Main Manuscript for

Herbaceous production lost to tree encroachment in United States rangelands.

Scott L. Morford[a*], Brady W. Allred[a,b], Dirac Twidwell[c], Matthew O. Jones[a,d], Jeremy D. Maestas[e], Caleb P. Roberts[f], David E. Naugle[a,b]

[a] Numerical Terradynamic Simulation Group, University of Montana, Missoula, MT 59812, USA

[b] University of Montana, W. A. Franke College of Forestry and Conservation, Missoula, MT 59812, USA

[c] Department of Agronomy and Horticulture, University of Nebraska–Lincoln, Lincoln, NE 68588, USA

[d] Regrow Agriculture, Durham, NH 03824, USA.

[e] US Department of Agriculture, Natural Resources Conservation Service, Portland, OR 97232, USA

[f] U. S. Geological Survey, Arkansas Cooperative Fish & Wildlife Research Unit, University of Arkansas, Fayetteville, AR, 72701, USA

*Corresponding Author: Scott L. Morford, Numerical Terradynamic Simulation Group. ISB 418, University of Montana, Missoula MT, 59812. (406) 461-4910.

Email: scott.morford@ntsg.umt.edu

Author Contributions: S.M. and B.A. designed the analysis with additional input from D.T. and M.J. S.M. developed the modeling framework and performed the analysis. All authors assisted in evaluating and interpreting analysis results. S.M. wrote the paper with contributions from B.A., D.N., D.T, and M.J. All authors reviewed and provided input on the manuscript draft.

Competing Interest Statement: None.

Keywords: Woody encroachment, herbaceous production, yield gap, global change, agricultural land use, afforestation

Data Availability: Model data and code will be archived at Zenodo upon manuscript acceptance and spatial data will be made available via Google Earth Engine.

This PDF file includes:

Main Text
Figures 1 to 6
Tables 1 to 2

Abstract

1. Rangelands of the United States provide ecosystem services that benefit society
and rural economies. Native tree encroachment is often overlooked as a primary
threat to rangelands due to the slow pace of tree cover expansion and the
positive public perception of trees. Still, tree encroachment fragments these
landscapes and reduces herbaceous production, thereby threatening habitat
quality for grassland wildlife and the economic sustainability of animal
agriculture.
2. Recent innovations in satellite remote sensing permit the tracking of tree
encroachment and the corresponding impact on herbaceous production. We
analyzed tree cover change and herbaceous production across the western
United States from 1990 to 2019.
3. We show that tree encroachment is widespread in U.S. rangelands; absolute
tree cover has increased by 50% (77,323 km^2) over 30 years, with more than
25% (684,852 km^2) of U.S. rangeland area experiencing tree cover expansion.
Since 1990, 302 ± 30 Tg of herbaceous biomass have been lost. Accounting for
variability in livestock biomass utilization and forage value reveals that this lost
production is valued at between $4.1 - $5.6 billion U.S. dollars.
4. Synthesis and applications: The magnitude of impact of tree encroachment on
rangeland loss is similar to conversion to cropland, another well-known and
primary mechanism of rangeland loss in the U.S. Prioritizing conservation efforts
to prevent tree encroachment can bolster ecosystem and economic
sustainability, particularly among privately-owned lands threatened by land-use
conversion.

1. Introduction

Native trees are invading global rangeland biomes (Nackley et al., 2017). Fire suppression, livestock overgrazing, nutrient pollution, and increasing CO_2 emissions contribute to extensive tree encroachment in rangelands (here defined as grasslands, shrublands, and open woodlands) (Asner et al., 2004). This encroachment exacerbates already substantial losses of rangelands to cropland conversion and threatens global rangelands' resilience and conservation potential (Fargione et al., 2018; Hoekstra et al., 2004; Kremen & Merenlender, 2018; Veldman et al., 2015).

Tree encroachment modifies the structure and function of rangeland ecosystems, thereby impacting a host of ecosystem services. Water storage and supply, wildlife and livestock habitat quality, biodiversity preservation, and climate regulation are all modulated by tree cover in rangelands (Archer and Predick, 2014; Bardgett et al., 2021). Importantly, tree cover is a key regulator of herbaceous production (the combined production of grasses and forbs; i.e., forage) upon which both wildlife and livestock depend. Substantial effort has been invested in disentangling the complex relationship between herbaceous production and tree cover (Anadon et al., 2014; Scholes, 2003). Yet, critical knowledge gaps still exist for how herbaceous production responds to tree encroachment at large scales.

Identifying where tree encroachment impacts ecosystem services such as carbon (C) storage and productivity has traditionally relied on historical image analysis, paired site investigations, and evaluations of the pollen record (Archer et al., 1988; Lubetkin et al., 2017). These methods have documented substantial tree canopy expansion in Africa, the Americas, Asia, and Australia. Unfortunately, critical knowledge on patterns, pace, and magnitude of tree encroachment to rangelands remains absent at large scales. While operational remote sensing products are applied globally to track forest cover changes, these analyses typically lack the sensitivity to track tree cover gains in rangelands or omit analysis of tree cover in rangelands altogether (Hansen et al., 2013; Rigge et al., 2020).

Recent technological advances in remote sensing collectively suggest large-scale tree cover expansion in United States (U.S.) rangelands (Allred et al., 2021; Filippelli et al., 2020; Jones et al., 2020), consistent with decades of empirical observations. Related

innovations in tracking annual herbaceous production now allow for an integrated

spatiotemporal analysis of production and tree cover (Jones et al., 2021)

Two-thirds of western U.S. rangelands are under private ownership, and conservation of

these lands requires addressing ecological and economic sustainability linkages.

Declining ranch income hastens the conversion of intact grasslands to row-crop

agriculture, fossil-fuel energy production, and dispersed housing developments (Allred et

al., 2015; Lark, 2020). For example, row-crop conversion has accelerated in recent

years due to commodity market fluctuations and declining economic returns from

livestock production. Tree encroachment can exacerbate declines in ranching

profitability as expanding woodlands out-compete and displace grasses and forbs

(Anadon et al., 2014; Fuhlendorf et al., 2008). Revealing the economic cost of tree

encroachment on forage production could help motivate livestock producers to

implement proactive, conservation-focused tree management in rangelands.

