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Vegetation responses to sagebrush-reduction treatments measured by satellites

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ABSTRACT

Time series of vegetative indices derived from satellite imagery constitute tools to measure ecological effects of natural and management-induced disturbances to ecosystems. Over the past century, sagebrush-reduction treatments have been applied widely throughout western North America to increase herbaceous vegetation for livestock and wildlife. We used indices from satellite imagery to 1) quantify effects of prescribed-fire, herbicide, and mechanical treatments on vegetative cover, productivity, and phenology, and 2) describe how vegetation changed over time following these treatments. We hypothesized that treatments would increase herbaceous cover and accordingly shift phenologies towards those typical of grass-dominated systems. We expected prescribed burns would lead to the greatest and most-prolonged effects on vegetative cover and phenology, followed by herbicide and mechanical treatments. Treatments appeared to increase herbaceous cover and productivity, which coincided with signs of earlier senescence − signals expected of grass-dominated systems, relative to sagebrush-dominated systems. Spatial heterogeneity for most phenometrics was lower in treated areas relative to controls, which suggested treatment-induced homogenization of vegetative communities. Phenometrics that explain spring migrations of ungulates mostly were unaffected by sagebrush treatments. Fire had the strongest effect on vegetative cover, and yielded the least evidence for sagebrush recovery. Overall, treatment effects were small relative to those reported from field-based studies for reasons most likely related to sagebrush recovery, treatment specification, and untreated patches within mosaicked treatment applications. Treatment effects were also small relative to inter-annual variation in phenology and productivity that was explained by temperature, snowpack, and growing-season precipitation. Our results indicated that cumulative NDVI, late-season phenometrics, and spatial heterogeneity of several phenometrics may serve as useful indicators of vegetative change in sagebrush ecosystems.

1. Introduction

Characterization of ecosystem responses to natural disturbances and management actions from local to landscape scales is fundamental to advancing strategies for ecosystem restoration and maintaining biological diversity (Folke et al., 2004). The evolution of theory on community development that provides guidance on ecological responses to management and natural disturbances has relied on field observations that have a limited spatio-temporal scope (Pickett et al., 1987; Walker et al., 2007; Vellend 2016). This limits discrimination of broad pattern from local anomaly and inhibits ability to obtain comprehensive, synthetic understanding of ecological phenomena. Spatio-temporally extensive assessment of ecological disturbance, now afforded by archives of satellite imagery with high spatial and temporal resolutions, can not only help assess efficacy of alternative management strategies, but also can aid understanding the organization and function of ecosystems (Kennedy et al., 2009; Wang 2012; Nauman et al., 2017). Measures of ecosystem components and change derived from satellite imagery can yield ecological indicators with desirable qualities (Noss 1990) because of their objectivity, repeatability, wide availability, and extensive spatio-temporal coverage at high resolutions (Klein et al., 2017).

The normalized difference vegetation index (NDVI) is derived from red and near-infrared bands of spectral reflectance in satellite imagery. The index measures vegetation greenness as an indicator of primary productivity (Tucker 1979). Time series of NDVI values provide a useful tool to measure spatially explicit changes in vegetation (Pettorelli et al.,

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2005). Such changes have been linked to other dynamics such as herbivore foraging behavior, movement, and fitness (Pettorelli et al., 2007, 2011; Merkle et al., 2014; Stoner et al., 2016). As such, NDVI has a long history of applications in studies of vegetation and as an indicator of ecosystem change (Yengoh et al., 2014). Despite the extensive use of NDVI for measuring ecosystem dynamics, novel indicators and applications in many ecosystems remain unexplored. No study has evaluated NDVI time series from satellite imagery to measure changes in vegetation resulting from management actions in sagebrush (*Artemisia* spp.) ecosystems. Biodiversity in this ecosystem is at risk from climate change and a history of management that has ultimately altered ecosystem function and composition (Noss and Cooperrider 1994; Chambers et al., 2017), e.g., via invasive grasses and consequently altered fire cycles.

The sagebrush ecosystem covers much of western North America and supports unique biota, but it has been diminished or altered through development, agriculture, livestock, invasive species, fire suppression, and management actions designed to reduce sagebrush cover (Davies et al., 2011; Miller et al., 2011; Beck et al., 2012). In the mid-20th century, most prescribed treatments sought to reduce sagebrush cover to stimulate production of grasses and forbs for livestock (Vale 1974; Beck and Mitchell 2000). More recently, sagebrush management has aimed to improve wildlife habitat and restore native ecosystems (Norvell et al., 2014, Dahlgren et al., 2015; Smith and Beck 2017). Management of sagebrush has come under increased scrutiny as recovery of imperiled species dependent upon these systems has become a priority for conservation groups and land management agencies (Knick and Connelly 2011; Chambers et al., 2017). Wildlife responses to sagebrush reduction have varied by species, sagebrush subspecies, and treatment application. Most studies have examined responses of sage-grouse (*Centrocercus* spp.; Dahlgren et al., 2006, Hess and Beck 2012; Dahlgren et al., 2015; Smith and Beck 2017), whereas few have examined other birds (Norvell et al., 2014; Lukacs et al., 2015), pygmy rabbits (*Brachylagus idahoensis*; Wilson et al., 2011), mule deer (*Odocoileus hemionus*; Bergman et al., 2014, 2015), and butterflies (McIver and Macke 2014). Still, the ecological effects of sagebrush treatments and whether they improve wildlife habitat or meet goals of ecosystem restoration remain poorly understood (Beck et al., 2012).

Remarkably little is known about alternative treatment effects on plant phenology, an important factor for wildlife within sagebrush ecosystems (Merkle et al., 2016). Birds and ungulates are known to time their migrations with the annual green-up period (van der Graaf et al., 2006; Merkle et al., 2016). Deer, for example, maximize foraging efficiency by following the green-up of vegetation as they migrate from winter to summer ranges (Aikens et al., 2017). This relationship has been effectively modeled with the date of maximum instantaneous rate of green-up (IRG) for vegetation based on time series of NDVI values (Bischof et al., 2012) from the Moderate Resolution Imaging Spectrometer (MODIS) aboard the Terra satellite (Gao et al., 2006). Measures of phenology (phenometrics) derived from satellite imagery reflect the collective phenologies of vegetative communities, known as land-surface phenology, because multiple plant species occur within individual image pixels (Henebry and de Beurs 2013). Although some differences between ground and satellite measures of phenology have been detected, overall correlation has been sufficient to identify phenometric patterns that influence resource use by animals (Coops et al., 2012; Merkle et al., 2014; Garroutte et al., 2016). Phenometrics may serve as relevant indicators of ecosystem change, but their application to date in assessments of natural disturbances or management activities has been limited. Sagebrush treatments are known to change composition and biomass of vegetation (Wambolt and Payne 1986; Pyke et al., 2014, Swanson et al., 2016), which in turn can change land-surface phenology (Kremer and Running 1993; Bradley and Mustard 2008). Furthermore, changes in soil chemistry and microclimate associated with sagebrush removal can alter phenology of some plants (Old 1969; Kauffman et al., 1997; Wrobleski and Kauffman, 2003).

We evaluated effects of three sagebrush treatments on metrics of vegetative cover, phenology, and productivity in southwest Wyoming, where treatments date back to the 1960s and cover about 5% of the landscape. Declining populations of ungulates in this region track phenology for their migrations, which has raised concern over habitat management and integrity of migration routes (Sawyer et al., 2009; Edmunds et al., 2016). Mismatches in plant phenology between treated and untreated areas could result in disrupted migration routes or suboptimal foraging for ungulates. We compared vegetative characteristics of treated sites to nearby untreated sites after accounting for the time since treatment and local environmental factors. Our objectives included: 1) quantifying effects of prescribed-fire, herbicide, and mechanical treatments on vegetative cover, productivity, and phenology, and 2) describing how vegetation changes with time following these treatments. We hypothesized that treatments would increase the ratio of herbaceous to sagebrush cover and accordingly shift phenologies towards those typical of grass-dominated systems. We expected prescribed burns would lead to the greatest and most-prolonged effects on vegetative cover and phenology, followed by herbicide and mechanical removal treatments (Wambolt and Payne 1986; Lesica et al., 2007).

2. Materials and methods

2.1. Study site

Our study domain was in the Upper Green River watershed in Sublette County, Wyoming, USA, where treatments to reduce sagebrush have been applied since the 1960s and were distributed across approximately 8000 km^2 (Fig. 1). Summers were dry with mean high temperatures of 22–28 °C in July based on 30-year normal temperatures (PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created 21 April 2017). Annual precipitation ranged from 20 to 80 cm. Winters were cold with mean daily low temperatures of −13 to −22 °C in January. Elevations of our study sites ranged from 2094 to 2565 m. Lower elevations were dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*), and higher sites were dominated by mountain big sagebrush (*A. t. vaseyana*) (Knight 1994). Other common sagebrush species in this area included black sagebrush (*A. nova*), silver sagebrush (*A. cana*), and low sagebrush (*A. arbuscula*). Rabbitbrush (*Ericameria nauseosa*, *Chrysothamnus viscidiflorus*), Gardner's saltbush (*Atriplex gardneri*), and winterfat (*Krascheninnikovia lanata*) were interspersed with sagebrush at relatively low densities. Common native grasses included Idaho fescue (*Festuca idahoensis*), needle and thread (*Hesperostipa comata*), thickspike wheatgrass (*Elymus lanceolatus)*, Letterman's needlegrass (*Stipa lettermani*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and bottlebrush squirreltail (*Elymus elymoides*). Invasive cheatgrass (*Bromus tectorum*) was a common annual grass. The forbs included aster (Asteraceae), buckwheat (*Eriogonum* spp.), clover (Fabaceae), fleabane (*Erigeron* spp.), and phlox (*Phlox diffusa*). Most lands were public and managed by the Bureau of Land Management for multiple use including energy development, livestock grazing, and recreation.

