Effect of woody-plant encroachment on livestock production in North and South America

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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 (LP), but the impacts of woody-plant encroachment on this crucial ecosystem service have not been assessed. We evaluate how tree cover (TC) has affected LP at large spatial scales in rangelands of contrasting social–economic characteristics in the United States and Argentina. Our models indicate that in areas of high productivity, a 1% increase in TC results in a reduction in LP ranging from 0.6 to 1.6 reproductive cows (Rc) per km^2. Mean LP in the United States is 27 Rc per km^2, so a 1% increase in TC results in a 2.5% decrease in mean LP. This effect is large considering that woody-plant cover has been described as increasing at 0.5% to 2% per y. On the contrary, in areas of low productivity, increased TC had a positive effect on LP. Our results also show that ecological factors account for a larger fraction of LP variability in Argentinean than in US rangelands. Differences in the relative importance of ecological versus nonecological drivers of LP in Argentina and the United States suggest that the valuation of ecosystem services between these two rangelands might be different. Current management strategies in Argentina are likely designed to maximize LP for various reasons we are unable to explore in this effort, whereas land managers in the United States may be optimizing multiple ecosystem services, including conservation or recreation, alongside LP.

global change | food production | social–ecological systems

Grasslands, shrublands, and savannas, collectively termed "rangelands," constitute about 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 (NPP) (2), contain >30% of the world's human population, and support the majority of the world's livestock production (LP) (3, 4). Besides LP, 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 y has been the proliferation of trees and shrubs at the expense of perennial grasses (6). In the United States, nonforest lands undergoing woody-plant encroachment are now estimated to cover up to 335 million ha (40% of the coterminous United States) (7) and the increase in woody cover ranges from 0.5% to 2% per y (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 nonnative 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 LP (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 US Natural Resources Conservation Service spent US$127 million 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 LP and the large amounts of federal, state, and private spending on brush management, the impact of woody-plant encroachment on LP has seldom been quantified (15). Here our objectives are (i) to quantify how woody-plant encroachment affects LP 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 LP depends on NPP, woody-plant cover, and other nonbiological determinants. NPP 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.

Social and ecological factors interact to determine livestock rate. For example, Oesterheld et al. (20) assessed the relationship between NPP and LP 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. In these rangelands, management practices, such as providing water and minerals; regulating animal distribution; and

Significance

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

reducing parasitism, predation, and diseases, resulted in stocking rates that were closely associated with NPP.