Here we investigate tree encroachment and its impacts to herbaceous production across

primary U.S. rangelands. We estimate the economic value of lost production to help

inform sustainable agricultural practices, the preservation of intact grasslands (Scholtz &

Twidwell, 2022), and the protection of grassland bird habitats threatened by tree

encroachment (Baruch-Mordo et al., 2013; Herse et al., 2018; Rosenberg et al., 2019).

Specifically, our analysis quantifies the difference between attainable and actual

herbaceous production as a function of tree cover expansion, a difference termed yield

gap that is commonly used in agriculture to investigate production losses (van Ittersum

et al., 2013). Yield gap estimates were combined with grazing rental rates from the U.S.

Department of Agriculture (USDA) to estimate foregone revenue to livestock producers

from tree encroachment.

2. Methods

We calculated tree cover change and herbaceous production lost to tree encroachment

using data from the Rangeland Analysis Platform version 2.0 (RAP-V2, Allred et al.,

2021). RAP-V2 geography spans 17 western states (**Fig. 1**) and includes the entirety of

intact semi-arid and arid rangelands in the U.S. (Reeves & Mitchell, 2011, Scholtz &

Twidwell, 2022). Our analysis incorporated data from 1990 through 2019. We used

Landfire Biophysical Settings (BPS) version 1.4.0, to identify where rangelands were

dominant prior to Euro-American settlement and to exclude primary forest areas from

our calculations. Our analysis also excludes contemporary lands that were mapped as
croplands, urban/built, or riparian. This analysis included 2,783,955 km^2 of historical
rangelands.

The multi-part modeling framework is presented below in four sections. Tree cover and
herbaceous production modeling are presented first. These data were used as inputs to
the yield gap modeling presented in section 2.3. Then, section 2.4 describes how the yield
gap biomass estimates were combined with economic data to produce a monetary
estimate of lost production.

2.1 Tree Cover Modeling and Analysis

In RAP-V2, fractional tree cover was calculated using a convolutional neural network.
The network used Landsat surface reflectance (bands 1-5,7 for Landsat 5 TM and 7
ETM+; bands 2-7 for Landsat 8 OLI), normalized difference vegetation index (NDVI), and
normalized burn ratio two (NBR2) for prediction. The model was trained using data from
52,012 vegetation field plots collected by Federal natural resource agencies. Model
performance was evaluated against 5,780 field plots; metrics evaluated include mean
absolute error (MAE = 2.8%), root mean square error (6.8%), residual standard error
(5.9%) and coefficient of determination (r2 = 0.65).

To improve the detection of real and significant tree cover change, we further processed
the tree cover data using the LandTrendr (LT) segmentation algorithm (Kennedy et al.,
2010) in Google Earth Engine (GEE). The LT parameters used in this analysis are
summarized in **Supplemental Table 1**. We applied two rules to remove spurious tree
cover trends in our analysis. First, to tally tree cover change, the difference in tree cover
needed to exceed the model MAE (2.8%). Second, we performed a Welch T-test (n = 4,
two-tailed, p-value = 0.01) on each pixel segment using the RAP-V2 uncertainty data.
For tree cover change to be tallied in a pixel, it had to have one or more segments where
the t-value < p-value.

Tree-free rangelands in this analysis were defined functionally at the pixel level (30m by
30m) as rangelands where tree cover was less than 4%, corresponding to tree cover
where sizable impacts to ecosystem function are observed (Baruch-Mordo et al., 2013).
Tree-free rangelands were further categorized as either *intact* or *vulnerable. Vulnerable*
tree-free rangelands were classified as *tree-free rangeland* pixels where tree cover was

greater than 2.8% (the tree cover MAE) in pixels within a 200-meter radius. In our

analysis we evaluate both the change in total tree-free rangelands on a per-pixel basis

and change in intact/vulnerable tree-free rangelands based on the neighborhood

analysis.

2.2 Herbaceous Production Calculations

Pixel-level estimates for herbaceous production were calculated using the Landsat

implementation of the MOD17 Net Primary Productivity algorithm and calibrated for

aboveground herbaceous production (Jones et al., 2021; Robinson et al., 2019). The

algorithm incorporated land surface reflectance, land surface cover from RAP-V2, and

meteorology data. Production calculations from this method show good agreement with

independent estimates of production from remote sensing and field-based compilations

(r^2 values of 0.79 and 0.82, respectively), but tend to under-estimate production in highly

productive environments (See Figure 2 in Jones et al., 2021 and supplemental text). In

the modeling for this analysis, herbaceous production estimates from the MOD17

algorithm are referred to as *Observed Production*.

2.3 Yield Gap Modeling

Next, we combined the tree cover and production data presented in sections 2.1 and 2.2

with other biophysical variables to calculate herbaceous production lost to increased tree

cover. We used XGBoost (Chen & Guestrin, 2016), an ensemble decision tree

supervised learning algorithm, to model herbaceous production as a function of the

variables presented in **Table 1.**

The XGBoost algorithm made two biomass predictions per pixel to estimate yield gap:

Estimated Production and *Achievable Production. Estimated Production* represents the

model's best estimate of actual biomass production; *Achievable Production* represents

potential production, assuming tree cover remains constant over their 30-year modeling

domain. The difference between these two production estimates represents the yield

gap.

More formally, our analysis applies the following framework to model herbaceous

production as a function of tree cover and biophysical variables (**equation 1**).

Production(YR) = f (YR, MU, LP, TC$_{(yr),}$, SP)   **eqn 1.**

In our framework, *YR* represents year, MU = soil map unit, LP = landscape position,

$TC_{(yr)}$ = tree cover for year YR, SP = spatial position/coordinates. Factor variables were

encoded as integers during training and inference. Model variables, source data, and a

rationale for their inclusion are presented in **Table 1**.

Model parameterization and training: We split our analysis area into 53 spatial units

using Level-3 EcoRegions from the U.S. Environmental Protection Agency. The training

data size for each unit was limited to 71,582,780 records due to computational

limitations; the remaining training data were used as hold-out (test) data. The models

were trained with 3.8 billion records randomly sampled from our dataset; the remaining

5.5 billion records were used for validation and evaluation. The optimization (loss)

function was mean squared error with L2 regularization; our ensemble used 60 trees

with a maximum tree depth of 15 **(Supplemental Table 2)**. Evaluation of the training

metrics showed that holdout MAE values closely matched training MAE values (r^2 >

0.99), suggesting the model did not overfit the data **(Supplemental Fig. 1)**.

