The elevational ascent and spread of exotic annual grasslands in the Great Basin, USA

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Abstract

In the Great Basin of the U.S., sagebrush (*Artemisia* spp.) and salt desert shrublands are rapidly transitioning to exotic annual grasslands, a novel and often self-reinforcing state that threatens the economic sustainability and conservation value of western grazing lands. Climate change is predicted to directly and indirectly favor annual grasses, potentially pushing annual grassland transitions into higher elevations. We used recently developed remote sensing-based rangeland vegetation data to retrospectively quantify expansion and elevational range shift of annual grassland transitions in the Great Basin from 1986–2019. During this period, we document an alarming six-fold increase in annual grassland area (to >75,000 km^2) occurring at a rate of 1,950 km^2 yr^{-1}. Annual grasslands now occupy one fifth of Great Basin rangelands. This rapid expansion has been in part facilitated by a broadening of elevational range limits, with the leading edge of annual grassland transitions moving upslope at 60–110 m $decade^{-1}$. Accelerated intervention is critically needed to conserve the fragile band of rangelands being compressed between annual grassland transitions at lower elevations and woodland expansion at higher elevations.

Significance

Exotic annual grasses became widespread throughout the western U.S. Great Basin in the last century and now rank among the most vexing challenges facing western rangelands. Once established, these invaders can transform native sagebrush (*Artemisia* spp.) and salt desert shrublands into virtual monocultures of highly flammable exotic annual grasses with severely diminished biological and economic value. Capitalizing on a recently developed remote sensing vegetation product providing continuous spatial and annual temporal coverage of western US rangelands, we map the expansion of exotic annual grasslands over the past three decades. Our analysis reveals the alarming pace at which native shrublands are transitioning to annual

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grasslands, and confirms the movement of these transitions into ever higher elevations as the climate of the western U.S. warms.

Keywords

Cheatgrass; invasion; grass-fire cycle; rangeland; transitions

Introduction

Grasses are highly successful invaders globally with the capacity to dramatically reshape rangelands (1, 2). Among diverse ecosystems across several continents, consequences of grass invasions include increased risk to human life and property from larger and/or more frequent wildfires (3), impacts on human health (4), disruption of hydrologic and nutrient cycles (5–7), loss of habitat for sensitive species (8), and reduced biodiversity across trophic levels (9, 10). Commonly, disruptions to invaded communities are sufficient to force transitions into alternative states characterized by dominance of exotic grasses (e.g., "grass-fire cycles;" 2). Despite advancements in our understanding of the mechanisms and outcomes of exotic grass invasions on recipient ecosystems, sporadic monitoring has limited our ability to quantify the scope and dynamics of such ecosystem transformations at broad spatio-temporal scales (11).

