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Research Paper

Land use change and habitat fragmentation of wildland ecosystems of the North Central United States

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A B S T R A C T

Wildlands and their ability to conserve biodiversity and provide ecosystem services are threatened by unprecedented land use intensification. Effective conservation of these wildlands depends on identifying their ecological boundaries and assessing land use change trajectories and habitat fragmentation within those boundaries. We evaluated the extent of land use intensification and fragmentation of six land cover classes and six ecosystem types within nine greater wildland ecosystems (GWEs) of three ecoregions in the north-central United States. Land use intensification across the ecoregions was characterized by assessing changes in NLCD land cover classes and housing density from 2000 to 2011. We used LANDFIRE BpS data to assess fragmentation effects on ecosystem types. We found relatively similar trends in land use intensification across the region with overall net changes by 1.2%, 1.1%, and 1% for the Central Plains, Western Mountains, and Western Plains, respectively. The study region has retained 58% of the area of original ecosystem types with a decrease of mean core area by −30% during the post-European period. The analysis revealed that some ecosystems either already lost over 70–80% area or are quickly approaching this threshold leading to an additional extinction of species due to land use intensification. This analysis can help managers in identifying sustainable conservation priorities to minimize surrounding land use patterns impacts on protected systems. We conclude that managers are likely to face multiple challenges to maintaining ecosystem conditions in their present or near present states while establishing connectivity with regional networks of protected lands.

1. Introduction

Wildlands are the areas dominated by natural process with relatively free from human impacts and chiefly occupied by native species that keep ecosystem services intact and biodiversity functioning (Balmford et al., 2002; Efroymson, Jager, & Hargrove, 2010; Kalisz & Wood, 1995). Wildlands are not necessarily free from human influences, but rather the degree of human influence is relatively low and consistent with the objectives of sustaining ecological services. Within the U.S., these areas of relatively intact natural vegetation are centered on federal lands and sometimes include surrounding state, county, and private lands that have not currently been subjected to intense land use. Besides recreational and aesthetic values, wildlands are vital in providing ecosystem services such as provisioning food and water, regulating pollination, nutrient cycles and floods, and providing habitat required for maintaining the viability of species' gene pools (Schulte, Pidgeon, & Mladenoff, 2005).

Within the US and in many countries, human populations and land use pressures are increasing around protected areas faster than in other rural lands and climate is changing in protected areas as in other locations (Radeloff et al., 2010; Wade & Theobald, 2010; Wittemyer et al., 2008). The aerial extent of wildlands has been declining in most of the Earth's biomes during recent centuries as industrial societies have expanded (Ellis, 2011). The wildlands that exist today are undergoing increased land use intensification in and around them (Gaston, Duffy, & Bennie, 2015; Radeloff et al., 2010; Wade & Theobald, 2010). These increases in human pressure caused a 10% decline in the area of large wildlands globally between 1993 and 2009 (Watson et al., 2016). In addition to increased human pressure on the periphery of protected areas, downgrading in legal protection, downsizing of area, and degazettement of protected areas is widespread globally (Mascia & Pailler, 2011). A recent analysis in the western US found that wildlands are being lost at a rate of "one football field every 2.5 min" Theobald et al. (2016). These changes have the potential to degrade biodiversity, ecosystem function, and the ecosystem services that we value in protected areas.

A challenge in wildland ecosystems conservation is delineating the surrounding area within which land use change can influence the

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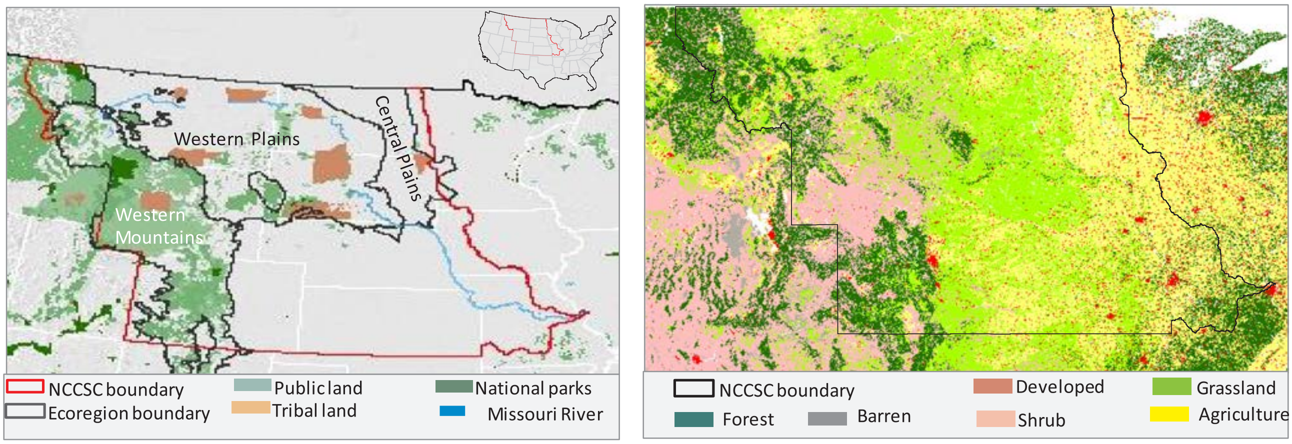

Fig. 1. Map of the study area showing land allocation types, state boundaries and ecoregion boundaries over shaded relief (left) and land cover map of study area from National Land Cover Data 2011 (right).

functioning of the wildlands. Accordingly, Protected Area Centered Ecosystems (PACEs), were defined as the ecological zone surrounding protected areas in which land use intensification can have undesirable influences on biodiversity and ecological processes of the protected areas (Hansen et al., 2011). An analysis of 60 PACEs in the contiguous U.S (Hansen et al., 2014) found that most PACEs experienced substantial change over the 20th century (> 740% average increase in housing density since 1940, 13% of vascular plants are presently non-native, temperature increase of 1 °C/100 yr since 1895 in 80% of PACEs), and projections suggest that many of these trends will continue at similar or increasingly greater rates (255% increase in housing density by 2100, temperature increase of 2.5°–4.5 °C/100 yr, 30% of PACE areas may lose their current biomes by 2030). Given these past and projected rates of change, maintaining ecological integrity within and connectivity among remaining wildlands is a high priority for conservation (Belote, Dietz, Jenkin, & et al., 2017).

Within the U.S, the north central region (Fig. 1) may present unique challenges and opportunities for sustaining and restoring wildlands. The region includes gradients in topography, climate, demography, and land allocations relevant to wildland conservation strategies. The topographically complex Rocky Mountains include large wildlands centered on iconic parks such as Yellowstone and Rocky Mountain. The natural amenities of the region have attracted high rates of population growth and land use development (Baron, 2002) and have motivated substantial efforts to maintaining ecological integrity within these wildlands and connectivity among them (Hansen, Monahan, Theobal, & Oliff, 2016). Precipitation and humidity are low in the rain shadow east of the Rockies and increase substantially eastward to the Mississippi Valley which receives moist humid air masses from the Gulf of Mexico. The extensive shortgrass prairie in the Western Plains support primarily livestock grazing while cultivated agriculture is widespread in the moister the Central Plains. Most of the Western and Central Plains are allocated as private lands, with public lands representing 28% of the region and tribal lands covering 14% of the region. Thus, wildlands in the plains region are relatively small and isolated by private lands. Mean annual temperature is projected to increase 4.9–5.3 °C by 2100 across the High and Central Plains (Adhikari et al., in review). The relatively flat topography here is a major driver of direction and rate of climate shifts, known as climate velocity, organisms will be required to move long distances to remain in climates similar to those of today (Belote, Dietz, McKinley, & et al., 2017; Ordonez, Martinuzzi, Radeloff, & William, 2014). Unlike the Rockies and most of the US, the Western Plains underwent a substantial loss of human population and abandonment of agricultural lands during 1950–2000 (Brown, Johnson, Loveland, & Theobald, 2005; Parton, Gutmann, & Travis, 2003; Sleeter et al., 2013). This depopulation event has been suggested to be an opportunity to “rewild” the plains, reintroducing keystone species and expanding the area allocated to conservation (Freese, 2015; Popper & Popper, 2006)

In this paper, we quantify changes in land cover and use, and fragmentation of natural habitats in and around wildlands of the north central US to provide a context for conservation planning across the region. We expand the concept of PACE from being centered on our most protected lands, national parks, to the areas in and around the national forests, national grasslands and tribal lands that represent the cores of wildlands in the region (Fig. 2). These ‘Greater Wildland Ecosystems’ (GWEs) represent the regions within which land use change may alter ecological processes and biodiversity within the core public and tribal wildlands. Our objectives are:

(1) Quantify trajectories and rates of change in land cover and land use for 2000–2010, the most recent period available, for GWEs across the climate, land allocation, and demographic ecotones of the north central US; and (2) Evaluate fragmentation of biophysical habitat types from pre-European settlement times to present within the GWEs. The results are relevant to the strategies for maintaining or restoring ecological integrity and connectivity that are likely to be most effective within each GWE.

2. Methods

2.1. Study area

We combine six EPA Level III ecoregions into three coarser ecoregions to represent the major biogeoclimatic units of the study area: Western Mountains, Western Plains, and Central Plains ecoregions (Fig. 1). Topography grades from folded mountains in the west to plains of decreasing elevation to the east. The climate across the study area includes: cold continental with pronounced elevational influences on precipitation in the mountains; cold, semi-arid continental climate in the Western Plains with north-south temperature gradients; and subhumid in the Central Plains. Soil fertility generally increases from west to east. Vegetation transitions from sagebrush/grassland valley bottoms and coniferous forests in uplands in the mountains to shortgrass and mixed grass prairie to the tall-grass prairie in the east. Major rivers dissect the Western and Central Plains and support deciduous riparian vegetation communities.

We delineated nine GWEs in the study area confined to six EPA Level III ecoregions (ERs) (Fig. 2). We grouped them into three ecoregions that represented aggregations of these five ecoregions. These three ER includes: 1) Western Mountains representing Middle Rockies, Wyoming Basin, and Southern Rockies ERs, 2) Western Plains representing North Western Great Plains ER and Northwestern Glaciated