Inference: XGBoost generated two predictions: *Estimated Production* and *Achievable*

Production **(equations 2 and 3),** assuming that tree cover remained constant at 1990

levels.

$$\textit{Estimated Production}(YR, TC_{(yr)}) \;=\; E[\textbf{\textit{m}}|\; YR,\, MU,\, LP,\, TC_{(yr)},\, SP] \qquad \textbf{eqn. 2}$$

$$\textit{Achievable Production}(YR, TC_{(1990)}) \;=\; E[\textbf{\textit{m}}|\; YR,\, MU,\, LP,\, TC_{(1990)},\, SP] \qquad \textbf{eqn. 3}$$

The yield gap attributable to tree cover expansion since 1990 is calculated by

subtracting *Estimated Production* from *Achievable Production* for each pixel-year

combination (**equation 4**).

$$\textit{Yield Gap}(YR) \;=\; \textit{Achievable Production}(YR, TC_{(1990)}) -$$

$$\textit{Estimated Production}(YR, TC_{(yr)}) \qquad \textbf{eqn. 4}$$

Prediction Error for each pixel was calculated as the absolute difference between

*Observed Production and Estimated Production **(equation 5). Model Error* was**

represented as the MAE **(equation 6)**, aggregated by year and map unit to provide

some localization; *n* is the number of observations for each MU.

Prediction Error(YR) =

180   *|Observed Production(YR) – Estimated Production(YR,TC$_{(yr)}$)|*   **eqn. 5**

Model Error(MU | YR) =[∑*Prediction Error*(MU | YR)] / n   **eqn. 6**

For this analysis, the yield gap was tallied when *Yield Gap > Model Error* for 3 or more

consecutive years.

2.4 Monetary calculations

We calculated the dollar value of herbaceous production lost to tree encroachment by

combining yield gap calculated in section 2.3 with estimates with annual state-level

grazing rental rates from the USDA National Agricultural Statistics Service (NASS, U.S.

Department of Agriculture, 2020). Producer-to-producer rental rates are the most direct

way to estimate the market value of herbaceous production. In the U.S., rental contracts

are most commonly negotiated using Animal Unit Month (AUM) lease rates. AUM is a

measure of forage use by livestock. The value of herbaceous production was calculated

from AUM rental rates using **equation 7**.

$$\frac{\$}{kg\ production} = \frac{\$}{AUM} \times \left(\frac{kg\ forage}{AUM}\right)^{-1} \times UF \qquad \textbf{eqn. 7}$$

Dollars per Animal Unit Month ($/AUM) represents the grazing rental rate; *kg forage / AUM*

represents the mass of consumed forage per AUM and is assumed to equal 344.73 kg

forage/AUM. UF is the utilization factor and represents the fraction of total herbaceous

production consumed as forage by livestock. The UF is required to convert between total

herbaceous production (what is grown) and forage (what is utilized).

The UF is difficult to estimate because it can vary in space and time. Literature based

estimates suggest that UF is equal to 0.43 under moderate grazing regimes (Holechek

et al., 2010), which generally conforms to the use-half leave-half principle prescribed in

U.S. grazing systems. Since 2008, NASS periodically reports rental rates negotiated on

an areal basis in addition to the AUM basis. When these records exist together, they can

be used with RAP-V2 production data to calculate UF as shown in **equation 8** (a full

derivation is provided in the supplemental text). This approach assumes that the value of
herbaceous production is comparable in the two rental schemes.

208
$$UF = \frac{\$}{hectare} \times \left(\frac{kg\ production}{hectare}\right)^{-1} \times \left(\frac{\$}{AUM}\right)^{-1} \times \left(\frac{kg\ forage}{AUM}\right)$$
eqn. 8

Using this method, we calculated a mean UF of 0.4011 (standard deviation = 0.0619, n =
168), slightly more conservative than the literature-based value. Importantly, military and
protected non-grazing lands (e.g., National Parks) were excluded from the monetization
calculations, but other federal grazing lands (i.e., BLM and USFS allotments) were
included. Finally, dollar estimates were inflation-corrected to 2019 dollars using the
consumer price index from the U.S. Bureau of Labor Statistics.

2.5 Evaluation of model uncertainty and error

To assess uncertainty in our yield gap estimates, we used Mean Absolute
Percentage Error (MAPE) to provide upper and lower bound yield gap estimates
for our annual data (**equations 9 and 10**).

219
$$\text{MAPE} = \frac{1}{n}\sum_{i}^{n}\left|\frac{(Observed\ Production)_i - (Estimated\ Production)_i}{(Observed\ Production)_i}\right|$$
eqn. 9

220
$$Yield\ Gap\ Uncertainity = Yield\ Gap \pm (Yield\ Gap * MAPE)$$
eqn. 10

To incorporate uncertainty in the monetary estimate, we used a Monte Carlo
simulation (n = 10,000) to account for variability in biomass estimates, forage
rental rates ($/AUM), and UF. We assumed forage rental rates ($/AUM) varied by
± 20% (random uniform distribution) and used random normal UF estimates
derived from ***equation 8.***

Uncertainty in production estimates attributable to satellite signal quality and
atmospheric noise (e.g., clouds) was assessed by calculating the yield gap with
and without data imputation and filtering measures. Further details of the
approach and results are presented in supplemental text.

3. Results

Rangelands gained 77,323 ± 1,222 km^2 of tree cover between 1990 and 2019 (**Fig. 2**). Absolute tree cover increased from 154,502 km^2 to 231,825 km^2 (**Table 2**). Tree cover grew on average 2,577 km^2 per year, with annual increases in all years. Tree cover in grasslands grew by 85% over this period, with shrublands and open woodlands increasing by 43% and 40%, respectively. In total, we observed increased tree cover on 25% (684,852 km^2) of rangeland area (pixels) between 1990 and 2019. In contrast, tree cover declined across roughly 6% of rangelands (180,461 km^2).