Invasions of several species of annual grasses into western North America have given rise to one of the best known and most studied examples of ecosystem transformation by exotic grasses. In the arid and semi-arid Great Basin of the western U.S., exotic annual grasses including cheatgrass (*Bromus tectorum*), red brome (*B. rubens*), medusahead (*Taeniatherum caput-medusae*), and ventenata (*Ventenata dubia*) have become virtually ubiquitous (12–14). These annual grasses colonize interstices between native perennial bunchgrasses and shrubs, increasing the amount and continuity of fine fuels (15). Consequently, annual grass-invaded vegetation communities burn 2–4 times more frequently than uninvaded communities (16, 17). Post-fire reestablishment of native vegetation, which is relatively fire intolerant, often proves exceedingly challenging due in part to pre-emptive resource use by early-germinating annual grasses (18–20). Ultimately, this cycle of invasion, fire, and exclusion of native competitors often results in undesirable near monocultures of exotic annual grasses, hereafter annual grasslands. Similar to grass invasions globally (1), annual grassland transitions are eroding both the economic and conservation value of Great Basin landscapes (21).
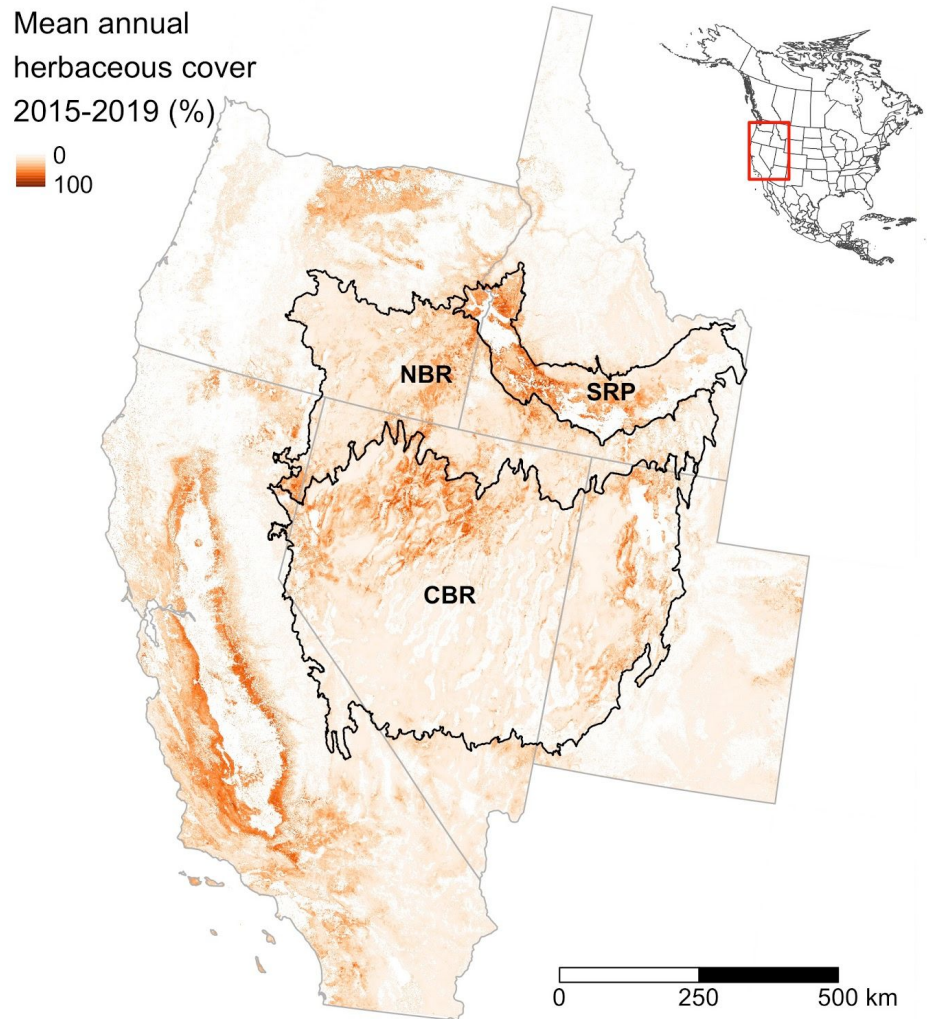
Figure 1. The Great Basin encompases parts of 5 US states. Ecoregions comprising the Great Basin include the Central Basin and Range (CBR), Northern Basin and Range (NBR), and Snake River Plain (SRP).

Climate change is hypothesized to facilitate exotic annual grass dominance in the Great Basin. Projected warmer temperatures and earlier snowmelt are predicted to favor establishment, growth, and reproduction of annual grasses throughout much of the region (22, 23). Larger and more frequent wildfires resulting from extended fire seasons may accelerate rapid transitions to annual grassland (24). Potentially exacerbating these dynamics, rising atmospheric CO_2 will increase annual grass biomass and flammability (25). In combination, these factors threaten to hasten the expansion of annual grasslands and broaden the geographic area at risk of transitioning in the western US (22, 26).

Elevational range shifts are among potential hypothesized responses of annual grasses to climate change (26). The Great Basin is mountainous, with elevations ranging from <700 m to

>4000 m. As temperatures warm and timing of snowmelt advances, higher elevations are predicted to become suitable for establishment of annual grasses (27). In addition to directly affecting reproduction and survival of annual grasses, warming may indirectly assist the spread of annual grasslands into higher elevations via effects on fire regimes, e.g., lengthening of fire seasons (22).

