

WOODY PLANT EXPANSION IN THE NORTHERN GREAT PLAINS:
A MULTI-SCALE ASSESSMENT OF THE DRIVERS AND
ECOLOGICAL IMPLICATIONS OF INCREASING WOODY
ABUNDANCE IN A TEMPERATE OPEN ECOSYSTEM

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Land Resources and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 2022

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DEDICATION

For my grandparents Don and Anne Currey, who have provided me with every opportunity I could have ever dreamt of, and then some.

ACKNOWLEDGEMENTS

I would not be where I am today without my grandparents, Anne and Don, to whom this document, and my lifetime, are dedicated.

To my mentors, my intellectual faculties are forever indebted to you. In particular, to Paul Stoy, Bruce Maxwell, and Dave McWethy for always being available and encouraging, and for being confident in me. And especially to Jack Brookshire, without whom none of this would be possible. Thank you for believing in me, setting a high bar, and instilling in me the understanding that I now hold a degree in, not just “ecology and environmental science,” but also a degree in philosophy. Inquisition is why we have all been drawn to the academy, and you have taught me to never forget this. To quote the great Richard Feynman, “Never confuse education with intelligence, you can have a PhD and still be an idiot.” I will try my best to not be an idiot.

To my friends, many of whom I am lucky to call family, I offer my thanks to you as well. Specifically, to Carson Szarek, Patrick Foster, David Strebel, and Kelly Cote for teaching me compassion, teaching me perspective, teaching me to always do the right thing, and teaching me true curiosity. And finally, to Justin Gay. More than just a lab mate, I would never have guessed that I was signing up for a lifelong friendship and brotherhood when I signed up to pursue a Ph.D. And to the many other friends, a list too long to write here, I am nothing but a compilation of small parts of each of you.

Finally, to Hannah Duff. Your companionship has been the most important aspect of my Ph.D. While I have learned so much over these past few years, you have taught me so much more than can be read in journal articles and books. Without you, I would struggle to find purpose.

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ABSTRACT

Open ecosystems (i.e., non-forested ecosystems) are inherently dynamic ecosystems that are essential to the persistence of humankind; yet many are being altered, degraded, or lost. One of the largest changes to open ecosystems globally is an increase in greenness, driven by increasing plant photosynthetic capacity or altered species composition. Often this transition in species composition occurs when woody species (i.e., trees and shrubs) increase in dominance or replace contemporary herbaceous species, a phenomenon referred to here as woody plant expansion (WPE). WPE has been proposed as a possible solution to climate change, yet ultimately has the potential to alter grasslands into a novel state.

This dissertation improves the understanding of how open ecosystems have been altered by WPE. The chapters within this document offer a multi-scalar examination of the drivers and ecological implications of WPE in the Northern Great Plains (NGP) of North America, one of the largest grasslands remaining globally. Specifically, I answer three main questions: (1) What is the extent and magnitude of WPE across the NGP? (2) What are the drivers, ecosystem implications, and biogeochemical impacts of WPE? and (3) Moving forward, how should research be prioritized in ecosystems like the NGP, particularly concerning climate mitigation and management? I begin with an introduction to the NGP, the implications of WPE, and an overview of this dissertation. I then examine the drivers and interactions of WPE and the recent increase in vegetative productivity. Next, I couple high-resolution estimates of WPE from the heart of the NGP with data from sampling plots to examine the impact that WPE has on ecosystem biogeochemistry. Next, WPE is examined against agricultural expansion and I propose that future work examining large-scale changes and the subsequent management of open ecosystems be reframed towards weighing the impacts on biodiversity, carbon storage, and ecosystem resilience. Finally, I summarize all findings with implications for future research. The NGP has the potential to represent the future of North American grasslands and, while this dissertation answers many questions, the future remains highly uncertain.

CHAPTER ONE

INTRODUCTION

Throughout Earth's history, ecosystems have developed, shifted, collapsed, and evolved innumerable times. Today, this is still the case. However, while we have typically viewed these ecosystem dynamics through a palaeoecological lens, today we can observe large and rapid ecological changes on a timescale that is measurable within a few generations (IPCC, In Press).

This is particularly true regarding grasslands and other open ecosystems (i.e., non-forested ecosystems). Humans have used these ecosystems since our earliest origins, giving rise to many of the habits and practices we maintain today (Manning, 1997). Moreover, while dynamism is a key feature of the grassland biome, the rate at which grasslands are currently changing is unprecedented. Despite this, most grasslands globally remain unprotected (Dinerstein et al., 2017; Carbutt et al., 2017).

One of the larger changes to grasslands globally is the increase in greenness (Chen et al., 2019a). Since the 1980s, using earth observation satellites, we have been able to examine this vegetative greening, which is typically defined as the increase in vegetative greenness resulting from increasing leaf size, leaf density, plant density, duration of green-leaf presence, leaf photosynthetic capacity, or changing species composition (Piao et al., 2020). Greening is largely driven by rising atmospheric CO₂ concentrations, climate change, nitrogen deposition, and land-use changes, although management dynamics or altered disturbance regimes can cause greening at local scales (Zhu et al., 2016). Greening is typically measured via Normalized Differenced Vegetation Index (NDVI), defined as the normalized difference between near-infrared light (~700-1100 nm) and red light (~620-700 nm), or Leaf Area Index (LAI), defined as half of the

summation of leaf area per unit ground area. How greening is measured can provide different insights into the drivers and consequences of greening. Irrespective of measurement, however, greening increases the photosynthetic capacity of vegetation and, thus, enhances vegetative productivity (Chen et al., 2019b). As a result, terrestrial carbon storage increases, consequently slowing anthropogenic climate warming (Piao et al., 2020). As such, understanding greening is exceedingly important.

While the phenomenon of greening comes with a unique catalog of consequences, greening alone cannot shift the biome into a new state unless other underlying changes also drive greening. One of these underlying drivers of greening is the phenomenon of woody plant expansion (WPE). WPE is a highly consequential change in species composition occurring across contemporary grasslands and open ecosystems around the planet (Bond, 2019). The average absolute rate across global grasslands was estimated to be 0.3% cover per year (Deng et al., 2021). WPE has large consequences for the ecology of the system where it occurs. The increase of woody species leads to higher biomass and aboveground carbon storage (i.e., productivity), increased structural complexity, and decreased grass abundance (i.e., forage for cattle; Archer et al., 2017). However, there is large uncertainty regarding generalizations of the global consequences of WPE. For instance, equivocal findings have been documented regarding the impacts of WPE on biodiversity (Eldridge et al., 2011; Ratajczak et al., 2012; Andersen & Steidl, 2019; Wieczorkowski & Lehmann, 2022), soil biogeochemical cycling (Jackson et al., 2002; Barger et al., 2011), and biophysical processes (Maestre et al., 2009; Qiao et al., 2017). Similarly, the role of WPE in climate mitigation is highly contentious. WPE has been proposed as a solution to climate change (e.g., Bonn Challenge, the Atlas of Forest Restoration

Opportunities, and the Great Green Wall of Africa, to name a few), albeit with large pushback due to the ancient history and cultural importance of these open ecosystems (Veldman et al., 2015; Feurdean et al., 2018).

This dissertation improves our understanding of how grasslands have changed due to the expansion of woody vegetation. To accomplish this, I leverage the ecoregion known as the Northern Great Plains (NGP) of North America. The NGP comprises $\sim 450,000 \text{ km}^2$ of short- and mixed-grass prairie, with a large portion of shrubland. The second-largest land cover type within the NGP is agricultural use, comprising roughly $220,000 \text{ km}^2$. Finally, the smallest vegetative biome of the NGP is forest ($< 50,000 \text{ km}^2$). Notably, the NGP has a population density of $\sim$ two persons km^{-2} (CIESIN, 2018), likely contributing to the lack of fragmentation. Of note, in much of this dissertation, I use the term “grassland” to include both shrub and prairie ecosystems or “open ecosystems” to emphasize non-forested ecosystems (e.g., grasslands, shrublands, and savannas).

While species composition change is a key driver of greening, this has not been thoroughly explored at high spatial resolution in the NGP. In Chapter Two, I start by answering simple yet fundamental questions regarding this ecoregion: What are the extent and magnitude of greening and WPE across the NGP, and What is driving these potential changes? Subsequently, we ask: How are WPE and greening spatiotemporally coupled across the grassland biome of the NPG? Said another way: To what degree does WPE lead to increased vegetative greening? To answer these questions, my coauthors and I use relatively high-resolution data ($\sim 500 \text{ m}$) to examine significant percent tree cover change, and greening measured three across the $450,000 \text{ km}^2$ of grasslands in the NGP. We examine 26 potential climatic, disturbance, and topographic

variables to understand the drivers of these vegetative changes and use machine learning and statistical approaches to disentangle the relative strengths and direction of each driver of vegetative change. Finally, we examine the degree of spatiotemporal synchrony between greening and WPE.

In Chapter Three, I focus on a study region in the heart of the NGP that has undergone large WPE, according to the findings from Chapter Two. In the Musselshell and Missouri River Breaks region, we established 25 long-term monitoring plots in which every tree was measured for height and diameter, up to four trees were cored per plot, soils and plant tissue chemistry were sampled, and the relative portion of woody versus herbaceous plant composition was measured. These long-term plots were established in concert with a prescribed-fire investigation by the Bureau of Land Management in which the larger Musselshell and Missouri River Breaks region was divided into discrete management units. In this chapter, we focus on one of the largest units that spans ~4,600 ha and represents the larger area. Furthermore, we used aerial photography to investigate the past and compare it with contemporary imagery to quantify the rate of WPE across the study system. This chapter answers the questions: To what degree is WPE occurring in the study region? and How is WPE impacting the ecosystem (soil and biomass) carbon, nitrogen, and phosphorus pools? Combining all the data, we link soil biogeochemistry to the rates of woody cover change derived from aerial imagery analysis. Importantly, this also allows us to benchmark the satellite-based estimates of woody cover from Chapter Two with the aerial and ground-based measurements.

In Chapter Four, I return to the scale of the NGP and broader. Here, I provide a perspective offering a new ideological framework for how open ecosystems like the NGP can be

understood and appropriately managed to better inform climate change mitigation strategies. This chapter is meant to be a generative piece and inform the burgeoning conservation movement occurring throughout the NPG and other open ecosystems with similar ecology. The shifting nature of open ecosystems implies that they are out of alignment with their climate by definition and thus have the largest potential to change under continued climate change. This also suggests that open ecosystems have the largest potential for mismanagement. This work provides an improved framework for considering possible outcomes before management is applied. Namely, this chapter underscores the importance of weighing the impacts of natural and imposed ecosystem changes on biodiversity versus carbon storage and sequestration.

Finally, in Chapter Five, I provide a short synthesis of the findings presented throughout this dissertation, with considerations and recommendations for future study.

This dissertation builds off a large body of previous scientific work. In particular, I build off the research in Brookshire et al. (2020), which documents large climate-dependent greening driven largely by increased CO₂-based water-use efficiency increases. Simultaneous large decreases in nitrogen availability suggest increased nitrogen-use efficiency, yet these findings signal a potential bottleneck to future productivity. How WPE may or may not influence these trajectories is a principal goal of this work. Much of my understanding of open ecosystems comes from a large body of literature well documented in Archer et al. (2017) and Bond (2019). Much of this work pertains to the arid southwest US and the savannas of Africa. I have leveraged this body of work as both a guide for how the NPG is similar, but also how the ecology of the ecoregion is different. Similarly, WPE has long been relegated to the realm of anecdote within the boundaries of the NPG, as documented in Symstad and Leis (2017). Another goal of this

dissertation is to build the beginnings of a library with measured evidence of WPE across multiple scales in this ecoregion. Finally, the NGP is a complex social-ecological system with large uncertainty for the future of the ecological and human communities that persist within its boundaries. Furthermore, much of the region is unprotected, although large conservation entities have begun to acknowledge the value and ecosystem services that the ecology provides for this region (Epstein et al., 2021). My intention here is to provide objective, scientific evidence and dialogue that may provide conservation and land managers with the facts and ideas necessary to protect and manage the NGP.

Of note, throughout this dissertation, I use the phrase “woody plant expansion,” abbreviated WPE, to indicate the increasing abundance of woody plant species in regions that are contemporarily perceived as grasslands. Throughout the literature, this phenomenon is stylized as “woody plant encroachment” or “woody plant invasion.” I intentionally chose “expansion” over “encroachment” or “invasion” for two reasons. First, encroachment implies that grass species are preferential to woody species, given the Merriam-Webster definitions: “to enter by gradual steps or by stealth into the possessions or rights of another,” or “to advance beyond the usual or proper limits.” While this may be the case regarding the management of some systems, such as the ancient grasslands of Europe, the cerrado of Brazil, or the savannas of South Africa (Ratter et al., 1997; Bond, 2016; Feurdean et al., 2018), it is not my intention to define the proper limits of vegetation in the NGP but rather to discover them. Second, many (albeit not all) of the species expanding into the grasslands of the NGP are not invasive (Richardson et al., 2000) and have existed here for millennia (Wells, 1970; Norris et al., 2016; Shinneman et al., 2016). Thus,

woody plant invasion may be a misleading term to describe the dynamics of this particular ecoregion.

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CHAPTER TWO

LARGE CONTRIBUTION OF WOODY PLANT EXPANSION TO
RECENT VEGETATIVE GREENING ON THE NORTHERN GREAT PLAINS

Contribution of Authors and Co-Authors

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Manuscript Information

Bryce Currey, David B. McWethy, Nicholas R. Fox, E. N. Jack Brookshire

Journal of Biogeography

Status of Manuscript:

☐ Prepared for submission to a peer-reviewed journal

☐ Officially submitted to a peer-reviewed journal

☐ Accepted by a peer-reviewed journal

☒ Published in a peer-reviewed journal

John Wiley & Sons Ltd

June 01, 2022

DOI: 10.1111/jbi.14391

LARGE CONTRIBUTION OF WOODY PLANT EXPANSION TO RECENT VEGETATIVE GREENING ON THE NORTHERN GREAT PLAINS

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ABSTRACT

Aim: Extensive portions of high-latitude grasslands worldwide have recently experienced increased vegetative productivity (i.e., greening) and have undergone a rapid transition towards woody plant dominance via the process of woody plant expansion (WPE). This raises the underlying question: To what degree are WPE and greening spatiotemporally linked? Given that these vegetative changes are predicted to continue, we seek to understand how recent changes in vegetation extent and productivity have interacted under recent climate change and anthropogenic disturbance to provide insights surrounding the future trajectory of temperate grasslands broadly.

Location: Northern Great Plains (NGP), North America

Taxon: Woody plants

Methods: Greening was measured as the significant increase in three metrics between 2000 and 2019: leaf area index (LAI), annual maximum normalized difference vegetative index (NDVI), and annual mean NDVI. WPE was measured as the significant proportional increase in percent

tree cover change between 2000 and 2019 in grasslands. We then examined these variables across a host of 26 potential driving variables.

Results: We show that average proportional greening increased by 0.2-1.3% yr⁻¹ (depending on metric), and proportional WPE increased by 6.9% yr⁻¹ since 2000 across the NGP. Both changes are largely driven by the absence of wildfire and changing climate. Furthermore, WPE was spatially coherent and positively associated with a large component of recent greening, as revealed by their coupling across 34.1-40.6% of grassland area and as evidenced by the 9.7-19.7% of the variability in greening explained by WPE.

Main conclusions: WPE and greening are spatiotemporally coupled across large portions of the NGP. Under continued climate change and wildfire suppression, WPE and greening are likely to continue across large swathes of grasslands globally. Furthermore, our results show that using a single greening metric may be insufficient to capture the large-scale vegetative changes such as the expansion of woody vegetation.

KEYWORDS

Woody plant expansion, woody plant encroachment, greening, leaf area index, normalized difference vegetation index, Northern Great Plains, temperate grasslands

INTRODUCTION

Globally, large areas of temperate grasslands are undergoing vegetative shifts towards an increased prevalence of shrubs and trees, hereafter referred to as “woody plant expansion” (WPE; Barger et al. 2011, Stevens et al. 2017, Criado et al. 2020). Simultaneously, large

increases in vegetative photosynthetic activity or productivity (“greening”) have been documented across temperate grasslands (Chen et al. 2019c, 2019a). Independently, these two vegetative changes have large consequences for grassland biophysical processes, biodiversity, and biogeochemistry (Eldridge et al. 2011, Ratajczak et al. 2012, Andersen and Steidl 2019, Brookshire et al. 2020, Welty et al. 2020). Furthermore, dynamic global vegetation models (DGVMs) have projected that both changes will continue in the future (Reeves et al. 2014, Shafer et al. 2015, Hufkens et al. 2016, Klemm et al. 2020). Increased woody plant cover has been hypothesized to be responsible for recent greening trends across grassland and savanna ecosystems (Xiao and Moody 2005, Chen et al. 2019b, Deng et al. 2021), but to what extent WPE contributes to greening and to what degree these two phenomena are spatiotemporally coupled in extent and driving mechanisms at fine resolution remains unresolved.

The most common approaches for measuring greening use the normalized difference vegetation index (NDVI) or leaf area index (LAI; Piao et al. 2020). LAI provides information on photosynthetic surface area (i.e., canopy structural complexity), whereas NDVI is biomass-independent and a more direct proxy of photosynthetic activity. NDVI is often measured using the maximum value across a time series (*peak* NDVI) or the mean value from a time series (*mean* NDVI). Peak NDVI highlights the maximum photosynthetic active radiation and subsequent maximum vegetative productivity (Myneni et al. 1995), whereas mean NDVI integrates annual vegetative production. Peak NDVI is often preferred over other metrics as it is best at minimizing error from cloud, reflectance, shadow, and aerosol effects (Myneni et al., 1995). However, changes in peak NDVI may be insufficient to distinguish between WPE dynamics and background greenness if the expanding shrubs and trees are primarily evergreen

(thus, maintain a relatively constant NDVI year-round). In this case, mean annual NDVI would capture the elongated NDVI signal across the year under WPE, whereas the maximum values may not change. Furthermore, both NDVI metrics may be inadequate compared with LAI, which captures the higher canopy complexity of trees than herbaceous vegetation. Although LAI and aboveground net primary productivity (ANPP) have both been associated with higher woody cover (Knapp et al. 2008, Barger et al. 2011), and NDVI and ANPP have been linked at coarse scales (Reeves et al. 2020), how these associations and their underlying assumptions apply to WPE is uncertain.

That WPE and greening are coupled at local scales is reasonable, but how both phenomena and their drivers are linked in space and across time at the landscape scale remains largely unknown. WPE and greening are most commonly attributed to increasing CO₂, changing climate, and shifts in disturbance regimes (Zhu et al. 2016, Archer et al. 2017), yet disentangling these drivers and their interactions have proven challenging. For example, elevated CO₂ can promote greening via directly stimulating photosynthesis and indirectly via increased water- and/or nutrient-use efficiency (WUE/NUE), but the strength of this effect can vary greatly among plant functional types (Feng et al. 2015, Terrer et al. 2019) and may be constrained by climate and nutrient availability (Frank et al. 2015, Brookshire et al. 2020). Precipitation dictates the bioclimatic limits of woody cover (Scholtz et al. 2018), and higher temperatures are strongly correlated with increased shrub cover (Criado et al. 2020). However, increases in temperature and precipitation also drive enhanced vegetative productivity, particularly in semi-arid environments, irrespective of WPE (Zhu et al. 2016, Knapp et al. 2017). Similarly, fire and herbivory can provide a check on expanding tree cover (Fuhlendorf et al. 2009), yet these disturbances may have negative,

neutral, or positive effects on greening (Frank et al. 1998, Geremia et al. 2019). Therefore, it is crucial to disentangle regionally specific climatic and disturbance drivers of WPE and greening at fine spatial and temporal resolution to understand the degree to which WPE contributes to greening.

We examined potential synchrony between WPE and greening across the Northern Great Plains (NGP) of North America. The current extent of WPE across the NGP has not been quantified, despite anecdotal (Symstad and Leis 2017) and historical photographic evidence (Phillips and Shantz 1963) of WPE. Peak photosynthetic productivity has increased in recent decades (Brookshire et al., 2020) and is predicted to continue in the future (Hufkens et al., 2016; Reeves et al., 2014). In addition, the climate of the NGP is predicted to get warmer and wetter (Polley et al. 2013, Conant et al. 2018), and DGVMs have projected extensive climate-driven increases in woody cover across NGP grasslands in the future (Klemm et al., 2020; Shafer et al., 2015). Importantly, these simulations have not been constrained by historical observations of WPE. It is thus essential to disentangle the recent trends and drivers of the potentially synchronous vegetative changes to benchmark and constrain these interactions for simulating future vegetative changes accurately.

Here we ask: 1) What is the magnitude and extent of WPE and greening across the NGP? 2) What are the drivers of WPE and greening across large topographic and climate ranges? And 3) to what degree are WPE and productivity synchronous across the landscape and through time? We use products from NASA's Moderate-Resolution Imaging Spectroradiometer (MODIS) to explore changes in peak NDVI, mean NDVI, LAI, and percent tree cover between 2000 and 2019. We examine these vegetative changes against 26 possible climate, physical, and

disturbance driving variables using a combination of random forest algorithms and linear regression.

METHODS

Study area

The NGP (as defined in this study) covers roughly 744,000 km², spans 15 degrees of longitude and 11 degrees of latitude (97.85 – 112.65W, 40.69 – 50.03N), and covers portions of five U.S. states and two Canadian provinces (Fig. 1). Mean annual precipitation (MAP) spans a wide gradient from 235 mm in the Northcentral-western regions to 1214 mm in the Southeastern and mountainous areas, and mean annual temperature (MAT) generally decreases with increasing latitude from 10.4°C to 0.8°C. Elevation in the NGP varies from 368 to >2500 m above sea level. According to the 2010 North American Land Change Monitoring System (NALCMS) 30m landcover dataset, 54.8% of the NGP is grassland, 28.4% is cropland, 7.6% is shrubland, 3% is forested (either deciduous, needleleaf, or mixed), and 6.2% is other (i.e., urban, water, and wetland; Fig. 1). For our research, we restricted our analyses to the combined grassland and shrubland layers (hereafter “grasslands”; 62.3% or ~463,000 km² of the NGP) as we were only interested in regions where tree cover was increasing in non-forested biomes. Across most of our study area, the primary trees implicated in WPE are *Pinus ponderosa* Douglas ex C. Lawson and numerous *Juniperus* species, including *J. horizontalis* Moench, *J. Communis* Linnæus, *J. scopulorum* Sarg., and *J. virginia* Linnæus (Brown and Sieg 1999, Symstad and Leis 2017). Some deciduous aspen (*Populus tremuloides* Michx) expansion has also been documented in the Northern regions (Köchy and Wilson 2001).

Data collection

All variables and their respective statistics can be found in Table S1.1 and are displayed in Figures S1.1-1.5. Table S1.2 contains information about the merged soils dataset. All analyses were conducted using *R* (Version 4.0.3). For a list of all packages used and the respective citations, see Table S3.1, and for a list of all datasets used, see Table S3.2. Finally, all data and analyses are publicly available at <https://doi.org/10.5061/dryad.z08kprrdj>.

Tree cover, NDVI, and LAI.

We examined a two-decade time series (2000-2019) of WPE, NDVI, and LAI data. Peak and mean NDVI were calculated from NASA's MODIS Vegetation Indices 16-day product (Version 6) at a 500m spatial scale. LAI was calculated as the mean yearly value from the MODIS 8-day LAI/FPAR product (V6) at a 500 m resolution. WPE is defined in this study as grassland pixels significantly increasing in percent tree cover. Percent tree cover was obtained from the MODIS Vegetation Continuous Fields 16-day product (V6) at a 250m spatial scale and resampled using the median pixel value to 500m. This product implements decision tree theory on a host of auxiliary variables (e.g., both MODIS and LANDSAT bands), which allows the algorithm to capture vegetation cover at lower percent tree cover values, although this product has been found to underestimate tree cover (Adzhar et al. 2022).

To determine significant ($p < 0.05$) changes in NDVI, LAI, and tree cover over time, we used a two-sided Mann-Kendal trend test across the 20-year period. Only for pixels showing significant changes, percent change was calculated relative to initial values, and the inner 99% of the data was kept, removing exceptionally large (e.g., $\pm 4\sigma$) outliers. A uniform 1% was added across all

tree cover values so that an increase from zero would not yield an infinite result but was subtracted for magnitude calculations and mapping. We also created a ‘Greening Index’ to examine areas that were increasing in all three greening metrics. This was done by scaling each metric between zero and one and taking the sum, excluding all areas not greening in all three metrics. As such, the theoretical maximum value of the greening index is three, and values lower than three indicate some degree of greening from all metrics. For greening and WPE statistics, we calculated the geometric mean and standard deviation (sd) as the distributions were highly right-skewed.

Climate data.

Climate data were obtained from NASA’s *Daymet* (1 km resolution resampled to 500m) gridded daily weather estimates. We determined the difference between the recent (2000-2019) and historical (1980-1999) periods for MAP, MAT, and mean seasonal climatologies. Relevant seasons were defined as spring (April, May, June; AMJ), summer (July, August, September; JAS), and winter (December, January, February, March; DJFM). We estimated precipitation variability by calculating the temporal coefficient of variation (CV) of MAP over the recent period. Finally, we included annual growing degree days (AGDD) and change in AGDD using a base temperature of 10°C at 1 km resolution data from the Coupled Model Intercomparison Project (Phase 5; *CMIP5*).

Physical and disturbance variables.

To examine the effect of topography, we calculated elevation, slope, aspect, and roughness from

the Shuttle Radar Topography Mission digital elevation model dataset at 30 m resolution. Roughness is calculated as the difference between the maximum and minimum elevation across the cell and the eight neighboring cells (i.e., larger values indicate rougher terrain). To examine the four cardinal directions of aspect as continuous variables, we calculated the sine and cosine of aspect (in radians) to examine the “northness” and “eastness,” respectively. Soils were obtained from the National Resource Conservation Service for soils within the United States and from the National Soils Database of Canada for Canadian soils and merged at the generalized order to create seven soil classifications.

We examined three disturbance variables: nitrogen (N) deposition, cattle per km² (a proxy for herbivory), and burned area. N deposition (kg N ha⁻¹ yr⁻¹) was obtained from the 1993 global product. Cattle per km² was obtained for 2010 from the areal-weighted cattle density global product. Finally, total burned area across the study period was obtained from MODIS and was converted into a binary variable of burned/unburned.