The magnitude and direction of tree cover change varied by region. Tree cover was found to be increasing in 11 of 14 regions examined, while substantial losses in tree cover were observed in parts of the desert southwest and along the Pacific Coast (**Fig. 3).** Tree cover trends appeared to be accelerating in the central and northern rangelands, while tree cover growth appeared to slow across portions of southeast rangelands**. Supplemental Fig. 2** shows a map highlighting areas (pixels) of increasing and decreasing tree cover.

Importantly, tree encroachment resulted in the loss of 147,700 km^2 (range: 135,283 - 150,827 km^2) of tree-free rangelands, transitioning roughly 8% of these lands into woodlands (**Fig. 2, Panel C**). Even where tree-free rangelands persist, they were increasingly vulnerable to encroachment due to their proximity to nearby tree seed sources. For example, the area of intact tree-free rangelands (rangelands greater than 200 meters from a tree seed source) declined by 15% (204,651 km^2) over the 30 years.

Tree encroachment contributed to sizable losses in herbaceous production (**Fig. 4**). Production losses totaled 302 ± 30 Tg (dry biomass) from 1990 through 2019. In 2019, the yield gap totaled 20.0 ± 4.2 Tg, representing 5% - 6% of the potential forage production for all western U.S. rangelands (**Fig. 4b**).

Locally, we observed that increasing primary productivity buffers production losses during early tree colonization of rangelands. We found that herbaceous production could remain stable or even increase following the establishment and expansion of woody encroachment (**Fig. 5**). In the absence of disturbance, however, yield gaps rapidly develop as tree cover continues to increase, resulting in large net declines in production

over short periods. For example, **Fig. 6** illustrates how a 30% yield gap developed in
only five years following 20 years of sustained tree cover expansion.

On an inflation-corrected basis, the value of herbaceous production lost to woody
encroachment totaled U.S. $4.84 ± 0.72 billion over the 30 years analyzed; losses for
2019 were estimated to be $307.2 million ($192.6 - $480.3 million). Our monetary
estimates were sensitive to biomass modeling error and under constrained economic
variables (i.e., uncertainty in rental rates and biomass utilization). Assumptions regarding
forage utilization by livestock may be particularly important but are also the hardest to
constrain in space and time.

Our yield gap results were generally robust to errors introduced from satellite signal
degradation and processing, particularly for years after 2000 (**Supplemental Fig. 3**).
Variability in yield gap calculations attributable to signal and processing errors was
approximately 3% in 2019 (yield gap range: 19.7 to 20.3 Tg). Prior to 2000, satellite data
processing relied heavily on gap-filling methods. However, the imputation of these data
had little impact on the interpretation of temporal trends.

4. Discussion

Our analysis shows that the conversion of grasslands to woodlands is widespread
among rangelands of the U.S., with estimated impacts to an area roughly the size of the
country of Germany (calculated as the sum of lost and vulnerable tree-free rangelands,
352,261 km^2). These findings are consistent with model-based projections of climate-
driven woodland expansion and impacts from a century of wildland fire suppression
(Bond, 2008; Klemm et al., 2020; Ratajczak et al., 2014). Modest increases in tree
density are well-known to have outsized impacts on ecosystem services and biodiversity
in rangelands. For example, many grassland and shrubland obligate bird species are
lost from rangelands when tree cover exceeds more than a few percent (Baruch-Mordo
et al., 2013; Herse et al., 2018; Lautenbach et al., 2017). These results further reinforce
scientific conclusions that woody encroachment is a primary change agent across broad
regions of U.S. rangelands (Engle et al. 2008; Wilcox et al. 2022).

The pace of tree encroachment is similar in magnitude to recent row-crop conversion,
another primary threat to the conservation and sustainability of U.S. rangelands. From
2008 to 2016, conversion of intact rangelands to cropland accelerated rapidly across the

western U.S; annual conversion rates were observed to be 1,649 to 4,385 km^2 annually

(median = 2,777 km^2, **Supplemental Fig. 4**) (Lark et al., 2020). In comparison, the

median annual loss of rangelands to tree encroachment was 1,899 km^2 over this same

period. Together, these data suggest that rangelands of the western U.S. are being lost

at a rate of 1,282 hectares (3,168 acres) per day, losses that are 68% higher than

estimates based solely on row-crop conversion. Importantly, not all areas are

experiencing tree encroachment. Large tree cover declines were observed in the

southwest of our study area, attributable primarily to long-term drought (**Fig. 3,**

Supplemental Fig. 4).

We found that tree encroachment creates sizable yield gaps in herbaceous production

across western U.S. rangelands. This production mediates critical ecosystem services

such as below-ground C storage and is the cornerstone of food and fiber production in

rangelands (Jackson et al., 2002). In an agricultural context, the annual 5% - 6% yield

gap observed in this analysis is comparable to sector-wide yield losses sustained to

commodity crops under extreme drought events (Lesk et al., 2016). Given that 25% of

U.S rangelands are seeing increasing tree cover, the continued expansion of yield gaps

this century could dramatically compound yield losses under intensifying drought cycles

resulting from climate change.

Rapidly accelerating woody encroachment and production losses in the northern Great

Plains are particularly concerning to working lands conservation (**Fig. 3**). This area is

central to ongoing efforts to protect the North American grassland biome. Here,

production losses resulting from tree encroachment may further exacerbate economic

harm to small ranching operations, promoting accelerated conversion of grasslands to

alternative land use types (Anadon et al., 2014; Haggerty et al., 2018; Lark, 2020).

Losses of these intact grasslands threaten the last remaining large-scale migrations of

native ungulates (*Antilocapra americana*) in the contiguous U.S. (Joly et al., 2019).

Further, the area is critical habitat for rapidly declining obligate grassland bird

populations which are particularly sensitive to habitat fragmentation and tree

encroachment (Brennan & Kublesky, 2005; Rosenberg et al., 2019).

Importantly, primary production is not fixed or constant in an era of global environmental

change. We observed sizable increases in herbaceous production among rangelands

where tree cover remained constant (averaging 195.7 kg ha^{-1} yr^{-1} more production in

2019 than in 1990), consistent with other studies showing increased productivity across

large swaths of the North American continent (Boone et al., 2018; Hicke et al., 2002;

Reeves et al., 2020). These increases are attributable to increases in precipitation and

growing season length as a result of climate change. Consequently, many areas

undergoing early stages of woody encroachment may experience little to no loss in total

herbaceous production (**Fig. 5, Supplemental Fig. 4**).