The spatio-temporal dynamics of state transitions to annual grasslands in the Great Basin remain poorly understood. Remote sensing has been successfully used to map exotic annual grasslands at ecoregional extents (28, 29), but these snapshots in time provide little insight into the rate or trajectory of transitions along ecological gradients. Using a recently developed remotely sensed vegetation cover product that provides continuous coverage across space and time of western US rangelands (30, 31), we quantify the expansion of annual grasslands in the Great Basin and test for elevational range shifts over the past several decades. To account for broad-scale variation in abiotic conditions across the region, we performed analyses at the Level III ecoregional scale, including the Central Basin and Range (CBR), Northern Basin and Range (NBR), and Snake River Plain (SRP) ecoregions (Fig. 1).

Results

The total area of annual grasslands in the Great Basin increased six-fold during the study period, from 12,499 km^2 in 1986 to 75,008 km^2 in 2019 (Fig. 2). In 2019, annual grasslands occupied 15% (40,368 km^2) of CBR, 13% (20,718 km^2) of NBR, and 26% (13,923 km^2) of SRP. Estimated annual rates of increase ranged from 380 ± 185 (SE) $km^2\,yr^{-1}$ in SRP to 977 ± 301 $km^2\,yr^{-1}$ in CBR (Fig. 2; Table S2) and yearly totals were consistent with single-year estimates from 1992 (32) and 2001 (28).
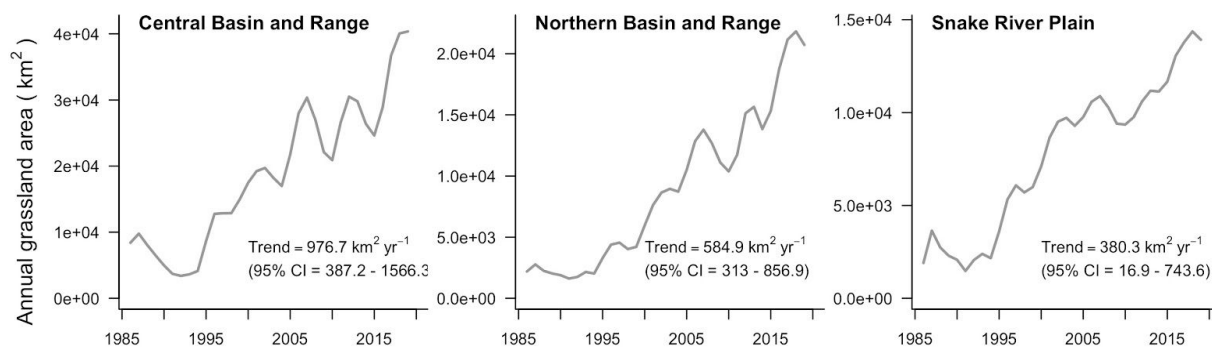

Figure 2. Growth in area of annual grasslands in Great Basin ecoregions, 1986–2019. One fifth (19%) of Great Basin rangelands are now occupied by annual grasslands. Yearly increases in annual grassland area represent 0.5%, 0.4%, and 1.2% of the total rangeland area of the Central Basin and Range, Northern Basin and Range, and Snake River Plain, respectively.

Elevations of annual grassland transitions increased through time (Fig. 3), though the rate of increase differed among ecoregions. For all quantiles, the year × ecoregion interaction model