Random forest and statistical analyses

We examined the variable importance metric from random forest models to determine the relative importance of each climate, topographic, and disturbance variable on greening and tree cover changes. Each variable’s relative importance is calculated by randomly permutating the data to induce randomness to each variable and comparing these simulations to the observation-driven simulations (known as ‘decreased accuracy’). The most significant variables have the largest differences between observation-driven versus randomly permuted runs. The error rate of random forest models is calculated as the average of all individual trees’ misclassification

rates across the forest. Before modeling, feature selection determined only the aspect variables ('northness' and 'eastness') non-relevant and were thus removed from all analyses. We examined the relative importance of all 24 remaining drivers of LAI change, peak and mean NDVI change, tree cover change, and 2019 tree cover. We also examined the drivers of 2000 tree cover for variables with historical data (1980-1999, $n = 15$). We also assumed constant cattle density, N deposition, and soil type across time. Finally, we calculated the variance explained by the predictor variables for all models (i.e., pseudo- R^2). All variables were resampled using median values to the resolution of the greening and tree cover variables (500 m resolution), on which we used 500 classification trees and four variables at each candidate node. These analyses were performed on the Hyalite High-Performance Computing System operated by University Information Technology Research Cyberinfrastructure at Montana State University.

Because random forest models cannot determine how individual variables interact with the response variables (i.e., the relationship's direction), we examined all 24 variable's responses against WPE, peak NDVI, mean NDVI, and LAI using ordinary least squares (OLS) regression models. Before modeling, all variables were standardized (z-score) to examine the effect size on a uniform scale. Effect sizes (slopes from the bivariate OLS models) were combined with the random forest rank importance analysis to examine each variable's importance score and direction concurrently. As such, a higher variable rank indicates higher importance, and a larger z-score indicates a steeper directional slope. It should be noted that a steep relationship (z-score far from the zero line) does not necessitate high variable importance, nor does higher rank importance necessitate a steep slope. For instance, a high importance value but a small z-score indicates a strong spatial coupling but a less steep relationship.

Similarly, we conducted bivariate analyses examining all greening metrics versus tree cover change to examine the variance explained within each greening variable by WPE. We then examined the correlation of WPE and greening variables in two ways: first, we examined each variable's spatial correlation using Tjøstheim's coefficient (A) and, second, we examined Spearman's rank correlation (ρ) between the drivers of each response variable (both bounded between 1 and -1). Tjøstheim's coefficient examines the spatial similarity of the response variables, whereas Spearman's coefficient examined the correlation in both z-score and importance of all 24 driving variables of each response variable. Said another way, Tjøstheim's A examines the degree of co-occurrence, whereas Spearman's ρ examines the similarity between each vegetative change's driving variables. For the rank correlation analysis between tree cover in the year 2000 and other response variables, we only examined the correlation between the 15 variables used in the 2000 tree cover random forest model.

RESULTS

Climate, Topography, and Disturbance

Climate

Recent (2000-2019) MAP increased by 24.5 mm on average over the entire study area compared with the 1980-1999 climatology (Table S1.1 and Fig. S1.2) but was regionally heterogeneous. For instance, some areas experienced large declines (decreased < 100 mm; primarily in the northern and central regions), yet others experienced substantial increases (increased > 200 mm; primarily in the southern region). The greatest seasonal precipitation increases were in the spring, with winter and summer mean precipitation barely changing on average. MAT also

increased on average by 0.1°C (Table S1.1 and Fig. S1.3), with the largest average increases in the summer months ($\sim 0.7^{\circ}\text{C}$). Consequently, AGDD increased across the entirety of the NGP, with the biggest increases in the southwestern areas (Fig. S1.4).

Disturbance

Over the 20-year study period, $\sim 2.7\%$ of grassland pixels experienced fire (0.135% probability yr^{-1} across all pixels), translating to $\sim 20,000 \text{ km}^2$ of burned area (Table S1.1 and Fig. S1.5). N deposition across the region was relatively homogenous after being upscaled yet with an evident east-west gradient from a high of 7.4 to a low of $1.8 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, and well within the range of *in situ* studies from the region (Symstad et al., 2019). Finally, the average distribution of cattle across the NGP was $12.5 \text{ head km}^{-2}$, but regions in the southern NGP showed densities as high as $\sim 137 \text{ head km}^{-2}$.

Greening and WPE

Extent of greening

We document extensive but variable greening across most NGP grasslands (Table 1; Fig. 2). LAI increases were the most extensive, occurring across 76.0% of grassland pixels. LAI-based greening also had the largest proportional 20-year changes of $26.8 (2.1)\%$ on average, or $\sim 1.3\% \text{ yr}^{-1}$. Next, peak NDVI increased significantly across 62.7% of grasslands, with a magnitude of $9.9 (1.7)\%$, or $\sim 0.5\% \text{ yr}^{-1}$. Finally, mean NDVI increased in over half (57.3%) of grassland pixels by $4.2 (1.9)\%$, or $\sim 0.2\% \text{ yr}^{-1}$. Synchronous increases in all three metrics (i.e., the extent of the greening index) occurred across 30.6% of NGP grassland area, and all three metrics had a

moderately high Tjøstheim's coefficient ($A \geq 0.42$; Table S2.1). We note slightly higher greening in shrubland versus grassland pixels, although the magnitude of changes was similar (Table S2.2).

Driving variables of greening

All random forest classification models for greening performed exceptionally well with error rates for LAI, peak NDVI, and mean NDVI changes of 1.43%, 0.44%, and 1.49%, respectively. Despite strong model performance, the 24 predictor variables only explained 32.7%, 24.4%, 53.9% of each greening metric's respective variance.

Roughness, slope, and elevation were negatively associated with increasing LAI (Fig. 3a), indicating that LAI-based greening was largest on smooth, flat topographies. High precipitation variability and absence of fire were also strong predictors. Precipitation drivers of LAI greening were seasonally dependent, although increasing MAP was correlated with increasing LAI. Warming summer temperatures were also positively associated with LAI. For peak NDVI (Fig. 3b), greening was positively associated with higher precipitation variability and increasing precipitation (save for winter precipitation). Peak NDVI-based greening was strongly associated with smoother topographies and low cattle density. Interestingly, fire was a poor predictor of peak NDVI-based greening. Conversely, the absence of fire was the strongest predictor of mean NDVI increases (Fig. 3c). The highest mean NDVI-based greening was associated with smoother topographies and lower elevations. Lastly, year-round wetting, albeit variably, and warming temperatures were strong driving variables of higher mean NDVI greening.

Overall, smoother topographies and the absence of fire (save for peak NDVI) were strong

predictors of greening. Seasonally-dependent changes in precipitation and temperature were apparent, in which warmer and wetter summers, but cooler and drier winters, led to the highest proportional greening, apart from mean NDVI, which was driven by a year-round increase in precipitation. Higher precipitation variability was also associated with the largest proportional changes of all three metrics. Lower cattle densities (i.e., herbivory) were a moderately strong predictor of NDVI-based greening. N deposition, AGDD, baseline climatology, and soil variables were less important driving variables for greening metrics. Despite climatic differences, the driving variables of all greening metrics had high Spearman correlations ($\rho \geq 0.75$; Table S2.1).

Extent of tree cover and WPE

Initial (year 2000) median percent tree cover in NGP grasslands was 1.6% and generally very low across the entire region (Table 2, Fig. 4a). Nonetheless, close to half (46.8%) of grassland pixels observed a significant increase in percent tree cover over the two decades (Table 1, Fig. 4b). As a result, proportional tree cover changes were large, with the average increase at 137.8 (2.3)%, or $\sim 6.9\% \text{ yr}^{-1}$, compared to tree cover in 2000. These large proportional changes increased the median percent tree cover to 3.4% by 2019, a 1.8% cover increase over the 20-year period ($0.09\% \text{ cover yr}^{-1}$; Fig. S2.1a). Interestingly, the inner quartile range in 2000 was 1.7% but increased to 4.7% over the two-decade period, signaling larger changes at higher tree cover densities (Table 2). Nonetheless, 2000 and 2019 tree cover had a large degree of spatial similarity ($A = 0.79$).

Driving variables of tree cover and WPE

Models of both static percent tree cover and changing percent tree cover performed well, with an error of 1.6% for the year 2000 tree cover model, 0.9% for the 2019 tree cover model, and 1.8% error for the changing tree cover model. Based on the random forest models, the 15 driving variables of 2000 tree cover explained 54.5% of the variation, and the 24 predictors for 2019 tree cover and tree cover change explained 39.3% and 32.8% of the variability, respectively. Initial tree cover was concentrated in areas with high topographic roughness and steeper slopes, with low precipitation variability and high winter precipitation (Fig. 5a). Drivers of tree cover in 2000 and 2019 were highly correlated ($\rho = 0.79$), although many of the changing climate variables became important to tree cover in 2019 (Fig. S2.1b).

In contrast to static tree cover, tree cover change was primarily driven by high precipitation variability, the absence of fire and other disturbances, and occurred on smoother topographies with lower slopes (Fig. 5b). All changing precipitation variables were positively associated with WPE, indicating that the most significant proportional changes occurred where it has gotten wetter year-round. Finally, tree cover in 2000 and tree cover change had a low Tjøstheim coefficient ($A = -0.11$), and their respective drivers had a $\rho = -0.52$ Spearman correlation (Fig. S2.1). This indicates that areas with the highest rates of WPE were not where tree cover was initially highest, nor were they associated with the same driving variables, emphasizing the point that tree cover change is occurring primarily as expansion rather than infilling.

Concurrent Greening and WPE

Both WPE and greening occurred across vast areas of NGP grasslands. Here, we document that

these changes were often concurrent and influenced by similar drivers. While 6.3-12.7% of WPE and 23.0-35.5% of greening occurred independent of one another (depending on which greening metric is examined in conjunction with WPE; i.e., WPE and LAI, WPE and peak NDVI, or WPE and mean NDVI), the largest proportion of vegetative changes were concurrent (Table 3).

This was particularly true for LAI and percent tree cover, which increased simultaneously across 40.6% of grasslands (Table 3, Fig. S2.2a). A doubling of percent tree cover corresponded with a $5.2 \pm 0.04\%$ increase in LAI ($p < 0.001$), and WPE explained 11.1% of the variability in LAI greening. Indeed, we found a relatively strong spatial correlation ($A = 0.49$) and a very strong correlation between drivers of WPE and LAI ($\rho = 0.67$; Table S2.1).

We found similar results for NDVI variables; 34.1% of all grasslands experienced increases in peak NDVI and WPE (Table 3, Fig. S2.2b), and 34.2% underwent mean NDVI-based greening and WPE (Table 3, Fig. S2.2c). For every doubling of percent tree cover, peak NDVI increased by $1.28 \pm 0.01\%$ ($p < 0.001$) and mean NDVI increased by $0.91 \pm 0.01\%$ ($p < 0.001$). WPE explained 9.7% of the variation in peak NDVI-based greening and 19.7% of mean NDVI increases. Interestingly, the Spearman correlation between drivers of WPE and peak NDVI was the lowest ($\rho = 0.56$), suggesting that even though WPE and peak NDVI co-occurred across large areas, the primary drivers of each differed. Conversely, drivers of mean NDVI and WPE were highly correlated ($\rho = 0.76$), and both peak and mean NDVI had similar Tjøstheim's coefficients ($A = 0.43$ and $A = 0.44$, respectively, Table S2.1).

Finally, we document that 19.0% of NGP grasslands have simultaneously undergone increases in all three greening metrics and WPE (Fig. 6a; Table 3). Greening and WPE were strongly and positively associated; a doubling of woody plant cover corresponded to a proportional 15.0%

increase in the greening index ($p < 0.001$; Fig. 6b). Although WPE and the greening index were mutually exclusive across large portions of grasslands (Table 3), WPE explained 17.0% of the variability in the greening index across the NGP.

DISCUSSION

We document a strong coupling between WPE and vegetative greening at high-resolution (~500m) across broad disturbance, climate, and topographic gradients within one of the last remaining relatively intact high latitude grasslands globally. Significant increases in percent tree cover occur on smooth topographies and are primarily driven by the absence of fire and increasing temperature and precipitation. We demonstrate that a doubling in proportional tree cover drives a concurrent 15% proportional increase in our integrative greening index and that these synchronous vegetative changes occur across roughly one-fifth (roughly 90,000 km²) of all NGP grasslands. Indeed, WPE alone accounts for 17% of the variability in the greening index. Comparatively, all 24 other climatic, topographic, and disturbance variables combined explained 17.4-50.7% of the variance, depending on the greening metric. These results highlight that WPE is a large component of vegetative greening in the NGP and imply that it may be an underappreciated component of greening trends in other semi-arid biomes.

Our results provide necessary observations to benchmark and parameterize models of vegetation change over the next century. While our results point to a more tree-covered NGP in the future, observed rates of change are much lower than required to result in a fully forested NGP by 2100 suggested by some DGVM projections (Shafer et al., 2015). Despite large proportional changes in percent tree cover, absolute changes of percent tree cover across the NGP were small. Median

percent tree cover increased by 1.8% over the two-decade period ($\sim 0.1\% \text{ yr}^{-1}$), with the upper quartile showing a slightly larger increase of 3.8% ($\sim 0.2\% \text{ yr}^{-1}$). A linear extrapolation of these trends suggests that WPE rates would have to increase more than 5-fold to obtain full woody cover by end-of-century across the NGP (i.e., median tree cover of at least 50%).

Our analyses of recent WPE point to critical interactions between topography, fire, and climate change in explaining the spatial distribution of this vegetative change. Early studies of vegetation distributions in the NGP observed that *P. ponderosa* and *Juniperus* spp. were historically restricted to fire-protected rocky scarps and uplands (Wells 1965). In alignment with these findings, we show that initial (year 2000) tree cover was highest in rough terrain, yet the highest rates of WPE occurred on smooth terrain in the absence of fire. Furthermore, drivers of established tree cover in 2000 and subsequent vegetative changes differed, indicating that what once allowed for the establishment of trees is distinct from what is associated with their expansion and greening today. Although the spatial resolution of this study cannot fully examine questions at the stand level, we find evidence that past tree cover and present WPE are negatively associated across space. This indicates that the majority of increasing percent tree cover is not where percent tree cover is currently the highest, providing evidence that trees are expanding. Facilitating this expansion was very low fire occurrence across the NGP, as less than 3% of NGP grasslands experienced fire over the 20-year period. Likely the result of active fire suppression, the dominant fire regime across much of the NGP has shifted from one with a relatively frequent fire return interval (FRI) of $< 30\text{-}50$ years to one of infrequent and small fires (e.g., $> 50\text{-year}$ FRI; Umbanhowar 1996, Reid and Fuhlendorf 2011). This trend could sustain WPE and greening further into the 21st century. It is also possible that, under a warming climate,

higher woody fuel loads resulting from continued WPE could trigger novel vegetation-fire feedbacks characterized by more frequent high-intensity fire activity (Moritz et al. 2012).

Enhanced vegetative growth and WPE were strongly associated with spring and winter precipitation increases, with the highest proportional increases occurring in more arid areas characterized by high long-term precipitation variability and lower baseline productivity and tree cover. In fact, precipitation CV ranked as a more important driver than any other climate variables for all greening and tree cover change measures. These results are consistent with high precipitation sensitivity and higher marginal gains in vegetation growth in response to increasing water supply in more arid areas (Hufkens et al. 2016, Ritter et al. 2020, Hoover et al. 2021). The NGP has been getting wetter over the last few decades (Polley et al. 2013, Bromley et al. 2020) and is predicted to continue to get wetter in the future (Conant et al. 2018), a trend that may sustain increases in vegetative activity. At the same time, enhanced moisture stress associated with higher evaporative demand and continued declines in summer precipitation could potentially dampen greening and WPE trends.

Our documented greening rates of 0.2-1.3% yr⁻¹ align with climate-driven model simulations showing 20-100% increases in NGP vegetative productivity over the next century (Hufkens et al., 2016; Reeves et al., 2014), but our results further suggest that shifts in vegetation composition and phenology may underlie some of these changes. While WPE has contributed disproportionately to greening relative to its spatial extent, enhanced vegetative productivity occurred across 23.0-35.5% of NGP grasslands in the absence of WPE. This is likely in part due to an elongated growing season, consistent with the warming temperatures we observe in this study. Nonetheless, the fact that LAI and mean annual NDVI were strongly correlated with WPE

suggests that increases in evergreen conifer cover enhance greening due to year-long photosynthetic activity and increased biomass. In contrast, peak NDVI had the lowest correlation with WPE, suggesting peak NDVI is largely driven by herbaceous-driven greening (Brookshire et al., 2020). Similarly, that peak NDVI had the lowest variance explained by climatological changes in our models may indicate that peak NDVI is more sensitive to interannual-to-annual climate variability than mean NDVI or LAI, both of which were better explained by our random forest models. These differences in model responses across greening variables highlight the importance of examining multiple greening metrics to capture the various aspects of phenology when examining greening phenomena of large-scale vegetative changes (Wood et al. 2021).

In addition to the elongation of photosynthetic activity associated with WPE, the increasing abundance of conifers raises important questions about potential shifts in plant resource acquisition and use-efficiency that may affect future greening and WPE. Foliar isotope analysis shows that WUE of grassland vegetation across the NGP has increased by 37% on average since the 1960s in response to atmospheric CO₂ enrichment, while N availability has declined (Brookshire et al., 2020). Although declining N availability suggests a potential bottleneck to future greening, it also indicates enhanced NUE given sustained productivity. How coniferous WPE may affect these trajectories is less certain. For example, *P. ponderosa* and *Juniperus* spp. may have advantages over grasses in access to soil nutrients via differences in rooting depth or mycorrhizal nutrient acquisition strategies (Policelli et al. 2019) that could sustain tree expansion and greening, particularly under elevated CO₂ (Terrer et al. 2019).

Our machine learning approach highlights the challenges of using empirical modeling to benchmark process-based DGVM projections of vegetative changes. A notable disadvantage is a

reliance on accurate and heterogeneous spatial data. For instance, atmospheric CO₂ enrichment likely drives some of the patterns we observe through direct stimulation of photosynthesis and/or indirect enhancement of WUE and NUE (Brookshire et al., 2020), but we did not account for CO₂ due to its spatial homogeneity. In addition, although the MODIS VCF tree cover product has been validated across 442 WPE sites (Deng et al., 2021), this product has been shown to consistently underestimate tree cover by 0-18% (Adzhar et al., 2022). Therefore, our estimates of WPE are conservative as we cannot capture trees too small or young to be included in the algorithm. Indeed, the WPE rate we document ($\sim 0.1\%$ cover yr⁻¹) is lower than field estimates in other western North American grasslands (0.5-0.6%, Barger et al., 2011), but closer to global estimates that use the same product (0.3% cover yr⁻¹; Deng et al., 2021).

Our findings document the pace of vegetation change and its dominant controls across one of the last remaining relatively intact grasslands worldwide and provide insight into alternative future ecosystem states. We have shown that the greening of the NGP is driven by interactions between large-scale vegetative shifts and cooccurring photosynthetic enhancement from established herbaceous vegetation. While recent WPE has clearly contributed to enhanced CO₂ sequestration, WPE is also associated with a host of ecosystem and socio-economic tradeoffs, including loss of grassland biodiversity, transformation of biogeochemical cycles, and changes to wildlife habitat (Barger et al. 2011, Symstad and Leis 2017, Wilcox et al. 2018, Epstein et al. 2021). Furthermore, the combination of higher conifer densities and a warmer climate dramatically increases the probability of large wildfires (McWethy et al. 2019). As such, assessment of these large-scale and interactive vegetative changes should be disassociated from values-based ideologies regarding whether woody encroachment and greening are entirely

beneficial or detrimental processes. Instead, it is important to examine the complex tradeoffs between these vegetative changes to guide understanding, evaluation, and management of future vegetative states and functions under projected climate change.

AUTHOR CONTRIBUTIONS

B.C., E.N.J.B., and D.B.M. conceived and designed the study. N.R.F. handled the soils data.

B.C. conducted all analyses and wrote the first edition of the manuscript. All authors contributed to the revision of the manuscript.

ACKNOWLEDGEMENTS

We thank Simon Scheiter, Anping Chen, and an anonymous reviewer for their insightful improvements to this manuscript. This work was supported by the National Science Foundation, Award Numbers: OIA-1632810 (ENJB) and BCS 1832486 (DBM), the Montana Agricultural Experiment Station, and the Department of Interior, Bureau of Land Management award L16AS00082 to ENJB.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

All large datasets are in .csv format and are available on datadryad.org at <https://doi.org/10.5061/dryad.z08kprrdj>. All other datasets, code, and figures are publicly

available on this project's repository on github.com at <https://doi.org/10.5281/zenodo.6473246>.

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TABLES

Table 1. Vegetative change metric statistics for NGP grasslands. *Inc* is the fraction of total area undergoing respective vegetative increase, decrease (*Dec*) represents the fraction decreasing. $\text{inc}_{(sd)}$ is the geometric average (geometric sd) magnitude of increases in the respective increasing proportion. $\text{dec}_{(sd)}$ is the geometric average (geometric sd) magnitude of decreases in the respective decreasing proportion.

	<i>Proportion of NGP grasslands</i>	<i>Inc</i>		<i>Dec</i>	
Tree Cover Δ	48.0	46.8	137.8 (2.3)	1.2	-17.7 (3.5)
LAI Δ	77.6	76.0	26.8 (2.1)	1.6	-3.9 (4.3)
Peak NDVI Δ	63.0	62.7	9.9 (1.7)	0.3	-1.9 (4.6)
Mean NDVI Δ	58.9	57.3	4.2 (1.9)	1.6	-1.7 (4.1)

Table 2. Vegetative metrics for NGP grasslands. *Q1* and *Q3* are the inner quartiles for the respective vegetative metric, *IQR* is the inner quartile range, and $\bar{x}$ is the geometric average.

	<i>Year 2000</i>				<i>Year 2019</i>			
	<i>Q1</i>		<i>Q3</i>	<i>IQR</i>	<i>Q1</i>		<i>Q3</i>	<i>IQR</i>
Tree Cover	1.0	1.6	2.7	1.7	1.8	3.4	6.5	4.7
LAI	0.28	0.38	0.51	0.23	0.48	0.50	0.65	0.17
Peak NDVI	0.37	0.46	0.58	0.21	0.51	0.60	0.71	0.20
Mean NDVI	0.22	0.26	0.31	0.09	0.26	0.30	0.34	0.08

Table 3. Percent of NGP grasslands undergoing synchronous versus mutually exclusive WPE and greening categorized by greening metric. As an example, 40.6% of NGP grasslands increased in LAI and tree cover synchronously. Conversely, 35.5% of the NGP experienced only LAI-based greening and 6.3% only WPE. Examining the *greening index and WPE*, we see that 19% of NGP grasslands increased in all three greening metrics and WPE.

<i>Greening metric with WPE</i>	<i>Synchronous</i>	<i>Mutually exclusive</i>	
		Greening Only	WPE Only
LAI and WPE	40.6	35.5	6.3
Peak NDVI and WPE	34.1	28.7	12.7
Mean NDVI and WPE	34.2	23.0	12.6
Greening Index and WPE	19.0	11.6	13.5

FIGURES

Figure 1. Study area schematic for the Northern Great Plains (NGP). (a) The extent of the NGP within North America. Dark grey indicates the five states and two providences partially occupied by the NGP. (b) Seven land cover types within the NGP. Grassland and shrubland layers were combined under the umbrella term ‘grassland.’ (c) The ‘grassland’ composite layer, covering roughly two-thirds of the study area. The largest non-grassland area is comprised of cropland.

Figure 2. NGP grassland (shaded grey) proportional greening changes from 2000 to 2019 measured as (a) LAI changes, (b) peak NDVI changes, and (c) mean NDVI changes. White areas represent non-grasslands (i.e., forested, cropland, urban, wetland).

Figure 3. Relative importance from random forest models in descending order of importance for the three greening indices: (a) LAI increases, (b) peak NDVI increases, and (c) mean NDVI increases. On the x-axis, standardized (z-score) effect size coefficients from ordinary least-squares regression. Positive values indicate a significant positive relationship with the greening metric; negative values indicate a significant negative relationship. Dots farther away from the zero line indicate a steeper slope. The fire product was converted to a numeric variable, with positive one indicating fire presence and zero indicating absence. Soil is on the zero line as it was kept a categorical variable. Grey circles signify topographic variables, gold circles signify disturbance variables, and blue circles signify climate variables.

Figure 4. NGP grassland (shaded grey) tree cover and tree cover changes. (a) Percent tree cover

from MODIS for the year 2000 and (b) the statistically significant proportional change between 2000 and 2019. White areas represent non-grasslands (i.e., forested, cropland, urban, wetland).

Figure 5. Relative importance from random forest models in descending order of importance for (a) percent tree cover (year 2000) and (b) tree cover percent increase. On the x-axis, standardized (z-score) effect size coefficients from ordinary least-squares regression. Positive values indicate a significant positive relationship with the tree cover metric; negative values indicate a significant negative relationship. Dots farther away from the zero line indicate a stronger directional relationship. The fire product was converted to a numeric variable, with positive values indicating fire presence. Soil is on the zero line as it was kept a categorical variable. Grey circles signify topographic variables, gold circles signify disturbance variables, and blue circles signify climate variables. Percent tree cover (a) has only variables that are relevant to the year 2000.

Figure 6. Greening and WPE across NGP grasslands (shaded grey; white areas represent non-grasslands). (a) Mapped changes. *WPE Only* represents areas where only tree cover has increased. *Greening Only* represents pixels where only greening has occurred. Greening is represented here as the ‘greening index,’ where peak NDVI, mean NDVI, and LAI have increased simultaneously. *Concurrent Δ* represents where greening and WPE have co-occurred. (b) Relationship between cells undergoing greening and concurrent tree cover increase. (c) Distribution of greening index values.