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 LP might be less driven by ecological drivers. Ecological factors, including NPP and woody-plant cover, determine potential stocking rates but actual stocking rates are modulated by manager's decisions (22). In some cases, land managers overstock rangelands leading to degradation and desertification (23), whereas 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 LP decreases with woody-plant encroachment; (*ii*) the effect of woody-plant encroachment on LP is modulated by NPP, with a larger negative impact of woody-plant encroachment in those areas with higher NPP; and (*iii*) the role of ecological drivers [NPP and tree cover (TC)] on LP 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 LP reflects the difficulties of addressing this issue by means of conventional field approaches. An experimental approach necessitates monitoring the change in LP 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 LP varies at a regional scale along sites with different NPP and woody cover. We thus assessed the consequences of the process of woody-plant encroachment by evaluating the relationship between TC and LP 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 this 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, however, 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 LP from agricultural census data. Woody-plant encroachment occurs when there is an increase in the cover of trees or shrubs. The type of woody component depends on mean annual precipitation, arid systems invaded by shrubs, and mesic ecosystems invaded by trees. In our study areas, the transition between shrub and tree domains occurs approximately at 600 mm annual precipitation (Fig. S1). In the present work, we focused on encroachment of trees (i.e., areas >600 mm) because current remote-sensing tools assess TC with accuracy, but do not adequately estimate shrub cover (29), reducing our confidence to address this cover type. We aggregated data at the county level and combined remote-sensing and census data into a model that yields estimates of the impact of woody-plant cover on LP at large scales. To account for the effects of social–economic factors, we quantified the impact of TC on LP in two regions of the world that have extraordinary environmental similarity but contrasting social–economic characteristics (30, 31). The two regions are the US 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 social–economic differences in the rural sector, specifically regarding LP (Fig. S2). During the last decades in
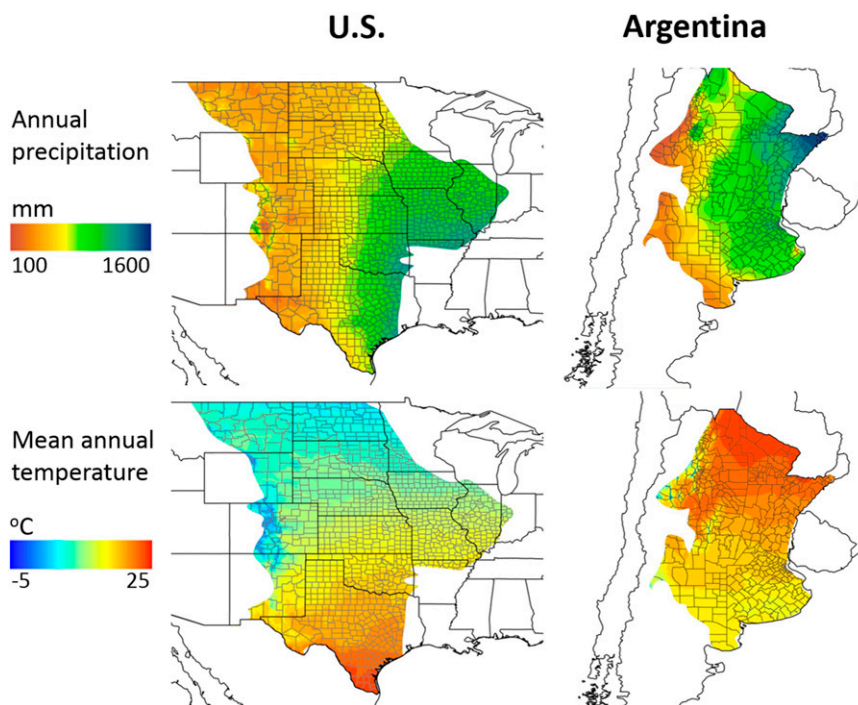
Fig. 1. Main environmental gradients (mean annual precipitation and mean annual temperature) in the US and Argentinean rangelands. Rangelands in this paper are defined as those areas encompassing the regular and regime mountain divisions of prairie, savanna, temperate and subtropical desert, and steppe, according to Bailey's ecoregions (1). Within these areas, our work focused on those counties with mean annual precipitation values between 600 and 1,260 mm (*Methods* and Fig. 2). For both areas, national (bold lines) and county (thin lines) borders are shown. In the United States, state borders are also shown (bold lines).

the United States, there has been a reduction of people making a living from agriculture (40% reduction since 1980s) and a negative trend in the number of cattle in the region (22% reduction since the 1970s). At present, a large proportion of stakeholders in the United States are not full-time ranchers but maintain LP as a source of secondary income or for cultural or recreational reasons [US Department of Agriculture (USDA) Economic Research Service, www.ers.usda.gov; ref. 32]. 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 1970s; Fig. S2); beef is still the agricultural commodity with the largest output value (28% of the total agricultural production 2005–2007) (33). 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 United States (20).

Results and Discussion

In both the United States and Argentina, LP shows a west-to-east gradient of increasing density of reproductive cows. The maximum value in the United States 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 United States, reaching maximum values of 43 Rc per km^2 (Fig. 2). This directional gradient is the same for NPP and TC 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 LP. An increase of 1% in TC resulted in an overall decrease in LP ranging from 0.6 to 1.6 Rc per km^2 (Fig. 3 and Table 1). In the United States, an increase in TC of 1% decreased LP by 0.57 Rc per km^2. Mean LP in the US is 27 Rc per km^2, so a 1% increase in TC results in a 2.5% decrease in the mean LP of the region. In NPP units, a 1% increase in TC had the same impact on LP 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 y (8).