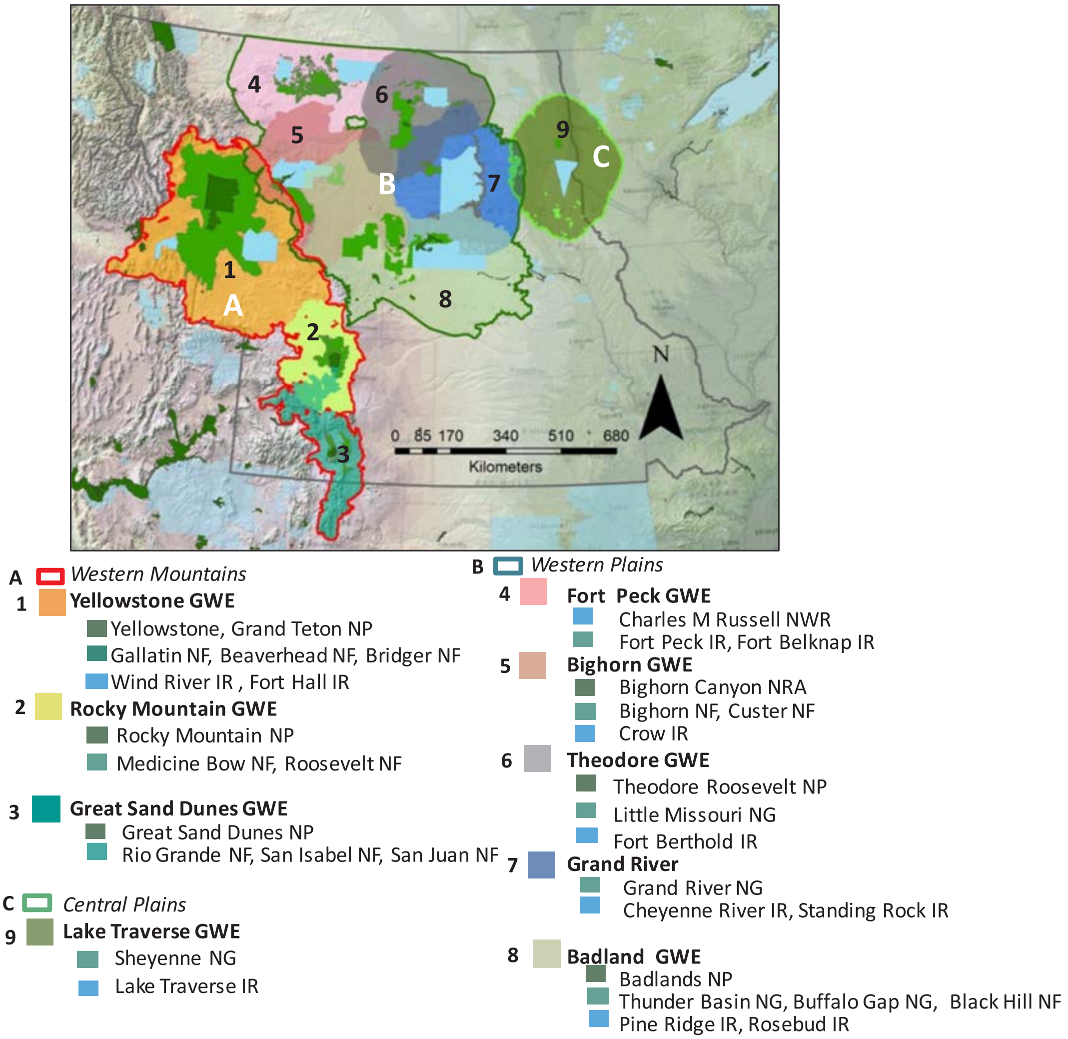

Fig. 2. Boundaries derived for three ecoregions and nine Greater Wildland Ecosystems across north central U.S. Each GWE includes multiple land units such as national parks, national forests, recreational areas, and tribal lands. Different colors represent different GWE boundaries.

Plains, and 3) Central Plains representing Northern Glaciated ER.

2.2. *Greater wildland ecosystems*

The nine GWE boundaries were generally derived following the methods of Hansen et al. (2011), (Fig. 2, see Online supplement). Rather than including only national parks as the core wildlands as was done with PACEs, we also included national forest, national grassland, and tribal lands as core areas. This was done because national park units are now well represented across all the large wildland units in the study area and we were specifically interested in including national grasslands and tribal lands, which are well represented. The boundary of land allocation types were extracted from a land classification spatial dataset available at the Conservation Biology Institute (Protected Area Database; http://consbio.org/). The GWE boundary delineation process then expands beyond the core wildlands based on criteria related to: watershed boundaries, contiguity of surrounding natural habitat required to maintain healthy populations of non-flying mammal species, and extent of human edge effects (Hansen et al., 2011). These criteria are considered to have strong influences on natural ecosystems of protected units (Davis & Hansen, 2011). The final GWE boundary was determined by overlaying and merging the boundaries derived for each criteria (Fig. 2). More details about our methods for delineating GWE boundaries are in the Online supplement.

2.3. *Spatial analysis*

Land cover and land use change (LCLUC) assessments across the study area were carried out analyzing two data sets; 1) the USGS 2001 and 2011 National Land Cover Database (NLCD, http://www.mrlc.gov/, Homer et al., 2015) which includes the major LCLUC types: and 2) the Spatially Explicit Regional Growth Model (SERGoM) products for 2000 and 2010, which define land development classes based on housing density (Theobald, 2005). NLCD is more informative about changes in natural cover, agriculture, and developed areas. SERGoM distinguishes five classes of home density, which has been shown to be a meaningful fine-scale measure of human pressure on ecological processes and species (Theobald, 2005). Habitat fragmentation of biophysically-based ecosystems types was evaluated using LANDFIRE vegetation layers (Zahn, 2015).

2.3.1. *Changes in NLCD land cover classes*

NLCD is the most recent spatially explicit land cover product for conterminous U.S. We regrouped 16 NLCD land use land cover classes into six classes: Developed (all four NLCD Developed cover classes), Barren, Forest (all three NLCD forest classes), Shrubland, Grassland, and Agriculture (NLCD Hay/Pasture and Cultivated classes) classes (Fig. 1). Changes in each new land use class within each GWE were analyzed by comparing net and percent changes in area of each cover class from 2001 to 2011 (Appendix 1 – Table S1). We did not consider

Open Water, Ice/Snow and two Wetland class categories in our analysis.

2.3.2. Changes in developed land classes based on housing density

To assess changes in developed land classes based on housing densities within each GWE from 2000 to 2010, we pulled out all developed land classes from the SERGoM data and grouped into four mutually exclusive developed land classes: Undeveloped land class (private undeveloped/very low density with 0–0.031 housing units/ha), Rural land class (≥0.031–0.063 units/ha), Exurban land class (≥0.063–1.45 units/ha), and Urban land class (>1.45 units/ha) (Appendix 1 – Table S2). For each year of analysis, the housing density was calculated by multiplying the midpoint of each housing density range by the area covered by that housing class.

2.3.3. Ecosystem fragmentation

We considered six major ecosystem types including Shrubland, Grassland, Conifer, Riparian, Hardwood, and Sparse vegetation ecosystems for the assessment of fragmentation extent across the region. For this, we used the biophysical setting (BpS) data layer of modeled historical LANDFIRE vegetation data (https://www.landfire.gov/) as the baseline following the methods of Piekielek and Hansen (2012). The BpS data layer was generated by simulating current vegetation and their biophysical settings, which represents dominant vegetation patterns of pre-European settlement (Barrett et al., 2010; Comer et al., 2003; International Terrestrial Ecological Systems or ITES). This layer represents present-day biophysical environments along with simulated historical ranges of natural disturbances. The current human land use layer from NLCD (agriculture land), SERGoM (land developed classes based on housing density), and US Census Tiger roads data (primary and secondary roads) were overlaid on the modeled historical vegetation layer to simulate present-day vegetation layer. We then estimated present-day fragmentation extent of each ecosystem type within each GWE by comparing historical and present day vegetation layers.

We estimated loss of each ecosystem types as change in aerial extent from pre-European settlement to present. Change in each ecosystem type extent was quantified by land allocation types: public lands, tribal lands, and private lands. The total change in each ecosystem area was determined by dividing the difference between historical and present-day ecosystem area by the historical total area of that ecosystem type.

Changes in spatial configuration was estimated as relative changes in core area. Relative Core Area was estimated as Core Area/Patch Area. The edge distance to estimate core area was 100 m. This metric is an integrated index of change in patch shape, edge length and perforation controlling for patch size.

All analyses were done within the nine individual GWEs across the study area (Fig. 2; Table 1). Comparisons on land use change impacts and fragmentation extent include average changes among GWEs within each ecoregion. In our analysis, the Central Plains ecoregion is represented by only one GWE while Western Plains and Western Mountains ecoregions were represented by five and three GWEs, respectively.

3. Results

3.1. Land use land cover change (2001–2011)

Across the nine GWEs, the major change in NLCD land cover and use was an increase in Developed (+7.22%) and a decrease in Forest (−3.26%) (Fig. 3). Shrublands increased by 2.13% while Agriculture changed was relatively little (+0.23%). Forest loss was due to conversion to Shrubland and Developed. Agriculture was converted to Developed and Shrubland. Increases in Agriculture came from loss of Grassland. Among SERGoM housing density classes, Undeveloped decreased by −8% while Rural, Exurban, and to a lesser extent, Urban/Suburban increased by 9%, 27%, and 4%, respectively. Rates and trajectories of changes were relatively similar for GWEs among ecoregions.

The Central Plains ecoregion had a net change in LUCLC of 1.2% compared to 1.1% for the Western Mountains and 1.0% for the Western Plains. Developed increased in GWEs in all three ecoregions and Forest decreased (Fig. 4). Agriculture and Barren increased in the Western Plains (except for the Fort Peck GWE) but changed relatively little in the other ecoregions. Similarly, the Undeveloped housing density class decreased and the higher density classes increased in all three ecoregions (Fig. 5). The highest losses of Undeveloped were in the Western Mountains and Central Plains ecoregions. The largest increases in Exurban were in the Western Mountains and in the Bighorn GWE in the Western Plains.

The Rocky Mountain GWE stood for the highest in net LULC change of 2.7%. The estimated LULC change for other GWEs was 1.3% for Lake Traverse, 1.7% for Fort Peck, 1.3% for Theodore Roosevelt, 1.9% for Bighorn, 1.5% for Badland, 1.0% for Grand River, 0.4% for Yellowstone, and 1.4% for Great Sand Dunes GWEs.

Table 1
Proportion of pre-settlement natural cover types (%) converted to human use by ecoregion and GWE. We excluded value for Sparse ecosystem type while estimating total average for Lake Traverse GWE.

Ecoregions and GWEs	Biophysical habitat type						
	Shrubland	Grassland	Conifer	Riparian	Hardwood	Sparse	Total
Western Mountains							
Yellowstone	−18.32	−37.85	−6.12	−52.97	−14.25	−1.65	−21.86
Rocky Mountain	−25.91	−63.81	−16.21	−43.50	−20.31	−8.14	−29.64
Great Sand Dunes	−51.56	−44.66	−23.93	−51.71	−18.51	−8.34	−33.12
Western Plains							
Fort Peck	−13.10	−42.47	−15.08	−47.03	−38.19	−7.97	−27.31
Bighorn	−13.29	−21.90	−15.76	−41.34	−19.86	−6.89	−19.84
Theodore Roosevelt	−25.06	−59.82	−9.44	−65.13	−10.39	−1.63	−28.58
Grand River	−38.49	−48.34	−19.10	−55.38	−41.94	−11.51	−35.79
Badland	−21.55	−26.88	−22.78	−36.56	−42.72	−9.91	−26.73
Central Plains							
Lake Traverse	−68.42	−91.82	−81.94	−79.10	−87.25	−2.32	−81.71
Average	−26.53	−45.55	−15.09	−51.01	−23.35	−6.59	−28.02

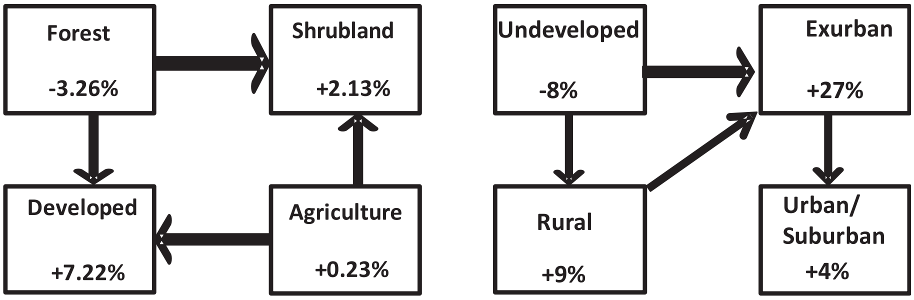

Fig. 3. Pathway of net gains and losses of major NLCD land cover classes from 2001 to 2011 averaged across the nine GWEs (left) and SERGoM housing density classes (right). Numbers inside the boxes represent area loss/gain for that particular land use class. An increase in Agriculture cover class was from Grassland cover class.