These findings illustrate both challenges and opportunities to address tree

encroachment in U.S. rangelands. The lag between when trees colonize and when yield

gaps are detectable may incentivize some land managers to accommodate tree

encroachment until it reaches more advanced stages. In these cases, managing

encroachment becomes more expensive and complex due to removing additional tree

biomass and established seed stores (Roberts et al., 2018). Conversely, the time lag

provides an opportunity to implement cost-effective management to prevent further tree

encroachment, productivity decline, and economic losses to agricultural producers.

Removing trees in rangelands presents trade-offs between competing ecosystem

services and biodiversity goals, and the scale and severity of these trade-offs should be

considered by applied ecologists. In some areas, such as equatorial grasslands, tree

encroachment can enhance local provisioning of shade, fuelwood, and food and also

mitigate climate change impacts to communities (Linders et al., 2021). Similarly,

removing encroaching trees may unintentionally impact wildlife that utilize newly

developed woodland patches (Tack et al., 2022). In the context of U.S. rangelands,

preventing further tree encroachment is a key biome-level strategy to protect remaining

intact grassland and the obligate species that depend on tree-free landscapes (Scholtz &

Twidwell, 2022).

Yield gap estimates here are consistent with other studies that investigated tree-grass

interactions, including field measures from the Konza Long Term Ecological Research

Site (**Supplemental Fig. 5**). While there is consensus that herbaceous production

declines under moderate to high tree cover, there is less agreement on how incipient

tree encroachment impacts production (Anadon et al., 2014; Fuhlendorf et al., 2008;

Scholes, 2003). We did not find evidence for declining herbaceous production during

early tree colonization. However, our model-based findings should not be viewed as

definitive due to interactions between shifting baseline production and model sensitivity

to sparse tree cover (see **Supplemental Text**).

Our monetary estimates for lost revenues should be considered preliminary as they do

not incorporate economic, policy, and social considerations that drive market valuation

and the adoption of management alternatives. Locally, our estimates for forage value

agree well with independent agricultural economic data (**Supplemental Table 3)**. Still,

more sophisticated analyses will be required to assess how managing tree

encroachment impacts ranching economics.

The loss of rangeland production and corresponding impacts to ecosystem services are

often overlooked in the face of advocacy efforts calling for the afforestation of

rangelands (Bastin et al., 2019).Increasing tree cover in rangelands may not benefit

global climate change mitigation strategies due to biogeophysical feedbacks

(Friedlingstein et al., 2019; Nuñez et al., 2021). Tree encroachment can increase C

storage in rangelands (Asner et al., 2003; Connell et al., 2020), but these C storage

gains are typically offset by reducing land-surface albedo at mid- to high- latitudes (Bala

et al., 2007; Betts et al., 2007). For example, across the northern Great Plains of North

America, tree cover would need to reach 95+% to contribute to climate cooling; such a

scenario would result in the wholescale collapse of the northern Great Plains and its

biodiversity therein (Hoekstra et al., 2004; Mykleby et al., 2017). The most effective

climate mitigation strategy for rangelands remains preventing grassland conversion to

row-crop agriculture and ensuring the massive C reservoirs found in rangeland soils are

not lost to the atmosphere by land-use conversion (Bossio et al., 2020; Hoekstra et al.,

2004).

5. Conclusion

Identifying yield gaps and mitigating the impacts of forage losses provides a new

approach to support the economic sustainability of U.S. rangelands and slow land-use

conversion. Herbaceous production is the cornerstone of food and fiber economics in

working rangelands and evaluating it like other agricultural commodities provides a

means to stack market incentives with other conservation subsidies. Implementing

landscape-scale conservation strategies to close and prevent yield gaps will help

maintain the function and biodiversity of rangeland ecosystems, ultimately benefiting

nature and society.

Acknowledgments

397   **References**

398   Allred, B. W., Bestelmeyer, B. T., Boyd, C. S., Brown, C., Davies, K. W., Ellsworth, L. M., Erickson,
399   T. A., Fuhlendorf, S. D., Griffiths, T. V., Jansen, V., Jones, M. O., Karl, J., Maestas, J. D.,
400   Maynard, J. J., McCord, S. E., Naugle, D. E., Starns, H. D., Twidwell, D., & Uden, D. R.
401   (2021). Improving Landsat predictions of rangeland fractional cover with multitask
402   learning and uncertainty. *Methods in Ecology and Evolution*, *12*(5).

403   Allred, B. W., Smith, W. K., Twidwell, D., Haggerty, J. H., Running, S. W., Naugle, D. E., &
404   Fuhlendorf, S. D. (2015). Ecosystem services lost to oil and gas in North America.
405   *Science*, *348*(6233), 401–402.

406   Anadon, J. D., Sala, O. E., Turner, B. L., & Bennett, E. M. (2014). Effect of woody-plant
407   encroachment on livestock production in North and South America. *Proceedings of the
408   National Academy of Sciences*, *111*(35), 12948–12953.

409   Archer, S. R., & Predick, K. I. (2014). An ecosystem services perspective on brush management:
410   Research priorities for competing land-use objectives. *Journal of Ecology*, 14.

411   Archer, S. R., Scifres, C., Bassham, C. R., & Maggio, R. (1988). Autogenic succession in a
412   subtropical savanna: Conversion of grassland to thorn woodland. *Ecological
413   Monographs*, *58*(2), 111–127.

414   Asner, G. P., Archer, S., Hughes, R. F., Ansley, R. J., & Wessman, C. A. (2003). Net changes in
415   regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999.
416   *Global Change Biology*, *9*(3), 316–335.

417   Asner, G. P., Elmore, A. J., Olander, L. P., Martin, R. E., & Harris, A. T. (2004). Grazing systems,
418   ecosystem responses, and global change. *Annual Review of Environment and Resources.*
419   9:261-299.

420   Bala, G., Caldeira, K., Wickett, M., Phillips, T. J., Lobell, D. B., Delire, C., & Mirin, A. (2007).
421   Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of
422   the National Academy of Sciences*, *104*(16), 6550–6555.