2.2. Treatments

Locations of 545 vegetation treatments covering 587 km^2 in the Upper Green River Valley from 1955 to 2015 were documented by BLM, Wyoming Game and Fish Department (WGFD), and the University of Wyoming. Each record describes the treatment type, location, dominant vegetation, and year of treatment. Of these records, 175 treatments were applied exclusively to Wyoming big sagebrush, and 122 treatments were applied only to mountain big sagebrush. Sagebrush treatment areas covered 395 km^2 and ranged from < 1 ha to 2355 ha with a median of 13 ha. The remaining treatments were applied to aspen-dominated stands, crops, or other vegetation. Many historic treatment areas were mapped based on treatment records of general locations (e.g., Township, Range, Section, and Quarter), aerial

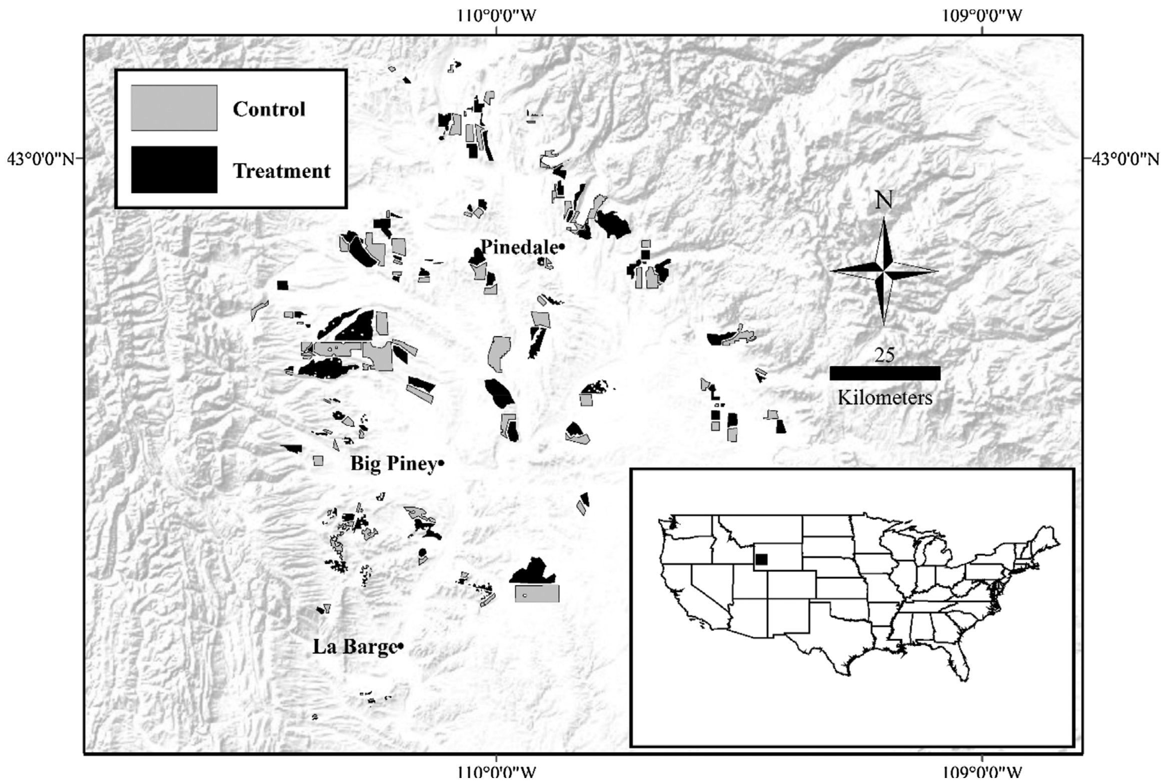

Fig. 1. Study area and sagebrush-reduction treatments within the Upper Green River Valley in southwest Wyoming, USA, 1960–2015. Control sites were untreated areas paired with adjacent or nearby prescribed-fire, herbicide, or mechanical treatments for analyses of vegetative characteristics. (black and white; two columns). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

photos, and consultation with range managers with first-hand knowledge of treatment areas dating back to the 1960′s. Most treatments were visible within aerial photos taken near the time of the treatment, which provided a means to delineate the spatial extent of the treatment with high confidence. Records of treatments not visible in historic photos or discernible with ancillary data were discarded.

We screened the treatments to ensure that selected sites met our analysis criteria for consistency across treated areas and representation of prescribed-fire, herbicide, and mechanical treatments. Specifically, we analyzed treatments that covered > 45 ha and ≥9 MODIS cells (250-m resolution), to ensure that measures of phenology and productivity were derived from several pixels within each site. All treated areas met this area requirement after omission of 1) the outer 125 m of the treatment area, to ensure that associated MODIS cells (250 m) did not cover areas outside the treatment; and 2) any areas disturbed by energy developments. This resulted in 58 total sites that included 11 fire-treated sites (3 Wyoming big sagebrush, 8 mountain big sagebrush), 38 herbicide-treated sites (29 Wyoming big sagebrush, 9 mountain big sagebrush), and 9 mechanically treated sites (7 Wyoming big sagebrush and 2 mountain big sagebrush). Across the 58 sites, treatments were applied between 1960 and 2008 (Table 1).

Treatment records varied in the amount of information to describe applications. Some records specified the type of herbicide (e.g., Spike 20P) or mechanical (e.g., mowing or chaining) treatment, whereas many did not. Photos and treatment notes from a visit to several treated areas in 2006 indicated that 4-dichlorophenoxyacetic acid (2, 4-D) was commonly applied in the 1960′s, resulting in high sagebrush kill-rates (80–90%). Sagebrush at these sites had recovered to levels similar to untreated areas by 2006 but lacked sagebrush in older age classes based on visual inspection. Tebuthiuron (e.g., Spike 20P or Graslan Brush Bullets 250) was used in more recent treatments (> 1980), where applications of < 1.1 kg active ingredient/ha were administered from aircraft to thin sagebrush (e.g., 50–70% removal). Leave-strips or partial treatments were applied to create mosaics of variable sagebrush densities. Mechanical treatments of mowing, chaining, or aerating were applied in similar patterns that left old sagebrush in untreated strips (e.g., 30-m wide) within project areas. Prescribed-fire treatments were applied in the spring or fall and targeted 40–60% removal of sagebrush. Fire efficacy for sagebrush removal likely varied with fuels, weather, and local factors that contributed to a mosaic of varying sagebrush removal. Post-treatment monitoring at a subset of these sites indicated that all treatments increased herbaceous cover (Wyoming Game and Fish Department, 2011). Sites treated with Lawson aerators recovered canopy cover of sagebrush in < 7 years, whereas recovery was much slower in prescribed burns (Wyoming Game and Fish Department, 2015). The lack of outliers in our analysis suggests that any widely varying treatment effects from differences in application or sub-treatment (e.g., mow versus aerator) were not apparent in our measures of vegetation characteristics. We obtained original documentation with details of treatment applications for several sites from the Land Treatment Digital Library (Pilliod and Welty 2013).

For each treated area, we selected an untreated area nearby to serve as a paired control (Fig. 1), for which similarity to treated sites was maximized based on area, sagebrush subspecies, elevation, and soil type. In most cases, controls were immediately adjacent to their paired, treated sites except for a 125-m buffer between treated and control areas that ensured MODIS pixels in control sites did not overlap any treated areas. In addition, controls were not placed near major roads,

Table 1
Treatment sample sizes by sagebrush subspecies (WBS = Wyoming big sagebrush, MBS = mountain big sagebrush) and ranges of elevation, treatment areas, and application years.