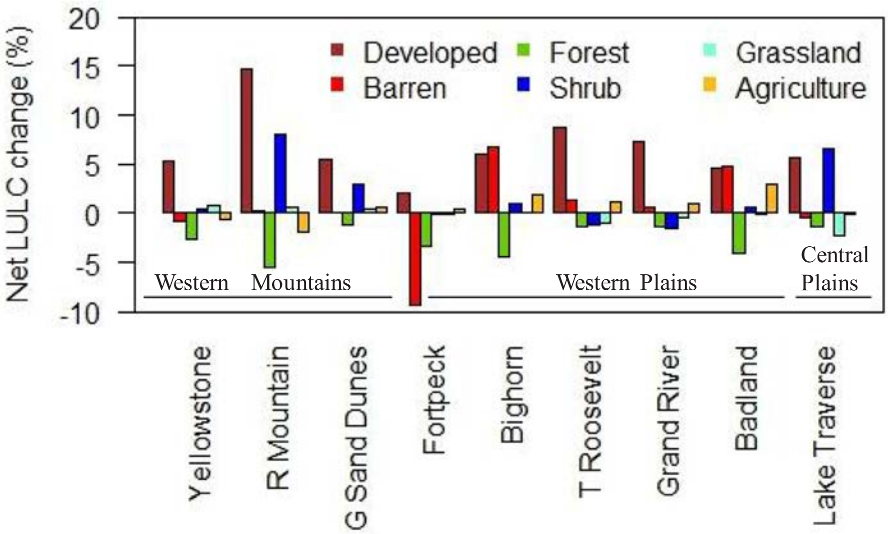

Fig. 4. Percent change in each land cover classes for nine Greater Wildland Ecosystems during 2001–2011. Six land cover classes were used to assess the LULC changes across north central U.S. (Abbreviation: T – Theodore, R – Rocky, G – Great).

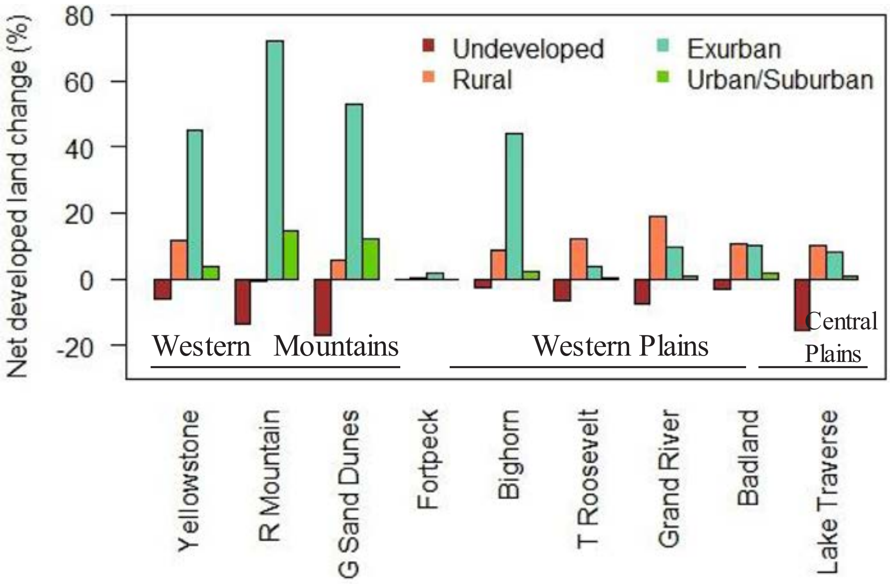

Fig. 5. Percent change in developed land classes based on housing density from SERGoM data for nine Greater Wildland Ecosystems across three ecoregions during 2000–2010. Based on housing density, four developed land classes were considered for our analysis (Abbreviation: T – Theodore, R – Rocky, G – Great).

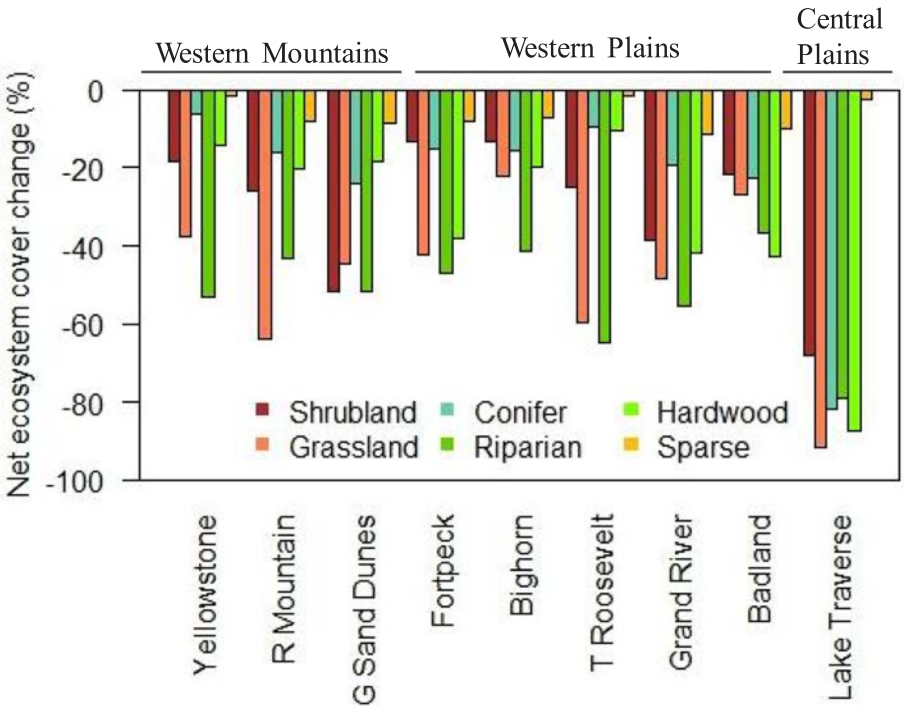

Fig. 6. Proportion of ecosystem loss estimated from the historical LANDFIRE BpS layer for each ecosystem type of nine Greater Wildland Ecosystems. Six ecosystem types were used to assess the extent of natural ecosystems loss across the three ecoregions after the European settlements. (Abbreviation: T – Theodore, R – Rocky, G – Great).

Table 2
Proportion of pre-settlement natural cover types (%) converted to human use by land allocation types across the ecoregions in the study domain.

Ecoregions and GWEs	US Public	US Tribal	US Private	Total
Western Mountains				
Yellowstone	−50.24	−20.97	−21.39	−30.87
Rocky Mountain	−20.01		−55.32	−37.67
Great Sand Dunes	−26.39		−65.55	−45.97
Western Plains				
Fort Peck	−7.81	−52.38	−37.10	−32.43
Bighorn	−10.76	−20.77	−20.65	−17.39
Theodore Roosevelt	−23.65	−64.52	−46.34	−44.84
Grand River	−50.93	−27.75	−41.10	−39.93
Badland	−18.31	−31.32	−32.62	−27.42
Central Plains				
Lake Traverse	−58.86	−69.01	−83.82	−70.56
Average	−29.66	−40.96	−44.88	−38.56

3.2. Ecosystem fragmentation across ecoregions

The pre-European settlement ecosystem types were converted to developed land use classes across the study area with an average loss of 41%. The highest average loss was for Riparian (53%) and Grasslands (49%), and the lowest loss was for Sparse (6%) (Table 1). Among ecoregions, habitat loss was greatest in the Central Plains (82%, excluding Sparse), intermediate in the Western Mountains (33%), and lowest in the Western Plains (31%). In the Central Plains, loss rates were −92% Grassland, −87% Hardwood, −82% Conifer, −79% Riparian, and −68% Shrubland (Fig. 6).

Loss of biophysical habitat types was relatively high on private and tribal lands and lowest on public lands (Table 2).

The highest Relative Core Area change was for Riparian (42%) and Shrubland (34%) (Table 3). The Relative Core Area for Sparse was increased in each ecoregion. Relative Core Area loss was greatest in the Central Plains (52%) and lowest in Western Plains (12%) among the ecoregions. In the Central Plains, the Relative Core Area loss rates were

Table 3
Relative Core Area change (in 100) % in each ecosystem type in ecoregions and GWEs from pre-settlement time to present time.

Ecoregions and GWE	Shrubland	Grassland	Conifer	Riparian	Hardwood	Sparse	Total
Western Mountains							
Yellowstone	−0.09	−0.35	0.05	−0.56	−0.04	0.11	−0.20
Rocky Mountain	−0.14	−0.61	0.00	−0.23	−0.06	0.13	−0.21
Great Sand Dunes	−0.47	−0.40	−0.15	−0.63	−0.09	0.04	−0.35
Western Plains							
Fort Peck	0.11	−0.19	0.14	−0.33	−0.19	0.28	−0.09
Bighorn	−0.01	−0.11	−0.04	−0.33	−0.09	0.06	−0.12
Theodore Roosevelt	0.11	−0.30	0.49	−0.54		0.30	−0.06
Grand River	−0.08	−0.19	0.08	−0.42	−0.10	0.41	−0.14
Badland	−0.08	−0.14	−0.09	−0.25	−0.33	0.06	−0.18
Central Plains							
Lake Traverse	−0.07	−0.79	−0.60	−0.46	−0.71	–	−0.52
Average	−0.08	−0.34	−0.01	−0.42	−0.20	0.17	−0.21