As in our second hypothesis, in Argentina, there is a significant interaction between NPP and TC as drivers of LP, although we did not find this interaction in the US data (Fig. 3 and Table 1). At high-productivity values (900 g C·m^{-2}·y^{-1}), an increase of 1% TC decreased LP by 1.6 Rc per km^2. However, at productivity values of less than 365 g C·m^{-2}·y^{-1}, TC enhanced LP. In low-productivity (300 g C·m^{-2}·y^{-1}) areas in Argentina, an increase in TC of 1% increased LP by 0.24 Rc per km^2. This result contradicts the current understanding of the impact of woody-plant encroachment, which is thought to have a negative impact on LP (6, 17–19, 34). Note that the lower limit of NPP in our study area in the United States occurs above 365 g C·m^{-2}·y^{-1}, obscuring a possible positive effect of TC on LP at low-productivity values. Potential explanations of this positive effect of woody-plant encroachment on LP at low-productivity values may be found in factors other than the amount of food available for LP. 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, TC might provide shelter and shade, decreasing overall near-ground temperatures and animal respiration costs (35).

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

Differences in the relative importance of ecological versus nonecological (social) drivers on LP in Argentina and the United States 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
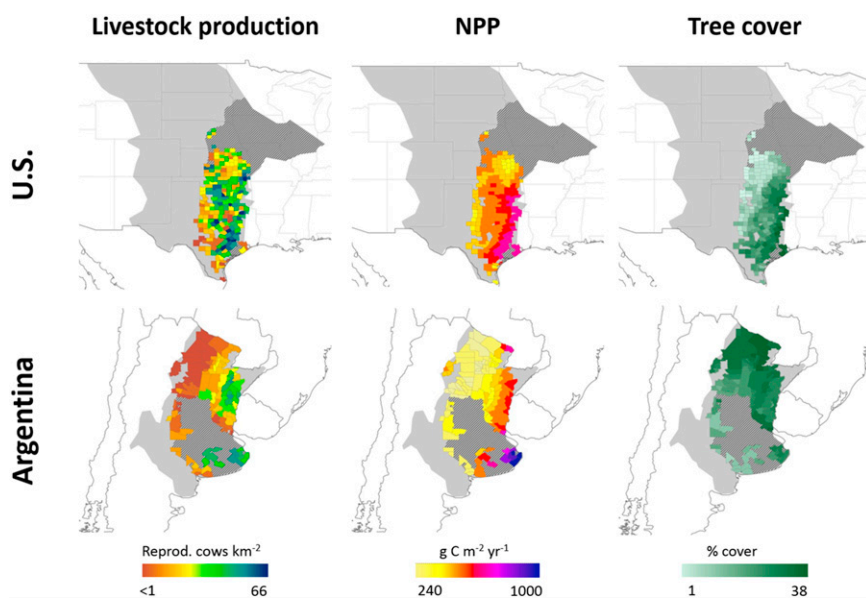
Fig. 2. LP, NPP, and TC for our study counties. Rangelands not included in the analyses (in gray) are those counties with an annual precipitation less than 600 mm or more than 1,260 mm (light gray) or those counties with less than 1,000 km^2 in rangelands or less than 25% of their total area in rangelands (dark gray; *Methods*).
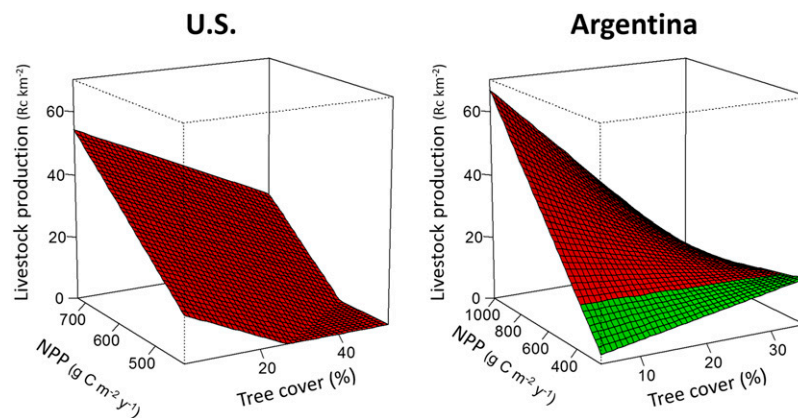
Fig. 3. Response models of LP to NPP and TC in the US and Argentinean rangelands. The equations for the response models are shown in Table 1. The red area indicates the NPP range where the impact of TC on LP is negative, whereas the green area indicates the positive effect.