received unequivocal support based on AIC (Table S3, Supplemental Information). The elevational floor (5th percentile) of elevations of annual grassland transitions changed at a rate of −0.4 (95% CI = −0.7– −0.1) m yr^{-1} in CBR, 7.4 (95% CI = 7.0–7.9) m yr^{-1} in NBR, and 3.5 (95% CI = 3.2–3.8) m yr^{-1} in SRP. The median elevation of annual grassland transitions increased by 4.2 (95% CI = 3.9–4.5) m yr^{-1} in CBR, 4.6 (95% CI = 4.3–5.0) m yr^{-1} in NBR, and 11.4 (95% CI = 11.0–11.8) m yr^{-1} in SRP. The elevational ceiling (95th percentile) of elevations of annual grassland transitions increased by 6.6 (95% CI = 6.0–7.3) m yr^{-1} in CBR, 7.7 (95% CI = 7.0–8.3) m yr^{-1} in NBR, and 1.4 (95% CI = 1.0– 1.9) m yr^{-1} in SRP.
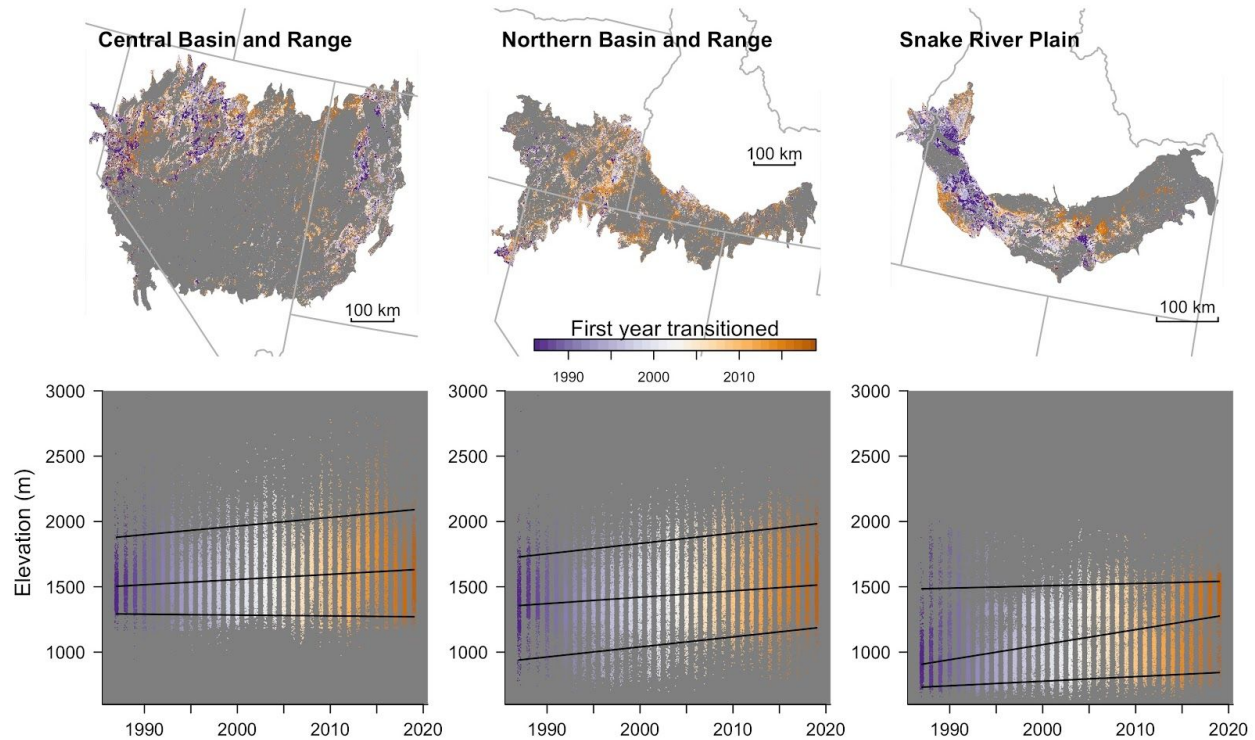

Figure 3. Elevational trends of annual grasslands in the Great Basin, USA, 1986–2019. Spatial extent of pixels classified as annual grasslands in ≥1 yr, with colors indicating the first year transitioned (top). Darkest purple indicates transition in or prior to 1986, the first year in the time series. Elevations of *n* = 1000 sampled annual grassland transitions in each year from 1987–2019, with fitted regressions for the 5th, median, and 95th percentiles (bottom). A small amount of random noise was added to x-axis values to aid visibility.