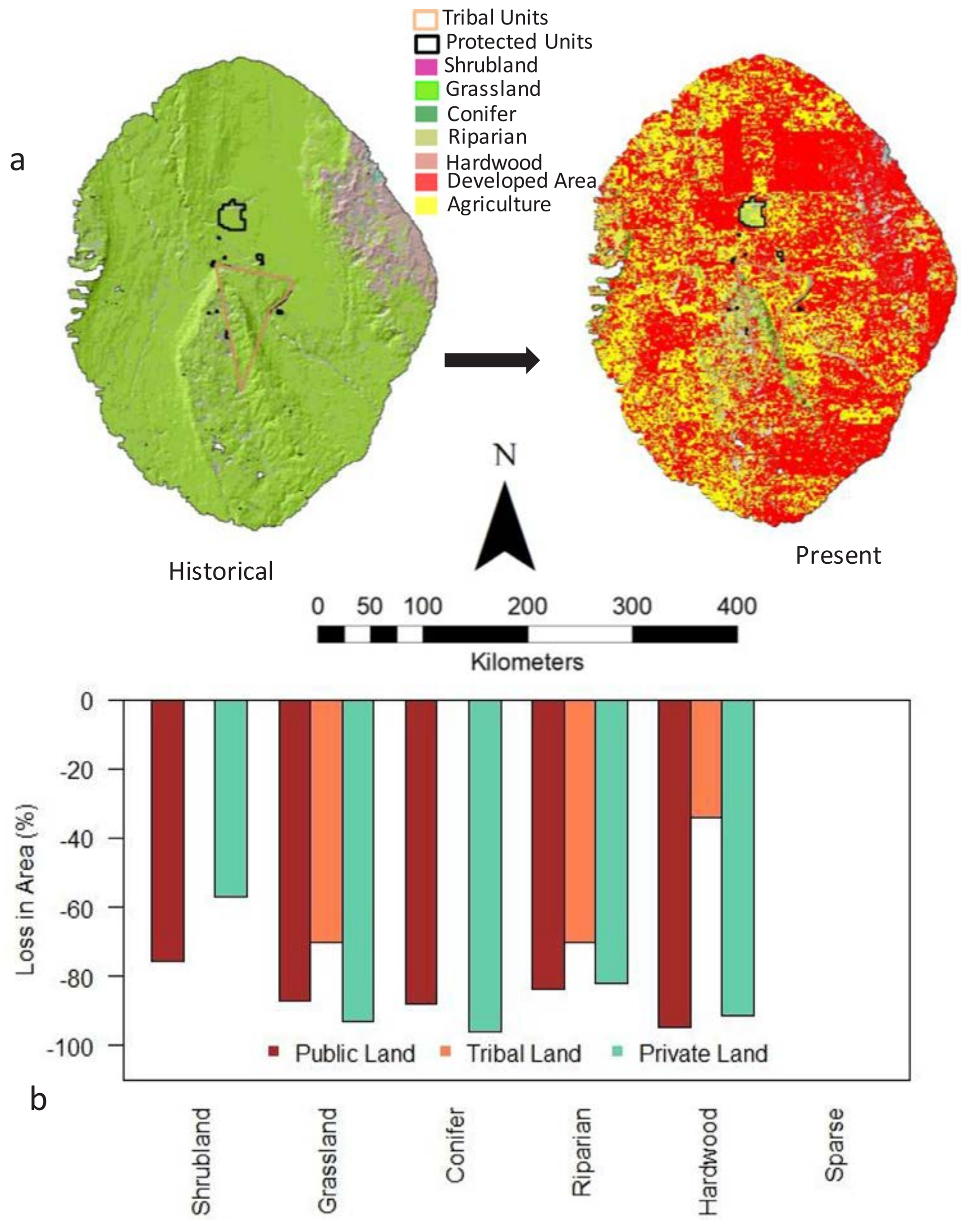

Fig. 7. Lake Traverse GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

highest for Grassland (79%) followed by Hardwood (71%), Conifer (60%), Riparian (46%) and Shrubland (7%).

The Lake Traverse GWE in the Central Plains illustrates high level of conversion of natural habitats to Agriculture and Developed (Fig. 7). The area was dominated by the Grassland and Hardwood habitat types. Agriculture expanded in these habitat types. Exurban, Suburban, Urban housing density classes and agriculture lands were placed especially in Grassland and Riparian habitat types, which were largely on private and tribal lands.

The Rocky Mountain GWE underwent substantial increase in Exurban, Suburban, Urban housing density classes (Fig. 8). Private lands were disproportionately placed in Grassland and Shrubland habitat types and these underwent high rates of conversion to the higher density housing classes, especially around Denver and the other cities on the Front Range of the Rockies. Figures in Appendix 2 represent loss in spatial extent of natural ecosystem types in six GWEs across Western Mountains and Western Plains ecoregions.

4. Discussion

We expected that land cover and use trends from 2001 to 2011 and conversion of natural cover types since pre-settlement times in the GWEs would differ among ecoregions based on their different patterns of human population growth and land use trends during 1950–2000. Instead, we found relatively similar trends of land use intensification and conversion of natural cover types, albeit with magnitudes of change

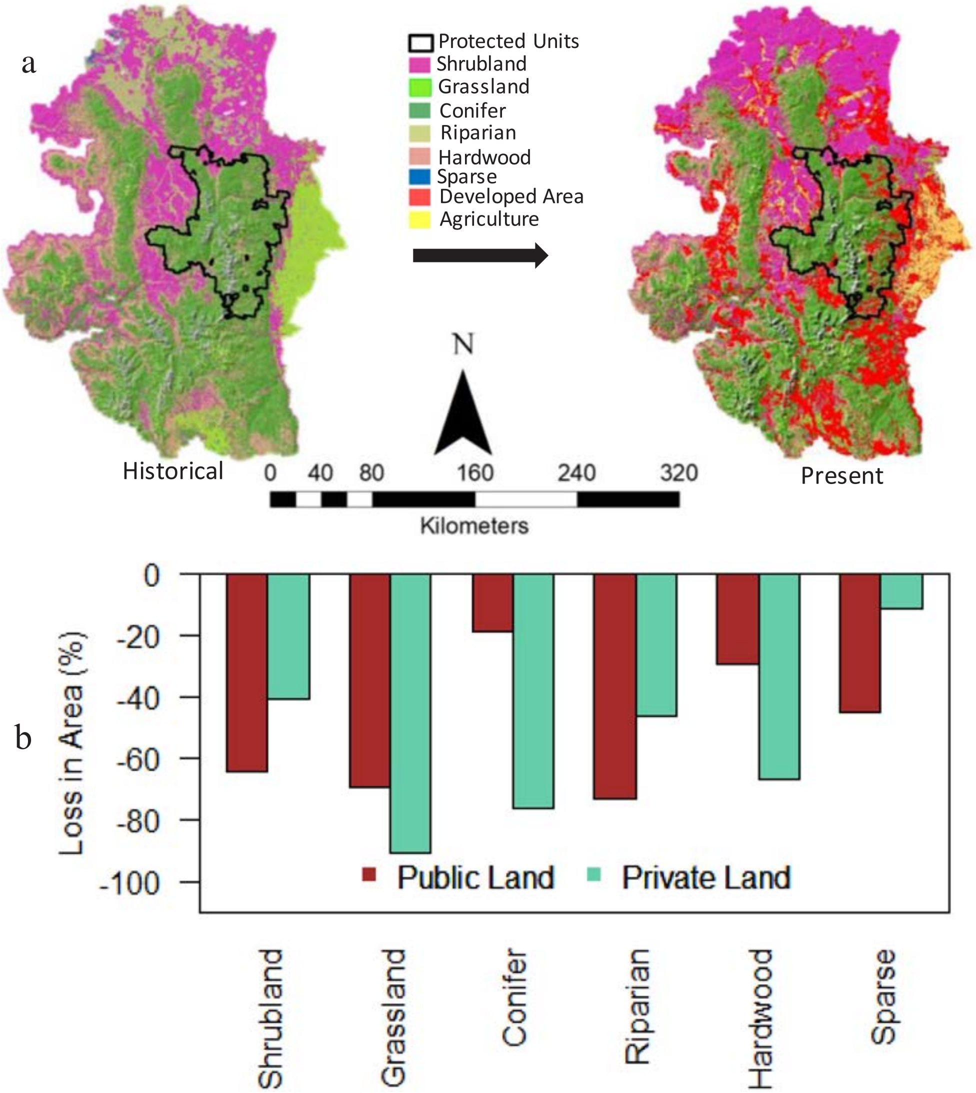

Fig. 8. Rocky Mountain GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

that varied among the ecoregions and GWEs. Land use patterns shifted from the wildland end of the land-use gradient towards the more human-dominated side of the gradient from 2001 to 2011. Forest area decreased, while the USGS Developed class and all the Rural to Urban/Suburban housing density classes increased. These changes occurred across all three ecoregions and all GWEs, regardless of previous demographic patterns. Conversion from grassland/shubland to agriculture or vice versa were not dominate trajectories of change and direction of change varied among GWEs. The increases in Developed area and/or home density classes were greatest in the faster growing Western Mountains and Central Plains Ecoregions than in the Western Plains. Rates of conversion and fragmentation of natural cover types since presettlement times was greatest in the Lake Traverse GWE in the Central Plains but were relatively similar among the Western Plains and Western Mountains. Among natural habitat types, Riparian and Grassland ecosystem types underwent the greatest reductions in aerial extents. As expected based on legal and policy frameworks, rates of land intensification were lower on public than private land but similar on private and tribal lands.

Demographic and land cover and use trends for the second half of the 20th century were summarized across study area or broader regions by Brown et al. (2005) for 1950–2000, and Drummond et al. (2012) and Sleeter et al. (2013) for 1973–2000. Human population density increased across all Type I ecoregions of the US during 1950–2000 (Brown et al., 2005). Rates of increase were 80% in the Great Plains (including our Western Plains and Central Plains ecoregions) and 53% in the Northwest Forest Mountains (including our Western Mountains Ecoregions), and were intermediate relative to all ecoregions. The High Plains was unique in loosing populations in rural counties over this time period. Nonmetro-nonadjacent counties in the High Plains declined by −20% in this time period while those in the Northwest Forested Mountains increased by 17%. The depopulation was especially pronounced across large portions of the Western Plains (Brown et al., 2005) and was due to decreases in farm numbers, larger farm sizes, and decreased in intensive labor required modern agricultural productions (Drummond et al., 2012).

The differences in population gain or loss across the study area during 1973–2000 did not correlate well with rates of change in land cover and use. Overall rates of change in land cover and use during 1973–2000 were relatively similar in the Rocky Mountain Ecoregion (overlapping with our Western Mountains ecoregion) (6.9% of area with 2.5%/decade) (Sleeter et al., 2013) and 7.8% (3.4%/decade) in the Great Plains ecoregion (Drummond et al., 2012). These rates of change were substantially higher than the 1.0–1.2% change per decade averages for GWEs within ecoregions in the study area during 2000–2010.

The major change in land cover and use in the Great Plains was expansion of Agriculture into Grasslands and Shrublands 1973 and 1986, but conversion back to Grasslands/Shrublands from 1986 to 2000 (Drummond et al., 2012). These changes primarily occurred in the western reaches of the region where the Conservation Reserve Program (CRP) had a substantial effect, including the Western High Plains, Northwestern Great Plains, and the Northwestern Glaciated Plains. The CRP established by the Food Security Act of 1985, which has encouraged landowners to retire millions of hectares of highly erodible and environmentally sensitive cropland from production using 10–15 year contracts, has had a substantial effect on land use patterns while also improving wildlife habitat, water quality, and soil carbon and nitrogen storage. Other changes in land cover and use included expansion of urban and other developed areas (+37%), decrease in Agriculture −4.75%, and decreased in Forest (−2.5%). The major changes in the Rocky Mountains Type I Ecoregion varied among the Type III ecoregions within in. Within the Middle Rockies, centered on Yellowstone, Forest declined by −5.7%, Grassland/Shrubland increased by 4.6% and Developed increased by 0.1%. The Montana Valley and Foothills Ecoregion to the north of the Middle Rockies had losses of Forest (−1.7%) Agriculture (−1.4%) and gains in Grassland/Shrubland (1.7%) and Developed (0.1%). The Southern Rockies, which includes Rocky Mountain and Great Sand Dunes National Parks experienced little change in land cover and use during this 1973 time period. This ecoregion excludes the Front Range of the Colorado Rockies which experienced high population growth rates and land use intensification during this time (Parton et al., 2003).

Thus, the major change in land cover and use occurring in GWEs during 2001–2011, increase in Developed, decline in Forest, variable change in Agriculture, Grassland, and Shrubland, are consistent with the changes documented for the study area as a whole for the period of 1973–2000. Despite the depopulation of the Western Plains prior to 2000, trends in expansion of Developed areas and decreases in Forest have occurred there in 2001–2011 as they have in the Western Mountain and Central Plains ecoregions.

Loss of natural habitat types from pre-European settlement to the 2000 has been addressed for the Yellowstone and Rocky Mountain Protected Area Centered Ecosystems by Piekielek and Hansen (2012) using similar methods to those used in this paper. Despite PACEs covering smaller areas and including proportionally less private lands than GWEs (see methods), the proportion of each habitat type remaining as of 2000 within PACEs was similar to our findings for GWEs in 2010. Both studies conclude substantial reductions in these natural cover types, especially on private lands.

4.1. Potential drivers of land use change across Greater wildland ecosystems

The factors known to be driving land use intensification across most of the U.S. are now also substantial forces in these ecoregions. Anthropogenic activities in recent years show large impacts even in the ecoregion with historically low rates of land use change such across the Western Plains. This may be associated with multiple drivers such as government policy, environmental policy, socio-economic condition, and climatic factors (Brown et al., 2005; Loveland et al., 2002).