Treatment	WBS	MBS	Total *n*	Elevation (m)	Year	Area (ha)
Herbicide	29	9	38	2103–2565	1960–2007	49–1906
Mechanical	7	2	9	2094–2357	1960–2008	47–1826
Fire	3	8	11	2263–2554	1989–2001	61–1550

cities, other vegetation treatments, or private lands, because of uncertainty in their management. Sagebrush distribution by dominant subspecies was available from a U.S. Geological Survey (USGS) GAP land cover map with classifications of dominant sagebrush subspecies. These classifications matched *in-situ* field data at all $n = 58$ treated sites. Elevation was acquired from the USGS National Elevation Dataset (10-m resolution). We used the State Soil Geographic (STATSGO) data set (Soil Survey Staff, 2017) to guide selection of control sites, and we were able to place nearly all controls within the same soil map unit as their paired treated site. We masked 150-m buffers around pad scars from energy development and 250-m buffers around oil wells from treatment and control polygons to omit these areas from data extraction and analysis. Finally, we visually inspected all treated and control sites in high-resolution satellite imagery (≤0.5 m resolution, DigitalGlobe, caltopo.com) to ensure sites represented sagebrush ecosystems. We omitted one forested and one developed site from the analysis that were not screened with our GIS layers. All data extraction and data analyses were performed in ArcMap 10.1 (Environmental Systems Resource Institute, Redlands, CA, USA).

We created indices of temperature, growing-season precipitation, and snowpack from weather station data (SNOTEL, ACIS) to serve as model covariates that might explain inter-annual variation in phenometrics and productivity. We averaged daily mean temperatures between February 5 to April 5 across 12 SNOTEL stations in the vicinity of our study area for each year from 2001 to 2016. This period represents the 60 days prior to the average Julian date (95) for the start of spring at our sites and is known to influence phenology (Cong et al., 2013). Growing-season precipitation was represented as the amount of precipitation from March through August, averaged over 12 SNOTEL stations and 3 ACIS stations, for each year. We averaged estimates of snow water equivalency (SWE) for April 1 across 12 SNOTEL stations to represent snowpack for each year.

2.3. Vegetative cover, phenology, and productivity

Within each treatment and control polygon, we extracted the mean and standard deviation of pixel values from rasters that represented vegetative cover, phenology, and productivity. We obtained cover percentages by sagebrush (all species), herbaceous vegetation, and bare ground from 30-m-resolution maps derived from LandSat and 2.4-m resolution QuickBird imagery acquired in 2006 and 2007 (Homer et al., 2012). These map products, developed by USGS, are publicly available on ScienceBase.gov. Mapped estimates of percent cover by sagebrush, herbaceous vegetation, and bare ground used in our analyses were rigorously validated with field measures by Homer et al. (2012). Root mean square errors for percent cover of each type based on an independent accuracy assessment were: sagebrush = 5.47, herbaceous = 12.9, and bare ground = 15.9. Phenology and productivity for years 2001–2016 inclusive were estimated from NDVI time series obtained from bands 1 and 2 (250-m spatial and 8-day temporal resolutions) of the MOD09Q1 data product from the MODIS Terra satellite. For each year and pixel, we fit a double logistic curve to smooth the NDVI time series following methods of Bischof et al. (2012) and Merkle et al. (2016). Prior to fitting curves, 1) NDVI values < 0 and pixels obscured by clouds were omitted; 2) values for November-February were defined as the 0.025 quantile of each pixel's time series; 3) a 3-window median filter was applied; and 4) the time series was scaled between 0 and 1 based on the upper 0.975 quantile of each pixel's time series. For sites with snow cover that persisted beyond February, winter values were assigned until snow cover was absent in 2 consecutive 8-day periods based on the snow cover band in the MOD09A1 data product (500-m spatial and 8-day temporal resolution). From the fitted NDVI curves, we extracted Julian dates for the start of spring as the highest values for the 2nd derivative of the spring side of the NDVI curve and the end of spring as the lowest value (Fig. 2). All derivatives were scaled from 0 to 1. We used the highest value of the 1st derivative on the spring side of the NDVI curve as the date of maximum instantaneous rate of green-up, and that of the fall side of the curve as the date of the maximum rate of senescence. We also extracted the dates of peak NDVI and calculated the length of spring as the number of days between spring start and end. For a measure of productivity, we calculated cumulative or integrated NDVI as the sum of the unscaled NDVI values for each year subtracted by the minimum value (Pettorelli et al., 2005).

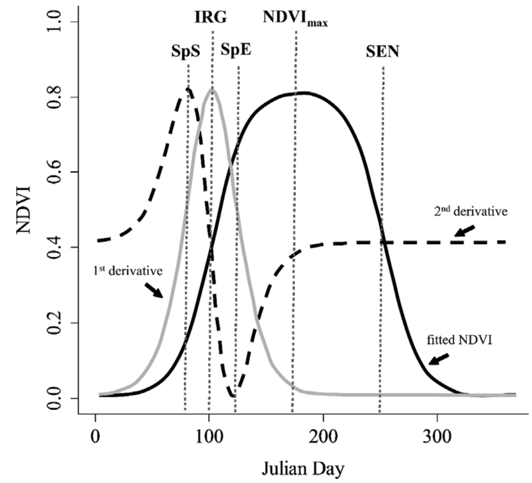

Fig. 2. Phenometrics derived from time series of NDVI values included the dates for spring start (SpS), spring end (SpE), maximum instantaneous rate of green-up (IRG), maximum NDVI ($NDVI_{max}$), and maximum rate of senescence (SEN). (black and white; one column).

2.4. Data analysis

We used linear models with mixed effects in R package LME4 (Version 1.1-12, https://cran.r-project.org/web/packages/lme4/index.html, accessed 7 Apr 2017) to test effects of

each treatment on vegetative cover, phenology, productivity, and the spatial heterogeneity of these metrics after accounting for the time since treatment and relevant environmental factors ($\alpha = 0.05$). Spatial heterogeneity was represented by the coefficient of variation (CV) calculated as the ratio of the standard deviation of pixel values within each site to the site mean (van Leeuwen et al., 2010). All models included a random factor that linked treated sites with their paired controls and, for the analyses of phenology and productivity, provided necessary structure for analysis of repeated measures from 2001 to 2016. There were 1796 observations among the 58 treated sites and their paired controls for analyses of phenology and productivity. Models also included the treatment as a fixed-effect with categories of control, prescribed fire, herbicide, and mechanical. We accounted for time since treatment as a fixed effect with a linear or nonlinear

function depending on model fit. For each response, we fit models with and without log transformation of the time since treatment, and then analysis proceeded with the form that resulted in the lowest Akaike information criterion with correction for small sample sizes (AIC_c; Burnham and Anderson 2002). All models included fixed-effect covariates for the mean elevation, dominant sagebrush subspecies (Wyoming or mountain big sagebrush), and area-to-edge ratio of each site. The area-to-edge ratio provided a means to account for differences in recovery associated with the size of treatment area and edge effects. We expected sites with high ratios to recover sagebrush more slowly because of lower likelihood of seed dispersal away from treatment edges. For analyses of phenology and productivity, fixed-effect covariates for temperature, snowpack, and growing-season precipitation were included as repeated measures from 2001 to 2016. For analyses of vegetative cover, we excluded treatments after 2005 because the cover maps were generated with Quickbird imagery acquired in 2006. We also excluded some sites where cover estimates were not available, which resulted in 50 treated areas and their paired controls that were suitable for analysis.

We tested interactions between treatments and time since treatment to determine whether treatment effects changed over time as vegetation recovered from the treatment. Although some interactions were statistically significant, most did not explain enough variation to warrant their inclusion in the models because AIC_c values for models with interaction were within 2 units of models with only main effects. We report significant interactions, but also present treatment effects from models without interactions because most were inconsequential. Treatment effects based only on analyses of main effects represent the difference between controls and treatments averaged over all years in the data. Coefficients for main effects in the presence of interactions represent the difference between treated and control sites one year after treatment, and interaction coefficients measure the annual change in trajectory of the treatment relative to controls. We also explored two- and three-way interactions among sagebrush subspecies, treatment, and time since treatment to determine whether recovery trajectories varied by sagebrush subspecies. Because there was little evidence of these interactions across responses, we reported results of models with only main effects for subspecies. Effects of covariates are reported from models without interactions because they were largely unaffected by interactions between treatments and the time since treatment. For all analyses with mixed-effects models, we constructed 95% profiled confidence intervals and tested effects with Type II Wald *F*-tests that used the Kenward-Roger estimate for degrees of freedom (Kenward and Roger 1997).

To investigate effects of mixed-vegetation communities on satellite-based estimates of phenology and productivity, we used linear models to relate our measures of phenology and productivity to the ratio of herbaceous to sagebrush cover after accounting for elevation. For this analysis, we used a subset of sites representing the 10 highest and 10 lowest values for the ratio of herbaceous to sagebrush cover based on estimates from Homer et al. (2012) data and the metrics of phenology and productivity from 2006. Cover ratios were expressed categorically as high or low. We expected sites dominated by herbaceous vegetation to have higher productivity and experience senescence earlier than sites dominated by sagebrush.

