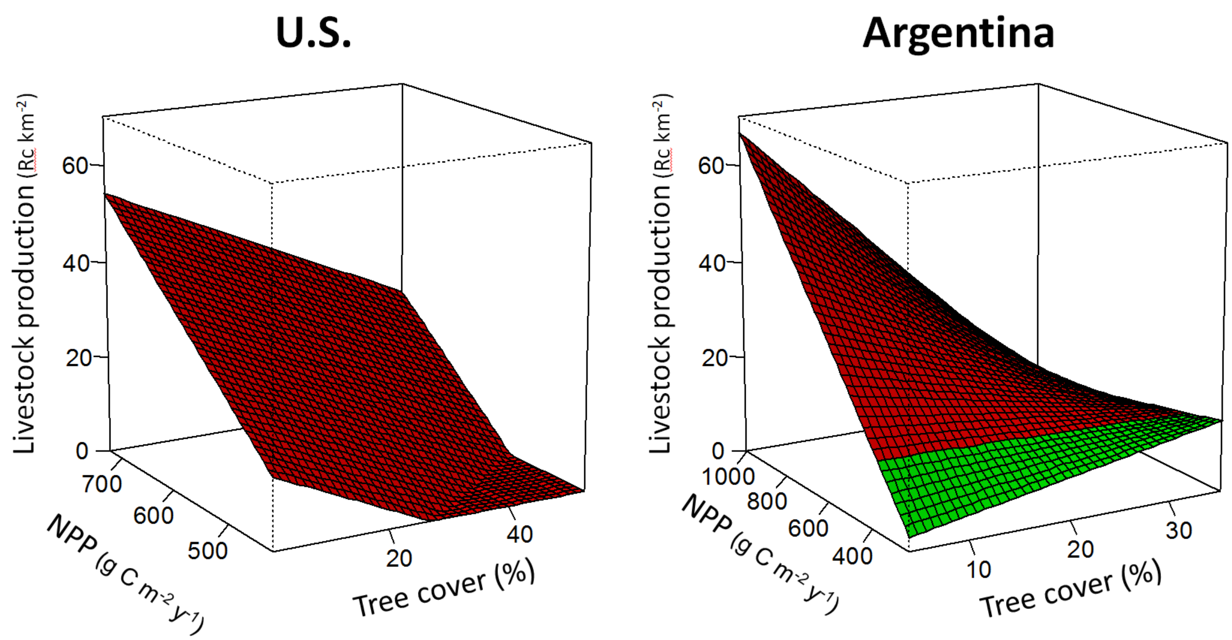
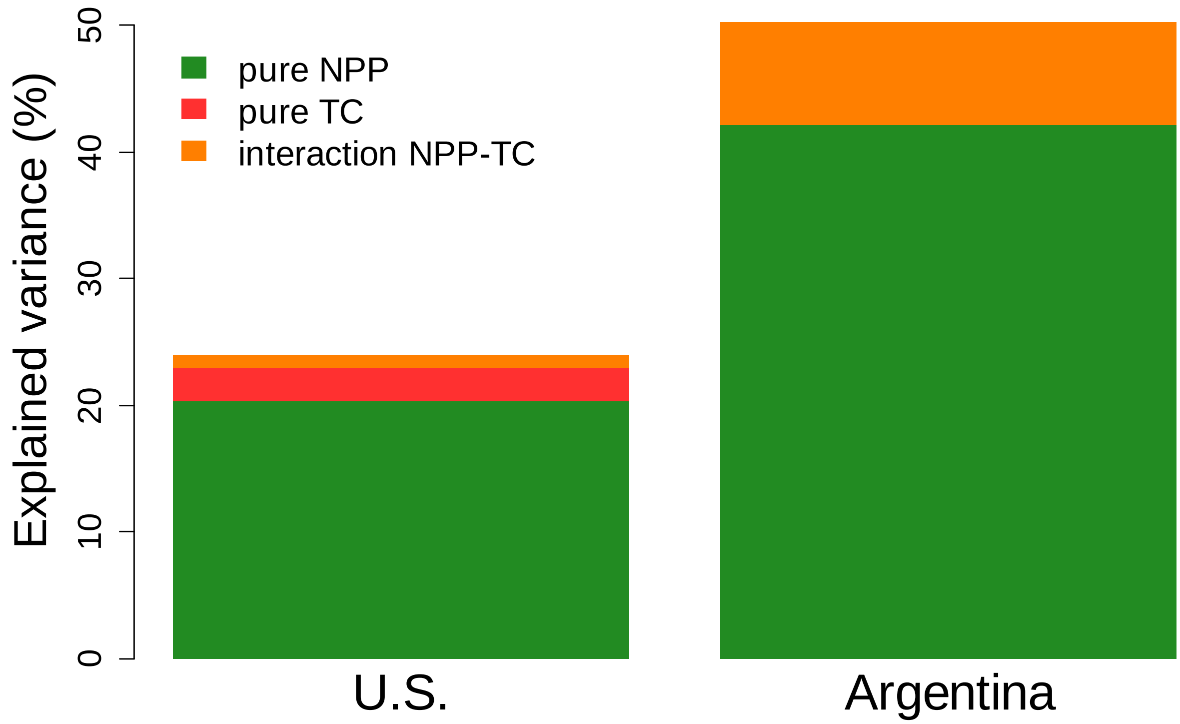
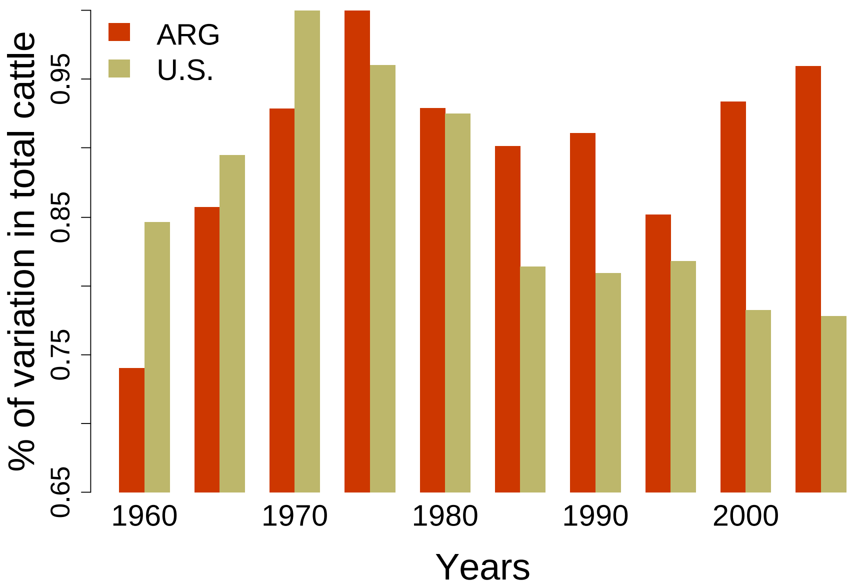