Amenity based population migration has been found to be the primary driver of agriculture land conversion to residential areas in Western Mountains GWEs. In many other GWEs, similar population based migration is underway which is in agreement with national trends (Brown et al., 2005; Cline, 2013). This type of land transformation has been reported to have serious ecological consequences to biodiversity and ecosystem services, such as species extinction due to habitat loss, degradation of soil and water quality, surface energy balances, and water balances (Foley et al., 2005; Su, Xiao, Jiang, & Zhang, 2012). Further, the abundant natural amenities are likely to continue to attract amenity migrants. Increasing land demands for the new migrants can drive continued conversion of wildlands for residential, commercial, and industrial uses questioning the sustainability of these wildlands (Cline, 2013).

Shrubland and grassland expansions at the expense of agricultural lands in relatively dry Yellowstone GWE and Bighorn GWEs across the northern Great Plains is associated with land abandonment due to low productivity (Gellrich, Baur, Koch, & Zimmermann, 2007). However, agriculture intensification in Western Plains can be attributed to the National Reclamation Act (1902) and advancement in irrigation technology that brings significant land areas into irrigation facilities from the High Plains Aquifer in the post-1950 era (Drummond et al., 2012). But limited irrigation due to groundwater depletion reportedly resulted in farm abandonment in relatively dry areas of High Plains after 1975 (Kettle, Harrington, & Harrington, 2007). Moreover, biofuels production for a substitute of energy source has been reported as an important driver of grassland conversion into agriculture lands in Great Plains, particularly after 1973's oil crisis (Searchinger et al., 2008).

Expansion of urban area has been found as the primary reason for land conversion within north-central region of U.S. In the Central Plains, agricultural land conversion to developed area reported in this study was the dominant land cover change can be associated with productivity and socioeconomic development (DeFries, Rudel, Uriarte, & Hansen, 2010). This study revealed the expansion of urban and suburban settlements at the expense of agricultural land. Hence a sharing of available resources (e.g. water) among these land classes may result in detrimental effects on these lands (Parton et al., 2003). The developed land and demographic expansions in urban and suburban areas of this depopulating region can be due to the establishment of agricultural industries that have created many employment opportunities (Harrington & Lu, 2002; USCB, 2015).

Forest cover class lost to shrubland was higher in Western Mountains ecoregion compared to the Central and Western Plains ecoregions. Some of these changes are the result of increases in forest fires and wildfire seasons due to elevated temperature in spring and summer, and early snowmelt in recent decades have resulted in the conversion of forest to shrubland cover (Westerling, Turner, Smithwick, et al., 2011). In addition, forest loss in these areas was reported to be associated with tree mortality due to warming and drought co-occurring with beetle outbreaks (Allen et al., 2010). Many conifer communities within the ecoregion have been seriously threatened by pine beetles, blister rust and disturbance factors which deserve special conservation attention (Bockino & Tinker, 2012).

However, the role of natural disturbances such as fire and disease in fragmentation cannot be ruled out because of long time span between pre-settlement and current vegetation across our study region (Burgess

& Sharpe, 1981). The past studies reported depletion of ground water in northern Great Plains, increasing drought in western U.S., and forest mortality due to beetle outbreaks, droughts and spread of forest pathogens as the additional contributing factors in ecosystem fragmentations in this region (Allen et al., 2010; Gellrich et al., 2007; Kettle et al., 2007; Westerling et al., 2011).

Barren cover class expansion in Western Plains, particularly from grassland, could be due to the spatially variation effects of recent drought (Drummnd, 2007) and increasing of fallow fields. However, the NLCD does not consider fallow cropland and other types of bare lands individually.

4.2. Scope and limitation

One limitation of this study is the period of land use intensification examined. The last year of analysis was 2011, rather than 2016, due to unavailability of comparable data with NLCD products. Hence, we are not sure of the land use trends since the end of the 2009 recession and the expansion of oil industries in the Western Plains. We have not considered land use change due to energy development including oil and gases, quarries and mines, wind farms, and solar plants which have contributed to considerable loss of land in the western U.S. (Theobald et al., 2016) as the data for these analysis are not publicly available. This paper is to our knowledge, however, the only published of LCLUC in the study area for 2000–2011 and is unique on focusing on wildlands and their surrounding ecosystems.

Species area relationships have been widely used to estimate species extinction based on the levels of habitat loss. This method predicts significant extinction of a species when the loss exceeds 70–80% of its natural habitat. However, this method has been called into question due to limitations in time lags, sampling issues, and non-random spatial settings of both human land use and habitats (He & Hubbell, 2011). Our analysis of impacts on ecosystem types revealed that some ecosystem types within the study area either have already exceeded 70–80% levels of habitat loss or are quickly approaching this threshold, which could lead to an additional extinction due to continued human land use intensification. These ecosystems need special attention in prioritizing the conservation and management efforts to meet the species conservation goals.

The scale and resolution of the remote sensing data is always an issue and this study is not an exception (Marceau & Hay, 1999). The LULC classes could be better differentiated to address existing fragmentation issues with finer grained data (Salmon, Friedl, Frolking, Wisser, & Douglas, 2015). In addition, mixed pixel problems associated with a wide range of spectral signatures have been reported during classification of developed cover class from a low to medium resolution data (Pena, 2012). Despite these problems, the accuracy of land cover classifications from NLCD 2006 data was found over ~ 85% (Wickham et al., 2013). Recent study by Wickham et al. (2017) reported the ~ 4% higher accuracy for 2011 NLCD data compared to that of 2006. Additionally, the authors found ~ 6% higher accuracy for the eastern region compared to the western region of the U.S. Long term field based monitoring across urban to rural gradients can overcome some of the uncertainty associated with our understandings of LULC impacts on ecological process (McDonnell, Pickett, Groffman, & Bohlen, 1997).

4.3. Conservation and management implications

Our results contribute to existing knowledge that provides a context for conservation for wildlands within the study area. The study area spans an important gradient in human modification and extent of remaining wildlands. Among regions of the contiguous U.S., the Rocky Mountains were found to have the lowest mean index of human modification and the North Central U.S. among the highest levels of human modification (Theobald, 2013). While the remaining wildlands in the Rocky Mountains are extensive and moderately well connected, those in Central and Western Plains Ecoregions are especially small and isolated.

Our results indicate that the wildlands within GWEs have continued to be converted to more intense land uses during 2000–2011. Of particular concern from a conservation perspective is the loss of lands in the Private Undeveloped class and the expansion of the Rural and Exurban classes. These findings indicate the remaining wildlands on private lands are undergoing conversion to rural homes, ranchettes, and subdivisions which are known to have strong negative impacts on native species and ecological processes (Hansen et al., 2005). It is notable that this trajectory of land use change is occurring across all the GWEs, including those dominated by tribal lands. Bighorn Canyon, Grand River, and Theodore Roosevelt GWEs, all focused on tribal lands and distant from urban centers and traditionally high-value natural amenities, yet are nonetheless undergoing increases in home density. The low proportion of natural habitats remaining in the GWEs, especially for Grassland and Riparian ecosystem types and on private lands, and the high rates of fragmentation of these is alarming.

The loss rates of wildlands in the Western and Central Plains presented in this paper may be conservative. Oil and gas development, largely not quantified by data sources used in this study, has grown dramatically in portions of the study area, particularly in North Dakota, eastern Montana, Wyoming, and eastern Colorado (USDA ERS, 2017) and may be reducing wildlands in ways not yet quantified. Future loss rates may accelerate due to changes in agriculture. In the Central Plains and east of Western Plains, changes in commodity prices and changing climate are driving conversion of grassland to corn and soybean cropping (Wright, 2013). This grassland conversion is also concentrated in close proximity to wetlands, posing a threat to waterfowl breeding in the Prairie Pothole Region.

Due to the small extent and fragmentation of remaining wildlands in the Western and Central Plains, levels of connectivity based on “natural” (i.e., least human-modified) corridors is among the lowest in the U.S. (Belote, Dietz, Jenkin, & et al., 2017). Corridors among large core protected areas are extensive in the Rocky Mountains but largely do not cross the Central Plains. Consequently, GWEs in the Western and Central Plains have among the lowest proximity to major corridors as any wildlands in the US (Belote, Dietz, Jenkin, & et al., 2017, Fig. 5A).

Conservation in the Western and Central Plains is additionally challenged by climate change. Temperatures are projected to rise 5 °C by 2100 across this region and water balance projected to decline by 25% (Adhikari et al. in review). The flat topography in this area results in high climate velocity, which is a measure of climate vulnerability that estimates the geographic distance species may need to travel to keep up with multivariate climate shifts. The Great Plains was found to have the highest climate velocity in the contiguous U.S. (Belote, Dietz, McKinley, & et al., 2017).

In the context of past and current land use and projected future climate, conservation goals for GWEs in the Western and Central Plains should emphasize: maintain existing wildlands; restoring degraded lands; and enhancing connectivity within and among GWES. Strategies for achieving these goals are described in Groves and Game (2016). Maps and analyses that could be used as a basis for managing for connectivity among GWEs are presented in Theobald, 2013; Belote, Dietz, Jenkin, & et al., 2017; Belote, Dietz, McKinley, & et al., 2017. An example of a comprehensive application of these strategies comes from the Prairie Foundation Project in eastern Montana that has implemented a public and private lands collaborative conservation effort (http://www.americanprairie.org/). Conservation planning for adaptation to climate change is especially challenging. Scenario planning has been found to be an effective approach for identifying management strategies that are most likely to be robust to the uncertainties of future climates. An example of scenario planning in the Badland GWE is described in Miller, Symstad, Frid, Fisichelli, and Schuurman (in review).

This study helps to identify candidate areas for protection and/or restoration where ecosystem degradation is rapid. Restoration work could be focused in most of the vulnerable ecosystems such as Grassland, Hardwood, and Conifer ecosystem types in Central Plains, Riparian ecosystem types in Western Plains, and Grassland and Riparian ecosystems in the Western Mountains ecoregion. This study may help to prioritize conservation areas close to the protected ecosystems potential for future development (Swenson & Franklin, 2000). For example, presence of high natural amenity keeps attracting migration in and around the Rocky Mountain GWE. Managers can identify the expanding urban and sub-urban areas around the surroundings of this GWE to formulate specific conservation strategies.

Lake Traverse GWE represents the agriculture-dominated GWEs which have recently undergone land conversion due to rapid urban and exurban expansion in their surroundings. The ecosystems in such GWEs are already at risk with higher rate of land conversion into developed area. Our findings call for an assessment of additional landscapes of high risks and urgent action with a conservation easement by regulatory restrictions on development to prevent further loss across those areas. Management and restoration actions should be implemented immediately considering future climate to preserve further loss of biodiversity and sustain the ecosystems from this ecoregion. Major initiatives are needed to maintain the assets in these remaining wildlands.

Agencies working for species conservation have a need to designate additional critical habitats for conservation, which may be approaching thresholds of local species extinction (Piekielek & Hansen, 2012). We believe analysis of longer temporal span data can help to identify such habitat that need critical attention for conservation. Therefore, this paper mainly focuses on the study of important habitat loss from European settlement to current period due to human land use intensification.