the genetic library (conservation), and recreation (5). Current management strategies in Argentina are likely to be designed to maximize a single ecosystem service (LP). In contrast, land managers in the United States appear to be optimizing multiple ecosystem services, including conservation or recreation, alongside LP. An alternative, and nonexclusive, explanation for the lower explanatory power of ecological drivers in the United States than in Argentina would be that in the United States supplementary feeding is more important than in Argentina. As a result, LP in the United States could be more decoupled from ecological drivers than in Argentina. Both processes—differences in the valuation of ecosystem services and in supplementary feeding—are likely to be acting simultaneously, yielding the observed differences between our two study areas. 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 ref. 34). Future quantitative studies taking into account multiple ecosystems services are needed to assist in deciding whether to implement brush-management actions or not. LP is currently one of the most important ecosystem service provided by rangelands but the development trajectory highlighted by the differences between Argentina and the United States points 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 LP is part of an integrated social–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 LP 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 of temperature, a possible linkage that requires examination. The demand for ecosystem services from rangelands becomes more diversified as economic development increases. 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

Study Areas. We modeled the impact of woody-plant encroachment on LP at a county resolution for both US and Argentinean rangelands (Fig. 1). Both areas share a similar latitudinal temperature gradient and a longitudinal precipitation gradient, with precipitation increasing from west to east. These similar climatic patterns yield vegetation types that are remarkably similar (31). These similarities contrast with large social–economic differences (Introduction and Fig. S2), which make them a perfect study system to address the impact of woody-plant encroachment on LP at a regional scale and the variation of this impact between different social–economic regions.

The US and Argentinean rangelands constitute, together with the Brazilian Cerrado, the two main rangelands of the Americas (36). 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 United States and Argentina as those encompassing the prairie, savanna, temperate and subtropical desert, steppe, and regime mountain divisions of prairie, savanna, temperate and subtropical desert, and steppe (1). Within those areas, we excluded those counties with mean annual precipitation values below 600 mm, thus focusing on the tree dominion (Fig. S1) and minimizing woody cover due to shrubs. The resulting areas in the United States and Argentina had the same precipitation lower limit (600 mm) but differed in their upper limit (United States: 1,260 mm; Argentina: 2,270 mm). To make the analysis of both areas fully comparable, we limited the upper precipitation limit of Argentina to that of the United States (i.e., 1,260 mm). The resulting study area in the United States extended to colder areas than our study area in Argentina (mean annual temperature range in the United States was 8.7–22.9 °C vs. Argentina at 13.5–23.1 °C.). However, the bulk of samples (i.e., counties) in both study areas presented a much more similar temperature range, as defined by their 10th and 90th percentiles (United States: 12.6–20.2 °C; Argentina: 14.8–21.8 °C.). Taking into account also counties excluded due to high representation of crop lands (see *Environmental Data*), the number of sampling units (i.e., counties in the United States and departments in Argentina) was 242 for the United States and 125 for Argentina.

LP Data. Data on LP were obtained from the USDA Census Database (www.agcensus.usda.gov/Publications/2007/) and Argentinean Food and Agriculture

Table 1. Models assessing the effect of ecological drivers NPP and TC on LP in US and Argentinean rangelands

	United States		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
TC	−0.5754	0.0005	1.1360	0.0006
NPP × TC		n.s.	−0.003	0.0001
R^2	24.01		50.26	

R^2 is the percentage of explained variance. n.s., nonsignificant effect (not included in the final model).

Table 2. Explanatory power (percentage of explained variance) of NPP and TC on LP in US and Argentinean rangelands, as assessed by a variance partitioning analysis

Explanatory fractions	United States	Argentina
NPP, pure effect	20.34	42.17
TC, pure effect	2.64	0
TC ∩ NPP	0	0
TC × NPP	1.03	8.09
Total	24.01	50.26

This analysis breaks down the explained variance of the model into (*i*) pure effects of NPP or TC (i.e., the portion of the variance explained exclusively by one this factors), (*ii*) the joint effects of NPP and TC (TC ∩ NPP, i.e., the portion of the variance explained jointly by NPP and TC, due to, for example collinearity between them), and (*iii*) the interaction between NPP and TC (TC × NPP).

Administration [Servicio Nacional de Sanidad y Calidad Agroalimentaria (SENASA, www.senasa.gov.ar] (Fig. 2). In both cases, we used the last available livestock data (2007 for the United States 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 databases. 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 km² for the United States and Argentina, respectively). In the United States we subtracted the number of cows on feedlots, also available in the US Census Database, from the total number of cows.