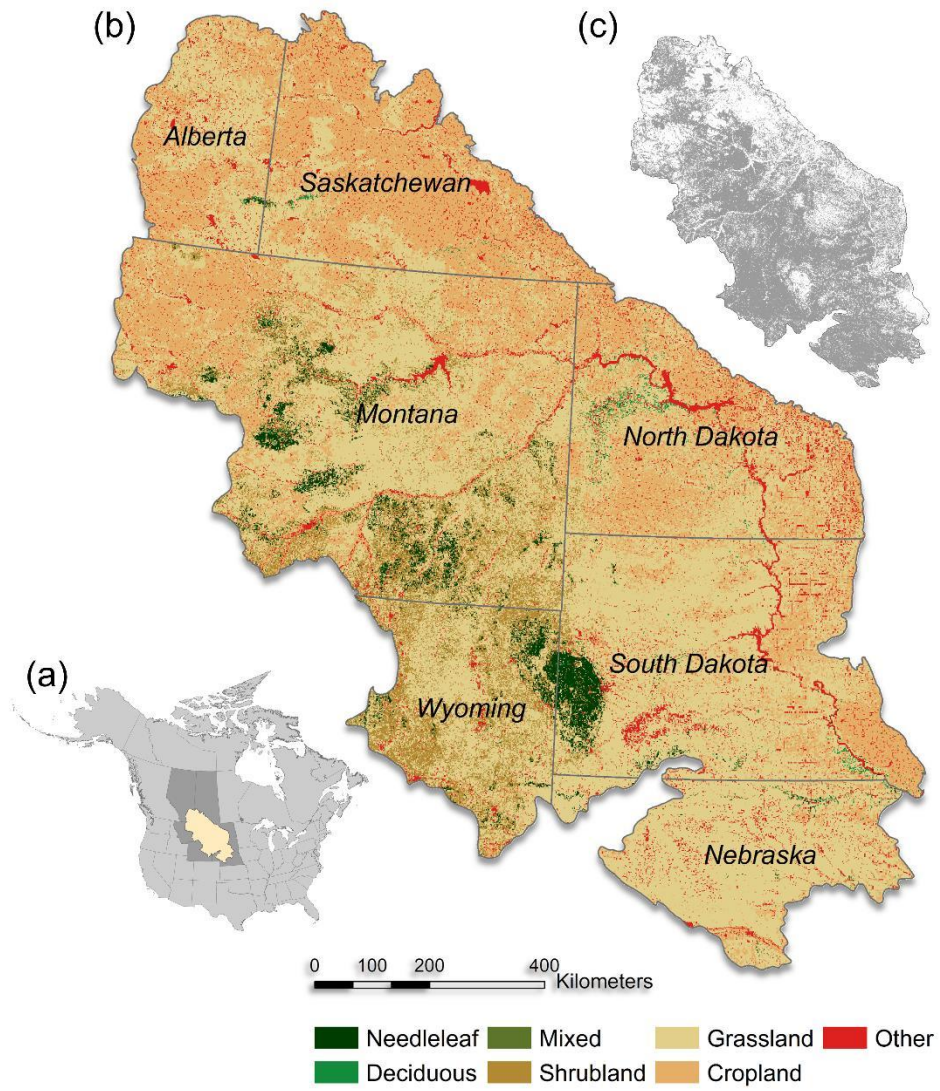


Figure 1.

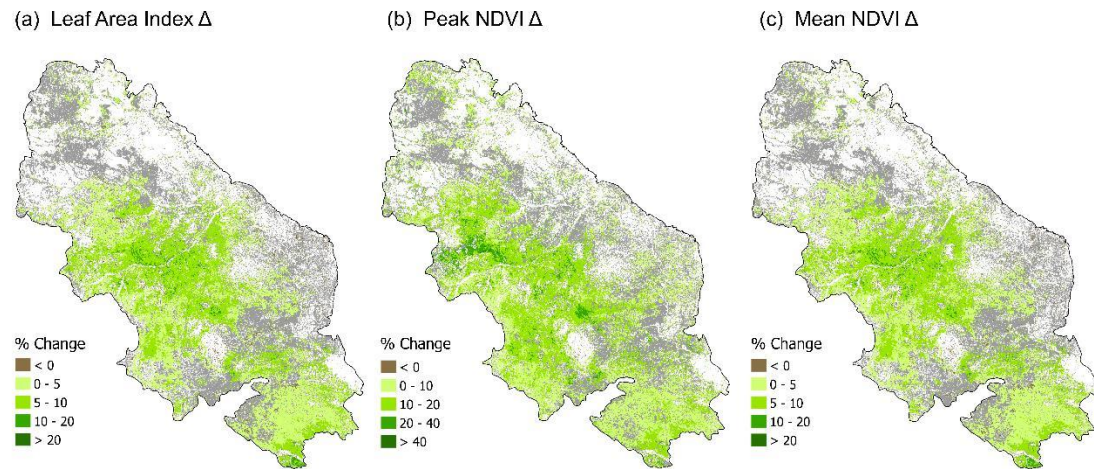


Figure 2.

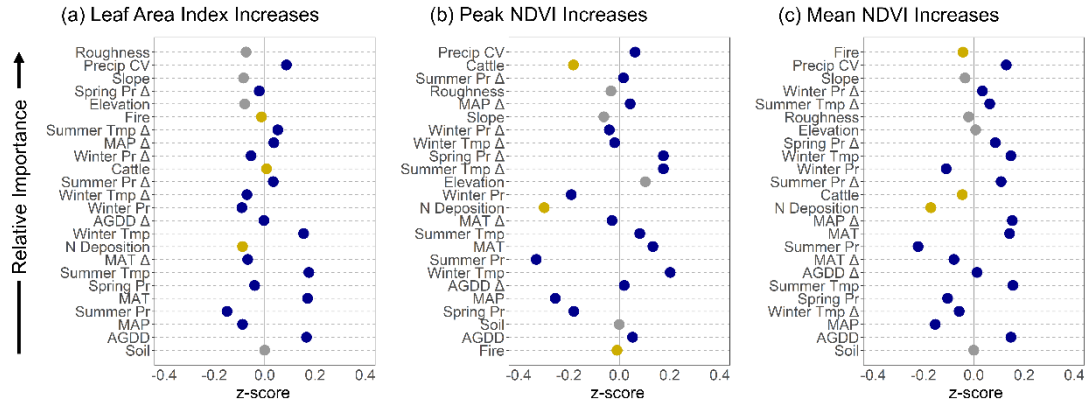
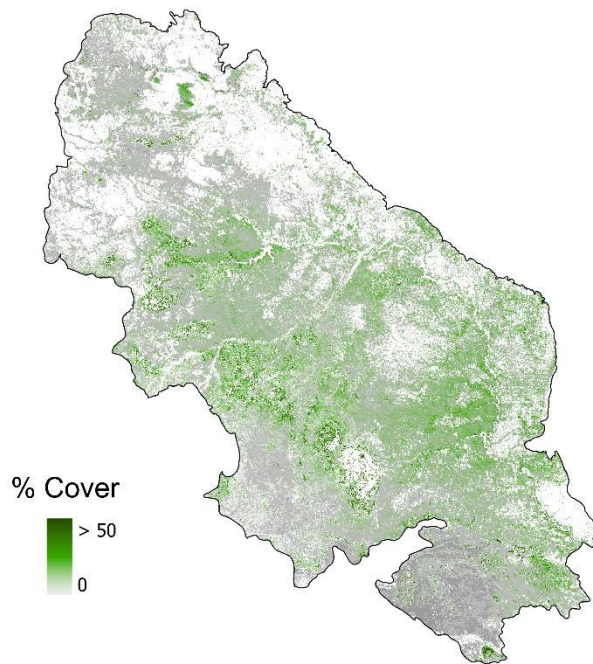


Figure 3.

(a) Tree Cover (year 2000)



(b) Tree Cover Change

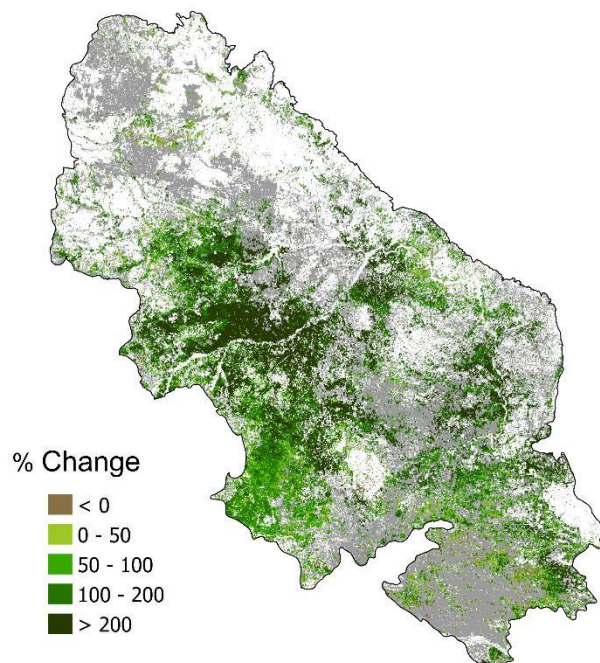
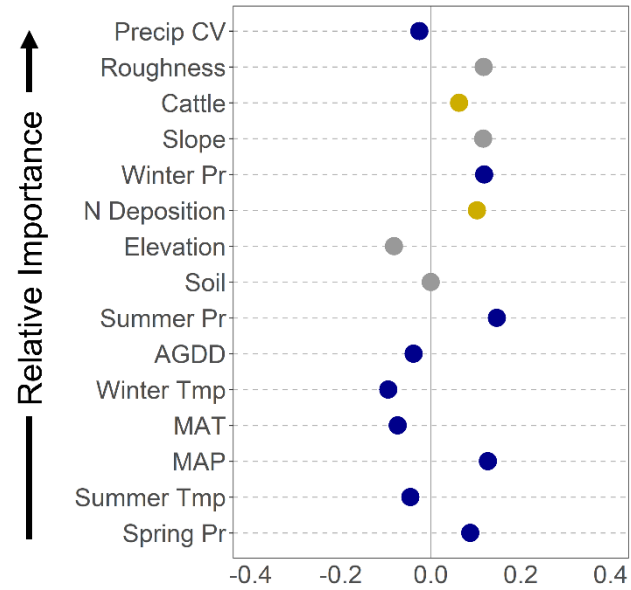


Figure 4.

(a) Tree Cover



(b) Tree Cover Increases

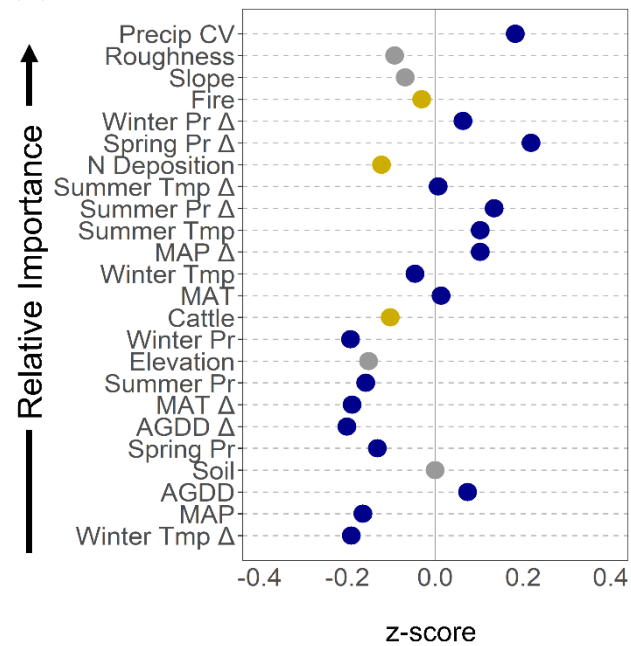


Figure 5.

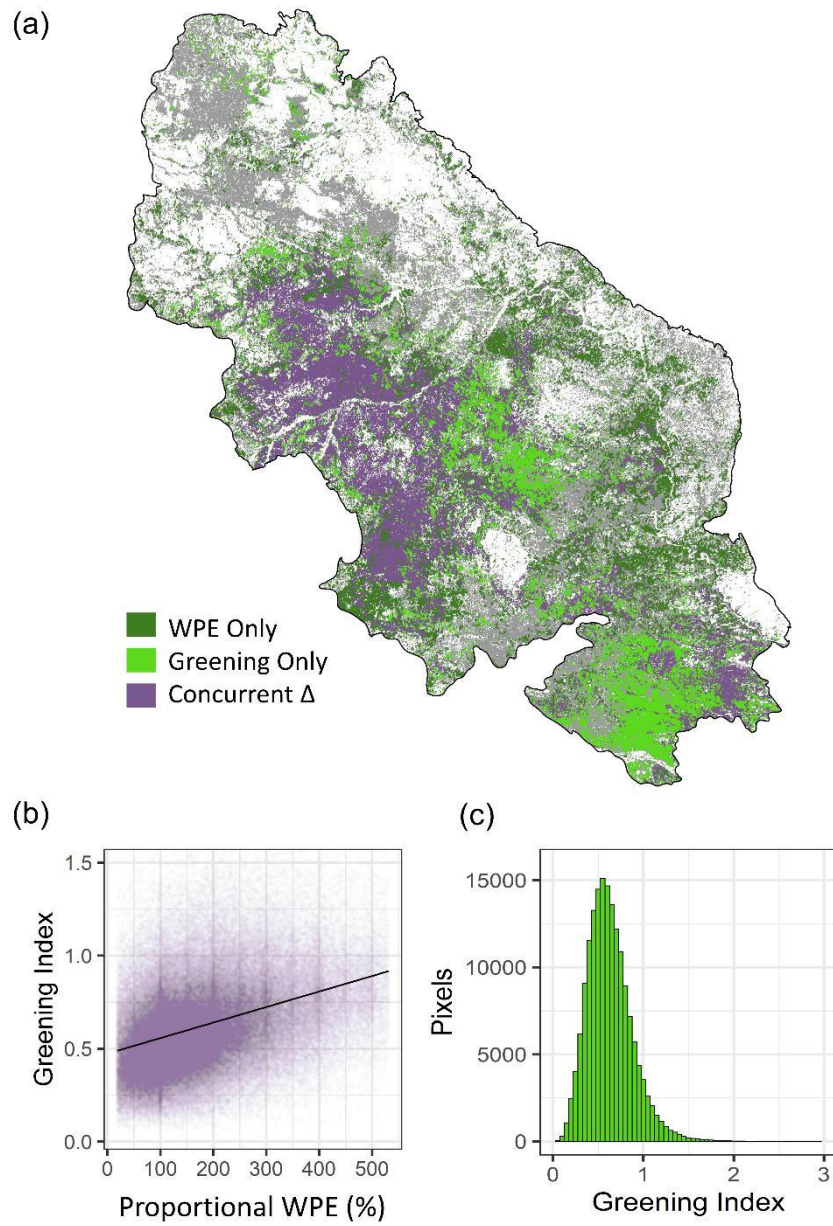


Figure 6.

Contents and brief description

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APPENDIX S1

Table S1.1. Predictor variable statistics. Climatologies from the recent (2000-2019) period. Differences are between the recent and historical (1980-1999) periods. April, May, June (AMJ); July, August, September (JAS), December, January, February, March (DJFM).

Variable	Statistics				Units
<i>Precipitation</i>	Min	Mean	Max	Std. Dev.	
Mean Annual Precipitation	235.2	436.8	1213.8	95.2	mm
Mean Annual Precipitation Difference	-131.1	24.5	217.7	31.6	mm
Spring (AMJ) Precipitation	101.5	196.3	517.9	40.7	mm
Spring Precipitation Difference	-55.5	22.0	117.0	15.9	mm
Summer (JAS) Precipitation	58.1	134.1	258.4	36.1	mm
Summer Precipitation Difference	-53.4	0.8	57.5	13.1	mm
Winter (DJFM) Precipitation	21.9	59.8	263.8	16.9	mm
Winter Precipitation Difference	-50.9	1.7	68.7	10.1	mm
Precipitation Coefficient of Variation	0.14	0.26	0.42	0.03	(-)
<i>Temperature</i>					
Mean Annual Temperature	0.8	6.6	10.4	1.8	°C
Mean Annual Temperature Difference	-0.8	0.1	1.7	0.3	°C
Summer (JAS) Temperature	10.2	18.9	22.5	1.7	°C
Summer Temperature Difference	-0.4	0.7	2.8	0.3	°C
Winter (DJFM) Temperature	-10.7	-4.9	0.0	2.6	°C
Winter Temperature Difference	-1.4	-0.1	1.5	-0.3	°C
Annual Growing Degree Days	458.9	1306.8	1909.3	235.2	(-)
Annual Growing Degree Days Difference	19.3	66.9	128.4	21.5	(-)
<i>Physical</i>	Min	Mean	Max	Std. Dev.	
Elevation	367	932	2757	285	m
Slope	0	4.0	54.6	3.2	degrees
Roughness	0	47.43	708.1	34.0	(-)
	North	East	South	West	
Aspect	32.6	14.3	29.7	23.4	% of pixels
<i>Disturbance</i>	Min	Mean	Max	Std. Dev.	
Cattle	0	12.5	137.4	8.6	head km ⁻²
N Deposition	1.8	3.3	7.4	1.0	mg N m ⁻² yr ⁻¹
	Burnt	Unburnt			
Fire	2.6	97.4			% of pixels

Table S1.2. Soil order information for the NGP.

Soil Order	Pixels	% of NGP	Description	US equivalent
Brunisolic	444,665	45.0	Found on sandy glacio-fluvial and till sediment parent material. Often where precipitation < 700 mm yr ⁻¹ . Often acidic.	Inceptisols, Mollisols
Luvisolic	99,595	10.1	Found on sedimentary or clayey lacustrine parent material. Typically, loamy or clayey in texture. Often neutral or alkaline.	
Vertisolic	285,921	29.0	Found on parent materials high in clay. Parent materials were deposited in lakes that existed during the retreat of the last (Wisconsinian) glaciers.	Vertisols
Gleysolic	43,396	4.4	High in clay, resulting from prolonged water saturation. Typically have a clay-depleted layer above a clay-enriched layer. Often found in wetlands.	Entisols, Inceptisols, Mollisols,
Regosolic	55,382	5.6	Associated with landforms with little soil development time. The B horizon is absent or only has limited development. Their properties are essentially those of the parent material.	
Solonetzic	251	0.03	Found on parent materials derived from glacial re-working of sedimentary rocks. High in calcium, magnesium, and sodium. These soils have B horizons that are very hard when dry and swell up when wet.	Alfisols, Mollisols, Vertisols
Chernozemic	58,975	6.0	Parent materials range from coarse sands to fine-textured silts and clay loams. Darkened A horizon from addition of organic matter. If parent materials are high in clay, the shrinking and swelling causes mixing of the soil horizons and development of Vertisolic soils. Marine shale parent material (often high in sodium) lead to properties associated with the Solonetzic development.	Aridisols, Mollisols

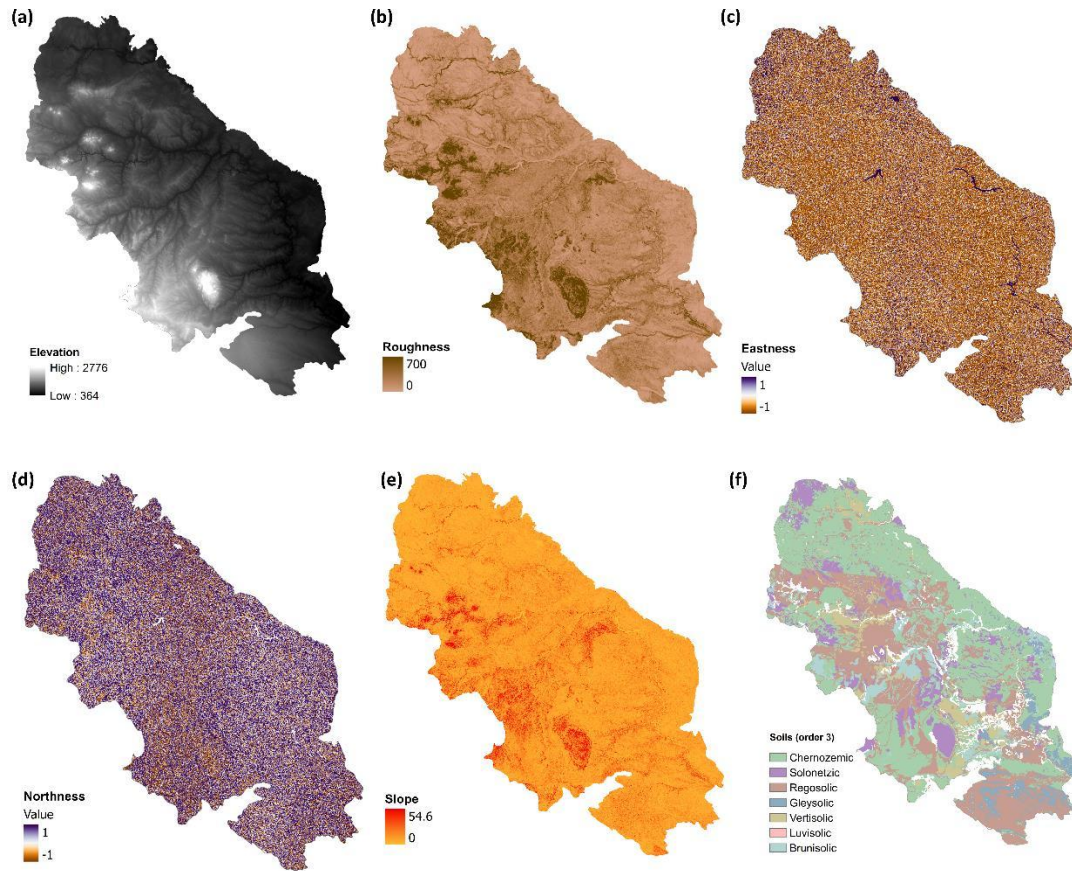


Figure S1.1. Mapped physical variables. (a) Elevation (masl) (b) topographic roughness, (c) *eastness* (sine of aspect), (d) *northness* (cosine of aspect), (e) slope (degrees), and (f) soil order

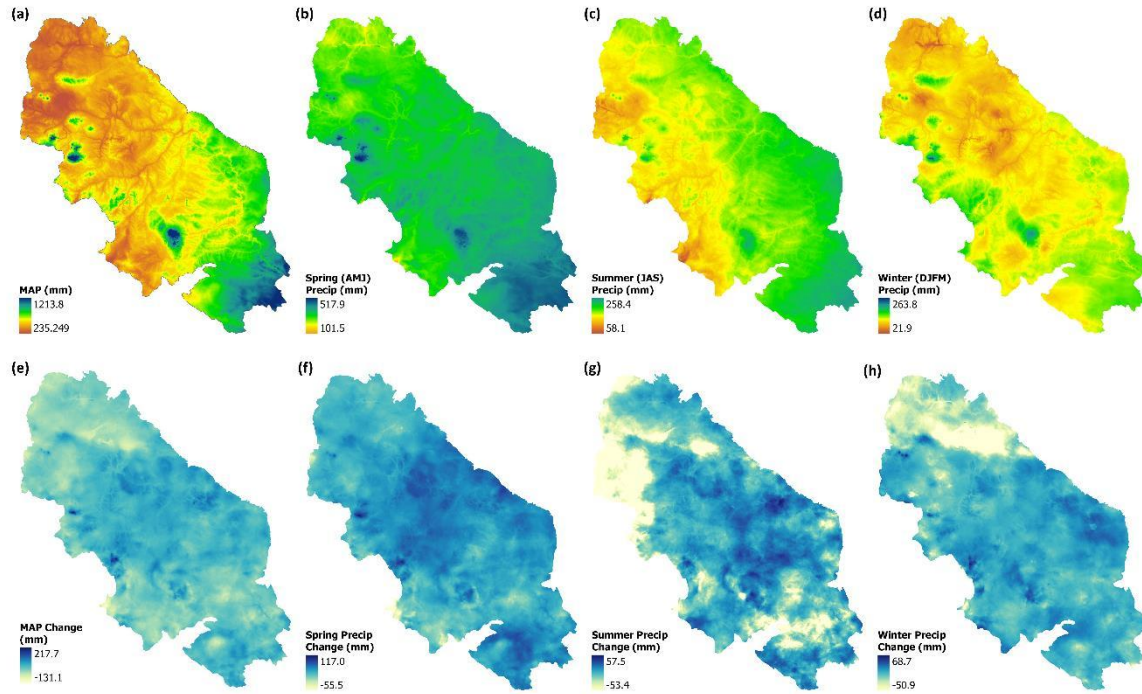


Figure S1.2. Mapped precipitation climatology variables for the period 2000-2019 (Precipitation CV on Figure S4). (a) Mean annual precipitation (MAP), (b) mean spring precipitation, (c) mean summer precipitation, and (d) mean winter precipitation. (e) The difference between MAP 1980-1999 climatology and 2000-2019 climatology. (f) The same as panel *e* for spring, (g) summer, and (h) winter. All units of mm. April, May, June (AMJ); July, August, September (JAS); December, January, February, March (DJFM).

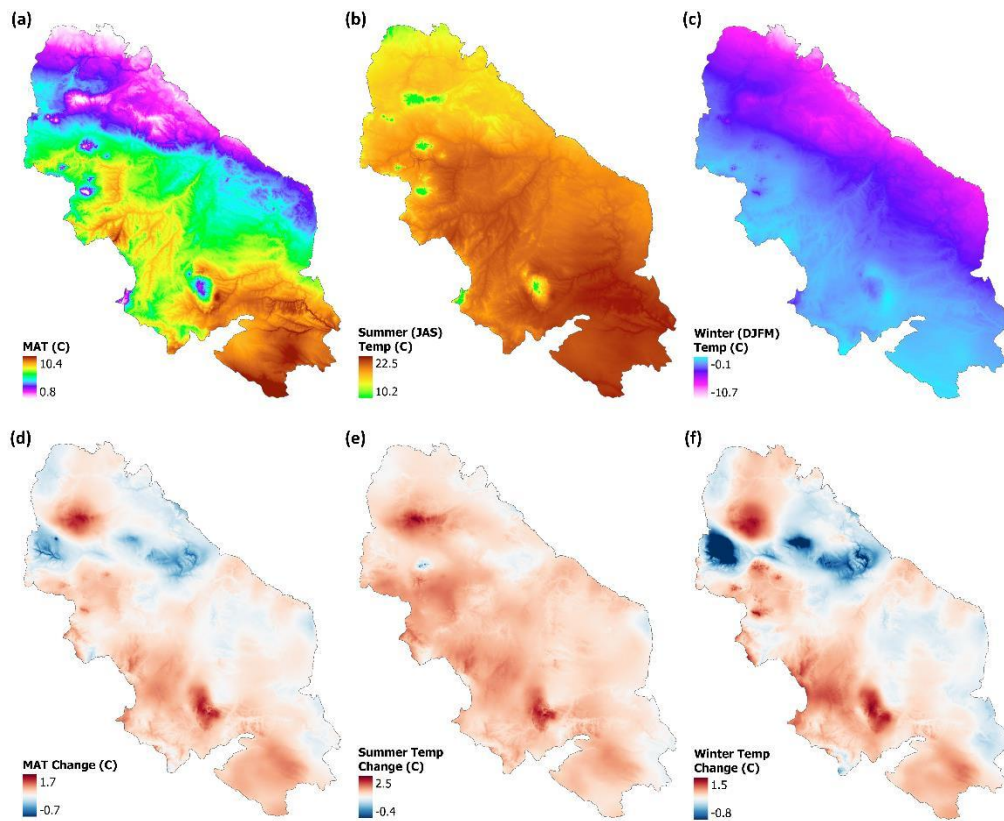


Figure S1.3. Mapped temperature variables (AGDD on Figure S5). (a) Mean annual temperature (MAT), (b) mean summer temperature, and (c) mean winter temperature. (d) The difference between MAT 1980-1999 climatology and 2000-2019 climatology. (e) The same as panel *d* for summer and (f) winter. All units of degrees Celsius. July, August, September (JAS); December, January, February, March (DJFM).