423   Bardgett, R., Bullock, J., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan,
424   G., Fry, E., Johnson, D., Lavallee, J., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X.,
425   Zhou, H., Ma, L., Ren, W., & Shi, H. (2021). Combatting global grassland degradation.
426   *Nature Reviews Earth & Environment*, *2*. https://doi.org/10.1038/s43017-021-00207-2

427   Baruch-Mordo, S., Evans, J. S., Severson, J. P., Naugle, D. E., Maestas, J. D., Kiesecker, J. M.,
428   Falkowski, M. J., Hagen, C. A., & Reese, K. P. (2013). Saving sage-grouse from the trees:
429   A proactive solution to reducing a key threat to a candidate species. *Biological
430   Conservation*, *167*, 233–241.

431   Bastin, J.-F., Finegold, Y., Garcia, C., Mollicone, D., Rezende, M., Routh, D., Zohner, C. M., &
432   Crowther, T. W. (2019). The global tree restoration potential. *Science*, *365*(6448), 76–79.

Betts, R. A., Falloon, P. D., Goldewijk, K. K., & Ramankutty, N. (2007). Biogeophysical effects of
land use on climate: Model simulations of radiative forcing and large-scale temperature
change. *Agricultural and Forest Meteorology*, *142*(2), 216–233.

Bond, W. J. (2008). What Limits Trees in C4 Grasslands and Savannas? *Annual Review of Ecology,
Evolution, and Systematics*, *39*(1), 641–659.

Boone, R. B., Conant, R. T., Sircely, J., Thornton, P. K., & Herrero, M. (2018). Climate change
impacts on selected global rangeland ecosystem services. *Global Change Biology*, *24*(3),
1382–1393.

Bossio, D. A., Cook-Patton, S. C., Ellis, P. W., Fargione, J., Sanderman, J., Smith, P., Wood, S.,
Zomer, R. J., von Unger, M., Emmer, I. M., & Griscom, B. W. (2020). The role of soil
carbon in natural climate solutions. *Nature Sustainability*, *3*(5), 391–398.

Brennan, L. A., & Kublesky, W. P. (2005). North American grassland Birds: An unfolding
conservation crisis? *Journal of Wildlife Management*, *69*(1), 1–13.

Chen, T., & Guestrin, C. (2016). XGBoost: A Scalable Tree Boosting System. *Proceedings of the
22nd ACM SIGKDD International Conference on Knowledge Discovery and Data Mining*,
785–794.

Connell, R. K., Nippert, J. B., & Blair, J. M. (2020). Three decades of divergent land use and plant
community change alters soil C and N content in tallgrass prairie. *Journal of Geophysical
Research: Biogeosciences*, *125*(8). https://doi.org/10.1029/2020JG005723

Engle, D. M., Coppedge, B. R., & Fuhlendorf, S. D. (2008). From the dust bowl to the green
glacier: Human activity and environmental change in Great Plains grasslands. In Western
North American Juniperus Communities (pp. 253–271). Springer.

Fargione, J. E., Bassett, S., Boucher, T., Bridgham, S. D., Conant, R. T., Cook-Patton, S. C., Ellis, P.
W., Falcucci, A., Fourqurean, J. W., Gopalakrishna, T., Gu, H., Henderson, B., Hurteau, M.
D., Kroeger, K. D., Kroeger, T., Lark, T. J., Leavitt, S. M., Lomax, G., McDonald, R. I., …
Griscom, B. W. (2018). Natural climate solutions for the United States. *Science Advances*,
4(11), eaat1869. https://doi.org/10.1126/sciadv.aat1869

Filippelli, S. K., Falkowski, M. J., Hudak, A. T., Fekety, P. A., Vogeler, J. C., Khalyani, A. H., Rau, B.
M., & Strand, E. K. (2020). Monitoring pinyon-juniper cover and aboveground biomass
across the Great Basin. *Environmental Research Letters*, *15*(2), 025004.

Friedlingstein, P., Allen, M., Canadell, J. G., Peters, G. P., & Seneviratne, S. I. (2019). Comment on
"The global tree restoration potential." *Science*, *366*(6463), eaay8060.

Fuhlendorf, S. D., Archer, S. A., Smeins, F., Engle, D. M., & Taylor, C. A. (2008). The Combined
Influence of Grazing, Fire, and Herbaceous Productivity on Tree–Grass Interactions. In O.
W. Van Auken (Ed.), *Western North American Juniperus Communities: A Dynamic
Vegetation Type* (pp. 219–238). Springer New York.

Ge, J., & Zou, C. (2013). Impacts of woody plant encroachment on regional climate in the
southern Great Plains of the United States. *Journal of Geophysical Research:*
Atmospheres, *118*(16), 9093–9104.

Haggerty, J. H., Auger, M., & Epstein, K. (2018). Ranching Sustainability in the Northern Great
Plains: An Appraisal of Local Perspectives. *Rangelands*, *40*(3), 83–91.

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau,
D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L.,
Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century
forest cover change. *Science*, *342*(6160), 850–853.

Herse, M. R., With, K. A., & Boyle, W. A. (2018). The importance of core habitat for a threatened
species in changing landscapes. *Journal of Applied Ecology*, *55*(5), 2241–2252.

Hicke, J. A., Asner, G. P., Randerson, J. T., Tucker, C., Los, S., Birdsey, R., Jenkins, J. C., & Field, C.
(2002). Trends in North American net primary productivity derived from satellite
observations, 1982-1998. *Global Biogeochemical Cycles*, *16*(2), 2-1-2–14.

Hoekstra, J. M., Boucher, T. M., Ricketts, T. H., & Roberts, C. (2004). Confronting a biome crisis:
Global disparities of habitat loss and protection: Confronting a biome crisis. *Ecology*
Letters, *8*(1), 23–29.

Holechek, J. L., Pieper, R. D., & Herbel, C. H. (2010). *Range management: Principles and*
practices. (6th ed.). Prentice-Hall.

Huxman, T. E., Wilcox, B. P., Breshears, D. D., Scott, R. L., Snyder, K. A., Small, E. E., Hultine, K.,
Pockman, W. T., & Jackson, R. B. (2005). Ecohydrological implications of woody plant
encroachment. *Ecology*, *86*(2), 308–319.

Jackson, R. B., Banner, J. L., Jobbágy, E. G., Pockman, W. T., & Wall, D. H. (2002). Ecosystem
carbon loss with woody plant invasion of grasslands. *Nature*, *418*(6898), 623–626.