Figure 4. Explanatory power of net primary productivity (NPP) and tree cover (TC) on livestock production in the U.S. and Argentinean rangelands as assessed by a variance partitioning analysis. This analysis breaks down the explained variance of the model into a) the pure effects of NPP or TC (i.e. the portion of the variance explained exclusively by one this factors), b) the join effects of NPP and TC (i.e. the portion of the variance explained jointly by NPP and TC, due to, for example collinearity between them), and c) the interaction between NPP and TC.



SUPPLEMENTARY INFORMATION

Figure S1. Evolution of the number of cattle (top) and agricultural population (bottom) by five-year periods in the U.S. and Argentina. Source: FAOSTAT *(http://faostat.fao.org/*; last accessed Jul 13th, 2013).



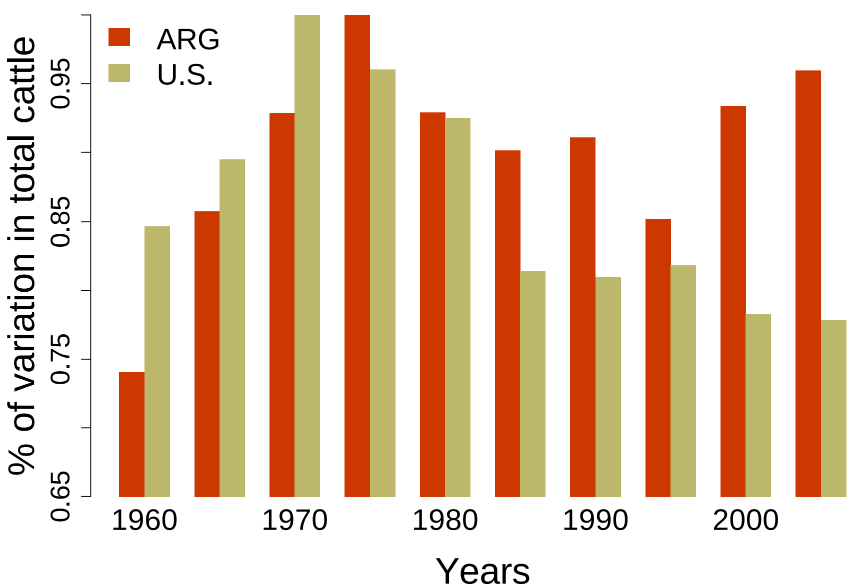


Figure S2. Mean annual precipitation range (600-1260 mm) in relation to tree cover in the U.S. The lower limit of our study area was set at 600 mm, thus excluding those areas where tree cover is marginal (<10%). 1260 mm equals the maximum annual precipitation value for a county in our study area. Annual precipitation from WorldClim database (*http://www.worldclim.com/*), tree cover from MODIS (see Methods section).