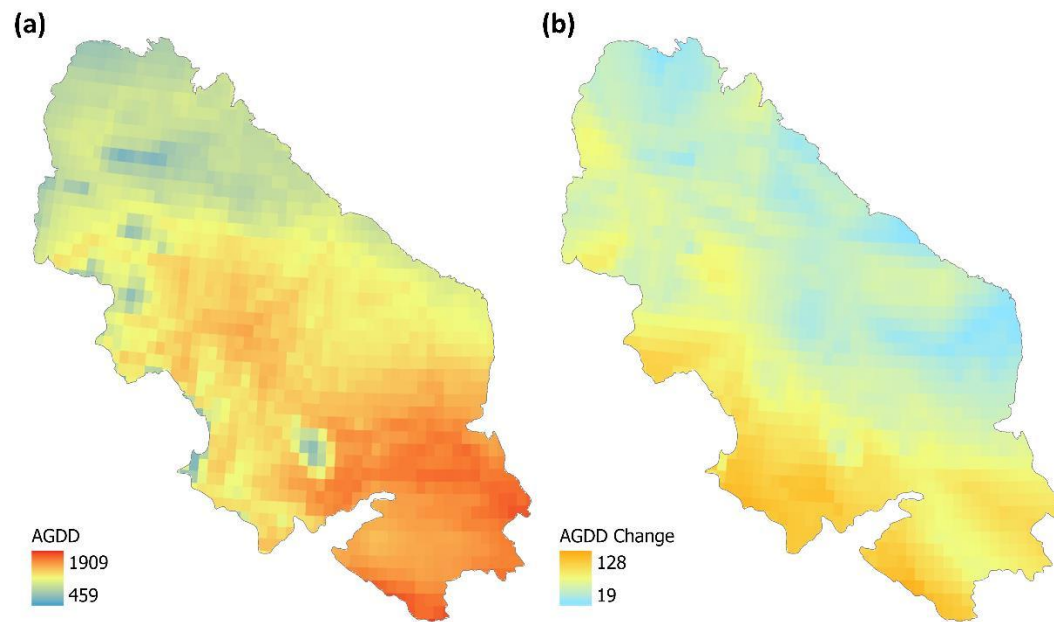


Figure S1.4. (a) Mapped average annual growing degree day (AGDD) from 2000-2019 and (b) the change between average AGDD from 1980-1999 and AGDD from 2000-2019.

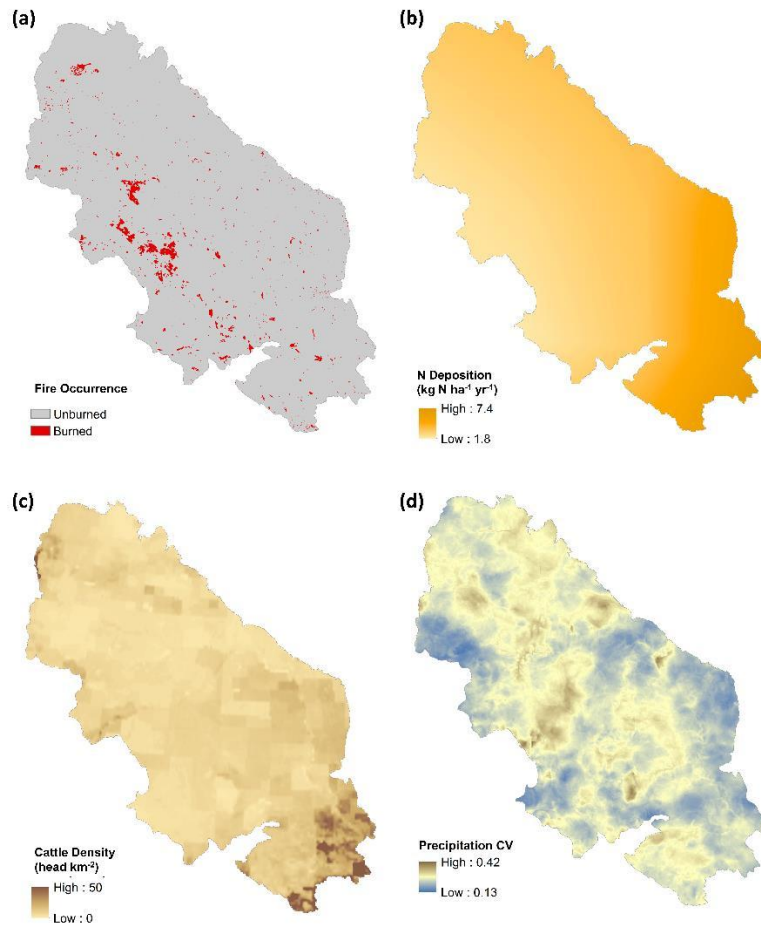


Figure S1.5. Mapped disturbance variables. (a) Annual cattle density (head km⁻²), (b) N deposition (kg N ha⁻¹ yr⁻¹), (c) fire presence/absence, and (d) mean annual precipitation CV.

APPENDIX S2

Table S2.1. Spearman's correlation (yellow, upper diagonal) between importance rankings of response variables from random forest models and Tjøstheim's coefficient (blue, lower diagonal) between spatial extent of response variables. It should be noted that Spearman's and Tjøstheim's coefficients are calculated using separate analyses but displayed on the same matrix above and below the diagonal for simplicity.

	<i>LAI Δ</i>	<i>Peak NDVI Δ</i>	<i>Mean NDVI Δ</i>	<i>Tree Cover Δ</i>	<i>2000 Tree Cover</i>	<i>2019 Tree Cover</i>
<i>LAI Δ</i>		0.75	0.86	0.67	-0.88	-0.44
<i>Peak NDVI Δ</i>	0.48		0.84	0.56	-0.43	-0.62
<i>Mean NDVI Δ</i>	0.50	0.43		0.76	-0.45	-0.29
<i>Tree Cover Δ</i>	0.49	0.43	0.44		-0.52	0.10
<i>2000 Tree Cover</i>	-0.13	-0.21	0.02	-0.11		0.71
<i>2019 Tree Cover</i>	0.09	0.02	0.03	-0.11	0.79	

Table S2.2. Response variable changes discretized into shrub- and grassland categories. Vegetation *Inc.* and *Dec.* columns indicate proportional grass or shrubland area undergoing respective directional change. The column directly right indicates the proportional increase or decrease. For all other results, shrub- and grassland are aggregated under the term *grassland*.

Vegetation metric changes by grassland category								
	<i>Grass Inc.</i>		<i>Grass Dec.</i>		<i>Shrub Inc.</i>		<i>Shrub Dec.</i>	
Tree Cover Δ	44.7	138.3	1.1	-30.5	61.6	135.2	1.8	-15.6
LAI Δ	74.9	27.0	1.5	3.7	84.1	25.7	1.9	-5.4
Peak NDVI Δ	60.6	9.8	0.2	-1.9	78.2	10.1	0.4	-1.4
Mean NDVI Δ	55.8	4.1	1.5	-1.6	67.5	4.5	2.3	-2.4

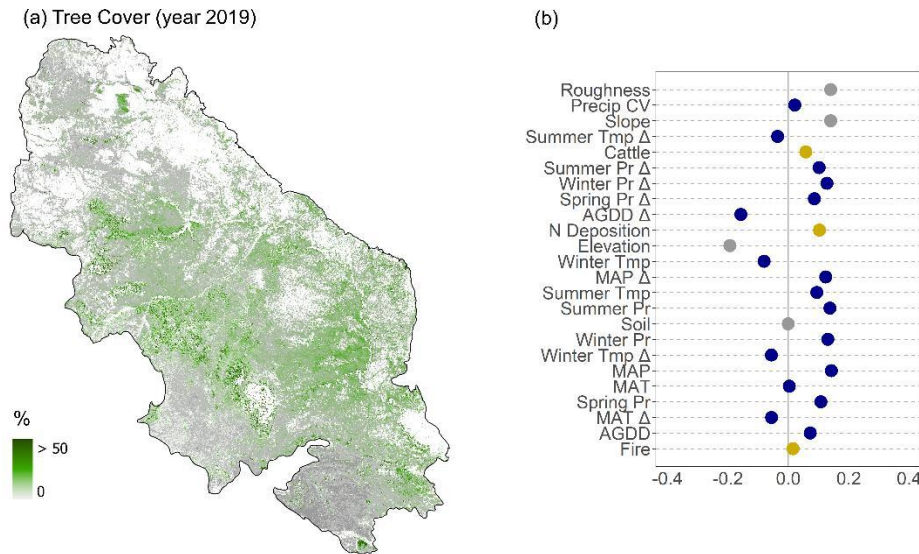


Figure S2.1. (a) Percent tree cover for the year 2019 in NGP grasslands (shaded grey). White areas represent non-grasslands (i.e., forested, cropland, urban, wetland). (b) random forest variable importance ranking. Dots farther away from the zero line indicate a steeper slope. Fire was converted to a numeric variable, with positive values indicating fire presence. Soil is on the zero line as it was kept a categorical variable. Grey circles signify topographic variables, gold circles signify disturbance variables, and blue circles signify climate variables.

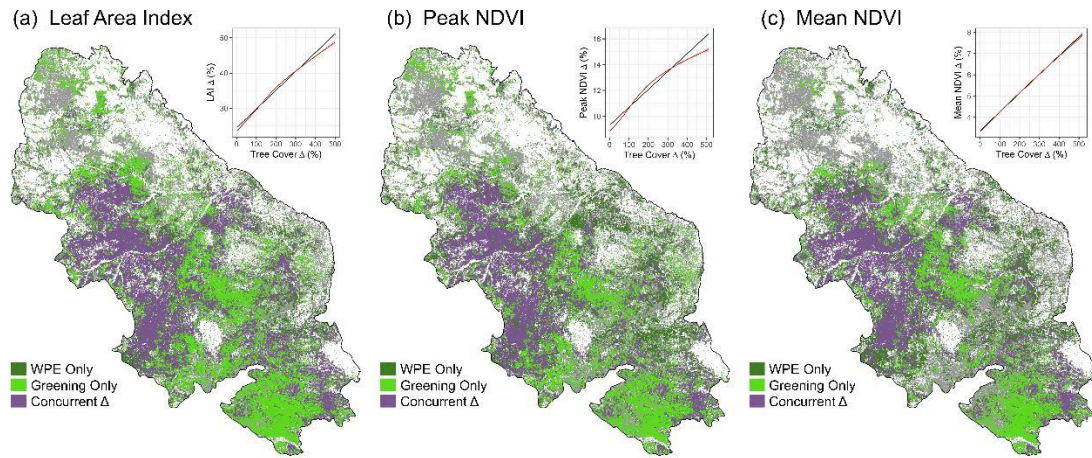


Figure S2.2. Concurrent analysis for the three greening metrics with percent tree cover changes in NGP grasslands (grey shading). Inset plots show the bivariate relationship between tree cover increase and respective greening increase. Black lines are linear fits; red lines are loess fits. White areas represent non-grasslands (i.e., forested, cropland, urban, wetland).

APPENDIX S3

Table S3.1. R packages used, their specific usage, and citations.

<i>R package</i>	<i>Use</i>	<i>Relevant citation(s)</i>
<i>MODISTsp</i>	Obtaining MODIS data	(Busetto and Ranghetti 2016)
<i>Kendall</i>	Mann-Kendall trend test	(McLeod 2011)
<i>Boruta</i>	Variable selection	(Kursa and Rudnicki 2010)
<i>Randomforest</i>	Random forest models	(Breiman 2001, Liaw and Wiener 2002)
<i>SpatialPack</i>	Tjøstheim's coefficient	(Vallejos et al. 2020)

Table S3.2. Datasets used, the associated variable type, their specific usage, and relevant citations.

<i>Dataset</i>	<i>Variable type</i>	<i>Use</i>	<i>Relevant citation</i>
2010 North American Land Change Monitoring System	Landcover	Determining landcover	(Canada Centre for Remote Sensing et al., 2020)
MODIS Vegetation indices; MOD13A1, version 6	Response	NDVI greening	(Didan 2015)
MODIS LAI/FPAR; MOD15A2, version 6	Response	LAI greening	(Myneni et al. 2015)
MODIS Vegetation Continuous Fields; MOD44B1, version 6	Response	Tree cover change (WPE)	(Dimiceli et al. 2015)
NASA Daymet temperature and precipitation	Climate	Climatological analysis	(Thornton et al. 2016)
NASA NEX-DCP30 (CMIP5) temperature	Climate	AGDD	(Thrasher et al. 2013)
Shuttle Radar Topography Mission	Physical	Digital Elevation Model	(Farr et al. 2007)
National Resource Conservation Service	Physical	United States soils	Soil Survey NRCS Soils (usda.gov)
National Soils Database of Canada	Physical	Canadian soils	The National Soil Database - Agriculture and Agri-Food Canada (AAFC)
1993 N Deposition	Disturbance	N-Deposition	(Dentener, 2006)
2010 Cattle Density	Disturbance	Grazing metric	(Gilbert et al. 2018)
MODIS Burned area product; MOD44B, version 6	Disturbance	Burned area	(Giglio et al. 2015)

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CHAPTER THREE

WOODY PLANT EXPANSION DRIVES THE REDISTRIBUTION
OF ECOSYSTEM NITROGEN FROM SOIL TO BIOMASS

Contribution of Authors and Co-Authors

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Contributions: Contributed to the conception of the idea, provided feedback on the analyses and figures, and edited the text.

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Manuscript Information

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Ecology

Status of Manuscript:

- ☒ Prepared for submission to a peer-reviewed journal
- ☐ Officially submitted to a peer-reviewed journal
- ☐ Accepted by a peer-reviewed journal
- ☐ Published in a peer-reviewed journal

WOODY PLANT EXPANSION DRIVES THE REDISTRIBUTION
OF ECOSYSTEM NITROGEN FROM SOIL TO BIOMASS

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Abstract: The structural and functional consequences of woody plant expansion (WPE) into grasslands have been documented across much of the globe, yet the ecosystem-level carbon and nutrient implications of WPE remain unclear. This is particularly pertinent regarding temperate systems where non-invasive gymnosperm expansion does not increase ecosystem nitrogen through fixation. By tracking the ecosystem development of elemental soil and biomass pools over 60 years in the heart of Northern Great Plains (NGP) in the U.S. across a woody expansion gradient, we ask: how does WPE affect ecosystem carbon (C), nitrogen (N), and phosphorus (P) pools? By comparing 1953 and 2013 aerial imagery, we quantify the degree of WPE across the 60-year period. We then integrate permanent ecological monitoring plots in which we have measured dendrochronology, allometry, and plant and soil chemistry and use statistical models to evaluate the extent of nutrient redistribution across an increasingly woody-dominant temperate grassland. Furthermore, we examine and isolate the topographic controls on contemporary

woody cover and soils to examine the potential direct effects of WPE on soil C, N, and P pools. We document WPE rates of 0.18-0.29 % cover yr⁻¹, which have driven large biomass C, N, and P changes between 1953 and 2013. We find a direct link between woody biomass growth and soil N pool declines after accounting for topsoil effects. We speculate that continued WPE could progressively limit N availability in this ecosystem by immobilizing N in conifer biomass, with the continuation of these trends suggesting a potential bottleneck for continued WPE in the NGP. Furthermore, the increasing aboveground biomass pools could become a vector for immense losses of C, N, and P given future disturbances.

Key Words:

Woody plant expansion, woody plant encroachment, progressive nutrient limitation, Northern Great Plains, gymnosperm, conifer, nitrogen, carbon, phosphorus

INTRODUCTION

Woody plant expansion (WPE) into grasslands and the associated structural and functional consequences have been documented across much of the globe (Archer et al. 2017, Deng et al. 2021), including in western North America, where WPE has been occurring at rates of ~0.1-2% cover yr⁻¹ for upwards of 150 years (Van Auken 2000, Barger et al. 2011). WPE is driven by complex interactions between long-term warming and altered precipitation (Knapp et al. 2008, Criado et al. 2020), increased nitrogen deposition and atmospheric CO₂ (Buitenwerf et al. 2012), and shifts in grazing intensity and fire regimes (Scholes and Archer 1997). WPE can increase the productivity of the ecosystem (Currey et al. 2022), although this can lead to increased strains on

soil nutrient pools with downstream effects on long-term nutrient availability (Brookshire et al. 2020). How WPE impacts the dynamics of ecosystem nutrient pools remains an outstanding question.

A comprehensive understanding of the impacts of WPE on ecosystem-level biogeochemical cycling of carbon (C) and primary production-limiting nutrients such as nitrogen (N) and phosphorus (P) has been elusive (Eldridge et al. 2011). While the storage of C, N, and P in biomass increases compared to pre-expansion levels, the effects of WPE on soil C, N, and P pools are far more equivocal with positive, negative, or no effects (Jackson et al. 2002, Barger et al. 2011, Eldridge et al. 2011, Zhou et al. 2018, Clemmensen et al. 2021). For instance, WPE has led to "islands of fertility" through localized nutrient uptake and recycling under tree canopies (Zinke 1962, Schlesinger et al. 1996, Pinho et al. 2011). Conversely, WPE could decrease soil N and P via plant uptake and long-term storage in biomass and induce shorter-term microbial immobilization in the soil pool (Walker and Syers 1976, Vitousek et al. 2010). WPE can slow soil decomposition via the high recalcitrance of leaf material slowing decomposition, which could drive increased soil C (Pinno and Wilson 2011, Blaser et al. 2014) or, alternatively, drive soil C priming in which new the addition of new plant litter stimulates the decomposition of existing SOM (McCarthy et al. 2010, Drake et al. 2011, Kuzyakov et al. 2019).

The long-term effects of WPE on soil chemistry are likely in part a function of the species that are expanding into grasslands. There is abundant documentation of WPE that focuses on species with symbiotic relationships with atmospheric N-fixing bacteria (e.g., mesquite; *Prosopis glandulosa* var *glandulosa*) or invasives expanding outside of their native range (Simberloff et al. 2010, Taylor et al. 2016, Zenni et al. 2022). Encroaching N-fixing trees

often lead to increased ecosystem N (Hughes et al. 2006, Zhou et al. 2018), though potentially at the cost of decreased soil P (Blaser et al. 2014, Zhou et al. 2018). Similarly, expanding non-native trees from their recent ranges often harbor different mycorrhizal associations than grasses that can liberate organically bound N and P in exchange for plant assimilated C (Policelli et al. 2019, Henriksson et al. 2021), thus increasing the overall bioavailability of soil N and P (Kuzyakov et al. 2019)

How the expansion of native gymnosperms (e.g., conifers) within their historical or native ranges into grasslands alters ecosystem C, N, and/or P pools remains an outstanding question. In the absence of significant external inputs, It can be assumed that the increased nutrient demand from increased woody biomass must be met by the turnover of soil organic matter N and P, and as the mycorrhizal communities may already be established, it is unclear whether there are strong impacts due to the ectomycorrhizal (ECM) fungal associations. Furthermore, disentangling the degree to which WPE is driven by pre-existing soil and nutrient gradients, or follows them, requires further investigation (Wu and Archer 2005, Farella et al. 2020, Zhou et al. 2022). While native conifer expansion is less well studied than WPE in subtropical savannas, temperate low-latitude grasslands, and high-latitude shrublands, it is documented to be occurring globally and has been proposed as a potential management solution for sequestering atmospheric CO₂. As such, examining the degree to which WPE influences ecosystem N and P cycling is imperative in better understanding the overall trajectory of ecosystem development and associated changes in C uptake and storage.

Here, we ask to what degree does WPE impact ecosystem (biomass + soil) C, N, and P pools? To answer these questions, we examine ecosystem C and nutrient pool changes over 60

years of WPE in the central Northern Great Plains, USA (NGP; Figure 1). Conifers have existed across the NGP for centuries to millennia (Wells 1970, Norris et al. 2016, Shinneman et al. 2016), yet recently there has been large-scale WPE driven largely by elongated growing season, increased precipitation, and the absence of fire (Currey et al. 2022). To answer our question, we first had to calculate the rate and magnitude of WPE across our study system. To do this, we calculated and compared percent tree cover from historical and contemporary aerial images. We then linked this to permanent stem dynamics and soil monitoring plots established in 2017 in central Montana. We examined and isolated the topographic and edaphic (hereafter, *topoedaphic*) controls on contemporary woody cover and soils to estimate the direct effects of WPE on soil C, N, and P pools. Finally, we integrated *in situ* dendrochronological methods, allometry, bulk tissue chemistry, and mineral soil chemistry with aerial imagery analysis to understand the ecosystem development of a conifer-encroached savanna in the NGP.

METHODS

Study region

We investigated WPE and its ecosystem consequences in a ~4,600-ha temperate grassland-savanna matrix in the Missouri and Musselshell River Breaks region in central Montana (47.44 N, 108.15 W; Figure 1). The study region is part of a Bureau of Land Management prescribed-fire study in which portions of the region are burned periodically. Mean annual precipitation (MAP) across the region is 358 mm and mean annual temperature (MAT) is 8.4°C. The area is topographically complex and is representative of the savanna-like mosaic of trees and grasses scattered across the NGP. Soils in the region are predominantly entisols and vertisols (SSURGO)

and are relatively shallow (Bliss et al. 2017). Soil texture ranges are from 10-50% sand (mean = 24%) and 16-51% clay (mean = 37%). The historical fire return interval in the region was ~30-50 years (Reid and Fuhlendorf 2011) although there was no known fire activity between the 60-year study period of 1953 and 2013. The primary woody species in the study area consist of *Pinus ponderosa* and various *Juniperus* species, including *J. horizontalis*, *J. scopulorum*, and *J. communis*, and their hybrids. Herbaceous vegetation is dominated by C₃ grasses (e.g., *Pseudoroegneria*, *Elymus*, and *Pascopyrum*), bluestem (*Andropogon*), grama (*Bouteloua*), needlegrass (*Stipa*), and fescue (*Festuca*).

Plot establishment

In 2017, we established twenty-five 20x20m sampling plots across a gradient of woody cover accessed from four hike-in locations (“plot-clusters,” Figure 1D). Plots were quasi-randomly chosen to maintain a semi-balanced mix of grassland, mixed grass-woody, and woody-dominant plots. The mean distance between plot clusters was 3.1 km, and within plot clusters, mean distance between plots was 0.42 km. Every ponderosa that fell within a plot was measured for diameter at breast height (DBH) and height (n = 631). Percent cover for ponderosa, juniper, and all herbaceous cover (including sagebrush) was ocularly estimated by each researcher (n = 3) and averaged. From these ocular estimates, plots were categorized into three woody-cover-based classifications that are used throughout this study: *grass* plots (<33% woody cover, n = 6), *mixed* plots (33-66% woody cover, n = 10), and *woody* plots (>66% woody cover, n = 9; Figure 1A-C). Finally, we examined the demographics of the plots, namely seedling density, stand density, maximum tree age (as a proxy for stand age), and mean relative growth rate (mRGR, derived

from dendrochronology).

Dendrochronology

From each plot with *P. ponderosa*, we randomly sampled four trees across the gradient of DBHs for dendrochronology using a 5mm increment borer (Speer 2010). If less than four ponderosas were present, all were cored. Two opposing cores were sampled 30 cm from the base for each tree, scanned using a ~3000 dpi scanner, and measured using Coorecorder (version 9.8.1). Because there is no historical chronology in the region, the cores in each plot were cross-dated using CDendro (version 9.8.1), and ring width correlation was evaluated in COFETCHA. In total, we examined ~150 cores from 77 trees from 21 plots which yielded a mean inter-series correlation (Spearman) of 0.4 ± 0.2 . As the morphology of the juniper stems in the study area made them hard to core, we destructively sampled 47 junipers at their bases from just outside the plots. The cross-sections were counted twice from opposing edges to determine the age of the trees.

Vegetation and soil sampling and analysis

We determined C, N, and P concentrations for woody and foliar biomass in both ponderosa and juniper. Ponderosa foliar samples were collected from similarly aged trees in the upper and sunlit sections of the canopy using a shotgun. Juniper sunlit foliar samples were collected by hand-clipping. For each species, we aggregated five random samples from separate trees across all plots and oven-dried them at 40 °C for 48 hours for analysis. We randomly chose five ponderosa tree cores and five juniper cross-sections for wood C, N, and P concentrations and ground them

using an electric rotary tool. Needles were dried and hand-milled in liquid nitrogen. Samples were sent to Agvise Laboratories (Northwood, ND) for analysis, where total C and N were determined via dry combustion, and total P was analyzed via nitric-acid digestion and quantification on an ICP-OES. Because wood P concentrations were below the detection limit (0.01%), we used values from Kaye et al. 2005 for ponderosa and DeBano et al. 1987 for juniper.

Organic mineral horizons were uncommon but, when present, were removed before taking five randomly sampled fixed-depth cores to 10 cm and composited before being passed through a 2 mm sieve to remove roots. Sub-samples were isolated from each plot for pH and phosphate (PO_4) analysis. pH was analyzed using a 2:1 Milli-q deionized water to soil solution and glass pH electrode. PO_4 analysis was done via the Bray I extraction technique based on neutral to > 7 pH of soils across the plots (Bray and Kurtz 1945). $\text{PO}_4\text{-P}$ was extracted by shaking (200 RPM) a 1:10 soil to Bray's solution (0.025M HCl and 0.03 M NH_4F) for five minutes before determination by the molybdate-blue method on a Lachat Quickchem autoanalyzer. The remaining samples were oven-dried at 60 °C for 48 hours and then milled to a fine powder over 12 hours. Total C and N were determined using the dry combustion method on a Costech ESC 4010 elemental analyzer, and duplicates were run on 10% of the samples to ensure analytical precision. All soil analyses were conducted at Montana State University's Environmental Analytical Laboratory. To convert SOC and nitrogen concentrations to spatial estimates of total soil stocks, we quantified bulk density in each of the plots by compositing three fixed depth cores (0-10 cm) from the mineral layer. Remaining soil from bulk density samples were used to calculate soil texture using hydrometry analysis (NRCS 2009).