Discussion

Exotic annual grasslands in the Great Basin are expanding with alarming speed in recent decades, increasing nearly six-fold in area since the mid 1980s. We estimate annual grasslands occupy one fifth (19%, 75,000 km^2) of Great Basin rangelands, and expand by 1,950 km^2

annually, a rate proportionally greater than recent deforestation of the Amazon[2]. The most rapid growth occurred in the last decade (2010-2019), averaging >3,800 km^2 annually across the Great Basin. Consistent with predictions based on warming trends, rapid movement into higher elevations has allowed expansion to continue more-or-less unabated (Fig. 3). This steady ascent of annual grasslands now threatens higher elevation rangelands formerly thought to be minimally vulnerable to transition (33, 34).

Elevational ascent of annual grass dominance has long been assumed (e.g., 35, 36), but we are the first to empirically confirm this widespread phenomenon by capitalizing on advanced remote sensing products (Fig. 4). Throughout most of the Great Basin, the median rate of elevational ascent was 40–50 m/decade, while the leading edge (i.e., 95th percentile) ascended substantially faster at 65–80 m/decade. Ecoregional differences in movement of elevational floors may reflect variation in the identities of annual grasses, with *B. rubens*, *Schismus arabicus,* and *S. barbatus* prevalent in the southern Great Basin near the Mojave desert, where they are associated with hotter and drier conditions and lower elevations (37). However, recent invasion of salt desert shrub vegetation by *B. tectorum* may also account for movement into lower elevations in the Central Basin and Range (38). The unique physiography and land use of the Snake River Plain, a large valley occupying a narrow band of latitude, resulted in nearly stationary floors and ceilings but also the fastest elevation ascent within those confines (>110 m/decade; Fig. 3).
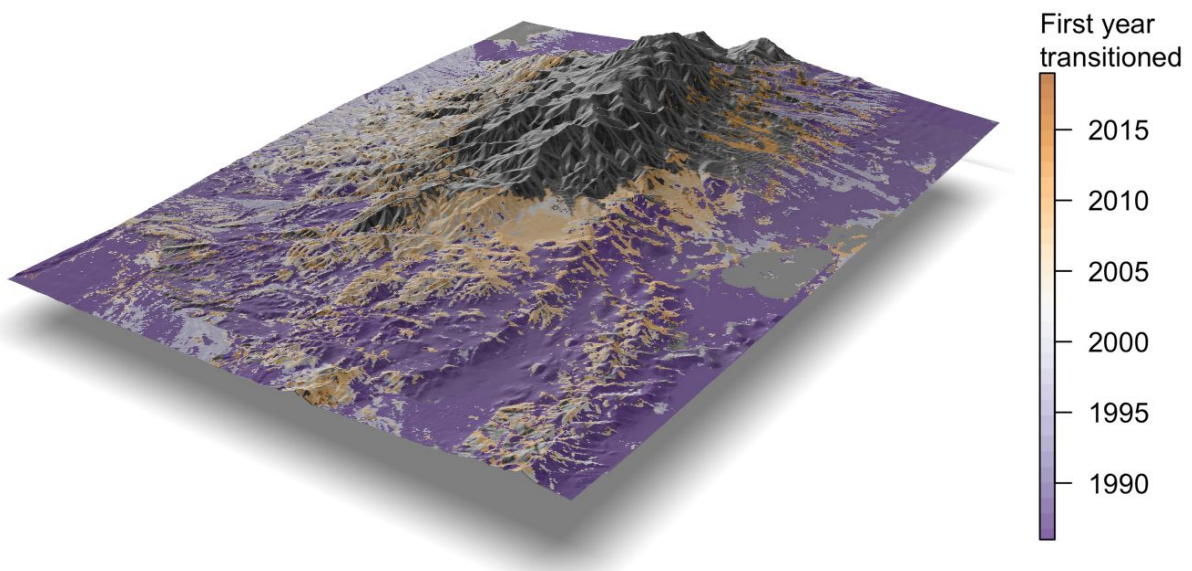
Figure 4. Example of elevational movement of annual grassland transitions at Cain Mountain, Central Basin and Range ecoregion, NV, USA. Non-annual grassland land cover in grey. The high elevation margin of annual grasslands ascended from approximately 1400 to 2000 m from 1986–2019.