Environmental Data. NPP, TC, and land uses per county were quantified by using Moderate Resolution Imaging Spectroradiometer (MODIS) products (http://modis-land.gsfc.nasa.gov) (Fig. 2). All environmental variables were characterized by the mean annual values of the year of the livestock data (2007 for the United States and 2010 for Argentina) and the previous 4 y. The value of the NPP was assessed using Photosynthesis and Net Primary Productivity algorithm MOD17A3 (37). Here, production is determined by first computing a daily net photosynthesis value which is then composited over an 8-d interval of observations over a year to produce a NPP measure. TC 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 TC, percentage of non-TC, and percentage of bare ground. Land uses were assessed by MODIS product MCD12Q1 (38). 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 NPP available for livestock consumption per county. Additionally, to remove those counties with a low-sampling size, we also excluded from our analyses those counties with less than 1,000 km² or 25% 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 (http://trmm.gsfc.nasa.gov) at a 0.25° of resolution. In the United States, annual climatic data at a 2.5° resolution were obtained from the PRISM Climate Group (Northwest Alliance for Computational Science & Engineering, Oregon State University, Corvallis, OR; www.prism.oregonstate.edu).

Hypotheses Testing. Our first two hypotheses describe the impact of NPP and TC on LP and were tested by means of the model $LP = \beta_0 + \beta_1 \times NPP + \beta_2 \times TC + \beta_3 \times NPP \times TC$. The sign and significance of β_2 and β_3 in the models fitted for the two study areas (US and Argentinean rangelands) tested the first and second hypotheses.

The third hypothesis, that the role of ecological drivers (NPP and TC) on woody-plant encroachment on LP would be larger in regions where the demand for ecosystem services is concentrated exclusively on food production, was tested by examining model results in the US and Argentinean rangelands separately. In particular, we examined the explained variance of the model in each country. The relative explanatory power of NPP and TC was assessed by variance partitioning analysis (39, 40), 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), joint effect of NPP and TC (i.e., variance explained simultaneously by NPP and TC), and effect of the synergistic interaction between the two drivers (variance explained by NPP × TC).

The model $LP = \beta_0 + \beta_1 \times NPP + \beta_2 \times TC + \beta_3 \times NPP \times TC$ was fitted with three candidate sets of variables describing NPP and TC considering 1, 3, or 5 y of previous information: (*i*) variables describing NPP and TC values for the year of census (2007 for the United States and 2010 for Argentina), (*ii*) variables describing the average NPP and TC values of the year of the census and the previous 2 y, and (*iii*) the average NPP and TC values of the year of the census and the previous 4 y. For both the United States and Argentina, the three candidate sets of variables yielded very similar patterns, although the models with the 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.

Our models are relatively robust to interannual variations in our system regarding the three hypotheses. Whereas year-to-year changes in TC are typically slow, LP and NPP might show important, more rapid, interannual changes. For example, LP might change due to changes in prices or an annual drought. These processes, however, would be expected to affect LP in the entire study area. For example, if prices increase, ranchers all along the encroachment gradient would be expected to reduce their number of animals. As such, we would expect a change in the intercept of the regression model but not in the metrics that we use here as test statistics for our hypotheses (slope and values of explained deviance).

We are aware that our dependent and independent variables are subject to measurement errors. Errors in the dependent variable (LP census data) are, however, of lesser concern because the linear regression model $Y = \beta_0 + \beta_1 X + \varepsilon$ takes for granted that observations of Y (Y_i) are subject to error ε (41). Errors in the independent variables will produce bias in the regression parameters when the variance of the error in X is large in comparison with the variance of X (41). In our case, our MODIS-based estimator of TC is known to be subject to errors, ranging from 10 and 31 units of rms error at the pixel scale (250 × 250 m) with a tendency of overestimation in areas of low cover and underestimation in areas of high cover (42). Here, it is important to note that our TC variable represents mean values of TC at a county scale, with each county containing tens of thousands of pixels. Because of their large size, single counties include a wide range of pixel cover values. As a result, the magnitude of the error of this variable at the county scale, although admittedly unknown, is actually much smaller than that described at the pixel scale in the literature (42). Thus, we assume that our models are robust in relation to the errors in our variables.

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