Estimating ponderosa biomass through time

We estimated ponderosa biomass using species-specific allometric scaling of total and needle biomass from Tinker et al. 2010 (Appendix S1, Equations S1-2). Allometry was applied to measured stems ($n = 631$) and we then used dendrochronologically-derived BA increment (BAI) from tree cores to simulate total and needle biomass through time. This was accomplished by cumulatively summing BAI to calculate BA through time and simulating tree height using a saturating function with BA derived *in situ* (Appendix S1, Figure S1). Needle biomass was subtracted from total biomass to obtain woody biomass. Percent C, N, and P derived from *in situ* vegetation sampling were multiplied by the respective biomass pools (i.e., woody or needle) through time to obtain total ponderosa biomass C, N, and P through time.

Because we only cored a maximum of four trees in each plot, we scaled up the dendrochronologically-derived biomass estimates to the plot scale by multiplying the biomass estimates by a correction factor calculated by dividing total plot BA by cored tree BA. The average correction factor was 4.28 ± 5.43 , indicating ~4.3-fold higher cumulative plot BA than the BA of the cored trees. We then scaled all plot-scale estimates up to the per-hectare scale. Finally, we conducted a breakpoint analysis of the dendrochronological-derived biomass pools over time. Although we do not specifically address differences in growth rate between the different sized stems, the dendrochronologically-simulated cumulative total biomass was derived from a range of tree sizes in each plot. As such, when we examined simulated total biomass versus measured *in situ* total biomass from allometry, the coefficient of determination was 0.97, and the mean absolute error was relatively small at 7.8 Mg ha^{-1} (Appendix S1, Figure S2).

Estimating juniper biomass through time

For contemporary juniper aboveground biomass (AGB), we calculated AGB using canopy area (CA) allometry. Because no CA allometry is known for the dominant juniper species in the region, we calculated AGB estimates using the average of 4 other known allometric equations to obtain a genus-level approximation (Appendix S1, Table S1). Juniper CA was first estimated ocularly but corrected using a correction factor derived via ground measurement of 102 juniper crown areas. Ocular estimates tended to underestimate measured CA by $33 \pm 2\%$ (Appendix S1, Figure S3). Similarly, for juniper belowground biomass (BGB), there are no known species- or genus-level allometric equations. Thus, we simulated BGB using known BGB:AGB (i.e., root:shoot) ratios from three other published studies (Appendix S1, Table S2). The final BGB:AGB ratio we used was 0.33 ± 0.08 . Total juniper biomass is then the summation of BGB and AGB.

To simulate juniper biomass back through time, we used the current ratio of juniper biomass relative to ponderosa biomass for each plot. We next calculated the proportion of wood versus needle biomass using the relationship found in Ansley et al. 2012. We then multiplied the respective biomass pools (woody vs. foliar) with the respective percent C, N, and P to obtain total juniper biomass C, N, and P through time. This was then added to the ponderosa total biomass to estimate woody plant biomass C, N, and P across the ecosystem and through time.

Aerial imagery analysis

We obtained historical aerial imagery from 1953 (~3m resolution) from the USGS EROS archives and present-day (2013) aerial imagery from the USDA NAIP program (~1m) from

Google Earth Engine for the study area. Historical imagery was georeferenced and orthorectified to the 2013 NAIP imagery using Spline Transformation in ESRI ArcGIS Pro, reducing RMS errors to near zero (Appendix S1, Figure S1). All imagery was resampled to a 2m grid cell size for supervised tree classification, and 500 randomly sampled training points were manually classified and double-checked as either Tree (1) or Not Tree (0; Appendix S2, Figure S2). Classified tree points were combined with auxiliary variables (Appendix S2, Table S1) for pixel-based supervised classification. Because the historical imagery only contained one band of pixel brightness, we included grey level cooccurrence matrices (GLCMs) to create more information about the image. We used a 3x3 cell window and created mean, variance, homogeneous, contrast, and dissimilarity GLCMs (Appendix S2, Table S1).

We used five supervised learner models to create an ensemble supervised meta-learner (h2o.ai, Appendix S2, Table S2). We ran this process 100 times (i.e., bootstraps) due to the random sampling of the 10-fold cross-validation used for model validation. We obtained the average Matthews correlation coefficient (MCC) on the cross-validation test data for model evaluation across the 100 runs (Chicco et al. 2021). MCC values of 1 indicate a perfect classifier, -1 indicate the classifier always predicts the opposite, and 0 indicate the classifier is no better than random guessing.

The meta-learner was run on all cells across the study area to classify each pixel as "Tree" or "Not Tree" (Appendix S2, Figure S3). Percent tree cover for both images was aggregated to 20m (plot-scale) and benchmarked with measured percent tree cover to check for accuracy (Appendix S2, Figure S4). For analysis, we aggregated 20m percent woody cover change up to 100m resolution using the third quartile to account for artificially inflated decreases

from errors produced from the misclassification of shadows as trees in the 1953 model. This allowed the average woody cover change at the 20m resolution (13.34% cover) to match the resampled 100m resolution (13.29% cover). Finally, we subtracted the two percent tree cover maps to calculate percent tree cover change between 1953 and 2013 and binned these changes by the same vegetation stratification used across the plots (i.e., *grass* pixels: <33% woody cover; *mixed* pixels: 33-66% woody cover; and *woody* pixels: >66% woody cover) based on the 1953 image.

Statistical Analyses

We examined the bivariate relationships between woody cover and key topoedaphic variables, namely: slope, topographical position index (TPI; -1 indicating areas of local low points and 1 indicating local high points), two aspect variables (cosine of aspect, or *northness* and sine of aspect, or *eastness*), soil moisture, and soil texture (percent sand and clay). We examined bivariate relationships between woody cover and soil C, N, and P pools and concentrations, soil pH, soil PO₄, and soil bulk density.

We next used stepwise model selection using the second-order Akaike's information criterion (AICc) from the *MuMIn* package (Bartoń 2022) to examine which topoedaphic variables influenced soil C and nutrient pools and concentrations (equation 1).

$$\text{soil CNP} \sim \text{selected topoedaphics} \quad 1)$$

where *soil CNP* is the measured soil C, N, or P pool or concentration, and *selected topoedaphics* are the topoedaphic variables described above that have been selected by the AICc stepwise

process (Appendix S3, Equation S1). We then extracted the residuals from these models and fit these against woody cover to examine the topoedaphically-corrected relationship between woody cover and soil C, N, and P pools and concentrations (Equation 2).

$$\text{soil } CNP_{resid} \sim \% \text{ woody cover} \quad 2)$$

where $\text{soil } CNP_{resid}$ is the residuals from all models following the form of equation 1, referred to hereafter as "topoedaphically-corrected" soil C, N, and P pools or concentrations (as specified). We compared these with uncorrected versions of these models (Appendix S3, Table S1)

Ecosystem changes through time

We applied the slope coefficients from the topoedaphic-corrected soil pool models (slope of Equation 2) to the woody cover changes calculated from the aerial imagery analyses. The slope from Equation 2 estimates the change in soil (C, N, or P) pool per unit increase in woody cover. Thus, by applying this estimate across the woody cover change maps, we estimated woody cover-driven soil C, N, and P changes by substituting space-for-time across the 60-year study period. Importantly, slope estimates were only applied if found to be statistically significant ($p < 0.05$; all p-values are reported per Wasserstein et al., 2019). Soil pool changes were then compared to plot-level biomass C, N, and P changes.

All analyses were conducted in *R* (version 4.1.1), all statical models were ordinary least squares (OLS) regression models, and any missing data were imputed using the predictive mean matching method from the *mice* package (Buuren and Groothuis-Oudshoorn 2011), which is required for the stepwise model selection process. When reporting the uncertainty around soil

pools and changes, plant stoichiometry, and biomass C, N, and P accumulation estimates, the mean $\pm$ standard deviation (sd) was reported since the variables and model residuals were normally distributed. Tree cover and tree cover changes were skewed so the geometric mean (geometric sd) was reported. Furthermore, we report the slope coefficient indicated by β when necessary.

RESULTS

Stem structure and biomass

Stem density across our study system spanned a wide range (0 to 1025 trees ha⁻¹) and had a large standard deviation around the mean for ponderosa (density: 376 ± 273 stems ha⁻¹; BA: 14.7 ± 11.3 m² ha⁻¹) and juniper (density: 182 ± 94.8 trees ha⁻¹; CA: 2107 ± 1257 m² ha⁻¹). Because the region had not burned during the study period, this translated into a large and variable density of recently recruited (<10 cm) ponderosa (408 ± 729 saplings ha⁻¹). Average woody cover across all plots was ~49% and scaled linearly with woody biomass ($R^2 = 0.63$; $p < 0.0001$). This corresponded to an average overall total woody biomass of 99.5 ± 68.3 Mg ha⁻¹, which was highest in woody plots and lowest in grass plots (*grass*: 19.5 ± 22.9 Mg ha⁻¹; *mixed*: 97.8 ± 39.0 Mg ha⁻¹; *woody*: 154.8 ± 60.8 Mg ha⁻¹). The juniper to ponderosa biomass ratio was 4.1 ± 5.2 in *grass* plots, 1.2 ± 1.3 in *mixed* plots, and 0.69 ± 0.78 in *woody* plots, indicating more ponderosa in *woody* plots and more juniper in *grass* plots, with roughly equal biomass in *mixed* plots. Across all plots, the average ratio was 1.5 ± 2.5 , indicating slightly more juniper biomass than ponderosa.

Topoedaphic relationships with woody cover

We found strong negative associations between percent woody cover versus bulk density ($\beta = -0.004$, $p < 0.001$, Figure 2a) and pH ($\beta = 0.007$, $p = 0.009$, Figure 2b), and a slightly positive association with soil phosphate ($\beta = 0.018$; $p = 0.193$ Figure 2c), although this relationship becomes much stronger when removing one outlier ($>2\sigma$; $\beta = 0.019$; $p = 0.046$). We found a strong positive relationship between percent sand and woody cover ($\beta = 1.57$; $p = 0.003$; Figure 2e) and subsequently, a strong negative relationship with clay ($\beta = -1.71$; $p = 0.008$; Figure 2f). We found no correlation between woody cover and soil moisture ($p = 0.186$; Figure 2d). There was only slight evidence that topography influenced woody cover, with a slight negative relationship with TPI (e.g., more trees in the gullies; $p = 0.069$; Figure 2g) but no relationship between northness or eastness ($p = 0.457$ and $p = 0.543$; Figure 2h,i). Interestingly, we found no relationship between the average relative growth rate and any topoedaphic variables save for soil moisture, in which RGR decreased with increasing soil moistures ($p = 0.0479$).

Woody cover changes through time

The median age for all ponderosa cored was 113 years old (Figure 3) and 84.5 years for juniper. We find that average biomass accumulation to be $1.64 \pm 1.38 \text{ Mg ha}^{-1} \text{ yr}^{-1}$ across the study period (Figure 3). However, we find a breakpoint for the average biomass accumulation rate of change in 1941 (Figure 3) from $4.2 \pm 0.3 \text{ kg ha}^{-1} \text{ yr}^{-2}$ to $17 \pm 1.1 \text{ kg ha}^{-1} \text{ yr}^{-2}$ after 1941, indicating a >4-fold acceleration of woody biomass accumulation.

Overall model accuracy (MCC) for the aerial canopy cover model was 0.754 and 0.798 for the 1953 and 2013 models, respectively (Appendix S2, Table S2). Similarly, modeled 2013

tree cover matched the 2017 *in situ* woody cover well ($R^2 = 0.69$) and with minimal bias (Appendix S2, Figure S4), although the aerial imagery-based estimate of 20.8% cover was much lower than the plot-level average (49% cover). This suggests that the plots are well represented in the model, despite not reflecting the relatively high proportion of grassland across the entire study area.

Mean (geometric) tree cover increased by 11.6 (3.0)% cover ($\sim 0.19\%$ cover yr^{-1}) across the entire study system over the 60-year period (Table 1, Figure 4). Between 1953 and 2013, *mixed* pixels (33-66% woody cover) experienced the largest average increases of $\sim 0.27\%$ cover yr^{-1} . *Grass* pixels comprised the largest proportion of the study area at 79.4% in 1953 and underwent the second-largest increase of 0.22% cover yr^{-1} (Table 1). This large increase in woody cover led to a proportional decrease of 15.2% in *grass* pixels by 2013. In contrast, areas with *mixed* vegetation increased to comprise 24.0% of the landscape, and *woody* pixels increased to 9.0% of all areas (Table 1). These results, paired with a strong negative association between woody cover change and percent woody cover (in 1953; $p < 0.0001$), indicate that more trees expanded into areas with historically less tree cover. It should be noted that due to heavy right-skew, the difference between the geometric mean values is less than the overall pixel-based proportional change (e.g., overall percent cover change of 11.6% is less than the subtraction of the 2013 and 1953 geometric averages, which equals ~ 5.4 ; Table 1). Overall, we estimate that 58.3% of the region underwent tree cover increases, 23% did not undergo any change, and the remaining portion of the landscape underwent decreases.

Woody vegetation percent C, N, and P values

The resulting leaf mass-based C:N ratio for both species was ~48, although C:N ratio for wood was 1830 compared to 480 between ponderosa and juniper, indicating much higher relative N in the juniper wood than ponderosa (Table 2). Finally, the biomass N:P ratio in wood and foliage for both species did not vary greatly, nor were the N:P ratios differ much between species. Applying tissue concentrations to the total biomass estimates, we estimate that contemporary biomass stocks of $87.6 \pm 69.4 \text{ Mg C ha}^{-1}$, $474 \pm 341 \text{ kg N ha}^{-1}$, and $56 \pm 41 \text{ kg P ha}^{-1}$ (Table 3).

Soil characteristics and controls on soil C, N, and P

Soil C pools generally increased from grass-dominant to tree-dominant plots and woody cover was a significant predictor for soil C concentrations ($p = 0.002$, $R^2 = 0.34$; Figure 5a) but not for soil C pools ($p = 0.159$; Figure 5d). Conversely, we observed a strong decrease in soil N and P pools ($p = 0.0003$, $R^2 = 0.44$; $p = 0.0008$, $R^2 = 0.39$; Figure 5e,f) but not soil concentrations of N and P ($p = 0.432$ and $p = 0.132$; Figure 5b,c). This corresponds to increasing mass-based soil C:N ratios from *grass* plots (9.2) to *mixed* plots (12.4) to *woody* plots (15.1), but relatively constant soil N:P ratios of 2.2.

We then examined how topographic variables (clay, sand, TPI, northness, eastness, and soil moisture) influenced soil C, N, and P pools and concentrations. After AICc selection (Equation 1), no model had more than two predictor variables (Appendix S3, Table S1). Percent sand was a strong predictor of soil N pool, whereas percent clay predicted soil C concentrations and soil P pool and concentration. TPI was the only predictor variable identified for the soil C pool and soil N concentration (although R^2 was only 0.19 and 0.14, respectively; Table S2).

Overall, topoedaphic factors best explained soil C concentration (percent clay and soil moisture, $R^2 = 0.5$) and the soil P pool (percent sand and TPI, $R^2 = 0.43$; Table S2).

We then extracted the residuals from these models and fit them as a function of woody cover (Equation 2) to isolate the topoedaphic controls on soil C, N, and P. These results show qualitatively similar trends to the non-corrected data (Figure 5g-1, Appendix S3, Table S2). We find no evidence that WPE influences topoedaphically-corrected soil C pools or concentrations and minimal evidence that WPE influences soil P pool ($p = 0.142$; Figure 5l) but not concentrations ($p = 0.628$; Figure 5i). Conversely, we do find suggestive evidence that WPE is associated with declining soil N concentrations ($p = 0.107$, $\beta = 2.20 \times 10^{-4}$ % per percent increase in tree cover; Figure 5h; Appendix S3, Table S1) and stronger evidence that WPE impacts the soil N pool ($p = 0.0551$, $\beta = 3$ kg N per percent increase in tree cover; Figure 5h; Appendix S3, Table S1).

Ecosystem C, N, and P changes

Using dendrochronology and allometry, we estimated biomass C, N, and P changes at the ecosystem scale. We find that the average biomass C accumulation rate across the 60-year period was 836 ± 702 kg C ha⁻¹ yr⁻¹, 4.4 ± 3.6 kg N ha⁻¹ yr⁻¹ for biomass N, 0.53 ± 0.43 kg P ha⁻¹ yr⁻¹ (Figure 6a; Table 3). When discretized by vegetation type, C, N, and P accumulation rates increased from *grass*, to *mixed*, to *woody* plots, and at their maximum, rates reached 1.2 ± 0.7 Mg C ha⁻¹ yr⁻¹, 6.1 ± 3.6 kg N ha⁻¹ yr⁻¹, and 0.7 ± 0.44 kg P ha⁻¹ yr⁻¹ (Table 3).

We simulated the soil N decline since 1953 using the space-for-time substitution analysis. To do so, we combined the slope coefficient from the soil N pool topoedaphically-corrected

model and WPE (3 kg N per percent increase in tree cover) with the estimates of percent tree cover change from the aerial imagery analysis (Figure 4c). We estimate that soil N decreased by $0.79 \pm 0.69 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. The overall biomass N accumulation rate was ~5-fold higher than the rate of soil N decline, indicating that 17.7% of soil N rate changes could be explained via the growth of woody biomass.

DISCUSSION

Recent woody expansion

We document widespread WPE in our study area. We calculate rates of WPE between 0.18-0.29% cover yr^{-1} , leading to a simultaneous 15% decrease in grassland since 1953. We find that the highest rates of change occurred in areas with moderate woody cover (33-66% cover), likely due to a combination of seed source availability and lower density dependency pressures. Higher WPE rates at moderate tree cover may point toward a potential tree cover threshold in which tree cover has reached a sufficient abundance and return to primarily grass cover becomes unlikely, although more work is needed to test this potential. Importantly, our WPE estimates fall in line with other studies, both globally (0.3% yr^{-1} , Deng et al. 2021) and locally (0.1-2% yr^{-1} , Barger et al. 2011), as well as link satellite-based estimates of woody cover to aerial and ground-based measurements. We find that WPE rates in this region are around the upper third quartile of WPE in the NGP (Currey et al. 2022).

Ecosystem biogeochemical implications

Tree expansion across the MMRB has led to large increases in C, N, and P stored in biomass

pools. In particular, we highlight that the redistribution of soil N to the biomass pool has numerous ecosystem-level implications. While there were no known fires across the study region during the study period, it is part of a prescribed-fire experiment and was burned in 2018. While the natural fire return interval of the region is ~50 years (Reid and Fuhlendorf 2011), fire may become more frequent in the future. How this will impact increasingly large stores of C and nutrients in the biomass pool is important for understanding the trajectory of this ecosystem (Moritz et al. 2012). Furthermore, grasslands are potentially more resilient to climate extremes (Dass et al. 2018); thus, the growing C and nutrient pools in woody biomass may become a vector for large-scale losses of nutrients across these ecosystems.

We document a strong coupling between woody cover and soil N changes between 1953 and 2013. We find that $\sim 3 \text{ kg ha}^{-1}$ of N is lost per percent increase in tree cover. Since 1953, we estimate that $0.79 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ has been redistributed from the soil pool into the woody biomass pool. This equates to $\sim 220 \text{ Mg}$ of N throughout the 60-year period. Importantly, these changes are likely non-linear over large periods, yet our breakpoint analysis indicates a quasi-linear uptake rate during the study period. Thus, comparing the biomass N uptake rate with estimated soil N changes, we see that $\sim 20\%$ of biomass N uptake can be directly accounted for by changes in the top 10 cm of soil. Importantly, neither of the expanding species are N fixers, and N deposition across the ecoregion is quite low ($\sim 1.1 \text{ kg N ha}^{-1} \text{ yr}^{-1}$; Brookshire et al. 2020). Similarly, that pH and PO_4 decrease per percent increase in woody cover suggest other tree-based soil changes are occurring (Chen et al. 2008).

Long-term implications

We highlight a few possibilities regarding these findings' long-term implications, given

continued future WPE. The first possibility is that WPE could progressively limit nutrient availability at certain timescales (Thomas et al. 2015) by immobilizing N acquired from SOM into woody biomass faster than it can turnover. Importantly, soil C:N and N:P ratios across our study area confirm both strong N and P limitation regardless of vegetation cover (Koerselman and Meuleman 1996, Sterner and Elser 2002, Cleveland and Liptzin 2007). Similarly, a documented decline in N availability across the region over the past century signal an exacerbation of N limitation with continuing WPE. Although we find no change in soil C with increasing tree cover in this study, the C:N and C:P ratios increase across the gradient of woody cover. Taken together, these changes parallel the notion of progressive nutrient limitation (Luo et al. 2004), in which increasing CO₂ explicitly drives the progressive immobilization of soil nutrients from increased primary productivity. Nonetheless, the continuation of these trends could point toward a future bottleneck for continued WPE in the NGP.

A second possibility is that trees follow pre-existing nutrient gradients driven by abiotic environmental factors (e.g., soil texture, slope, etc). In this scenario, nutrients required by trees are met by nutrient inputs to the system, either from deposition, fixation (from other species), and weathering. Although N fixation is undocumented in the study system, we find some ancillary evidence for this possibility arising from the finding that, after correcting for topographic effects, the relationship between tree cover and C was nullified and was weakened for N and P. Soil texture can influence seedling propagation, and tree rooting depth, and thus partially influence the distribution of WPE, as has been eluded to elsewhere, particularly concerning sandier soils (Wu and Archer 2005, Farella et al. 2020, Zhou et al. 2022). Here we corroborate these findings, although we cannot parse apart the possible negative impacts from

clay versus potential facilitative impacts from sand. Conversely, that RGR was not associated with other topsoil variables except soil moisture signals that growth may primarily be constrained by climate rather than other topsoil factors or nutrient limitations.

Finally, a third possibility is that trees could create local areas of increased nutrient availability, although we find no evidence of this. This effect has been found elsewhere (Schlesinger et al. 1996), in which soil nutrients increase simultaneously with plant biomass elemental pools. While we find that WPE increases the productivity of this ecosystem, it comes at the cost of soil N, potentially P, and does not appear to impact soil C. Continuing to explore these hypotheses in the future will allow us to understand better ecosystem C storage and nutrient cycling in the context of WPE in a temperate savanna ecosystem.

Potential mechanisms and limitations

By substituting space for time, we examined the theoretical potential of WPE-derived soil nutrient changes. We speculate that the removal of top-down drivers such as fire or herbivory in recent decades and large climatic changes are in large part driving increased biomass (Currey et al. 2022), leading to more demand on soil nutrient pools. The coniferous expansion in our study system is likely increasing the abundance of ECM fungi, as evidenced by changes in PO_4 with increasing tree cover (Figure 2c), which could increase the capacity to liberate organic N and P reserves and promote tree growth (Chen et al. 2008, Policelli et al. 2019, Clemmensen et al. 2021). However, it is important to point out that the soils sampled were only from the top 10 cm of the soil profile. Nevertheless, increased ECM abundance may also explain how trees can continue to grow and expand in such a low nutrient environment, as ECM abundance and soil

nutrients can be negatively correlated due to increased root investment (Rygiewicz et al. 1997). Furthermore, the woody species that are expanding in the study system may have dimorphic root systems (Potter and Green 1964, Graham and Jain 2005), enhancing their ability to obtain both shallow and deep soil water and nutrients, although this has never been examined in this region.

Importantly, we do not account for herbaceous productivity and uptake, which may be higher in grassier plots than woody uptake, thus, our estimates of ecosystem C, N, and P changes through time are low in the grassier areas of the study systems. Furthermore, biomass P estimates are highly uncertain due to literature-derived values. This study highlights the challenges of tracking and estimating ecosystem nutrient pools, particularly P, in both soils and vegetation. Nonetheless, our simulations indicate that the potential for soil nutrient changes is large in grasslands with high rates of WPE.

Conclusions

We find a direct link between biomass accumulation and soil N decline across the study system. While it is challenging to predict the rate or magnitude to which these changes will continue, using topodaphic corrections and substituting space-for-time, we speculate that N availability may limit tree growth in the future, although perhaps not enough to prevent it. More work is needed regarding the potential applicability of progressive nutrient limitation theory to WPE in this system versus topodaphically-driven WPE. Nevertheless, this work highlights the potential for large changes in ecosystem stability given the large shift of nutrients into the biomass pool, which may be more prone to disturbance given the combination of higher conifer density and a warmer climate (McWethy et al. 2019). Conversely, WPE over the past 60 years has led to C

sequestration rates upwards of $1.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, similar to other tree-based climate mitigation solutions proposed across the US (e.g., $1.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$; Cook-Patton et al. 2020). However, the use of WPE should be thoroughly investigated before being suggested as a solution to climate change (Veldman et al. 2015), as WPE is also associated with a host of ecosystem and socio-economic tradeoffs, including changes to biodiversity and wildlife habitat (Wilcox et al. 2018, Epstein et al. 2021). Nonetheless, this work highlights that the ecosystem implications of WPE may be underappreciated in other temperate ecosystems across the globe and may become increasingly important given projected global climate changes.

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TABLES

Table 1. Woody cover changes (%) determined using a comparison between 1953 and 2013 aerial photographs.

Overall	Year	Percent woody cover	Proportion of study area (%)	Δ (%)	Percent cover change (%)	Rate (% yr⁻¹)
	<i>1953</i>	15.4 (3.3)				
	<i>2013</i>	20.8 (3.1)			11.6 (3.0)	0.19
Land cover						
<i>Grass</i>	<i>1953</i>	8.8 (2.8)	79.4			
	<i>2013</i>	17.3 (3.1)	67.0	-15.2	12.9 (2.6)	0.22
<i>Mixed</i>	<i>1953</i>	47.6 (1.2)	16.5			
	<i>2013</i>	50.8 (1.7)	24.0	7.5	15.9 (2.7)	0.27
<i>Woody</i>	<i>1953</i>	75.4 (1.1)	4.1			
	<i>2013</i>	61.3 (1.7)	9.0	4.9	10.7 (2.6)	0.18

Table 2. Percent C, N, and P values and C:N:P ratios (mass-based) for ponderosa and juniper wood and leaf tissues and bulk soil (0-10 cm). *Value from Kaye et al., 2005. **Value from DeBano et al., 1987

	C (%)	N (%)	P (%)	C:N	N:P	C:P
<i>Pinus ponderosa</i>						
Wood	51.2 ± 1.450	0.028 ± 0.011	0.004 ± 2e-4*	1829	12800	7
Leaf	49.3 ± 0.267	1.02 ± 0.191	0.098 ± 0.098	48.3	502	10.4
<i>Juniperus spp.</i>						
Wood	50.1 ± 0.431	0.104 ± 0.025	0.02 ± 0.01**	482	2505	5.2
Leaf	51.4 ± 0.441	1.07 ± 0.121	0.123 ± 0.019	48.1	416	8.65
<i>Soil</i>						
<i>Overall</i>	1.45 ± 0.403	0.114 ± 0.020	0.052 ± 0.006	12.7	2.2	28.8
Grass	1.07 ± 0.172	0.116 ± 0.019	0.053 ± 0.002	9.26	2.2	20.1
Mixed	1.47 ± 0.255	0.116 ± 0.022	0.053 ± 0.009	12.7	2.2	27.9
Tree	1.67 ± 0.469	0.110 ± 0.022	0.049 ± 0.004	15.1	2.3	35.2

Table 3. C, N, and P pools and rates of change for total woody biomass and soil (0 – 10 cm) from WPE. Soil C and P rates of change could not be determined because no significant relationship was found between topocedaphically-corrected soil C and P pools and percent woody cover.