3. Results

3.1. Vegetative cover

Results supported our hypotheses that treatments to remove sagebrush would increase herbaceous cover and result in phenology more indicative of grasslands (Figs. 3 and 4, A.1, A.2). However, effect magnitudes estimated from satellite imagery were small across all responses. At sites treated with fire, herbaceous cover was 3.7 percentage points higher than the control mean of 15.0% ($F_{1,55} = 23.7, p < 0.001$, 95% CI 2.3, 5.2). Some evidence suggested that herbaceous cover was higher on sites treated with mechanical removals ($F_{1,62} = 2.79$, $p = 0.100$) or herbicides ($F_{1,50} = 3.98$, $p = 0.051$) relative to controls, but 95% confidence intervals for mechanical effects slightly overlapped zero. We expected cumulative NDVI to increase with herbaceous cover, and it was slightly higher (≤3.6% of the mean) in areas treated with fire ($F_{1,1770} = 4.10, p = 0.043$), herbicides ($F_{1,1749} = 37.7, p < 0.001$), and mechanical removals ($F_{1,1784} = 7.62$, $p = 0.006$), compared to control areas.

3.2. Phenology

Most early-season phenometrics were similar between treatments and controls, regardless of treatment type and time since treatment (Fig. 4, A.2). In contrast, mid- or late-season phenometrics in treated areas often differed from their controls. Specifically, dates of maximum NDVI and senescence rate occurred earlier in most treated areas relative to controls. Effect magnitudes were small for phenometrics (< 7 days), in cases where treatments differed from controls. Plots of phenometrics and productivity for treatments applied during the MODIS time-series (i.e., 2001–2016) illustrate small effect sizes evident in our analyses (Fig. 5). For example, data points for IRG at treated sites followed those of their paired control sites with little deviation. Inter-annual differences in IRG exceeded 30 days within sites, but paired sites usually

achieved IRG within 5 days of each other in a given year. Clearly, factors other than sagebrush treatment had strong effects on phenology, as indicated by the influence of our covariates for temperature, snowpack, and growing-season precipitation (Table 2). Changes to plant

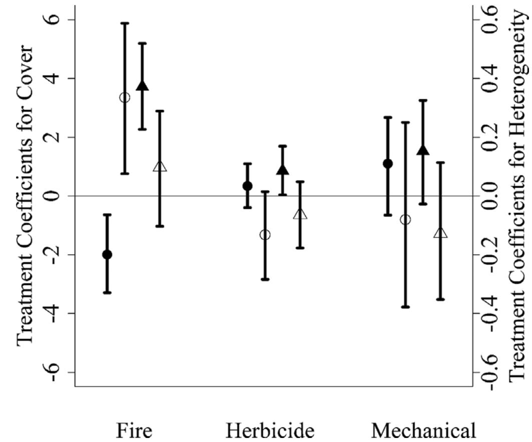

Fig. 3. Coefficients and 95% CIs for main effects of prescribed-fire, herbicide, and mechanical treatments on sagebrush cover (solid circles), spatial heterogeneity (CV) of sagebrush cover (hollow circles), herbaceous cover (solid triangles), and spatial heterogeneity of herbaceous cover (hollow triangles) in Wyoming, USA, 1960–2005. Main effects represent the difference between controls and treatments averaged over all years in the data. Units for vegetative cover are percentage points. Log transformations were applied to heterogeneity responses. (black and white, one column).

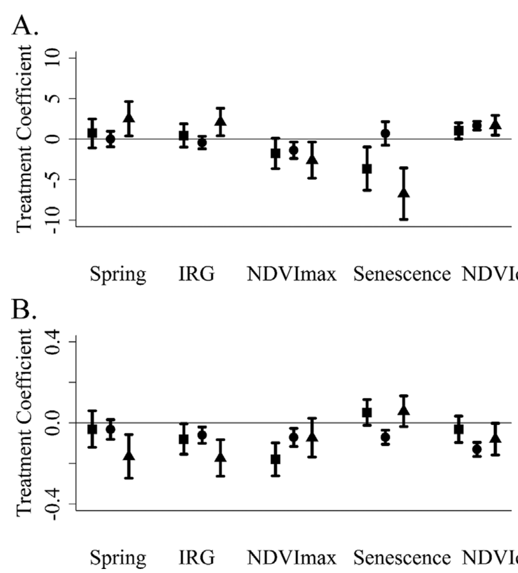

Fig. 4. Main effects (mean and 95% CIs) of prescribed-fire (square), herbicide (circle), and mechanical (triangle) treatments on phenology and productivity of vegetation in Wyoming, USA, 1960–2016. Main effects represent the difference between controls and treatments averaged over all years in the data. Units are Julian dates of occurrence (A) for start of spring, maximum instantaneous rate of green-up (IRG), maximum NDVI, and maximum rate of senescence. Cumulative NDVI (NDVIc) was the sum of vegetative indices over the year. The coefficients of variation for these metrics represented their spatial heterogeneity (B) and were log-transformed for analysis. (black and white; two columns).

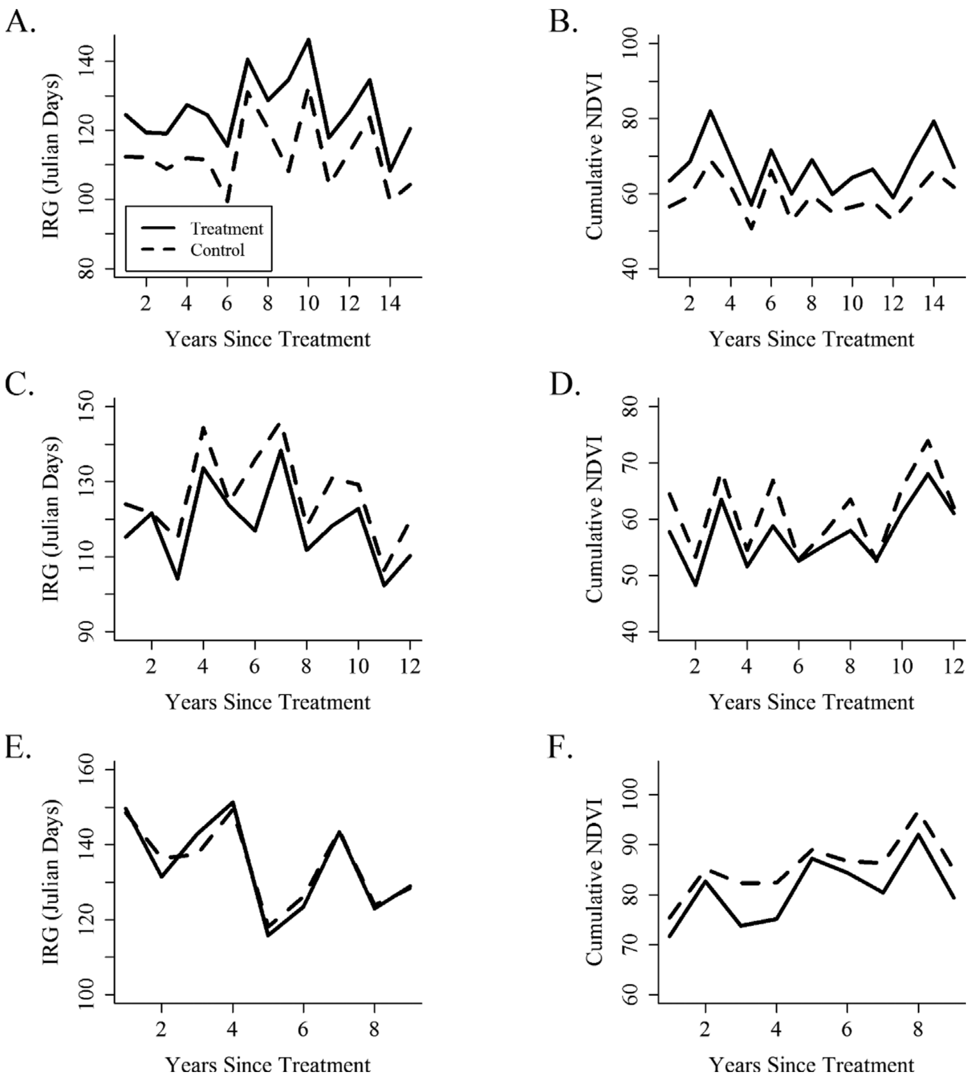

Fig. 5. The dates of occurrence for maximum instantaneous rate of green-up (IRG) and the cumulative NDVI for each year following treatment with prescribed fire in 2001 (A, B), herbicide in 2004 (C, D), and mechanical removals in 2007 (E, F) in Wyoming, USA. Each plot represents the measured response at a site that was treated during the time of image acquisition by MODIS. (black and white, 2 columns).

Table 2
Coefficients and SEs for abiotic covariates in the analysis of vegetative responses to prescribed-fire, herbicide, and mechanical treatments in sagebrush communities in Wyoming, USA, 1960–2016.

	Precipitation (cm)		SWE (cm)		Temperature °C	
	β	SE	β	SE	β	SE
Start of spring (days)	0.638*	0.036	0.240*	0.027	−5.31*	0.17
IRG (days)	0.317*	0.029	9.30e^{-2*}	2.16e^{-2}	−5.62*	0.14
Senescence (days)	1.94*	0.05	0.132*	0.041	2.63*	0.26
Max NDVI (days)	0.505*	0.038	−0.103*	0.028	−2.93*	0.18
Cumulative NDVI	0.597*	0.020	7.22e^{-2*}	1.49e^{-2}	3.48*	0.097

* Significant relationships ($p < 0.05$).

phenology associated with treatments were not substantial despite apparent differences in sagebrush and herbaceous cover that were evident in our analyses and visible in historical aerial imagery. Recent vegetative-cover estimates and satellite imagery revealed that sagebrush cover was high at many treated sites, which may reflect recovery and partial applications of treatments. Coefficients of variation (i.e., spatial heterogeneity) for phenometrics within sites were often lower in treated sites relative to controls, and differences were significant for several cases (Fig. 4, A.2). Mechanical and herbicide treatments initially decreased spatial heterogeneity of most phenometrics, but heterogeneity rebounded over time. These patterns may reflect homogenization of the plant community following treatments and subsequent recovery of sagebrush.