The vulnerability of Tribal lands to land use intensification is possibly because of tribe's reliance on natural resources to sustain sociocultural and spiritual practices (Thomas & Twyman, 2005). In addition, limited economic opportunities and dwindling federal supports have triggered land use intensification in these lands (Gautam, Chief, & Smith, 2013). Our study showed that tribal lands in Central and Western Plains ecoregions are the most vulnerable as half of their area has already been transformed into other land cover classes. With the loss of over two-third of land cover classes, land cover conversion on Lake Traverse tribal lands in Central Plains ecoregion will likely to continue due to socioeconomic development, recreational values, and high climate velocity. The sustainability of tribal lands in these ecoregions is extremely important to conserve the economic, spiritual, and cultural legacy of tribes. An integrated approach to conserve and to create opportunities for tribal people can be effective for the sustainability of tribal lands.

5. Conclusion

This study synthesized data about LULC patterns using socioeconomic and historical information across the north-central region of the United States, which represents various modes of land use, multiple pathways of land conversion, net land changes, and fragmentation of natural ecosystems in recent years. We believe this research can contribute to understanding the vulnerability and sustainability of land systems across the north-central U.S. which is considered as highly affected by climate change. Our study suggests that despite similar trends in net land use changes among the GWEs, land use/land cover types across the study area showed strong differences in land use dynamics and expanding, contracting, and stable land cover types. Differences in land use change among ecoregions call for actions to develop an integrated regional-scale adaption plans that include quantitative assessments of exposure to multiple global change factors. The restoration mission of American Prairie Foundation (http://www.americanprairie.org/), an organization that has purchased or leased ~123,429 ha land to maintain prairie based wildlife reserves across public and private lands of Montana serves as an ideal example for management of vulnerable landscapes in this region.

We captured the geographical characteristics of the ecoregions considering land use change dynamics and fragmentation of natural ecosystems across the north-central U.S. by categorizing GWEs into agriculture intensive, depopulating, and growing mountains. In our analysis, GWEs with lower quality land or climate limitations for agricultural production have shown little fluctuation in land use changes compared to the ecoregions of higher quality land with abundant agricultural resources. Expansion in Developed and Shrubland areas in expense of forest cover drives into net reduction of natural habitat, carbon stocks, and ecosystem services affecting sustainability of wildlands. The presence of natural amenities and natural lands across the mountainous ecoregion has made these areas unique, also creating unique challenges for maintaining their ecological integrity. As the study area represents one of the most productive agricultural regions in the world, vulnerability due to land use change of this region can have potential effects on the global economy. This work provides an opportunity to conservation stakeholders in identifying threats to prioritize conservation sectors.

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Appendix A

See Tables S1 and S2.

Table S1
Estimated land use class composition (%) 2001–2011 and net changes in class areas for nine greater wildland ecosystems.

Ecoregions and land cover classes	2001	2011	Net Change (km^2)	%change
Western Mountains Ecoregion				
Yellowstone GWE				
Developed	0.67	0.71	86.80	5.28
Barren	1.25	1.24	−26.19	−0.86
Forests	16.12	15.70	−1028.97	−2.61
Shrub	54.44	54.65	516.29	0.39
Grass	16.87	17.00	308.82	0.75
Agriculture	7.74	7.69	−132.51	−0.70
Rocky Mountain GWE				
Developed	1.72	1.97	156.48	14.73
Barren	2.00	2.00	4.22	0.34
Forests	44.27	41.82	−1510.47	−5.53
Shrub	26.42	28.55	1316.26	8.07
Grass	15.59	15.69	63.48	0.66
Agriculture	5.23	5.13	−60.02	−1.86
Great Sand Dunes GWE				
Developed	0.71	0.75	23.94	5.50
Barren	3.54	3.55	3.61	0.17
Forests	52.17	51.58	−363.61	−1.13
Shrub	15.59	16.06	288.38	3.01
Grass	22.99	23.09	58.78	0.42
Agriculture	2.68	2.70	9.83	0.60
Western Plains Ecoregion				
Fort Peck GWE				
Developed	0.29	0.29	8.35	2.00
Barren	0.42	0.38	−56.98	−9.28
Forests	3.81	3.68	−188.42	−3.40
Shrub	8.28	8.27	−10.23	−0.08
Grass	56.32	56.25	−102.87	−0.13
Agriculture	27.73	27.85	176.48	0.44
Bighorn GWE				
Developed	0.49	0.52	46.77	6.02
Barren	0.45	0.48	48.20	6.78
Forests	11.89	11.35	−840.49	−4.50
Shrub	28.81	29.13	490.77	1.08
Grass	51.17	51.21	68.28	0.08
Agriculture	5.29	5.39	159.56	1.92
Theodore GWE				
Developed	0.52	0.57	52.75	8.76
Barren	0.45	0.46	6.70	1.29
Forests	2.29	2.26	−36.72	−1.39
Shrub	5.16	5.11	−65.84	−1.11
Grass	47.12	46.66	−526.83	−0.97
Agriculture	39.14	39.59	512.04	1.14
Grand River GWE				
Developed	0.43	0.46	47.34	7.39
Barren	0.84	0.85	7.84	0.62
Forests	0.66	0.65	−13.73	−1.39
Shrub	0.83	0.82	−19.35	−1.56
Grass	65.66	65.35	−465.91	−0.48
Agriculture	27.20	27.46	396.88	0.98
Badland GWE				
Developed	0.40	0.41	45.94	4.68
Barren	0.94	0.98	110.06	4.72
Forests	5.92	5.67	−600.46	−4.09
Shrub	15.30	15.39	227.55	0.60
Grass	67.19	67.16	−75.25	−0.05
Agriculture	7.06	7.27	511.10	2.92
Central Plains Ecoregion				
Lake Traverse GWE				
Developed	1.18	1.24	73.37	5.62
Barren	0.05	0.05	−0.25	−0.44
Forests	2.93	2.89	−45.77	−1.41
Shrub	0.20	0.21	14.16	6.50
Grass	9.66	9.45	−236.53	−2.21
Agriculture	76.28	76.26	−23.77	−0.03

Table S2
Change in Developed class and housing density in each GWE within NCCSC domain.

Developed Land Class	2000 (%)	2010 (%)	Net Change (km^2)	%change	#household (2000)	#household (2010)	Net change	%change
Western Mountains								
Yellowstone GWE								
Undeveloped	71.92	67.38	−4992.38	−6.30	7921	7422	−499	−6.30
Rural	24.79	28.64	4248.24	15.56	47490	53057	5568	11.72
Exurban	2.36	2.69	370.41	14.27	27475	39842	12367	45.01
Urban/Suburban	0.85	1.19	373.73	39.98	91674	95188	3514	3.83
Commercial	0.09	0.09	0.00	0.00	0	40607	40607	
Rocky Mountain GWE								
Undeveloped	47.29	41.01	−1489.36	−13.29	1121	972	−149	−13.29
Rural	36.92	39.54	619.52	7.08	16128	15988	−140	−0.87
Exurban	8.51	4.94	−847.97	−42.03	32713	56339	23626	72.22
Urban/Suburban	6.76	14.01	1717.81	107.20	172185	197403	25218	14.65
Commercial	0.51	0.51	0.00	0.00	0	49378	49378	
Great Sand Dunes GWE	39.56	32.79	−1817.05	−17.11	1062	880	−182	−17.11
Undeveloped	52.10	56.95	1301.90	9.31	24187	25557	1370	5.67
Rural	5.24	5.22	−6.63	−0.47	19767	30190	10423	52.73
Exurban	2.94	4.88	521.78	66.10	53975	60550	6575	12.18
Urban/Suburban	0.16	0.16	0.00	0.00	0	17502	17502	
Commercial								
Western Plains								
Fort Peck GWE								
Undeveloped	80.49	80.45	−48.96	−0.06	8592	8587	−5	−0.06
Rural	18.82	18.86	39.20	0.20	32951	33007	56	0.17
Exurban	0.52	0.53	9.11	1.63	5020	5098	78	1.56
Urban/Suburban	0.14	0.14	0.65	0.43	16070	16080	10	0.06
Commercial	0.02	0.02	0.00	0.00	0	7000	7000	
Bighorn GWE	81.15	79.16	−2341.65	−2.45	9549	9315	−234	−2.45
Undeveloped	17.62	19.32	1999.14	9.64	34396	37354	2957	8.60
Rural	0.78	0.98	231.41	25.11	10422	14999	4578	43.93
Exurban	0.36	0.45	111.10	26.20	71274	73048	1775	2.49
Urban/Suburban	0.08	0.08	0.00	0.00	0	41138	41138	
Commercial								
Theodore Roosevelt GWE								
Undeveloped	65.09	60.84	−4127.89	−6.54	6311	5899	−413	−6.54
Rural	32.57	36.77	4070.92	12.89	52875	59327	6452	12.20
Exurban	1.86	1.91	45.60	2.52	16907	17515	608	3.60
Urban/Suburban	0.42	0.43	11.37	2.78	30519	30673	154	0.50
Commercial	0.05	0.05	0.00	0.00	0	20563	20563	
Grand River GWE								
Undeveloped	71.74	66.34	−7001.38	−7.53	9303	8603	−700	−7.53
Rural	26.54	31.83	6859.36	19.93	57315	68215	10900	19.02
Exurban	1.34	1.43	111.35	6.39	16464	18048	1583	9.62
Urban/Suburban	0.32	0.35	30.67	7.29	40986	41323	338	0.82
Commercial	0.06	0.06	0.00	0.00	0	31044	31044	
Badland GWE								
Undeveloped	77.39	74.88	−5371.30	−3.23	16608	16071	−537	−3.23
Rural	20.80	23.17	5096.80	11.42	75139	83175	8036	10.70
Exurban	1.29	1.38	195.27	7.04	32442	35727	3285	10.13
Urban/Suburban	0.48	0.51	79.23	7.73	71542	72872	1331	1.86
Commercial	0.05	0.05	0.00	0.00	0	41855	41855	
Central Plains								
Lake Traverse GWE								
Undeveloped	43.75	37.08	−6628.09	−15.25	4348	3685	−663	−15.25
Rural	44.26	50.31	6015.95	13.68	84168	92882	8713	10.35
Exurban	9.24	9.71	469.28	5.11	98250	106219	7969	8.11
Urban/Suburban	2.60	2.74	142.86	5.53	116569	117753	1184	1.02
Commercial	0.16	0.16	0.00	0.00	0	65599	65599	