Veg	C Pool (Mg ha⁻¹)	C Δ (kg ha⁻¹ yr⁻¹)	N Pool (Mg ha⁻¹)	N Δ (kg ha⁻¹ yr⁻¹)	P Pool (Mg ha⁻¹)	P Δ (kg ha⁻¹ yr⁻¹)
Biomass						
<i>Overall</i>	<i>87.6 ± 69.4</i>	<i>836 ± 702</i>	<i>0.474 ± 0.341</i>	<i>4.44 ± 3.56</i>	<i>0.056 ± 0.041</i>	<i>0.53 ± 0.43</i>
Grass	24.7 ± 23.1	224 ± 176	0.221 ± 0.205	1.55 ± 1.03	0.027 ± 0.025	0.19 ± 0.12
Mixed	63.0 ± 49.8	672 ± 605	0.404 ± 0.322	3.84 ± 3.27	0.048 ± 0.039	0.46 ± 0.40
Woody	136 ± 69.6	1220 ± 695	0.636 ± 0.342	6.07 ± 3.58	0.074 ± 0.041	0.772 ± 0.44
Soil						
<i>Overall</i>	<i>13.0 ± 2.76</i>	-	<i>1.05 ± 0.228</i>	<i>-0.79 ± 0.87</i>	<i>0.480 ± 0.107</i>	-
Grass	11.8 ± 2.29	-	0.240 ± 1.28	-0.82 ± 0.89	0.584 ± 0.035	-
Mixed	12.8 ± 2.38	-	0.185 ± 1.03	-0.79 ± 0.86	0.474 ± 0.120	-
Woody	14.1 ± 3.25	-	0.157 ± 0.927	-0.33 ± 0.54	0.418 ± 0.072	-

FIGURES

Figure 1. Study area extent and plot design. (a) Representative aerial images of the study design, with our 25 plots spanning a woody cover gradient of grass plots (< 33% cover), mixed grass and tree plots (33-66% cover), and woody plots (>66% cover). (b) Larger extent of the Northern Great Plains (light gray) and Montana (darker gray). (c) Our study unit, as designated by the Bureau of Land Management, which is part of a larger Rx fire study experiment in the area.

Figure 2. Bivariate relationships between percent woody cover and (a) bulk density (units: g/cm³), (b) pH, (c) phosphate concentrations, (d) percent soil moisture, (e) percent sand, (f) percent clay, (g) topographic position index (TPI), (h) cosine of aspect, or Northness, and (i) sine of aspect, or Eastness. Statistical significance follows the schema (***) = $p < 0.001$, (**) = $p < 0.01$, (*) = $p < 0.05$, and (·) = $p < 0.1$.

Figure 3. (a) Individual biomass changes (kg yr⁻¹) between 1800 and 2013 determined from dendrochronology measurements scaled up to biomass using allometry. The red line is a second-degree loess smoother with a span of 0.25. (b) Ecosystem biomass changes scaled up from the individual changes, with estimated Juniper biomass incorporated and the same parameterized loess smoother. A breakpoint was found just before the beginning of the study period (shaded red) in 1941, indicating an acceleration since then. The average ecosystem biomass change during the study period was $1.6 \pm 1.4 \text{ Mg ha}^{-1} \text{ yr}^{-1}$.

Figure 4. Tree cover change across 60 years in the study derived from historical and contemporary aerial photography. (a) Percent tree cover from 1953 and (b) 2013. (c) The change between the two in units that match our woody cover classification schema.

Figure 5. (a-c) Raw observed fits between elemental concentrations for carbon, nitrogen, and phosphorus across a gradient of woody cover. (d-f) Observed elemental pools across the same gradient. (g-i) Topoedaphically corrected relationships between woody cover and the elemental concentrations and (j-l) pools. Background boxplots represent the woody cover classification schema.

Figure 6. (a) Biomass C, N, and P accumulation simulated through time with the study period in the grey box. (b) Biomass and soil N change rates. Soil N change rate derived from slope coefficients visualized in Figure 5k. Rates are binned by woody cover classification, and the grey bar behind represents the ecosystem average with dashed 95% confidence intervals.

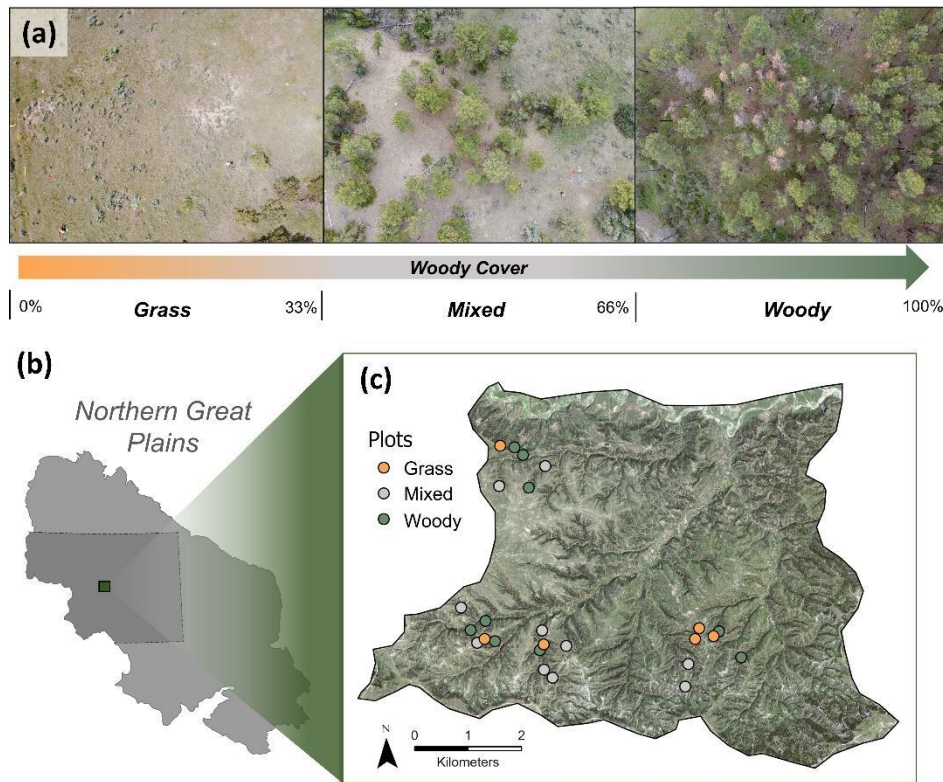


Figure 1.

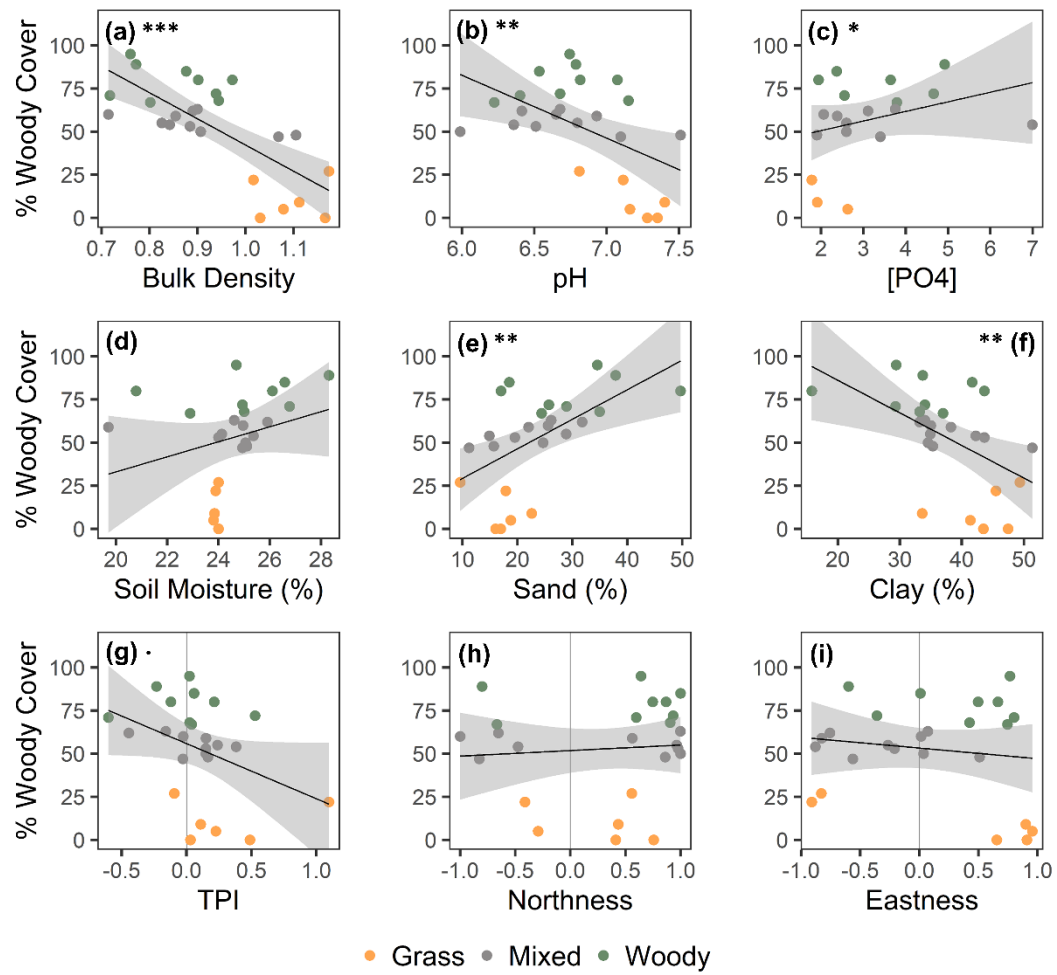


Figure 2.

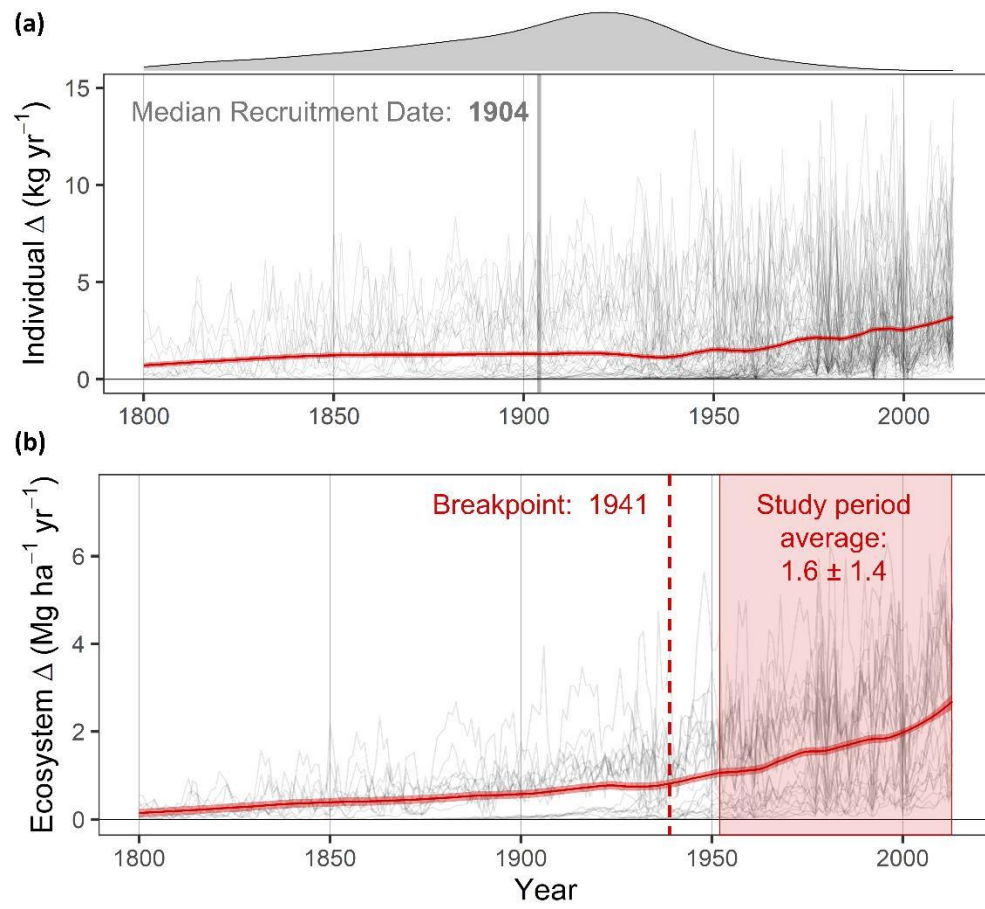


Figure 3.

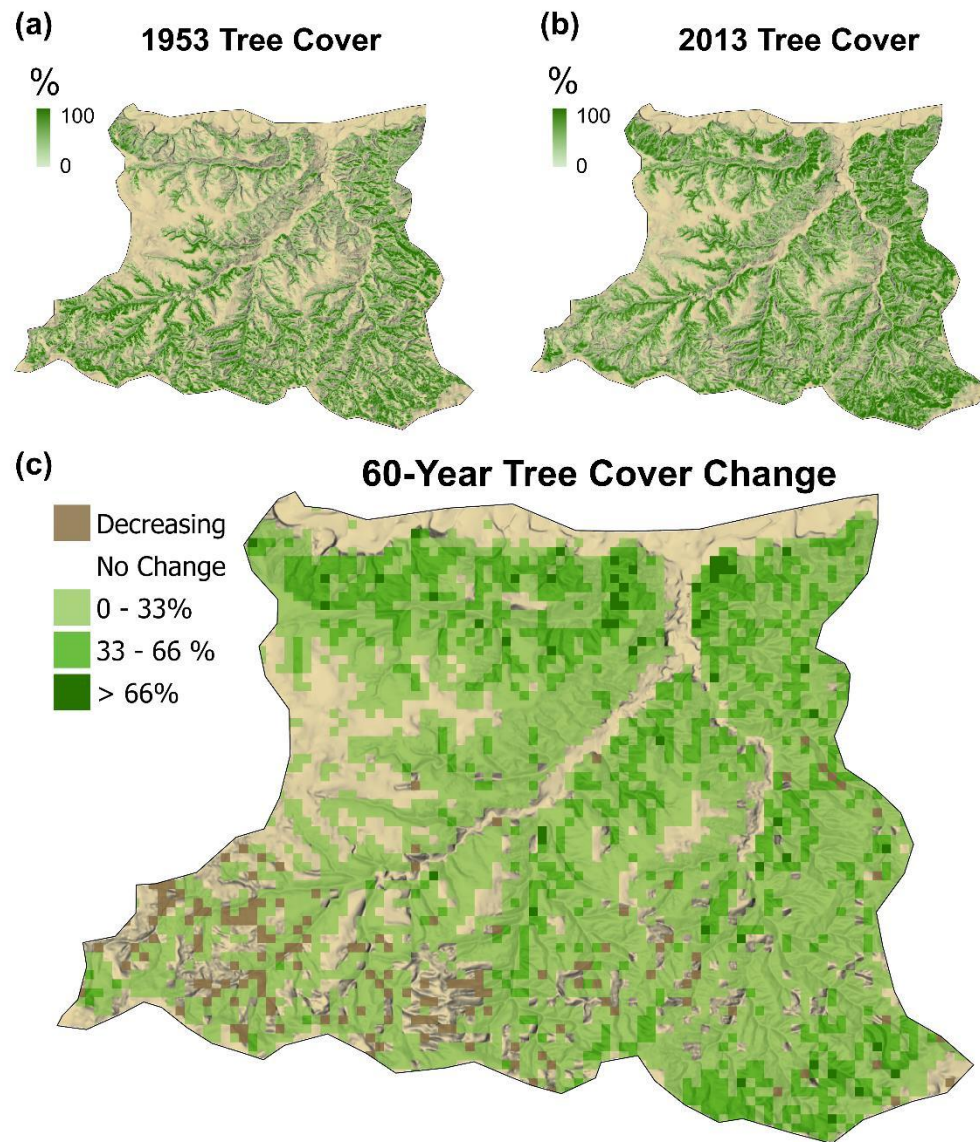


Figure 4.

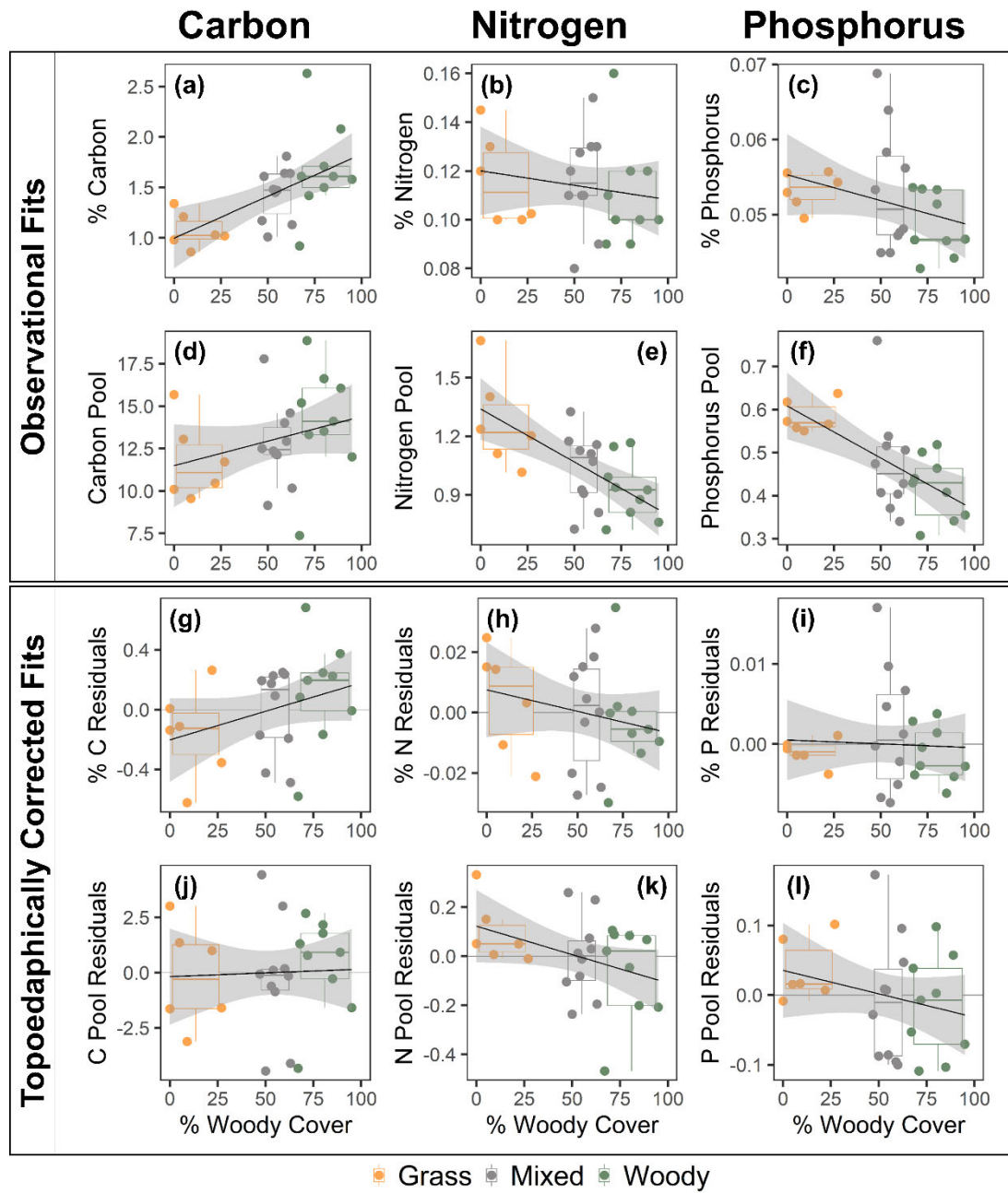


Figure 5.

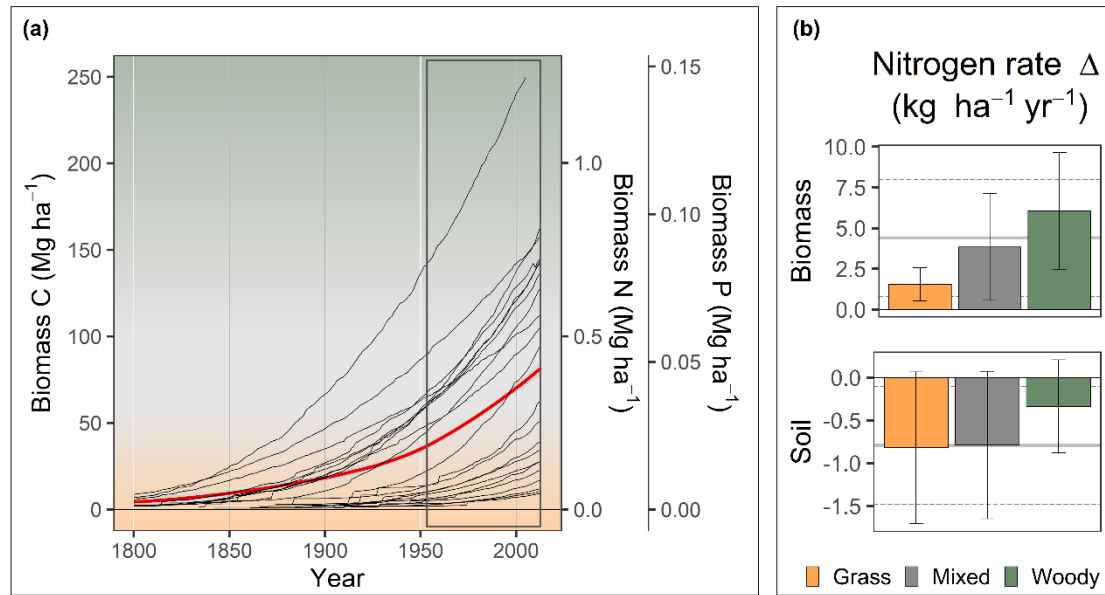


Figure 6.

APPENDIX S1

Allometric Scaling

Ponderosa pine allometry

Allometries obtained from Tinker et al using the following relationships:

$$Total\ biomass = 0.029 \cdot (H \cdot BA) + 14.365 + error \quad (1)$$

$$Needle\ biomass = 0.052 \cdot BA^{0.982} + error \quad (2)$$

Where H and BA are tree height and basal area, and $error$ was simulated following a normal distribution with the mean and standard error calculated from the original estimates.

To estimate biomass (equation S1 and S2) through time from dendrochronology measurements, we fit an saturation curve as a function of measured basal area and height.

$$H = \frac{ymax \cdot BA}{xhalf + BA} \quad (3)$$

Where $ymax$ followed a normal distribution $N(16.01, 0.34)$ and $xhalf$ followed the distribution $N(242.09, 13.08)$.

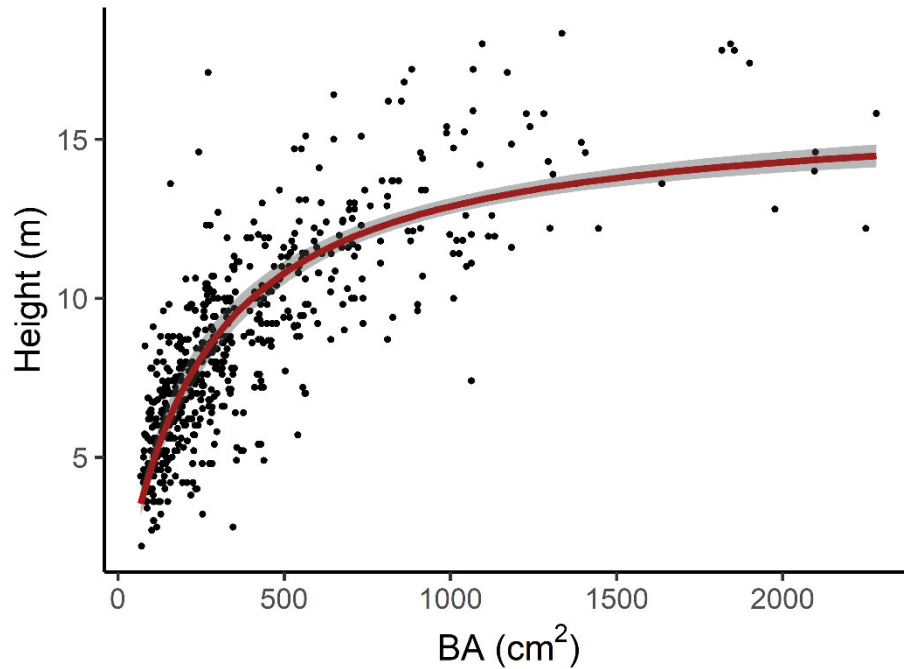


Figure S1. *In-situ* derived relationship between BA and Height for *P. ponderosa* seen in Equation S3 and used in the simulation of biomass through time using ponderosa allometry (e.g., Equation S1 and S2)

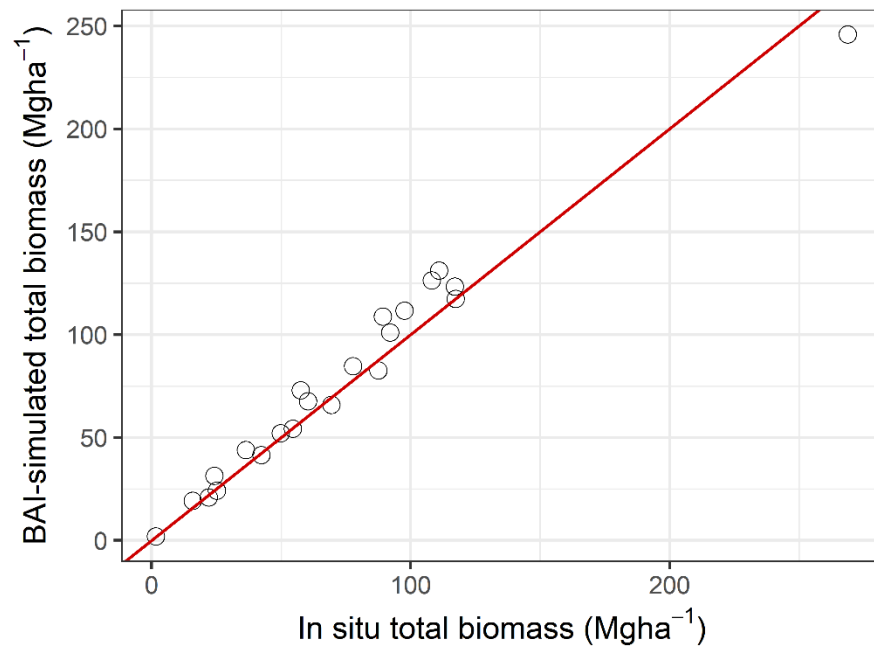


Figure S2. Comparison between simulated biomass using dendrochronology (BAI-simulated) and allometry (Equations S1 and S2), scaled to the plot level.