3.3. Recovery

Few interactions were evident to indicate that treatment effects on phenology changed with time since treatment (Fig. 6). Interactions between mechanical treatments and the time since treatment indicated that timing of spring start ($F_{1,1670} = 10.9$, $p < 0.001$), spring end ($F_{1,1676} = 13.3$, $p < 0.001$), and IRG ($F_{1,1673} = 17.1$, $p < 0.001$) occurred later at sites treated with mechanical removals relative to controls, but then occurred increasingly earlier over time. Mechanical treatments also hastened senescence, but this effect dissipated over time ($F_{1,1600} = 5.26$, $p = 0.022$). Herbicides increased cumulative NDVI over time relative to controls ($F_{1,1753} = 6.73$, $p = 0.010$).

Some evidence indicated that fire effects were more substantial than herbicide and mechanical treatments. For example, analysis of main effects indicated that sagebrush cover on fire-treated sites was 2.0 percentage points lower than the mean of 15.8% cover at controls based on differences between controls and treated areas averaged across all years following treatment ($F_{1,55} = 8.35$, $p = 0.006$, 95% CI 0.6, 3.3). In contrast, sagebrush cover was similar between controls and sites with herbicide or mechanical treatments. Also, the increase of herbaceous cover following treatments was greatest for fire. Furthermore, fire effects did not change over time based on phenometrics and their spatial heterogeneity, whereas these vegetative characteristics recovered

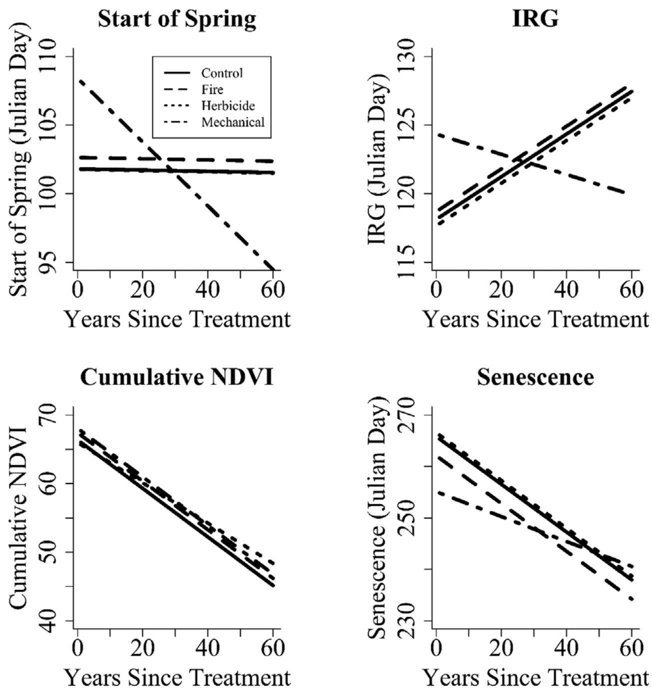

Fig. 6. Fitted values from mixed-effect models for phenology, and productivity for 1–60 years following sagebrush-reduction treatments. Interactions between mechanical treatments and time since treatments were evident for start of spring, IRG, and senescence, whereas effects of herbicides on cumulative NDVI varied with time relative to controls. Plots show estimated values for communties dominated by mountain sagebrush at average values for random intercepts, elevation, area-to-edge ratio, temperature, snow water equivalent, and growing-season precipitation for each year fitted. (black and white; two columns).

following herbicide and mechanical treatments. This suggests that sagebrush recovery occurred more rapidly following herbicide and mechanical treatments relative to fire.

3.4. Covariates

Temperature, snowpack, and growing-season precipitation strongly influenced ($p < 0.001$) most metrics of phenology and productivity (Table 2, A.1). All phases of phenology except senescence occurred earlier in years with warmer temperatures prior to green-up, whereas all phases occurred later with more growing-season precipitation. Cumulative NDVI increased with warmer temperatures ($F_{1,1778} = 1266$, $p < 0.001$), snowpack ($F_{1,1750} = 23.6$, $p < 0.001$), and growing-season precipitation ($F_{1,1743} = 928$, $p < 0.001$). Start of spring ($F_{1,1770} = 78.8$, $p < 0.001$), IRG ($F_{1,1770} = 18.5$, $p < 0.001$), and senescence ($F_{1,1772} = 10.6$, $p = 0.001$) occurred later in years with greater snowpack.

Covariates for time since treatment, elevation, sagebrush subspecies, and the area-to-edge ratio for treatments explained significant variation in most metrics for vegetative cover, phenology, and productivity (Table 3, A.2).

3.5. Vegetative cover and NDVI-based metrics

Our NDVI-based metrics varied little with the ratio of herbaceous cover to sagebrush cover, after accounting for elevation. Cumulative NDVI was higher on sites dominated more by herbaceous cover than sagebrush cover ($t_{17} = -2.66$, $p = 0.016$). Spring length and phenometrics did not differ between high and low ratios of herbaceous cover to sagebrush cover.

4. Discussion

4.1. NDVI metrics as indicators

Time series of NDVI values derived from satellite imagery can advance ecology and biological conservation by facilitating assessment of vegetative responses to disturbance and management activities at multiple spatial and temporal scales. The large seasonal and annual variations in NDVI within our time series indicate that temporal dynamics of vegetative communities in sagebrush ecosystems are substantial; such dynamics can be difficult to capture with field-based methods. Archives of satellite imagery can advance understanding of community change and disturbance (Nauman et al., 2017), especially when metrics like NDVI can discriminate vegetative communities explicitly in space and time (Bradley and Mustard 2008). The sensitivity of cumulative NDVI, late-season phenometrics (i.e., dates of maximum NDVI and maximum rate of senescence), and spatial heterogeneity of several phenometrics to sagebrush treatments suggest that they have good potential as ecological indicators for assessments of disturbance in sagebrush ecosystems. These metrics can complement static maps of vegetative cover (e.g., Homer et al., 2012, 2015) through their spatiotemporal coverage, wide availability, and biological relevance.

Several of the satellite-based measures of vegetative cover and phenology that were sensitive to sagebrush treatments have also explained habitat use by wildlife including Greater Sage-grouse (*Centrocercus urophasianus*; Kirol et al., 2015), Ferruginous Hawks (*Buteo regalis*; Wallace et al., 2016), Golden Eagles (*Aquila chrysaetos*, Tack and Fedy 2015), and several ungulate species (Merkle et al., 2016; Aikens et al., 2017). Ecological indicators that express biologically meaningful information for wildlife are particularly useful in assessments of management activities on habitat quality and biodiversity. The effects of sagebrush treatments or other disturbances on wildlife can be measured quantitatively with habitat suitability models. Such models include NDVI metrics sensitive to treatments as predictors of suitability. Under these circumstances, several extensions are possible to assess effects of sagebrush treatments on habitat amount, distribution, and connectivity (McRae et al., 2008). In addition, many habitat suitability models can be forecasted to assess risks to wildlife from proposed management actions or climate change (Lawler et al., 2009; Homer et al., 2015).

The archive of satellite imagery allowed us to retroactively assess effects of treatments applied over the past century. Short-term treatment effects were estimated for treatments applied before MODIS was launched, but were measured directly on recent treatments. Precision of effect estimates and understanding of long-term vegetation responses to disturbances should improve with lengthening of the archive of satellite imagery. This approach is efficient because it exploits existing data and analyses can be especially rapid in cloud-computing environments, where archives of satellite imagery now can be accessed and manipulated without cost (Klein et al., 2017). These techniques can be applied to other ecosystems (e.g., forests, meadows) or types of disturbances like wildfire (van Leeuwen et al., 2010) and management activites (e.g., timber harvest). Recent efforts by land-management agencies to catalogue vegetation treatments to support these types of analyses (Pilliod and Welty 2013) will provide rich datasets that should advance management and ecological theory on disturbance and recovery.

The primary challenges to this approach remain in validation and interpretation of results. Because indicators like IRG have explained resource use by wildlife (Merkle et al., 2016; Aikens et al., 2017), it is clear they are biologically meaningful and useful for research or management purposes. However, translating land-surface phenologies derived from satellite imagery to infer species-specific dynamics of vegetation can be difficult because NDVI values from individual image pixels often represent mixed-species communities (Henebry and de Beurs 2013). Efforts to map vegetation communities based on NDVI time series have shown that some communities have unique signatures,

Table 3
Coefficients and SEs for model covariates in the analysis of vegetative responses to prescribed-fire, herbicide, and mechanical treatments in sagebrush communities in Wyoming, USA, 1960–2016.