Appendix B

Fig. A. Yellowstone GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

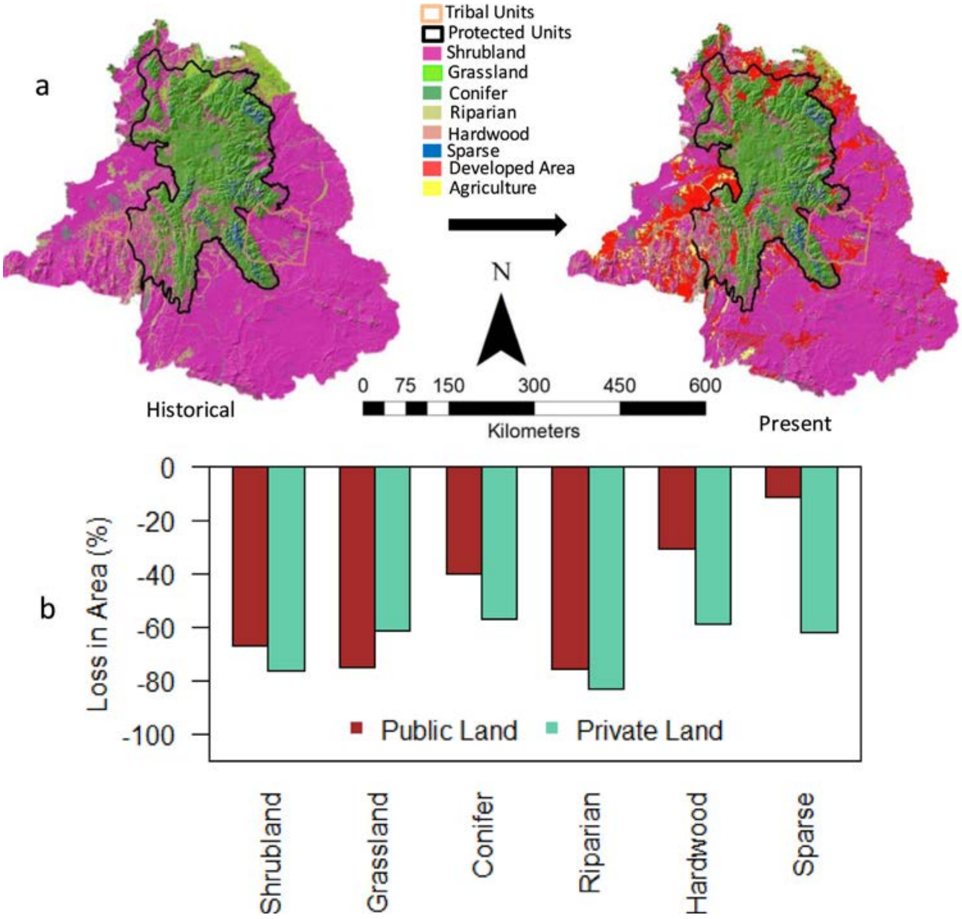


Fig. B. Great Sand Dunes GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

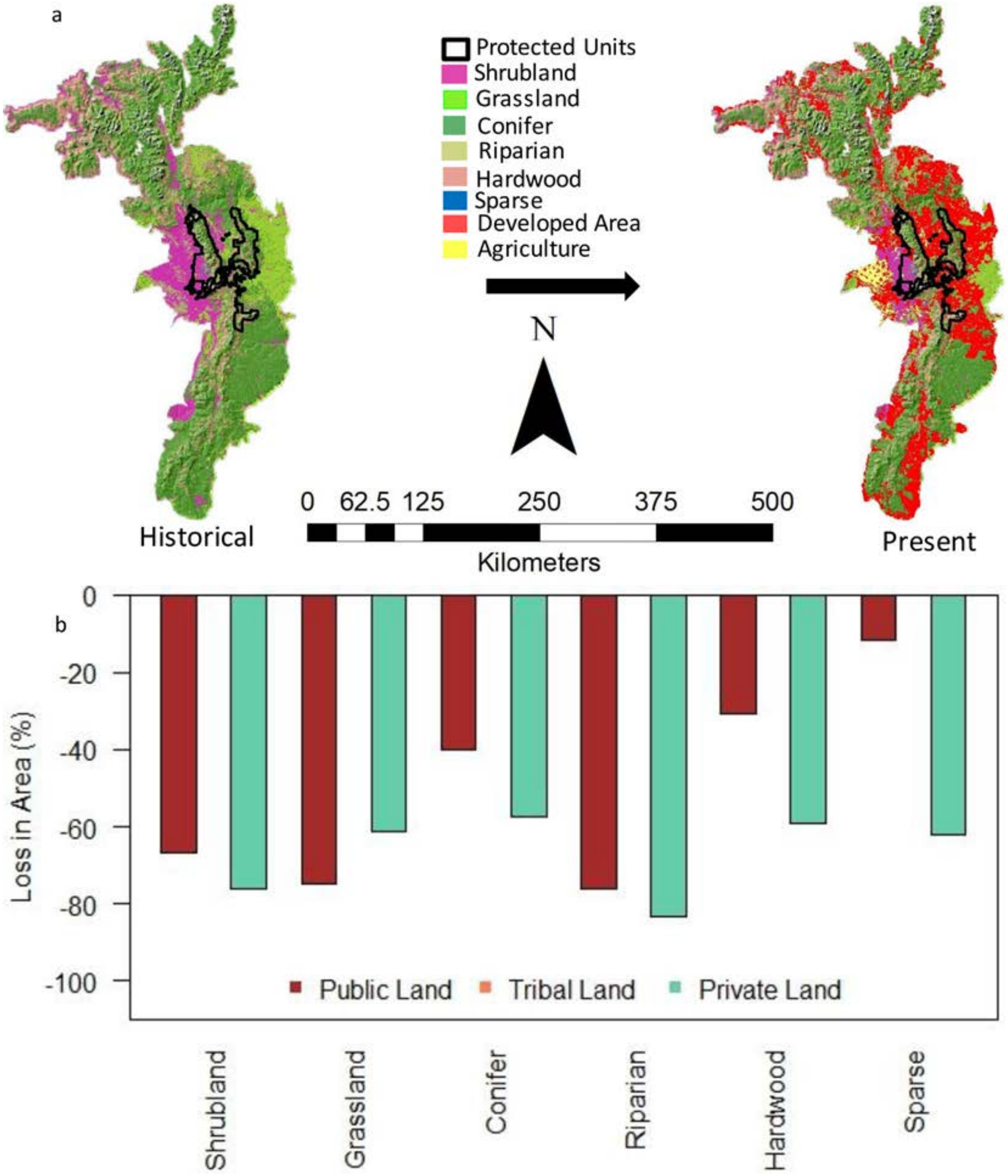


Fig. C. Fort Peck GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

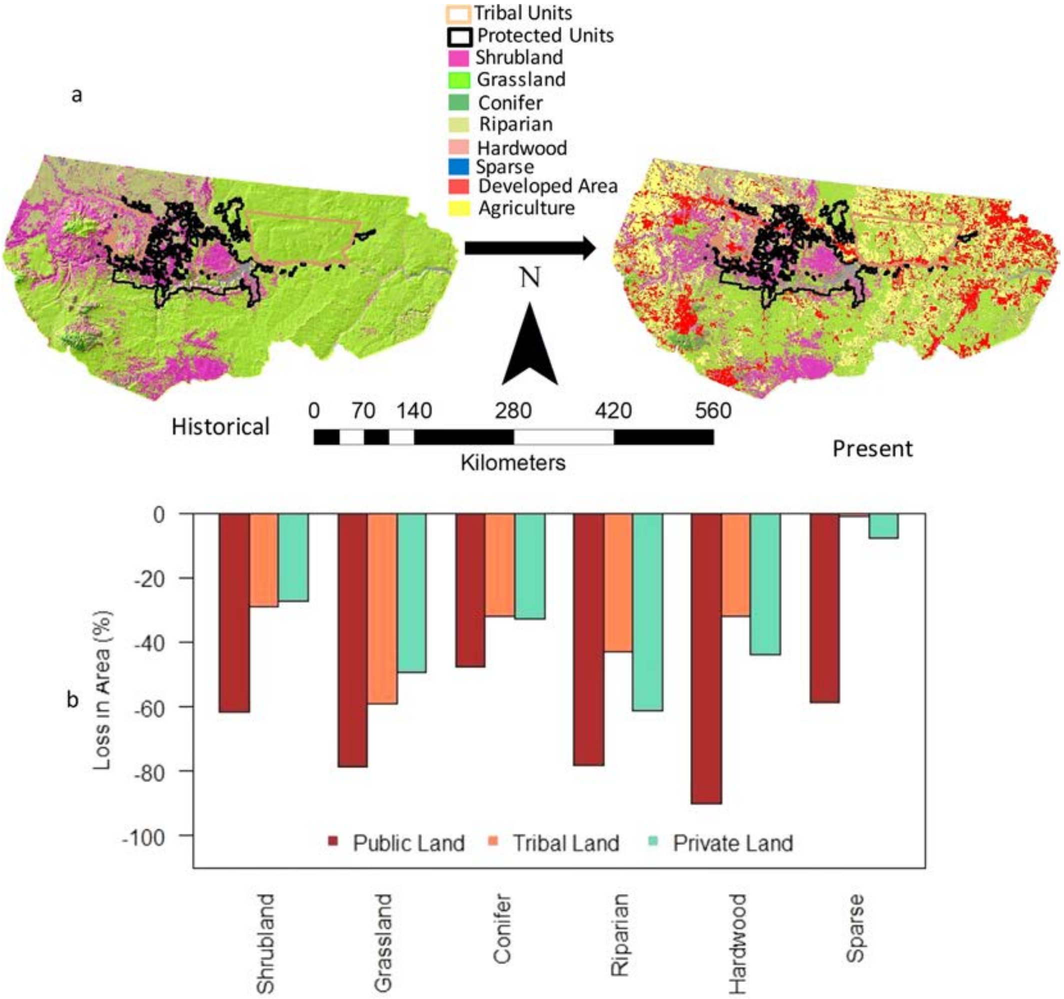


Fig. D. Bighorn GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

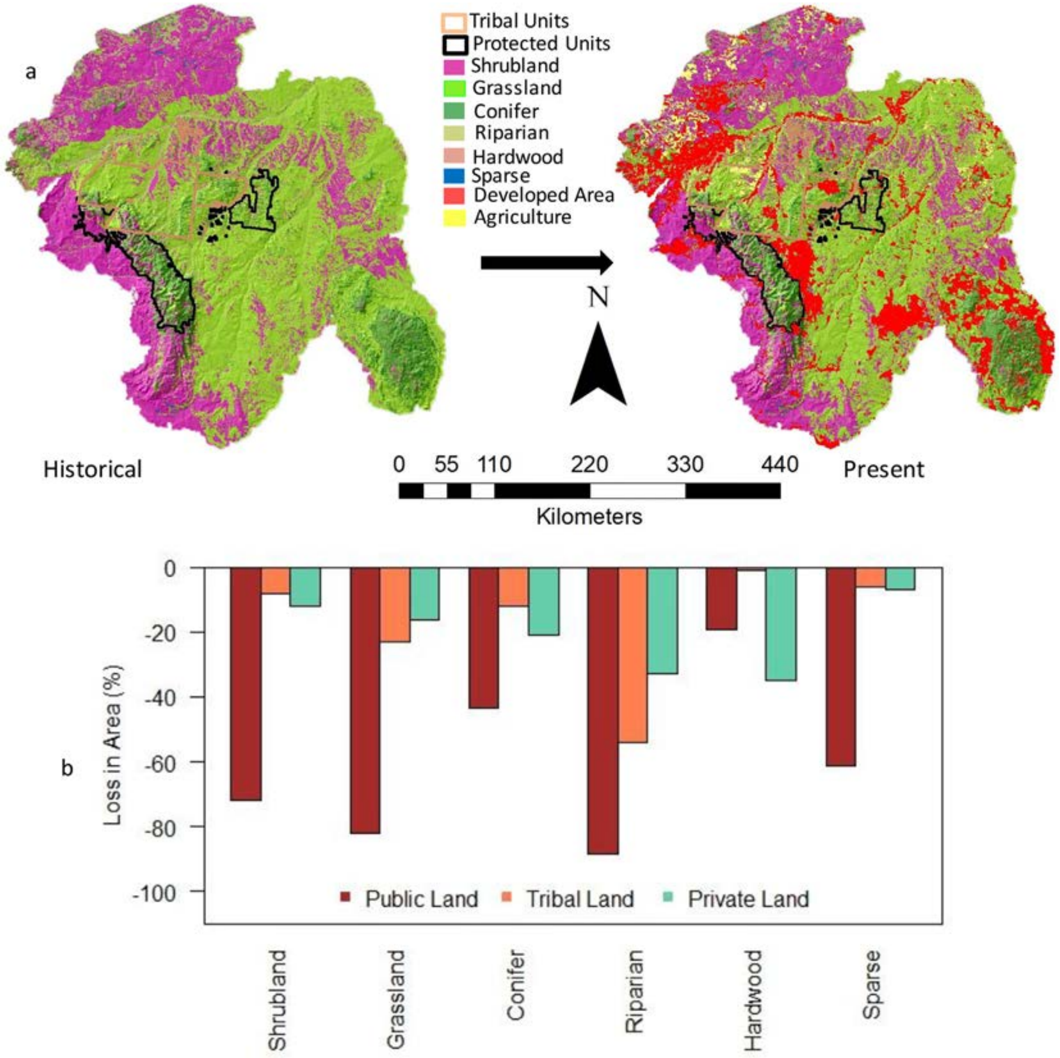


Fig. E. Theodore Roosevelt GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