*Juniper biomass*Table S1. Table of allometric models used to calculate *Juniperus* spp. aboveground biomass.

Equation	Species	Source
EQ	<i>J. monosperma</i>	(Cunliffe et al. 2020)
EQ	<i>J. osteosperma</i>	(Miller et al. 1981)
EQ	<i>J. pinchotii</i>	(Ansley et al. 2012)
EQ	<i>J. occidentalis</i>	(Sabin 2008)

Table S2. There are no known genus-level allometric equations for belowground juniper biomass. Thus, we simulated belowground biomass using known belowground:aboveground ratios from 3 other published studies. These ratios ranged from 0.18 to 0.43, from which we calculated an weighted average which increased the weight based upon how many trees the BGB:ABG ratios were derived from. Our final BGB:ABG ratio came out to be 0.33 +/- 0.08.

BGB:ABG ratio	species	n	Precip (mm)	Temp (C)	source
0.29 +/- 0.04	<i>J. thurifera</i>	21	450	13	Garcia Morote et al. 2012
0.43 +/- 0.05	<i>J. thurifera</i>	21	450	13	Garcia Morote et al. 2012
0.25-0.26	<i>J. virginiana</i>	12	835	13	Norris et al., 2001
0.18	<i>J. excelsa</i>	1	800	19	Evrendilek et al 2006

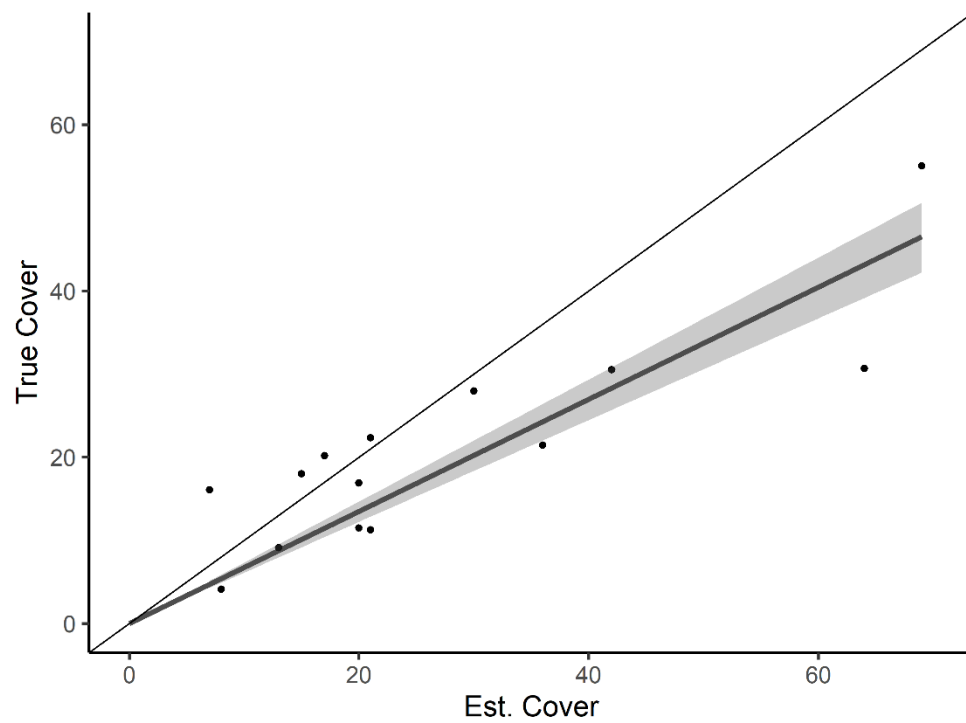


Figure S3. Estimated cover using ocular estimates vs. true cover using canopy cover allometry of the same individual juniper trees, used to correct other ocularly-estimated plots.

APPENDIX S2

Aerial Imagery analysis

Table S1. Ancillary data used to predict percent tree cover from the aerial images during the supervised classification.

1953 Model	Source	2013 Model	Source
1953 Image	USGS Archive	Red band	NAIP
Mean GLCM	Calculated	Blue band	NAIP
Variance GLCM	Calculated	Green band	NAIP
Homogeneity GLCM	Calculated	IR band	NAIP
Contrast GLCM	Calculated	NDVI	Calculated
Dissimilarity GLCM	Calculated	DEM	NASA SRTM (30m)
DEM	NASA SRTM (30m)	TPI	Calculated
TPI	Calculated	Roughness	Calculated
Roughness	Calculated	Eastness	Calculated
Eastness	Calculated	Northness	Calculated
Northness	Calculated	Slope	Calculated
Slope	Calculated	Available water storage 25cm	NRCS SSURGO
Available water storage 25cm	NRCS SSURGO	Available water storage 25cm	NRCS SSURGO
Available water storage 25cm	NRCS SSURGO	Soil order	NRCS SSURGO
Soil order	NRCS SSURGO	Percent clay	NRCS SSURGO
Percent clay	NRCS SSURGO	Percent sand	NRCS SSURGO
Percent sand	NRCS SSURGO		

Table S2. Matthew's correlation coefficients from all supervised classification models.

1953 supervised classification			2013 supervised classification		
Model	MCC	Probability threshold	Model	MCC	Probability threshold
Neural Network	0.722		Neural Network	0.764	
Random Forest	0.766		Random Forest	0.776	
Gradient Boosted Machine	0.758		Gradient Boosted Machine	0.789	
Generalized Linear Model	0.760		Generalized Linear Model	0.796	
Naïve Bayse	0.722		Naïve Bayse	0.768	
Ensemble	0.754	0.358	Ensemble	0.798	0.322

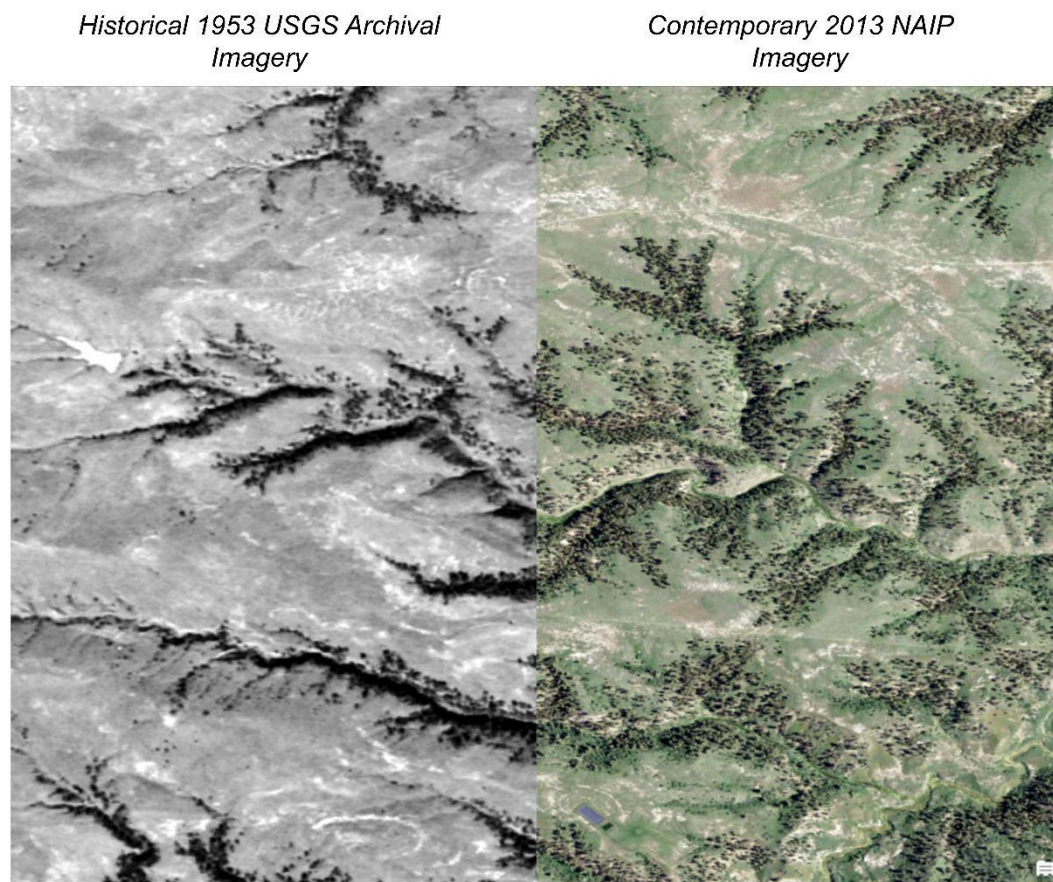


Figure S1. Example georeferenced comparison between 1953 and 2013 images.

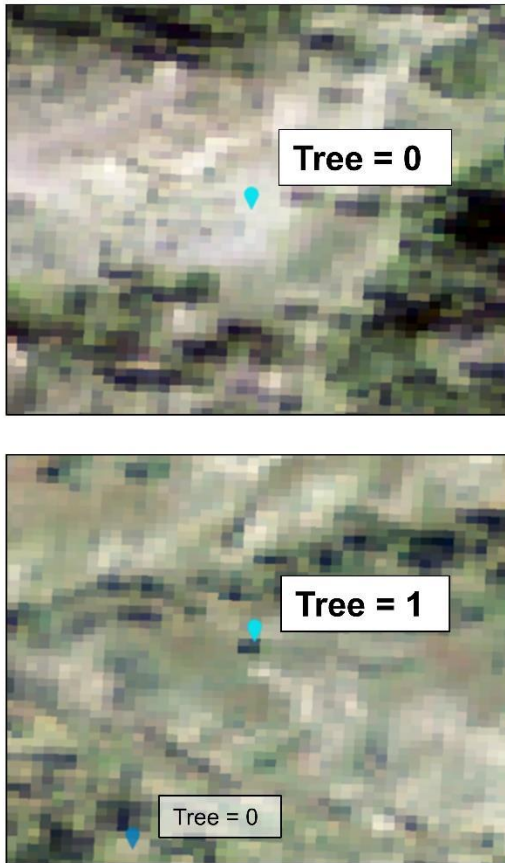


Figure S2. Example of a classified pixel.

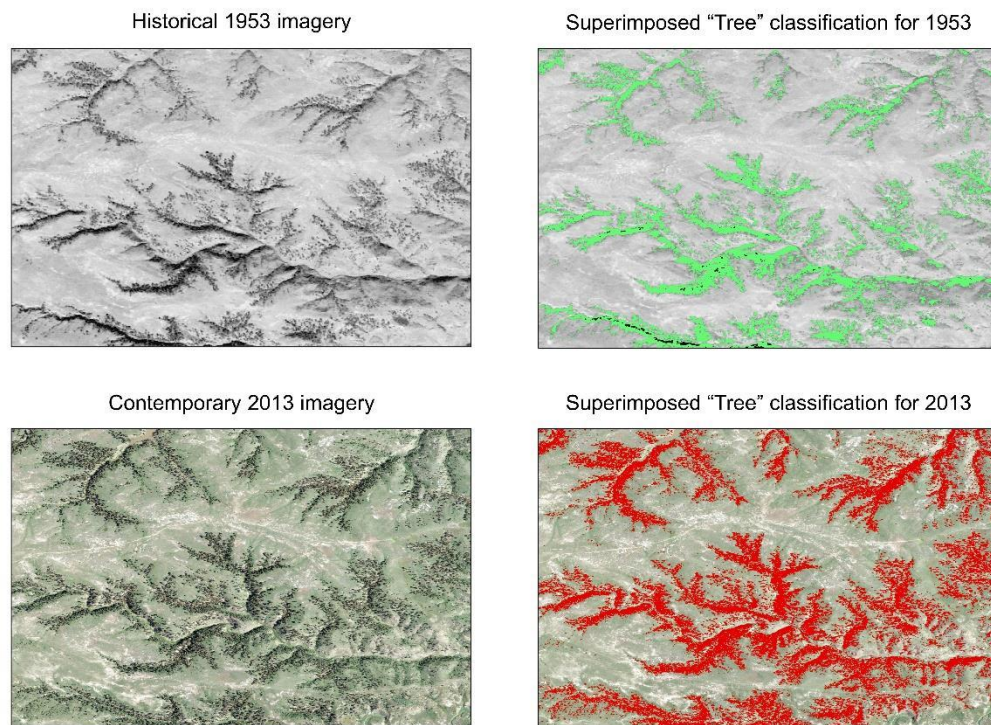


Figure S3. Tree classification for 1953 (green) and 2013 (red).

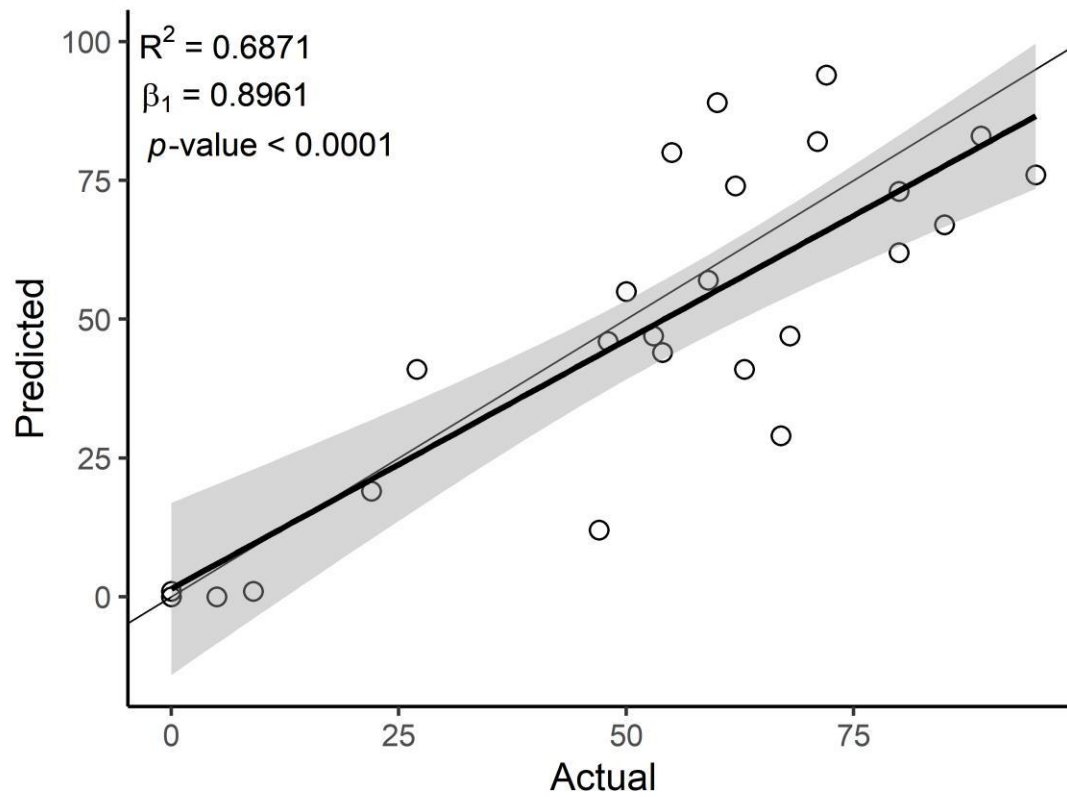


Figure S4. 2013 *in-situ* woody cover for 2013 versus predicted, remotely sensed tree cover as derived via the classification analysis.

APPENDIX S3

Topoedaphic corrections

The initial soil models for total C, N, and P pools and concentrations before being run refined using stepwise AICc selection using the *dredge* function from the *MuMIn* package in R as discussed in equation 2 in the main text. Coefficients in Table S2.

$$\text{soil CNP} \sim \text{TPI} + \text{clay} + \text{sand} + \text{eastness} + \text{northness} + \text{soil moisture} + \text{woody cover} \quad (1)$$

Where *soil CNP* is either total C, total N, or total P in Mg ha⁻¹ or C, N, or P concentration in %, *TPI* is topographic position index, *clay* and *sand* are in units of percent, *northness* is the cosine of aspect (calculated in radians), *eastness* is the sine of aspect, and *woody cover* is percent woody cover (from 0 to 100%).

Table S1. Uncorrected versus corrected model coefficients from equation 2 in the main text.

Response variable	Uncorrected models			Topoedaphically-corrected models		
	Coefficient	p-value	R ²	Coefficient	p-value	R ²
Soil C pool	0.029	0.159	0.08	0.013	0.502	0.02
Soil N pool	-0.005	<0.001	0.44	-0.003	0.055	0.15
Soil P pool	-0.002	<0.001	0.39	-8.78x10 ⁻⁴	0.142	0.09
Soil %C	0.008	0.002	0.34	0.001	0.576	0.01
Soil %N	1.18x10 ⁻³	0.432	0.03	2.20x10 ⁻⁴	0.107	0.11
Soil %P	-6.71x10 ⁻⁵	0.146	0.09	-1.80x10 ⁻⁵	0.628	0.01

Table S2. The resulting models and the coefficients after the stepwise AICc selection.

Response variable	Predictor 1	Coefficient	P-value	Predictor 2	Coefficient	P-value	R ²
Soil C pool	TPI	-3.646	0.030				0.19
Soil N pool	% Clay	0.019	0.002	Eastness	0.137	0.039	0.38
Soil P pool	% Sand	-0.006	0.003	TPI	0.092	0.099	0.43
Soil %C	% Sand	0.024	0.001	Soil Moisture	13.367	0.001	0.50
Soil %N	TPI	-0.023	0.065				0.14
Soil %P	% Sand	-2.91x10 ⁻³	0.011	Roughness	8.31x10 ⁻³	0.036	0.38

CHAPTER FOUR

ASSESSING POTENTIAL TRADEOFFS OF CLIMATE
CHANGE MITIGATION IN OPEN ECOSYSTEMSIntroduction

Grasslands, shrublands, and savannas (hereafter open ecosystems; i.e., non-forest ecosystems, box 1) play an important role in carbon sequestration and climate change mitigation (Poulter et al., 2014; Chang et al., 2021). Open ecosystems provide ecological and cultural services such as water regulation, erosion control, pollination, and cultural connections (Bengtsson et al., 2019). Furthermore, open ecosystems can harbor high rates of diversity and many are considered biodiversity hotspots (Mittermeier et al., 2011; Nogueira et al., 2011).

Box 1. Open ecosystems: We regard the matrix of ecosystems across the NGP as a temperate *open ecosystem* to attempt to continue momentum surrounding the use of the term coined in Bond, 2022. Open ecosystems are ecosystems in which the vegetation and the climate-defined potential vegetation differ. For instance, the Northern Great Plains has a climate-defined potential to be much woodier, like the boreal forests just to the North, and with other deciduous trees in the more southern reaches of the NGP. Why then is the ecoregion a grassland? Largely due to other disturbances such as grazing, fire, and climate extremes. Since open ecosystems are not in equilibrium with the climate by definition, there is a large potential for rapid change in these ecosystems.

Despite their ecological and cultural importance, open ecosystems are considered one of the most imperiled ecosystems on the planet, largely due to the ease of conversion to agricultural use (Hoekstra et al., 2005; Green et al., 2005; Dinerstein et al., 2017; Scholtz & Twidwell, 2022). For instance, 99% of North America's productive tall-grass prairie has been lost to agriculture (Dinerstein et al., 2017). Simultaneously, many remaining open ecosystems are undergoing

woody plant expansion (WPE; Deng et al., 2021), which has the potential to greatly alter the structure, biophysics, biogeochemical cycling, and overall function of these ecosystems (Archer et al., 2017). These changes have fragmented most of the last remaining open ecosystems into small remnants that are vulnerable to climate variability and further degradation from land use (Carbutt et al., 2017; Malhi et al., 2020; Scholtz & Twidwell, 2022).

Open ecosystems have been shown to be potential important systems for mitigating climate change as carbon sinks. Initiatives, such as the Bonn Challenge, the Atlas of Forest Restoration Opportunities, the Great Green Wall of Africa, and others, aim to promote carbon sequestration by planting trees in these ecosystems. Often placed under the umbrella of natural climate solutions (NCS), these tree-based solutions have immense potential to sequester large amounts of atmospheric carbon (Griscom et al., 2017; Cook-Patton et al., 2020b). However, these initiatives also have the potential to significantly degrade open ecosystems when poorly implemented (Veldman et al., 2015; Bond, 2016).

This article aims to build upon the discussion regarding an improved understanding of open ecosystems and their multi-objective management, including both production and conservation objectives. We believe that a framework in which management decisions optimize biodiversity and carbon storage is necessary to inform the management of open ecosystems. Improving the understanding of the trade-offs between competing management interests, when grounded in objective science, will allow these ecosystems to persist as part of a social-ecological system.

As a case study, we highlight the Northern Great Plains of North America as it is one of the least protected (Dinerstein et al., 2017; Carbutt et al., 2017) yet relatively intact (Scholtz &

Twidwell, 2022) open ecosystems remaining globally. The NGP ecoregion spans 744,000 km² and contains one of only four remaining, relatively intact temperate grasslands (58% grassland, Olson & Dinerstein, 2002), in addition to swaths of wooded areas (3%) and sagebrush steppe (8%). A large reason for the relatively intact nature of the ecoregion is its incredibly low population density (~2 persons km⁻² in 2020; CIESIN, 2018). Another is the climate; the NGP is semi-arid and relatively cool, with a mean annual precipitation around ~450 mm and a mean annual temperature around 6.5°C, leading to lower economic value. Furthermore, novel, large, and often private conservation efforts have been initiated throughout the region (Schrag & Forrest, 2012; Epstein et al., 2021). As such, the potential for mismanagement is great.

While many large ecological changes are occurring within these ecosystems, we restrict this examination to two significant transformations: increasing agricultural extent and increasing woody plant cover (Figure 1). We examine the current state of ecological change and how it impacts biodiversity and carbon sequestration. Where we can, we use accessible data to inform our case study of the NGP.

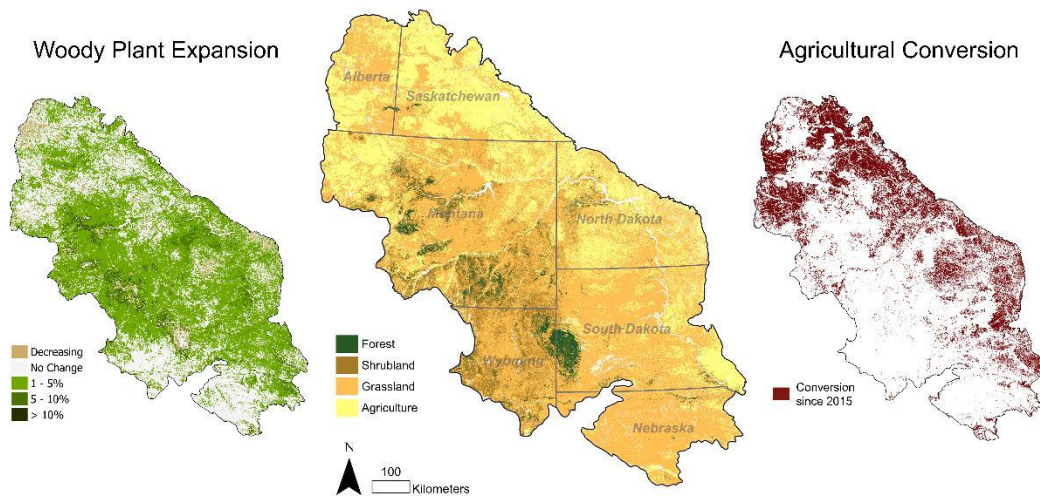


Figure 1. Landcover and the competing large-scale changes across the Northern Great Plains. Landcover data is from ESA CCI landcover product. Data from the woody plant expansion image is from a Sens-slope analysis of NASA's MODIS MOD44B woody cover from 2000–2019. Data from agricultural conversion is from WWF (2021).

Ecosystem Changes

Agricultural Expansion

The conversion of land for crop production is responsible for catastrophic biodiversity losses (IPCC, In Press) and has been identified as the single biggest hazard to bird species listed as threatened (Green et al., 2005). In large part, this is due to habitat fragmentation, or the division of the ecosystem into progressively smaller remnants that follows agricultural conversion (Haddad et al., 2015; Scholtz & Twidwell, 2022). Though maintenance of landscape heterogeneity within agroecosystems can sustain high levels of biodiversity at the local scale ((Martin et al., 2020), habitat fragmentation via agricultural conversion has negative implications for biodiversity at the landscape scale (Saura, 2021).

Globally, more than 50% of agriculturally usable natural habitat has been converted to crop production, with much of the rest used for grazing (Green et al., 2005). The US alone has

converted over one million acres of grassland to cropland each year since 2008 (Lark et al., 2020). Indeed, we will need improved agricultural paradigms and novel technologies to be part of the solution (Duff et al., 2022). However, new agriculture is now expanding into more marginal land (e.g., low soil fertility), lowering average crop yields and negatively impacting carbon pools and biodiversity (Tollefson, 2019).

As of 2019, 30% of the NGP ecoregion was used for agricultural production (not including grazing), with roughly half a million acres grasslands converted to agricultural use yearly (WWF, 2021). However, expansion of agriculture into grasslands is spatially limited and in competition with other emerging land uses (e.g., bioenergy production; Stoy et al., 2018), emphasizing the fact that continued agricultural establishment in the NGP will be pushed into increasingly marginal land (Lark et al., 2020).