	Time Since Treatment		Elevation (km)		Species[a]		Area-to-Edge Ratio (ha/km)	
	β	SE	β	SE	β	SE	β	SE
Sagebrush%	5.80e^{-2}	3.14e^{-2}	22.0[*]	4.1	−2.80[*]	0.93	1.44e^{-2}	1.75e^{-2}
Herbaceous%	−2.68e^{-2}	3.38e^{-2}	7.98	4.48	−4.20[*]	1.00	2.51e^{-2}	1.90e^{-2}
Start of spring (days)	−2.41e^{-2}	4.24e^{-2}	66.3[*]	6.7	−5.79[*]	1.96	-3.11e^{-3}	3.07e^{-2}
IRG (days)	0.135[*]	0.034	50.2[*]	5.4	−7.65[*]	1.57	-1.92e^{-2}	2.46e^{-2}
Senescence (days)	−0.444[*]	0.061	58.3[*]	9.3	−8.88[*]	2.60	−0.161[*]	0.044
Max NDVI (days)	3.40e^{-2}	4.26e^{-2}	36.8[*]	6.5	−8.44[*]	1.82	−0.103[*]	3.1e^{-2}
Cumulative NDVI	−0.334[*]	0.027	73.6[*]	4.7	−8.40[*]	2.08	−5.65e^{-2}[*]	1.97e^{-2}

[a] Coefficients represent the value added to means for sites with mountain big sagebrush to estimate sites with Wyoming big sagebrush.
[*] Significant relationships ($p < 0.05$).

which supports their use for measuring vegetative change (Bradley 2014).

Our results generally support expectations that treatments to remove sagebrush should increase herbaceous vegetation (Wambolt and Payne 1986 Davies et al., 2012a; Swanson et al., 2016), resulting in higher productivity (i.e., cumulative NDVI) and altered phenology. The consistencies in our results for higher herbaceous cover, higher cumulative NDVI, and lower heterogeneity of phenometrics associated with treatments suggest changes in vegetative composition were large enough to detect in satellite imagery. Where statistically significant differences between controls and treatments were evident, however, effect sizes were small, based on our metrics derived from satellite imagery. In contrast, inter-annual variation in phenometrics and productivity was high relative to treatment effects and was explained by temperature, snowpack, and growing-season precipitation. Treatment effects on phenology and productivity may seem small because they represent a shift in community dominance away from sagebrush and towards herbaceous species, but interpreting NDVI values and their variability across vegetative communities remains an active area of research (Garroutte et al., 2016).

4.2. Vegetative cover

Several studies have assessed effects of sagebrush treatments with field measures of vegetation where overall direction of effects were similar to ours, but effect sizes across studies have differed considerably (Beck et al., 2012). For example, our results are consistent with other studies in finding that fire was more effective than herbicide and mechanical treatments at achieving long-term reductions in sagebrush cover and increases in herbaceous cover (Wambolt and Payne 1986; Wambolt et al., 2001; Ellsworth et al., 2016). However, our differences in cover of sagebrush and herbaceous vegetation between controls and fire-treated sites were small compared to near-complete eradication of sagebrush cover commonly observed following fire treatments (Wambolt and Payne 1986; Lesica et al., 2007; Pyke et al., 2014; but see Ellsworth and Kauffman 2017). Likewise, mechanical and herbicide treatments have been effective at reducing sagebrush cover to extremely low levels of coverage (Wambolt and Payne 1986; Sturges 1993; Davies et al., 2009), but our results did not show statistical differences in sagebrush cover between controls and sites with these treatments. Full recovery of sagebrush following fire has been estimated to take > 30 years for mountain big sagebrush, and considerably longer for Wyoming big sagebrush (Baker 2006; Lesica et al., 2007; Ellsworth et al., 2016). We likely detected sagebrush removal by fire because of the long period required for sagebrush recovery following fire and all fire treatments occurred within 17 years of the imagery used to estimate vegetative cover. In contrast, recovery can occur within 15 years after mechanical or herbicide treatments (Wambolt and Payne 1986; Davies et al., 2009). Because few herbicide and mechnical treatments in our data set occurred near the acquisition time for the imagery used to estimate vegetative cover, it is likely that most of these sites experienced some recovery of sagebrush prior to cover estimation, which resulted in underestimation of short-term treatment effects on sagebrush removal. In addition, managers increasingly have used herbicide or mechanical treatments to thin sagebrush or remove sagebrush in spatially-mosaicked patterns (Olson and Whitson 2002; Baxter et al., 2017). Whereas field studies have estimated treatment effects by sampling only within treated areas that may have a mosaic distribution (Dahlgren et al., 2006), our approach found relatively small effects because it did not discriminate treated and untreated patches within sites.

Sagebrush treatments are commonly applied to stimulate herbaceous vegetation, but end results have varied (Sturges 1993; Olson and Whitson 2002; Pyke et al., 2014; Swanson et al., 2016). For example, Wambolt and Payne (1986) found that herbaceous vegetation (kg/ha) at sites treated with fire or herbicide was more than doubled the amount at controls, 18 years after treatment. In contrast, Wambolt et al. (2001) did not find significant increases in herbaceous vegetation following fire treatments. Our effect estimates of < 4 percentage points in herbaceous cover associated with treatments are small relative to the findings of Wambolt and Payne (1986) because mean percent cover at our control sites was 15%. Nevertheless, our effect sizes for herbaceous cover fall within the range of variability reported by field studies of vegetation responses to sagebrush treatements.

Many field studies have documented complex, short-term responses of vegetative cover to sagebrush treatments that were not evident in our assessment (Sturges 1993; Watts and Wambolt 1996; Olson and Whitson 2002; Lesica et al., 2007; Davies et al., 2012a, 2012b, 2012c). Responses are often lagged, nonlinear, and depend on treatment and vegetation type, yet, our models indicated that linear fit was adequate for many responses to treatments. Linear recovery of sagebrush has been documented (Lesica et al., 2007; Davies et al., 2009), but any nonlinear responses in our data may have been masked by low sample sizes for recent treatments and mosaicked or partial treatments. Our ability to detect nonlinear responses with satellite-based measures will improve as time series of vegetative cover become available (Homer et al., 2015).

4.3. Phenology and productivity

Phenologies and NDVI time series of cheatgrass, perennial bunchgrass, and sagebrush differ in their timing of senescence and cumulative NDVI values (Kremer and Running 1993). Sagebrush are evergreen but develop relatively large, ephemeral leaves in late winter or early spring that supplement smaller, perennial leaves during the growing season (Miller and Schultz, 1987; Evans and Black 1993). The emergence of ephemeral leaves increases leaf area, which likely contributes to spring increases in NDVI values (Baghzouz et al., 2010). Green-up of herbaceous vegetation coincides with emergence of ephemeral leaves on sagebrush, but senescence of cheatgrass precedes senescence of perennial grasses by a month (Kremer and Running 1993). New perennial leaves and a second set of small, ephemeral leaves that persist until fall begin to emerge on sagebrush in late spring. Perennial leaves from the previous year and the first set of ephemeral leaves senesce and begin abscission in summer. These events initiate the seasonal decline in NDVI indicative of sagebrush senescence, but, unlike cheatgrass and perennial grasses, overall leaf activity of sagebrush continues for two more months. Cumulative NDVI of sites dominated by grass consistently exceeds that of sagebrush-dominated sites because NDVI of standing dead grass that remains throughout the season is higher than NDVI of bare ground, which is common in sagebrush communities (Kremer and Running 1993; Bradley and Mustard 2008). We found few differences between treated sites and controls based on early season phenometrics (e.g., spring start, spring end, IRG), but greater cumulative NDVI scores and earlier senescence at treated sites. The increases in herbaceous cover following treatments suggest increased dominance by grasses that exhibit these phenological characteristics. Although our results are consistent with these patterns, effect sizes for senescence were far less than one month and differences in cumulative NDVI were small relative to year-end values.

Small magnitudes of treatment effects on senescence and productivity likely reflect the mixture of grasses and sagebrush, which exhibit distinct phenologies and NDVI values across our sites. Whereas previous descriptions of NDVI-based phenologies for sagebrush and grass communities examined sites strongly dominated by each vegetation type, our sites had greater mixtures of these communities that we speculate could yield land-surface phenologies that represent an average of the grass and sagebrush communities weighted by their relative abundances. Although phenology of dominant vegetation is expected to be reflected in NDVI curves, little is known about how curves behave for mixed communities. Despite the seasonal exchange of ephemeral and perennial leaves, it seems unlikely that sagebrush contributes much to intra-annual fluctuations in the NDVI curve because *Artemisia* species are evergreen. Lower amplitudes of NDVI curves for sagebrush-dominated communities may reflect lower abundances of herbaceous vegetation, given that fluctuations in the NDVI curve are primarily driven by the herbaceous component. Our results suggest that cumulative NDVI increases with the ratio of herbaceous to sagebrush cover, consistent with previous findings (Kremer and Running 1993; Bradley and Mustard 2008). We could not discriminate changes in land-surface phenology due to shifts in species composition from phenological shifts within plant species (Wrobleski and Kauffman, 2003), but increased dominance by herbaceous vegetation following treatments was probably most influential on land-surface phenology. The presence of cheatgrass at some of our sites may have contributed to variation in our phenometric responses. Sagebrush treatments can have variable effects on cheatgrass invasions that depend on range condition and exposure to cheatgrass (Davies et al., 2012b, 2012c; Swanson et al., 2016). New methods that use time series of NDVI to map cheatgrass distribution (Clinton et al., 2010; Bradley 2014) could improve our understanding of vegetative responses to sagebrush treatments by providing a means to account for composition of herbaceous species.