Joly, K., Gurarie, E., Sorum, M. S., Kaczensky, P., Cameron, M. D., Jakes, A. F., Borg, B. L.,
Nandintsetseg, D., Hopcraft, J. G. C., Buuveibaatar, B., Jones, P. F., Mueller, T., Walzer,
C., Olson, K. A., Payne, J. C., Yadamsuren, A., & Hebblewhite, M. (2019). Longest
terrestrial migrations and movements around the world. *Scientific Reports*, *9*(1), 15333.

Jones, M. O., Naugle, D. E., Twidwell, D., Uden, D. R., Maestas, J. D., & Allred, B. W. (2020).
Beyond inventories: Emergence of a new era in rangeland monitoring. *Rangeland*
Ecology & Management, *73*(5), 577–583.

Jones, M. O., Robinson, N. P., Naugle, D. E., Maestas, J. D., Reeves, M. C., Lankston, R. W., &
Allred, B. W. (2021). Annual and 16-day rangeland production estimates for the western
United States. *Rangeland Ecology & Management*, *77*, 112–117.

Kennedy, R. E., Yang, Z., & Cohen, W. B. (2010). Detecting trends in forest disturbance and
recovery using yearly Landsat time series: 1. LandTrendr — Temporal segmentation

algorithms. *Remote Sensing of Environment*, *114*(12), 2897–2910.

Klemm, T., Briske, D. D., & Reeves, M. C. (2020). Potential natural vegetation and NPP responses
to future climates in the U.S. Great Plains. *Ecosphere*, *11*(10).
https://doi.org/10.1002/ecs2.3264.

Kremen, C., & Merenlender, A. M. (2018). Landscapes that work for biodiversity and people.
Science, *362*(6412), eaau6020. https://doi.org/10.1126/science.aau6020

Lark, T. J. (2020). Protecting our prairies: Research and policy actions for conserving America's
grasslands. *Land Use Policy*, *97*, 104727.
https://doi.org/10.1016/j.landusepol.2020.104727

Lark, T. J., Spawn, S. A., Bougie, M., & Gibbs, H. K. (2020). Cropland expansion in the United
States produces marginal yields at high costs to wildlife. In *Nature Communications* (Vol.
11, Issue 1). https://doi.org/10.1038/s41467-020-18045-z

Lautenbach, J. M., Plumb, R. T., Robinson, S. G., Hagen, C. A., Haukos, D. A., & Pitman, J. C.
(2017). Lesser Prairie-Chicken Avoidance of Trees in a Grassland Landscape. *Rangeland*
Ecology & Management, *70*(1), 78–86

Lesk, C., Rowhani, P., & Ramankutty, N. (2016). Influence of extreme weather disasters on global
crop production. *Nature*, *529*(7584), 84–87.

Linders, T. E. W., Schaffner, U., Alamirew, T., Allan, E., Choge, S. K., Eschen, R., Shiferaw, H., &
Manning, P. (2021). Stakeholder priorities determine the impact of an alien tree
invasion on ecosystem multifunctionality. *People and Nature*, *3*(3), 658–672.

Lubetkin, K. C., Westerling, A. L., & Kueppers, L. M. (2017). Climate and landscape drive the pace
and pattern of conifer encroachment into subalpine meadows. *Ecological Applications*,

Mykleby, P. M., Snyder, P. K., & Twine, T. E. (2017). Quantifying the trade-off between carbon
sequestration and albedo in midlatitude and high-latitude North American forests.
Geophysical Research Letters, *44*(5), 2493–2501.

Nackley, L. L., West, A. G., Skowno, A. L., & Bond, W. J. (2017). The nebulous ecology of native
invasions. *Trends in Ecology & Evolution*, *32*(11), 814–824.

Nuñez, M. A., Davis, K. T., Dimarco, R. D., Peltzer, D. A., Paritsis, J., Maxwell, B. D., & Pauchard,
A. (2021). Should tree invasions be used in treeless ecosystems to mitigate climate
change? *Frontiers in Ecology and the Environment*, *19*(6), 334–341.

Ratajczak, Z., Nippert, J. B., Briggs, J. M., & Blair, J. M. (2014). Fire dynamics distinguish
grasslands, shrublands and woodlands as alternative attractors in the Central Great
Plains of North America. *Journal of Ecology*, *102*(6), 1374–1385.

Reeves, M. C., Hanberry, B. B., Wilmer, H., Kaplan, N. E., & Lauenroth, W. K. (2020). An
assessment of production trends on the Great Plains from 1984 to 2017. *Rangeland*
Ecology & Management, S1550742420300117.

Reeves, M. C., Mitchell, J. E., (2011). Extent of conterminous US Rangelands: quantifying
implications of differing agency perspectives. *Rangeland Ecology & Management*, 64(6)
585-597.

Rigge, M., Homer, C., Cleeves, L., Meyer, D. K., Bunde, B., Shi, H., Xian, G., Schell, S., & Bobo, M.
(2020). Quantifying western U.S. rangelands as fractional components with multi-
resolution remote sensing and *in situ* data. *Remote Sensing*, *12*(3), 412.

Roberts, C. P., Uden, D. R., Allen, C. R., & Twidwell, D. (2018). Doublethink and scale mismatch
polarize policies for an invasive tree. *PLOS ONE*, *13*(3), e0189733.

Robinson, N. P., Jones, M. O., Moreno, A., Erickson, T. A., Naugle, D. E., & Allred, B. W. (2019).
Rangeland productivity partitioned to sub-pixel plant functional types. *Remote Sensing*,
11(12), 1427.

Rosenberg, K. V., Dokter, A. M., Blancher, P. J., Sauer, J. R., Smith, A. C., Smith, P. A., Stanton, J.
C., Panjabi, A., Helft, L., Parr, M., & Marra, P. P. (2019). Decline of the North American
avifauna. *Science*, *366*(6461), 120–124.

Scholes, R. J. (2003). Convex relationships in ecosystems containing mixtures of trees and grass.
Environmental and Resource Economics, *26*, 559–574.