Woody Plant Expansion

WPE into grasslands and the associated structural and functional consequences have been documented across much of the globe (Deng et al., 2021). WPE is driven by complex feedbacks between long-term warming and altered precipitation, increased nitrogen deposition and atmospheric CO₂ concentrations, and shifts in grazing intensity and fire regimes (Archer et al., 2017; Hempson et al., 2019). However, the relative importance and feedbacks among these drivers are site- and scale-specific. The ecosystem consequences of WPE are also often localized, but typically include decreased herbaceous cover and altered biodiversity (Eldridge et al., 2011). WPE can increase the productivity of the ecosystem (Knapp et al., 2008; Currey et al., 2022), but can lead to increased strains on soil nutrient pools, with downstream effects for long-term nutrient availability (Brookshire et al., 2020). The proliferation of woody plants in grazing

lands typically reduces the production of economically valuable forage grasses (Scholes & Archer, 1997). While this may be economically destructive for some, heavy cattle grazing is detrimental to many grasslands and can even cause intensified WPE (Stevens et al., 2016).

Rates of WPE across North America span $\sim 0.1\text{-}2\%$ cover yr^{-1} (Barger et al., 2011), with the global average falling around 0.3% cover yr^{-1} (Deng et al., 2021). In the NGP, the rate is closer to 0.1% yr^{-1} (Currey et al., 2022), with an average percent tree cover within the region of around 5.7% in 2019 (up from 1.8% in 2000; Figure 1). The lower rate of WPE in the NGP is determined, at least in part, by the cooler and drier climate of the ecoregion, which sets the theoretical limits of tree cover in any ecosystem (Whittaker, 1962; Scholtz et al., 2018). As the globe warms and precipitation patterns change, the climate-derived limitations to tree cover will also change (Figure 2). Using a pixel-based Holt-Winters exponential forecast for all pixels, we estimate that tree cover has the potential to increase to 9.4% by 2050 and 15.8% by 2100, although it must be stressed that the uncertainty surrounding these simple forecasts is large (Figure 3).

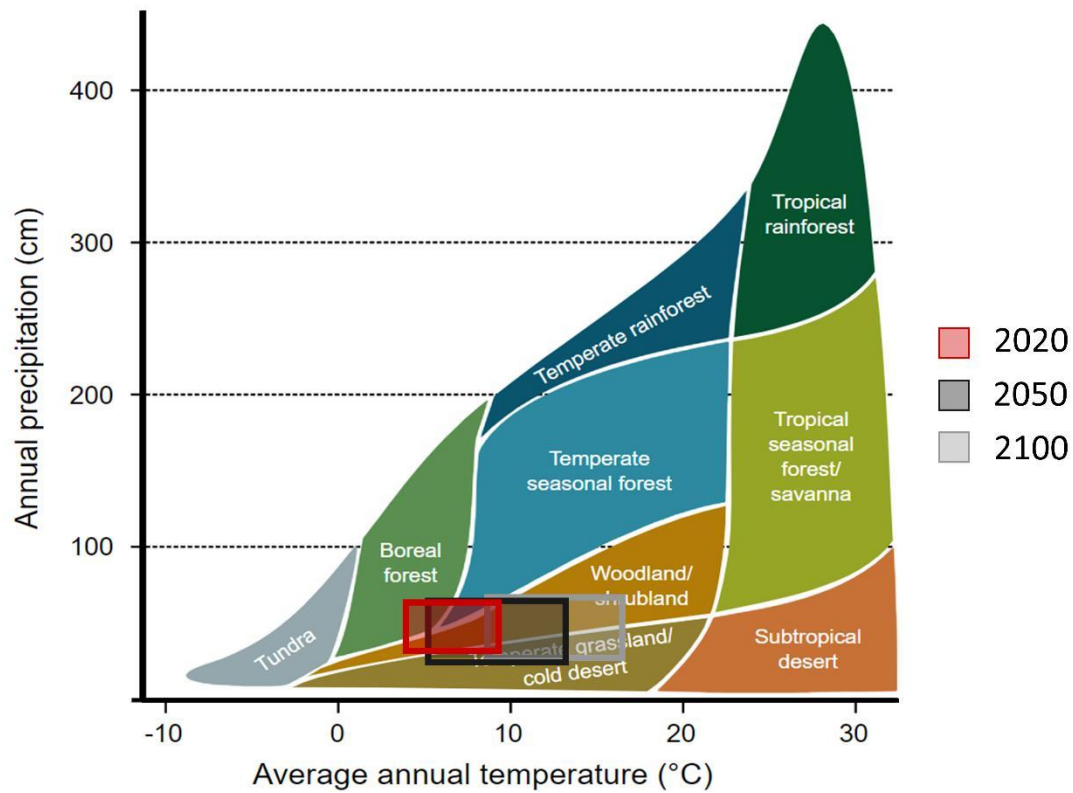


Figure 2. Whittaker diagram. The current climate of the NGP in red, and potential future climate envelopes in 2050 (black) and 2100 (grey). Climate data from the NASA Earth Exchange Downscaled Climate Projection (NEX-DCP30; Thrasher et al., 2013)

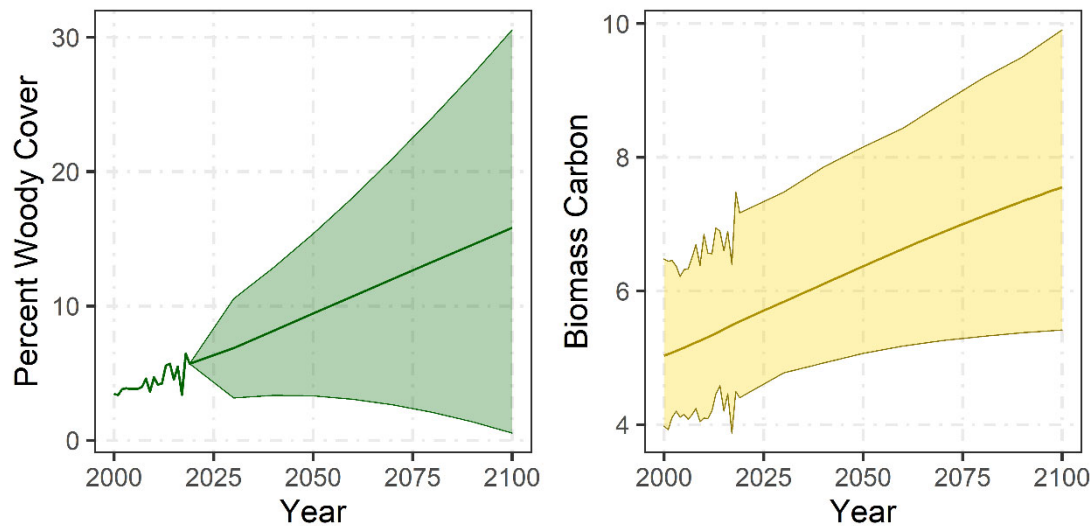


Figure 3. Projected tree cover and derived total biomass carbon estimates across the NGP. Shaded area for percent woody cover represents the 95% confidence interval around the mean. Shaded area for biomass carbon represents the first and third quartile around the median.

How will the Management Decision Impact Biodiversity?

Open ecosystems are losing biodiversity at an unprecedented rate, particularly concerning grasslands and their avifauna. Roughly 75% of grassland-breeding birds are in decline (Rosenberg et al., 2019), many of which may never be demographically viable to return (With et al., 2008). This has cascading implications for the function of key processes important to the stability and productivity of Earth's ecosystems (Hooper et al., 2012) and has negative consequences for the persistence of human existence (Cardinale et al., 2012). Biodiversity can induce biome stability via functional complementarity as different species survive given different conditions (MacDougall et al., 2013). Through similar mechanisms, biodiversity can also increase productivity (Tilman, 1996), leading to higher carbon sequestration (Yang et al., 2019).

Declines in grassland biodiversity has been attributed to WPE across the globe, particularly when woody cover has increased beyond one-third of the total percent cover

(Wieczorkowski & Lehmann 2022). For instance, *Juniperus virginiana* in the Central Plains can expand into grasslands at upwards of 6% per year, causing drastic declines in species richness (Briggs et al., 2002). Although, in some regions, this is not the case (Eldridge et al., 2011). For instance, where WPE is driven largely by the decline of human activity (e.g., pastoral activities), there have been increases in species richness (Maestre et al., 2009). Moderate WPE has even been shown to increase local avifauna diversity due to the recruitment of generalist species, although at the cost of some grassland-obligate species (Andersen & Steidl, 2019). Given the positive relationship between ecosystem structure and diversity in other biomes (Verschuyl et al., 2008), it is feasible that progression from grassland to a more heterogeneous savanna-type ecosystem could lead to increased diversity. The drivers, intensity, and regional history causing WPE likely determine the relationship between biodiversity and WPE in a context-specific manner.

Many open ecosystems across the globe are biodiversity hotspots and home to thousands of endemic species, such as the savannas of the Southeastern US (Noss et al., 2015), South Africa (Bond & Parr, 2010), and Brazil (Nogueira et al., 2011). Though many of these biodiversity hotspots have large sequestration potential, protecting biodiversity in these biodiversity hotspots likely outweighs their carbon sequestration potential due to high levels of endemism (Cook-Patton et al., 2020a). Comparatively, while the NGP is home to a relatively rich number of species, most of these are not endemic to the region (Forrest et al., 2004), largely due to the glacial history of the NGP (Wells, 1970). As such, unilaterally managing for biodiversity may come at the expense of other ecological and cultural benefits provided in a less biodiverse region.

How will the Management or Conservation Decision Impact Carbon Sequestration?

Human activities, such as the combustion of fossil fuels and land-use changes, have led to the addition of massive quantities of carbon to the atmosphere (IPCC, In Press). Tree-based NCSs have the largest potential to mitigate large climatic changes due to their large carbon sequestration potential (Griscom et al., 2017; Cook-Patton et al., 2020b). Implementation of these large-scale tree planting efforts has led to a range of controversy. Most controversial are calls to initiate tree plantings in any ecosystem absent of trees which can accomplish sequestration goals, but be problematic for conservation of native biodiversity (Nuñez et al., 2021). Conversely, efforts to allow or aid the regrowth of degraded forests is a useful objective. The middle ground is more uncertain.

The topic of carbon sequestration is the most numerically straightforward regarding the trade-off between agricultural conversion and woody expansion. Soil organic carbon (SOC) in the NGP is relatively low ($37.7 \text{ Mg carbon ha}^{-1}$; global average = $59.8 \text{ Mg carbon ha}^{-1}$; FAO); however, given the massive extent and relatively low land use across the NGP, the SOC pool is quite large ($\sim 2.7 \text{ Pg of carbon}$). Evidence of whether WPE has significant impacts on this pool is equivocal (Eldridge et al., 2011), although a study from within the heart of the NGP found no change in total soil carbon after more than 60 years of WPE (Currey et al., in prep.).

What is certain is that WPE increases carbon sequestered in biomass. The best biomass carbon data to date is from Spawn et al. (2020), which estimates both aboveground and belowground biomass carbon globally for 2010 at high resolution. Here we used a simple random forest model to examine the relationship between NASA's MODIS MOD44B V6

percent tree cover product, ESA CCI land cover data, and the biomass carbon data set. We then applied this relationship to a simple Holt-Winters percent tree cover forecast while holding the landcover constant at 2019 estimates (Figure 3). Based on this simple forecast of WPE-driven carbon changes, we estimate that 2.4 Tg yr⁻¹ (0.032 Mg carbon ha⁻¹ yr⁻¹) of carbon could potentially be sequestered each year by 2050 and 1.7 Tg carbon yr⁻¹ afterward until 2100 (0.024 Mg carbon ha⁻¹ yr⁻¹; Figure 3). Compared with other tree-based NCSs estimated to sequester between ~3.2-3.6 Mg carbon ha⁻¹ yr⁻¹ globally and ~1.3 Mg carbon ha⁻¹ in the US, these estimates from the NGP are relatively low (Griscom et al., 2017), although WPE requires no labor or financial inputs.

Open ecosystem conversion to agriculture often decreases carbon sequestered in soils and can remove the potential for carbon sequestration in woody biomass via tree planting NCSs or WPE. For instance, ~30% of carbon stocks are lost, upwards of 34 Mg carbon ha⁻¹, from the initial tilling of grasslands (Sanderman et al., 2017; Fargione et al., 2018). Conversely, through the adoption of sustainable agricultural methods, especially in perennial agroecosystems, croplands can sequester carbon from the atmosphere (Grandy & Robertson 2007), especially in soils previously disturbed, as soils farthest from carbon saturation have the highest potential of sequestration (Stewart et al., 2007). Similarly, improvements in agricultural systems through multiscale diversification strategies (e.g., agroforestry) offer the potential to mitigate climate risk by increasing carbon stocks and reducing emissions (Kirby & Potvin, 2007; Jose, 2009).

In the NGP, one study estimated that converting grassland to agriculture would release ~14 Mg carbon ha⁻¹ on average (Ahlering et al., 2016). Given that 234,700 ha yr⁻¹ of grassland is lost each year to conversion in the NGP (WWF, 2021), that is equivalent to roughly 3.3 Tg SOC

lost annually to tilling native grassland. Preventing these losses while also allowing tree cover expansion equates to a potential upper threshold of between 5 and 6 Tg of carbon saved each year (3.3 from not plowing grasslands and ~2 from woody biomass increase).

The role of carbon sequestration in management goals is potentially the most contentious. Many uncertainties remain regarding carbon permanence in soil in both natural grasslands and agriculture, and the verification methods used to validate sequestration goals are often inconsistent (Oldfield et al., 2022). Moreover, concern remains that trees and forests are reliable long-term carbon stores since climate change mitigation goals can be negated through carbon losses during disturbance (e.g., fires and beetle outbreaks; McKinley et al., 2011). Nonetheless, tree-based NCSs can provide the most benefit per dollar spent (Griscom et al., 2017) but may come at the cost of biodiversity loss and other values that lack a consistent method of quantification. Open ecosystems, such as the grasslands in the NGP, may not provide the most rapid carbon sequestration for climate change mitigation. However, they currently hold large stores of soil carbon that should receive high conservation priority.

Conclusion

It is time to reevaluate how management and conservation are conducted given the large and unprecedented climatic shifts and decline in biodiversity that are unequivocally human-driven (Tollefson, 2019; IPCC, In Press). This is particularly true concerning open ecosystems. The reevaluation of these open ecosystems should be local due to context-specific drivers, yet the overarching emphasis on multi-objective management strategies should be a global conversation. This may include the restoration of grasslands that have been heavily grazed, the

reduction of invasive trees expanding into grasslands, allowing native tree expansion in grasslands, the restoration of agricultural fields to grasslands or savanna, or the expansion of certain types of sustainable agriculture.

Our aim here is to build off the “protect, manage, and then restore” mentality proposed by Cook-Patton et al. (2021). Given the inherent dynamism and current transitions of many open ecosystems globally, neither protection nor restoration may be the correct direction. Furthermore, we argue that “managing” in the sense of maintaining a historical ecosystem state may also be incorrect. Instead, management should optimize for both biodiversity and carbon sequestration given future trajectories of the ecosystem. This starts by asking the question: How will the management decision impact biodiversity versus carbon sequestration and storage? While we do not claim to provide a universal formula here, we argue that too much attention and management prescription are unilaterally placed on the answers to either biodiversity or carbon. Critically, management will likely not be as simple when considering multiple conservation priorities simultaneously. For instance, biodiversity may slightly decline at the expense of large carbon sequestration, at which point carbon may be the intended target for preservation. Conversely, if changes in carbon sequestration potential are minimal, or the region is a biodiversity hotspot, biodiversity should be the target of action.

Maximizing both biodiversity and carbon storage is the ultimate target, yet often focusing on one of these aspects comes at the expense of another. One potential solution towards preserving these ecosystems is an idea recently proposed by Loisel and Walenta (2022) in which the NGP and other open ecosystems (or any ecosystem for that matter) become “Carbon Parks.” Loisel and Walenta explain that these parks would not necessarily be designated as protected

areas, rather they would be more broadly recognized as important to carbon stores and potentially offer them special conservation consideration and protection. They liken the idea to the “dark sky” designation across large areas of the western US. This designation would also likely have cascading benefits to the ecosystem's resilience, depending on how the policy was developed.

We find that the NGP has high biodiversity, although it has few endemic species. Agricultural expansion likely negatively impacts the biodiversity of this system, yet how WPE influences biodiversity is unknown. Both remain largely unquantified. Similarly, agricultural expansion is detrimental to carbon sequestration in the NGP, yet the slow spread of trees across the region does not provide strong sequestration potential either. As such, while WPE is a large perceived threat in the NGP, and indeed may be to many local stakeholders, a high-level cursory examination suggests that WPE in the NGP has potentially neutral impacts, particularly when weighed against agricultural expansion. Examining how WPE impacts diversity in the region and testing alternative stable state theory within the NGP is a useful starting point toward better understanding the ecoregion.

The IPCC 6th assessment states that the improvement and sustainable implementation of management and/or conservation of natural ecosystems can deliver large-scale greenhouse gas reductions (IPCC, In Press). Furthermore, realizing this potential “entails overcoming institutional, economic and policy constraints and managing potential trade-offs” (IPCC In Press; p44). Here, we highlight that these "potential trade-offs" are largely unquantified globally but should be weighed carefully before management or conservation decision-making occurs.

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CHAPTER FIVE

SYNTHESIS

“The Northern Great Plains in many ways represents North America’s grassland future.”
(Schrug and Forrest, 2009)

The Northern Great Plains (NGP) has the promise to represent the future of North American grasslands (Schrug & Forrest, 2012). With over 60% of the 744,000 km² representing relatively intact grass and shrublands (Scholtz & Twidwell, 2022), it offers incredible capacity to harbor one of the largest temperate grasslands left on the planet (Olson & Dinerstein, 2002). Furthermore, the NGP has relatively high biodiversity (Forrest et al., 2004) and provides numerous ecosystem services at multiple scales (MacDougall et al., 2013). Indeed, recent and large conservation efforts have initiated a movement towards private conservation of these lands (Epstein et al., 2021). However, as documented within the chapters of this dissertation, North America’s grassland future remains highly uncertain.

Here, we have presented a multi-scalar examination of the causes and consequences of woody plant expansion (WPE) in the Northern Great Plains (NGP). We examined the drivers and interactions of WPE and the recent increase in vegetative productivity using satellite-based remote sensing. These estimates were then benchmarked with estimates derived from high-resolution aerial imagery and paired with established permanent sampling plots in the heart of the NGP. This allowed us to examine the impact that WPE has on ecosystem biogeochemistry, specifically concerning ecosystem carbon (C), nitrogen (N), and phosphorus (P). Finally, we compared and examined WPE against another large transition occurring throughout the NGP:

agricultural expansion. We proposed that future work examining large-scale changes and the subsequent management of open ecosystems (i.e., non-forested ecosystems) like the NGP be reframed towards weighing the impacts of agricultural expansion and WPE, and their reversal via management efforts, on biodiversity, carbon storage, and ecosystem resilience.

Part of the importance of this dissertation is its regional contribution to the growing literature surrounding this important temperate grassland. The NGP remains understudied relative to other grasslands, both globally and across North America. For instance, a meta-analysis of WPE across Western North America, which included the Central Great Plains, omitted the NGP, likely due to lack of measurement (Barger et al., 2011). Similarly, before the publication of “Large Contribution of Woody Plant Expansion to Recent Vegetative Greening of the Northern Great Plains” (Currey et al., 2022), comprehensive documentation of the NGP was relegated to the realm of anecdote (Symstad & Leis 2017). That being said, it would be an oversight if we did not acknowledge some of the great mid-20th century work examining vegetation and history of the NGP, such as Phillips and Shantz (1963) and Wells (1965, 1970). Yet, to this day, much of the ecological changes that have been studied in other open ecosystems are undocumented or unknown within this large ecoregion. This dissertation attempts to answer some of these regional unknowns while contributing to the broader understanding of the ecological implications of large vegetation changes occurring within open ecosystems across the globe.

Within this dissertation, we find the occurrence of large WPE across the NGP since the turn of the millennium, with some areas likely having undergone WPE for decades or centuries. We note that WPE rates in the NGP, ranging between ~0.1 and 0.2% cover per year, are slower

relative to other open ecosystems globally (Deng et al., 2021), and average tree cover across the NGP remains less than 5% cover on average. Tree cover and these lower WPE rates across the NGP are largely determined by the harsh and semi-arid climate of the NGP, which imposes a theoretical maximum on the woody-cover potential. Nevertheless, as documented in Chapter Two, the climate across the NGP is changing, increasing the potential of future abundance of tree cover relative to the amount currently observed (Scholtz et al., 2018).

Previous work in the region has noted that these productivity changes are partly driven by the large and recent increase in atmospheric CO₂ (Brookshire et al., 2020). Increased vegetative productivity has large ecosystem consequences, including cascading impacts for herbivory, potential biophysical changes, and large implications for ecosystem biogeochemistry. Declining N isotope concentrations in plant tissues due to increased productivity suggests large and consistent decreases in N availability, the principal molecule of photosynthesis, since the mid-20th century. This research implicates the potential for a bottleneck on continued productivity and the capacity for C sequestration (Chen et al., 2019; Brookshire et al., 2020).

Here, we take this analysis further and examine the contribution to greening from species composition changes, i.e., WPE. We find a strong coupling between increasing vegetative productivity and WPE. Relative to other climate, disturbance, and topographic factors, WPE has had a disproportionately large impact on increased vegetative productivity, as measured by both normalized differenced vegetative index (NDVI) and leaf area index (LAI). We find that WPE across this large temperate grassland has increased the ecosystem's capacity to sequester atmospheric C in the short-term, though this trend cannot be assumed to continue in the future.

Regarding the future, potential productivity bottleneck highlighted in Brookshire et al.

(2020), we find that increases in tree cover have large implications for the biogeochemistry of the ecoregion. By pairing aerial imagery analysis with state-of-the-art machine learning modeling approaches, we documented the rate and extent of WPE across a 60-year interval (1953–2013) in the heart of the NGP in central Montana. This allowed us to benchmark previous findings from satellite-based estimates with more accurate ground-based measures. Furthermore, we paired these findings with ground-based biomass and biogeochemical measurements from established vegetation monitoring plots. In 2017 we established these plots to document the dendrochronological history, vegetation composition and chemistry, biomass, and soil chemistry through time. By combining the aerial photography analysis with these in-situ measures, using a simple statistical approach, we were able to directly link declines in soil N to WPE across the 60-year period. The large increases in biomass C, N, and P not only reduce the resilience of these elemental pools to future disturbances, but also indicate a potential mechanism for future progressive N limitation.

Notably, we find that rates of WPE are highest where tree cover is between 33% and 66%, likely due to increased seed source with reduced density dependency pressures. Higher WPE rates at moderate tree cover may point toward a potential threshold between 33% and 66% cover in which tree cover has reached an adequate abundance that returning the ecosystem to primarily grass cover becomes infeasible. However, more experimental work is needed to test the potential of this possible threshold.

Much of this dissertation examines the ecological and biogeochemical impacts of WPE on the grasslands of the NGP. However, these grasslands are shrinking annually due to their conversion to agricultural land uses. As noted by the World Wildlife Fund, ~2,350 km² of

grassland is plowed up every year (WWF, 2021). While WPE is a potential hazard to the persistence of grassland habitat and the species that exist within, we find that, with regard to the NGP, agriculture expansion has far more negative implications for biodiversity, carbon sequestration, and the resilience of the ecoregion. As such, management efforts across the NGP should prioritize decreasing the plow-up of grasslands into continually more marginal lands. We note that one possible solution is delineating the NGP as a “Carbon Park,” per Loisel and Walenta (2022), endowing the entire region with conservation and management privileges. We emphasize the decision-to-manage for the state that will be the most resilient to future change and maintain the highest carbon stores and biodiversity due to its ability to respond to perturbations. While this may not be the current ecological state of the ecosystem, the decision to manage for carbon sequestration or biodiversity unilaterally in lieu of resilience must be made very carefully. We highlight that much more work is needed in the NGP and ecologically comparable open ecosystems to understand the impacts of WPE and its removal on biodiversity and ecosystem resilience.

Indeed, this dissertation highlights many uncertainties of the NGP’s past and possible trajectories for its future. First, the historical role of indigenous peoples with regard to the maintenance of the grasslands, particularly regarding maintaining low tree cover, is largely speculative. While it is known that indigenous peoples used fire immensely for many purposes, the degree to which this maintained low tree cover is uncertain. Similarly, the impact of bison on preventing tree cover is largely unquantified. Many other large herbivores across the globe use mechanical means (browsing, stomping, rubbing) to prevent the growth and spread of trees (Asner et al., 2016). Indeed, there are large densities of cattle across the NGP; yet, the impact of

cattle on the ecosystem is ecologically different than bison (Allred et al., 2011) and actually may increase WPE due to heavier grazing practices than is sustainable by the productivity of the land (D’Odorico et al., 2012). As such, whether the precipitous declines of both native peoples and bison catalyzed the phenomenon of WPE remains unknown.

As aforementioned, whether a tipping point exists for an entirely forested NGP is unknown. Resolving this will require employing experimental and theoretical methods of alternative stable states. Importantly, we note that the fastest rates of WPE occur with moderate amounts of tree cover. If a tipping point does exist, it may be within this 33%–66% range, although, for a majority of the grasslands of the NGP, this point is very far off. Simple projections and calculations of future tree cover within this dissertation highlight that the potential for a forested NGP is largely impossible over the 21st century. Indeed, the current climate indicates a maximum threshold for tree cover of less than ~50% (Scholtz et al., 2018). Despite this, some dynamic global vegetation model (DGVM) projections indicate a forested NGP in the future. This discrepancy between what is modeled and reality is likely due to large unknowns mentioned here. Many DGVMs do not resolve historical land use well, nor do these models incorporate grazing or have robust fire mechanisms (Pachzelt et al., 2013; Baudena et al., 2015). Similarly, they largely lack accurate nitrogen cycling, which, as we have noted, may constrain WPE and productivity in the future (Thomas et al., 2015).

This dissertation indicates that there is much work to do in both the empirical and modeling communities to better understand the NGP and other open ecosystems. Within these chapters, we have answered many questions regarding the drivers and ecological implications of the expansion of trees into the NGP and have also put forth generative ideas for future directions

in the conservation and management of these ecosystems. As such, I hope this document and the manuscripts within can act as a catalyst to initiate future research regarding this important and immense ecosystem.

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