Several covariates consistently explained significant variation in the responses suggesting that the metrics were sensitive to broad-, if not always local-scale, factors. As expected, timing of green-up occurred later with increasing elevation and at sites dominated by mountain big sagebrush. Although the area-to-edge ratio explained significant variation in some of our responses, no clear pattern emerged to suggest that seed source and proximity strongly affected our results. Inter-annual variability in phenometrics commonly exceeded the differences between controls and treatments. Much of this variation was explained by temperature, snowpack, and growing-season precipitation, underscoring the importance of accounting for these factors in analyses of phenology (Cong et al., 2013).

5. Conclusions

Time series of NDVI from MODIS constitute a unique and valuable tool for assessing vegetation responses to natural disturbances and management activities over landscapes and many years. Cumulative NDVI and late-season phenometrics like senescence were sensitive to sagebrush treatments and may serve as good indicators of vegetative change in sagebrush ecosystems. Differences between control and treated sites based on these metrics most likely reflected increased dominance of herbaceous vegetation after treatments. Spatial heterogeneity for most metrics was also sensitive to treatment and may reflect homogenization of NDVI curves that arises when vegetation communities are shifted to a more uniform mixture of sagebrush and herbaceous vegetation. Phenometrics for vegetation dynamics known to influence wildlife migrations (e.g., mule deer, moose, and bighorn sheep; Merkle et al., 2016; Aikens et al., 2017) were largely unaffected by treatments, as evidenced by the lack of changes to the timing of green-up. However, the influences of productivity and senescence timing on fall migrations of wildlife and their forage quality are unknown. Further assessment of treatment effects on wildlife is needed because local-level treatment effects on important forage species may not be captured with the methods of this study. Fire appeared more effective than herbicides and mechanical treatments for removing sagebrush, but all three treatments increased herbaceous coverage. Several researchers have cautioned the use of fire when restoration of sagebrush communities is an objective, especially when invasion by exotic plants is likely (Wambolt et al., 2001; Lesica et al., 2007; Beck et al., 2012). However, fire has also aided restoration of sagebrush communities invaded by conifers (Bates and Svejcar 2009; Miller et al., 2014) and will continue to be an important tool in sagebrush management. Satellite imagery offers objective and spatiotemporally extensive assessment of change in vegetation that can complement field studies and inform complex decisions on sagebrush management, such as application of fire for restoration. As archives of satellite imagery and associated map products grow, refinement of our method should capture nuanced responses of vegetation to management and disturbances to aid managers and improve understanding of ecosystem dynamics.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ecolind.2017.12.033.

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Appendix A

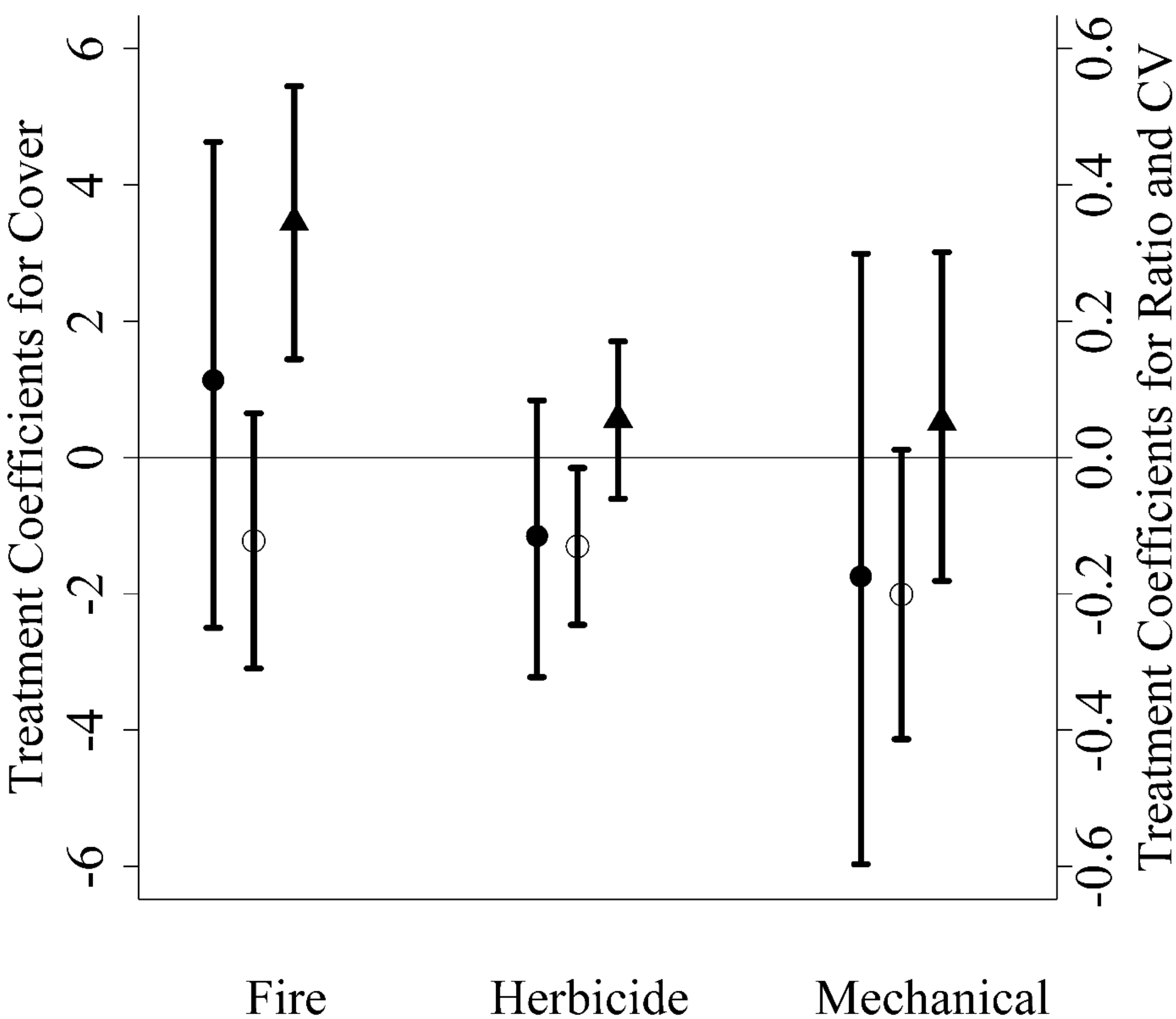

Figure A.1. Coefficients and 95% CIs for main effects of prescribed-fire, herbicide, and mechanical treatments on bareground (solid circles), CV (ie. spatial heterogeneity) of bareground (hollow circles), and the ratio of herbaceous to sagebrush cover (triangles) in Wyoming, USA, 1960-2005. Main effects represent the difference between controls and treatments averaged over all years in the data. Units for cover by bare ground are percentage points. Log transformations were applied to heterogeneity responses. (black and white; one column)