Scholtz, R., & Twidwell, D. (2022). The last continuous grasslands on Earth: Identification and
conservation importance. *Conservation Science and Practice*, *4*(3), e626.
https://doi.org/10.1111/csp2.626

Tack, J. D., Smith, J. T., Doherty, K. E., Donnelly, P. J., Maestas, J. D., Allred, B. W., Reinhardt, J.,
Morford, S. L., & Naugle, D. E. (2022). Regional context for balancing sagebrush- and
woodland-dependent songbird needs with targeted pinyon-juniper management in the
sagebrush biome. *BioRxiv*, 2022.05.03.490495.
https://doi.org/10.1101/2022.05.03.490495

United States Department of Agriculture. (2020). *National Agriculture Statistics Service Quick*
Stats Database. https://quickstats.nass.usda.gov/

van Ittersum, M. K., Cassman, K. G., Grassini, P., Wolf, J., Tittonell, P., & Hochman, Z. (2013).
Yield gap analysis with local to global relevance—A review. *Field Crops Research*, 14.

Veldman, J. W., Overbeck, G. E., Negreiros, D., Mahy, G., Le Stradic, S., Fernandes, G. W.,
Durigan, G., Buisson, E., Putz, F. E., & Bond, W. J. (2015). Where tree planting and forest
expansion are bad for biodiversity and ecosystem Services. *BioScience*, *65*(10), 1011–
1018.

Wilcox, B. P., Fuhlendorf, S. D., Walker, J. W., Twidwell, D., Wu, X. B., Goodman, L. E., Treadwell,
M., & Birt, A. (2022). Saving imperiled grassland biomes by recoupling fire and grazing: A
case study from the Great Plains. Frontiers in Ecology and the Environment, 20(3), 179–
186. https://doi.org/10.1002/fee.2448

FIGURES

547 **Figure 1.** Yield gap analysis area includes the western half of the United States of
548 America, covering approximately 2.8 million km^2 of rangelands.

Figure 2. Woody encroachment in western U.S. rangelands (1990 - 2019). a) Net tree canopy expansion in rangelands shown in green; converted agricultural lands and built environment shown in white. b) Cumulative net tree cover expansion totaled 77,323 km^2 over 30 years; error bands represent the cumulative 95% prediction interval. c) Woodland extensification has resulted in an 8% decrease (147,700 km^2) of tree-free rangelands in the past 30 years. Intact tree-free rangelands (lands without a tree seed source within 200 meters) have declined more rapidly than the total, showing that tree-free rangelands are increasingly vulnerable to woodland conversion due to the prevalence of nearby tree seed sources.

Figure 3. Rangeland tree cover by EPA Ecoregion Level 2 (1990 – 2019). Woody expansion is
accelerating in parts of the northern Great Plains (*Region C*) and Great Basin (*Region B)* and
slowing in parts of the southern Great Plains and Texas (*Regions F, J, M, and N)*. Sustained tree
cover losses were found in the desert southwest (Region L) and California (*Region G).*

Figure 4. Herbaceous production yield gap attributable to woody encroachment: 1990 -
2019. a) Map of 2019 yield gap; converted agricultural lands and built environment
shown in white. b) Total annual yield gap in Tg ± MAE; includes dry herbaceous biomass
(grass and forb); c) The monetary value of forage lost to woody encroachment; error
bars represent the 95% prediction interval.

Figure 5. Localized relationships between tree cover change and herbaceous production from years 1990 - 2019 for five diverse locations across U.S rangelands. Impacts on herbaceous production from tree encroachment vary by location due to local biophysical conditions and climate. These data are calculated at the county scale and are truncated at ±20% to emphasize dominant threshold behavior.

Figure 6. Local-scale evaluation of tree encroachment and yield gap development in the
Loess Canyons, Nebraska USA (W100.44° N40.95°). Herbaceous production decreased
by 34% percent between 1990 and 2019. **(Top)** Time series aerial imagery shows the
dramatic expansion of Eastern Red Cedar (*Juniperus virginiana*). (**Bottom**) Time-series
and spatial trends in achievable and observed forage production show the forage yield
gap's evolution as a function of tree encroachment.

Table 1. Yield gap modeling variables

Variable	Abbv.	Data Type	Source	Rationale
Independent				
SSURGO map units	MU	Factor	NRCS[a]	Segment site potential across the landscape.
Landscape position - Continuous Heat-Insolation Load Index	LP	Continuous	Conservation Science Partners [b]	Integrate topographic position and solar insolation to further segment site potential.
Year	Year	Factor	N/A	Proxy for annual weather conditions.
Tree cover	TC	Continuous	RAP[c]	Key independent variable.
Spatial Position - X	SPx	Continuous	N/A	Localization - rounded to 0.1 decimal degree (roughly 10 km).
Spatial Position - Y	SPy	Continuous	N/A	
Dependent				
Herbaceous Production	-	Continuous	RAP[c]	-

Notes: Factor data types were encoded as integers in the model because one-hot encoding was unfeasible to implement across thousands of map units.
(a) Map Units from NRCS gridded SSURGO product (https://gdg.sc.egov.usda.gov/).
(b) US NED CHILI product available on Google Earth Engine (asset: '*CSP/ERGo/1_0/US/CHILI*').
(c) Available on Google Earth Engine or https://rangelands.app/products/.

Table 2. Absolute tree cover change from 1990 - 2019

	Intact Biome Area(†)	Tree Cover 1990		Tree Cover 2019		Tree Cover Expansion	
	km^2	km^2	%	km^2	%	km^2	%
Grasslands	1,032,089	30,012	2.91	55,537	5.38	25,524	2.47
Shrublands	1,265,754	42,441	3.35	60,852	4.81	18,411	1.45
Open Woodlands	438,216	81,379	18.57	114,625	26.16	33,246	7.59
Sparsely vegetated (‡)	47,895	669	1.40	812	1.69	142	0.30
Total	2,783,955	154,502	5.55	231,825	8.28	77,323 ± 1,222	2.73 ± 0.04

Notes: † Intact biome areas calculated from Landfire BPS v1.4, NLCD 2016 and NASS data. Areas exclude row-crop agricultural lands and the built environment. ‡ Sparsely vegetated class includes all sparsely vegetated systems identified in BPS v1.4.0; these areas typically are found as subcomponents of the three primary biomes included in our analysis. The total tree data includes the 95% confidence interval based upon incorporating model error rate and trend analysis of the time-series data.