The multi-decadal increase in extent of annual grasslands was clear and unambiguous despite short-term fluctuations corresponding to increasingly severe episodes of spring drought (Fig. 2, S4). Consistent with the high interannual variability in cover of annuals previously described (28), short-term minima in extent observed in 1992, 2004, 2010, and 2015 followed prolonged droughts (Fig. S4). Although droughts may temporarily inhibit annual grasses, climate drying and warming may facilitate annual dominance over the long term by promoting larger and more frequent fires (3) and weakening competition from perennial grasses and shrubs (33).

Among the most threatened biomes of North America (39), sagebrush and salt desert shrublands and their biota occupy a fragile elevational band in the Great Basin that is compressed between annual grassland transitions at lower elevations and woodland expansion predominantly at higher elevations (40). Our analysis reveals that this squeeze is tightening as annual grasslands steadily expand upslope. Transformation of shrublands to annual grasslands comes with dire socio-ecological consequences. Sagebrush and other shrubs lost in transitions are keystones supporting much of the region's wildlife (8). Larger and more frequent wildfires directly threaten not only ecosystems, but also human health (41, 42). With or without fire, annual grassland transitions and woodland expansion threaten the forage base that sustains livestock operations and rural economies (43). The pace and scale of transitions supports rapid adoption of new triage approaches being proposed to manage invasive annual grasses in the region (44, 45). Strategies that proactively prevent less invaded rangelands from transitioning must quickly replace the urge to restore all annual grasslands to their historical native plant communities, which is costly and ineffective. Without a paradigm shift in management, the archetypal shrubland ecosystems of the Great Basin could be largely transformed into highly flammable, depauperate annual grasslands and woodlands within a lifetime.

Materials and Methods

Study area

We characterized expansion and elevational movement of annual grasslands within three level III ecoregions (46) that overlap the hydrologic Great Basin and share similar climates and potential vegetation (Fig. 1). These include the Central Basin and Range (CBR), Northern Basin and Range (NBR), and Snake River Plain (SRP). Within these ecoregions, we limited our analyses to rangeland land cover as defined by Reeves and Mitchell (47). We also excluded agricultural land cover identified as hay, alfalfa, and idle cropland in the Cropland Data Layer (48).

Characterizing trends

We summed the area of pixels classified as annual grasslands (see Supplemental Information for detailed classification methods) to derive annual estimates of the areal extent of annual grasslands within each ecoregion. We then fit ARIMA models to these time series to characterize trends in areal extent over the study period. We automatically selected the ARIMA error structure for the time series from each ecoregion using the auto.arima function from the 'forecast' package in R (version 8.12; 49), employing AIC_c to select the most parsimonious model structure. We set allowdrift = TRUE to recover estimates of the trend (or drift) of each time series, if present. This is equivalent to fitting a linear regression with ARMA errors.

We examined trends in the elevation of newly-appearing annual grasslands through time to test whether the elevational distribution of pixels transitioning to annual grasslands changed over the duration of the time series. For pixels classified as annual grassland in ≥1 yr, we determined the earliest year in the time series that the pixel was assigned to the annual grassland cluster (transition year). Omitting pixels already classified as annual grasslands in the beginning of the time series, we randomly sampled n = 1,000 pixels from each transition year in each ecoregion and determined their elevations from the USGS National Elevation Dataset ⅓ arc-second digital elevation model. We used quantile regression to test for temporal trends in the 5th percentile (τ = 0.05), median (τ = 0.50), and 95th percentile (τ = 0.95) of elevations. For each response, we compared 4 models: temporal trend (linear effect of year), ecoregion effect (factor with 3 levels), temporal trend + ecoregion effect (additive), and a year × ecoregion interaction using AIC. Quantile regression models were fit with the 'quantreg' package (v 5.67; 50) in R, and standard errors and confidence intervals of coefficients were computed from 1,000 bootstrap samples.

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