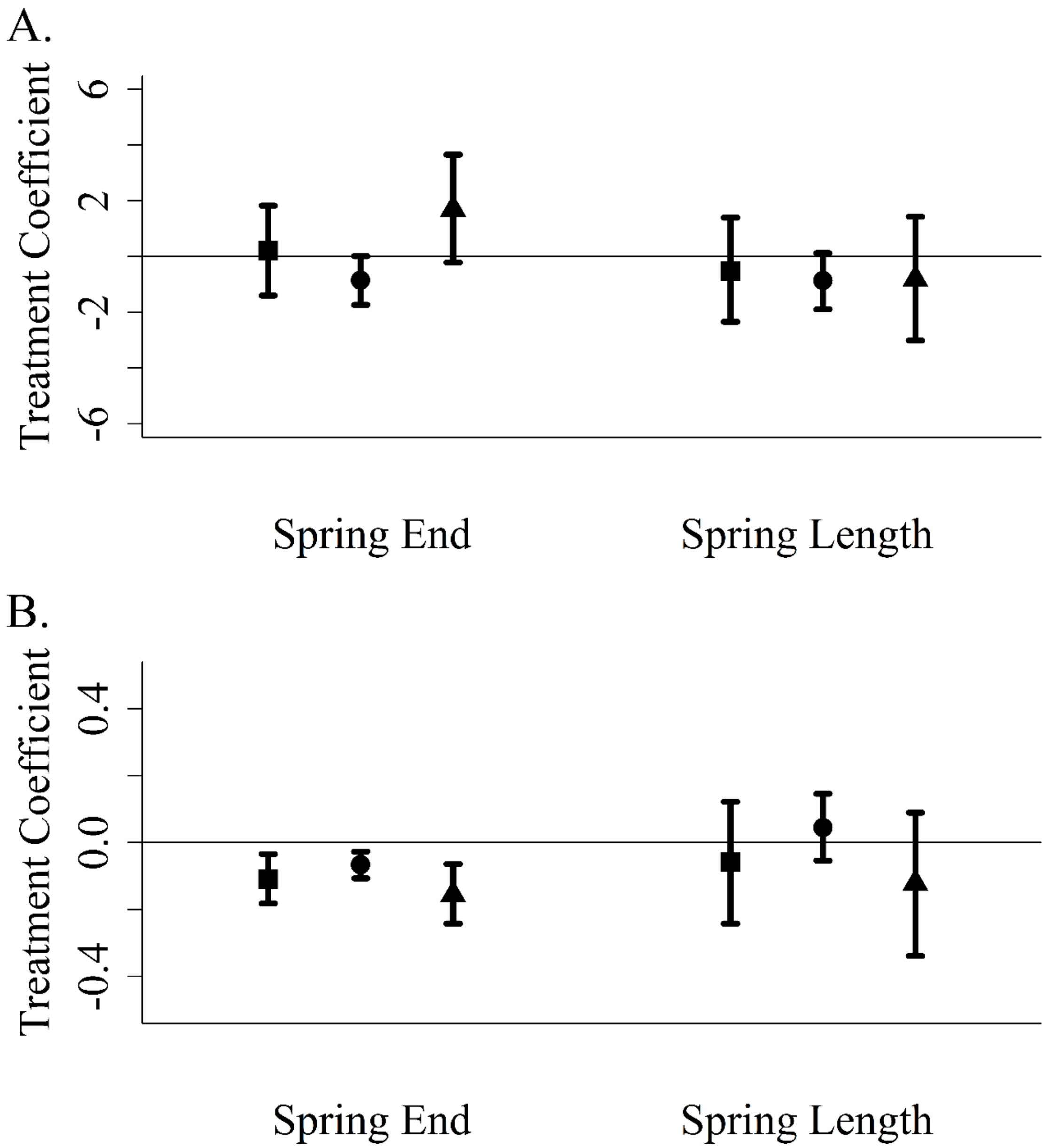

Figure A.2. Main effects (mean and 95% CIs) of prescribed-fire (square), herbicide (circle), and mechanical (triangle) treatments on vegetation in Wyoming, USA, 1960-2016. Main effects represent the difference between controls and treatments averaged over all years in the data. Units are Julian dates of occurrence for A) the end of spring and the number of days for spring length. The coefficients of variation for these metrics B) represented their spatial heterogeneity and were log-transformed for analysis. (black and white; one column)

Table A.1. Coefficients and SEs for abiotic covariates in the analysis of vegetative responses to prescribed-fire, herbicide, and mechanical treatments in sagebrush communities in Wyoming, USA, 1960-2016.

	Precipitation (cm)		SWE (cm)		Temperature °C	
	β	SE	β	SE	β	SE
SpE[a] (days)	$4.99e^{-3}$	$3.24e^{-2}$	$-5.38e^{-2*}$	$2.45e^{-2}$	-5.94^{*}	0.16
SpL (days)	-0.643^{*}	0.037	-0.293^{*}	0.028	-0.624^{*}	0.182
CV[b] SpS	$8.54e^{-3*}$	$1.80e^{-3}$	$-1.83e^{-2*}$	$1.4e^{-3}$	$6.62e^{-2*}$	$8.8e^{-3}$
CV SpE	$3.79e^{-3*}$	$1.49e^{-3}$	$-4.61e^{-3*}$	$1.12e^{-3}$	$3.41e^{-2*}$	$7.2e^{-3}$
CV SpL	$5.19e^{-2*}$	$3.7e^{-3}$	$1.22e^{-2*}$	$2.8e^{-3}$	$2.07e^{-2}$	$1.78e^{-2}$
CV IRG	$6.49e^{-3*}$	$1.49e^{-3}$	$-1.25e^{-2*}$	$1.1e^{-3}$	$5.55e^{-2*}$	$7.3e^{-3}$
CV SEN	$-4.00e^{-2*}$	$1.3e^{-3}$	$-1.75e^{-3}$	$9.6e^{-4}$	$-5.61e^{-2*}$	$6.2e^{-3}$
CV NDVImax	$1.28e^{-2*}$	$1.7e^{-3}$	$2.21e^{-5}$	$1.26e^{-3}$	$4.19e^{-2*}$	$7.9e^{-3}$
CV NDVIc	$-2.58e^{-2*}$	$1.3e^{-3}$	$-2.79e^{-3*}$	$9.8e^{-4}$	$-5.92e^{-2*}$	$6.4e^{-3}$

[a]Start of spring (SpS), end of spring (SpE), length of spring (SpL), maximum instantaneous rate of green-up date (IRG), maximum rate of senescence date (SEN), maximum NDVI date (NDVImax), and cumulative NDVI (NDVIc).

[b]All coefficient of variation (CV) responses (i.e., spatial heterogeneity) were log transformed.

[*]Significant relationships ($p < 0.05$)

Table A.2. Coefficients and SEs for model covariates in the analysis of vegetative responses to prescribed-fire, herbicide, and mechanical treatments in sagebrush communities in Wyoming, USA, 1960-2016.

	Time Since Treatment		Elevation (km)		Species[a]		Area-to-Edge Ratio (ha/km)	
	β	SE	*β*	SE	*β*	SE	*β*	SE
Herb/sage ratio	$-6.70e^{-3}$	$3.96e^{-3}$	-1.50^{*}	0.54	$-4.88e^{-2}$	0.116	$1.22e^{-3}$	$2.34e^{-3}$
Bare ground %	$-1.68e^{-2}$	$7.68e^{-2}$	-65.0^{*}	10.3	9.80^{*}	2.27	$-5.12e^{-2}$	$4.42e^{-2}$
SpE[b] (days)	0.296^{*}	0.039	34.3^{*}	6.1	-9.54^{*}	1.80	$-3.49e^{-2}$	$2.80e^{-2}$
SpL (days)	0.317^{*}	0.044	-32.0^{*}	7.0	-3.70	2.05	$-3.15e^{-2}$	$3.21e^{-2}$
CV[c] Sagebrush %	$-8.51e^{-3}$	$4.60e^{-3}$	-1.61^{*}	0.64	0.603^{*}	0.135	$-1.31e^{-3}$	$2.79e^{-3}$
CV Herbaceous %	$-9.35e^{-3*}$	$3.50e^{-3}$	0.535	0.486	0.353^{*}	0.102	$1.13e^{-3}$	$2.12e^{-3}$
CV Bare ground %	$-2.33e^{-3}$	$2.50e^{-3}$	1.49^{*}	0.35	0.371^{*}	0.071	$2.78e^{-3}$	$1.57e^{-3}$
CV SpS	$1.24e^{-2*}$	$2.2e^{-3}$	-0.666	0.350	$1.74e^{-2}$	0.106	$-3.64e^{-3*}$	$1.59e^{-3}$
CV SpE	$1.05e^{-2*}$	$1.7e^{-3}$	-1.14^{*}	0.26	-0.140	$7.2e^{-2}$	$-2.56e^{-3*}$	$1.22e^{-3}$
CV SpL	$-1.27e^{-2*}$	$3.9e^{-3}$	3.04^{*}	0.56	$1.87e^{-2}$	0.150	$2.95e^{-3}$	$2.77e^{-3}$
CV IRG	$1.56e^{-2*}$	$1.9e^{-3}$	-0.950^{*}	0.308	-0.117	0.098	$-3.72e^{-3*}$	$1.36e^{-3}$
CV SEN	$8.66e^{-3*}$	$1.51e^{-3}$	-1.36^{*}	0.24	0.228^{*}	0.069	$3.83e^{-3*}$	$1.09e^{-3}$
CV NDVImax[d]	$5.27e^{-2*}$	$2.50e^{-2}$	0.100	0.240	-0.121	$6.1e^{-2}$	$2.18e^{-3}$	$1.20e^{-3}$
CV NDVIc	$7.88e^{-3*}$	$1.64e^{-3}$	-0.267	0.272	0.133	0.089	$-4.97e^{-4}$	$1.20e^{-3}$

[a]Coefficients represent the value added to means for sites with mountain big sagebrush to estimate sites with Wyoming big sagebrush.
[b]Start of spring (SpS), end of spring (SpE), length of spring (SpL), maximum instantaneous rate of green-up date (IRG), maximum rate of senescence date (SEN), maximum NDVI date (NDVImax), and cumulative NDVI (NDVIc).
[c]Log transformations were applied to all coefficient of variation (CV) responses (i.e., spatial heterogeneity).
[d]Time since treatment was log transformed.
[*]Significant relationships ($p < 0.05$).