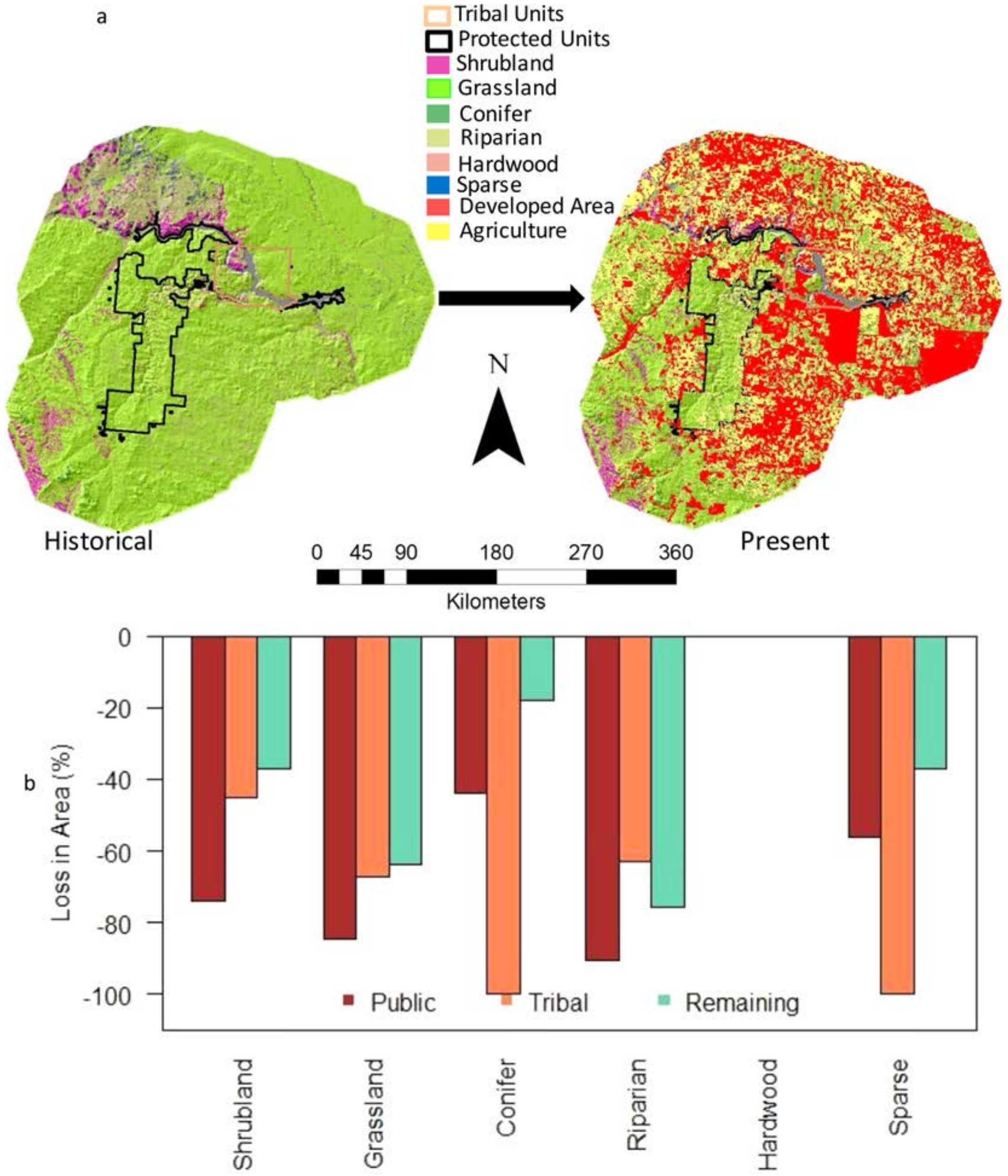


Fig. F. Grand River GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.

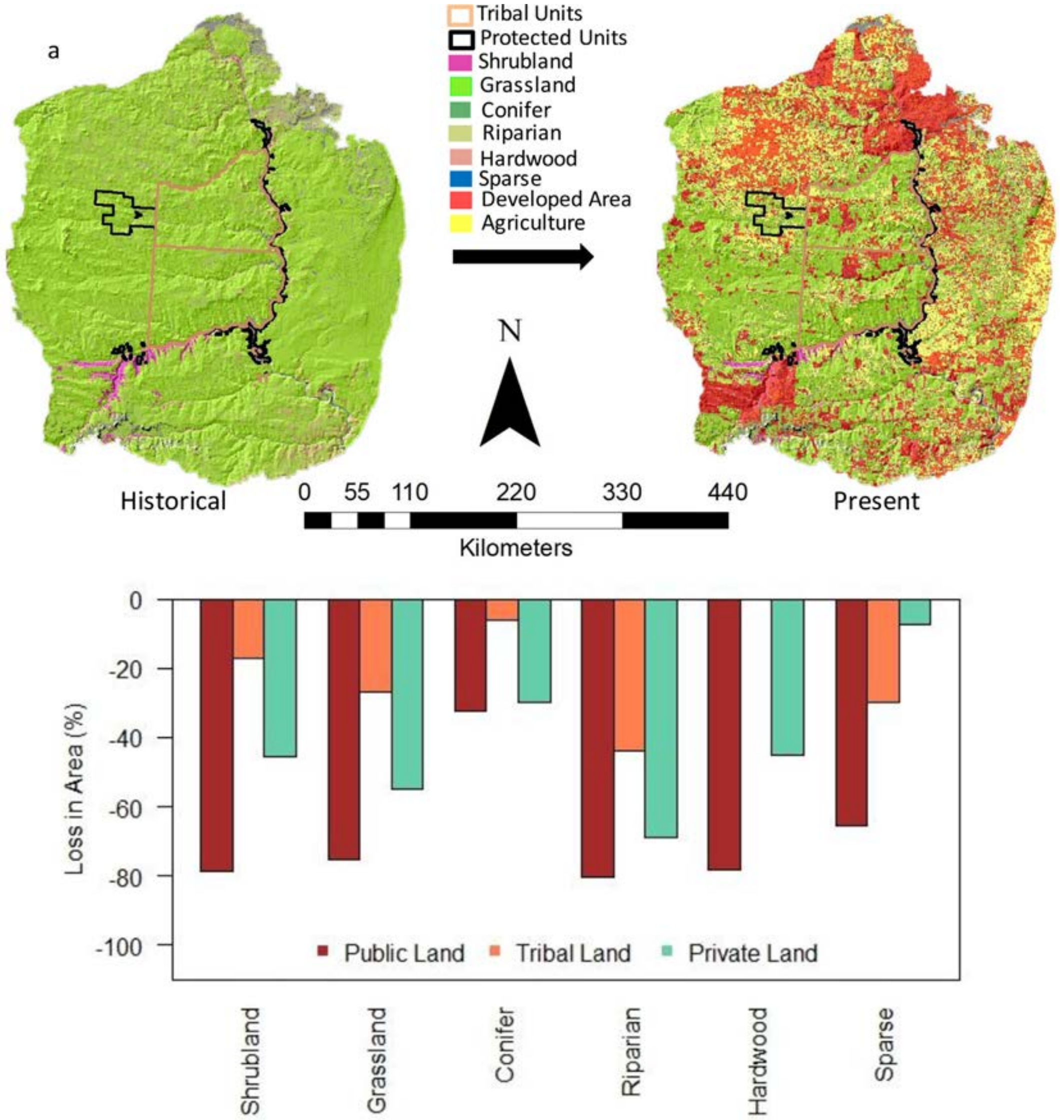
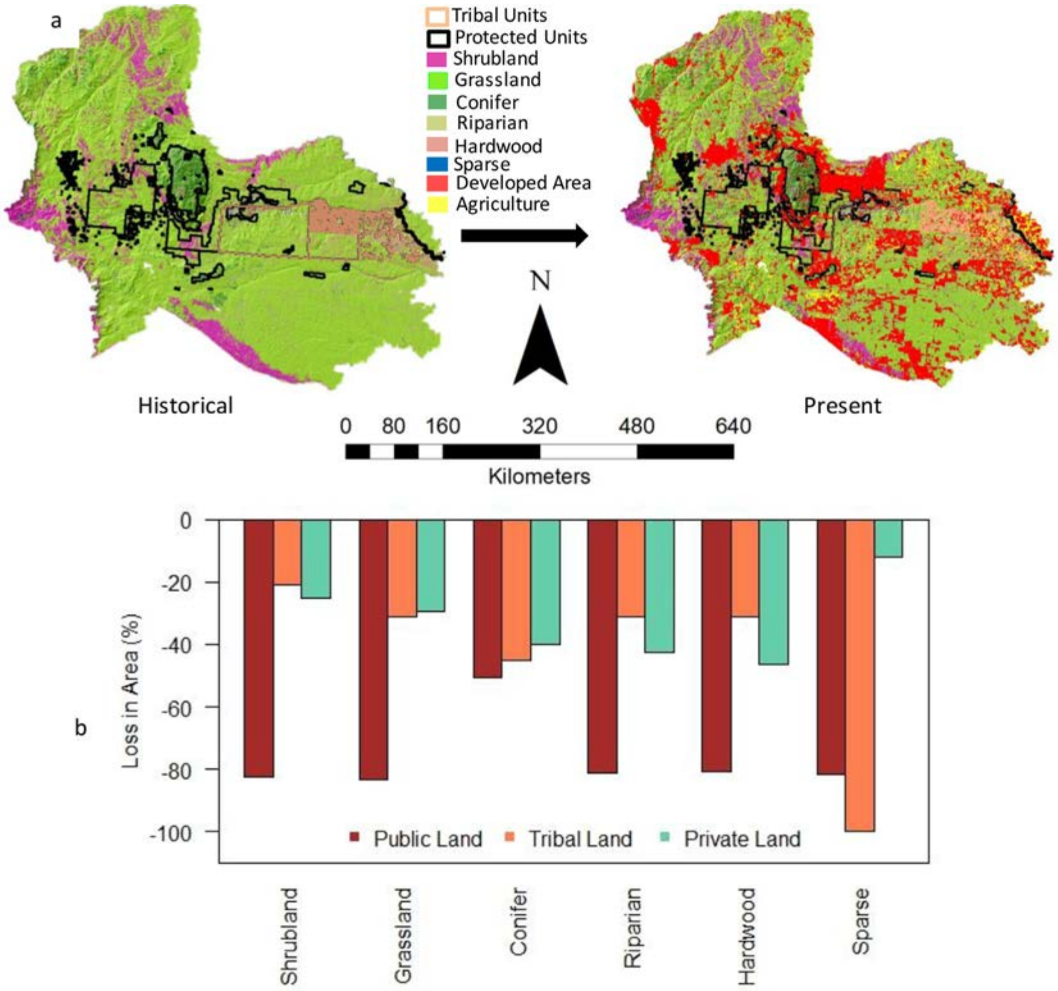


Fig. G. Badland GWE: a. Historical versus present-day ecosystem types, b. Reduction in areas of ecosystem types from pre-European settlement to the present-day by land allocation types.



Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2018.04.014.

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