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QUANTIFYING LEGACY EFFECTS OF MANAGED DISTURBANCE

ON SAGEBRUSH STEPPE RESILIENCE AND DIVERSITY

by

Julie Ripplinger

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

of

MASTER OF SCIENCE

in

Ecology

Approved:

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Thomas C. Edwards, Jr.   Peter Adler
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Committee Member   Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, UT

2010

ABSTRACT

Quantifying Legacy Effects of Managed Disturbance

on Sagebrush Steppe Resilience and Diversity

by

Julie Ripplinger, Master of Science

Utah State University, 2009

Major Professor: Dr. Thomas C. Edwards, Jr.
Department: Ecology

Land-use legacies can affect landscapes for decades to millennia. A long history of shrub management exists in the sagebrush steppe of the Intermountain West where shrub-removal treatments, a type of managed disturbance, have been implemented for over 50 years to reduce sagebrush cover. The assumption behind managed disturbances is that they will increase forage for domestic livestock and improve wildlife habitat. However, the long-term effects of managed disturbance on plant community composition and diversity are not well understood.

We investigated the legacy effects of three common types of managed disturbance (chemical, fire, and mechanical treatments) on plant community diversity and composition. We also examined sagebrush steppe resilience to managed disturbance. Based on management assumptions and resilience theory, we expected within-state phase shifts characterized by an initial reduction in biodiversity followed by a return to prior

state conditions. We also expected changes in species proportions, characteristic of within-state shifts in state-and-transition models. We also expected an increase in non-native contribution to overall diversity.

We found that plant communities experienced a fundamental shift in composition following disturbance, and responded in a flat linear fashion, giving no indication of return to prior community composition or diversity. As expected, we found post-disturbance increases in the number of non-native grass species present. However, native forb species made the largest contribution to altered diversity. Disturbance modified functional group composition, so contrary to our expectations, within-state changes did not occur as a result of disturbance. Our results indicated that sagebrush steppe plant communities are not resilient to chemical, fire, and mechanical treatments, and subsequent to managed disturbance, community composition tips over a threshold into an alternate stable state.

(48 pages)

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BACKGROUND

Research Context

Past land-use can have legacy effects on landscapes for decades to millennia. In the Intermountain West, shrub-removal treatments have been a prevalent management practice since the mid-1900s. This practice is designed to control sagebrush, improve wildlife habitat and increase livestock forage (Harniss and Murray 1973, Stoddart et al. 1975, Holechek et al. 2004), but it is unclear how these managed disturbances affect sagebrush steppe diversity, community composition, and resilience in the long-term.

Shrubsteppe and semidesert scrub are the dominant vegetation types of North America's Great Basin (ca. 584,000 km^2), and sagebrush steppe alone comprises at least 630,000 km^2 of the western United States (West and Young 2000). Historically, the sagebrush steppe vegetation type constituted more of the semidesert vegetation than any other type (West 1983). These shrub-dominated regions of diverse flora and fauna are semi-natural systems, having been impacted for over a century by widespread livestock grazing, fire suppression, and human use. This treeless, semi-arid ecosystem has analogues worldwide with similar physiognomy and land-use. Global analogues include Eurasian cold-desert shrublands (Petrov 1972, Stoddart et al. 1975), Patagonian steppe (Soriano 1956, 1972), Australian saltbush steppe (Stoddart et al. 1975), and Canada's Okanagan-Similkameen shrubsteppe. Because analogous systems exist that consist of similar vegetation and land-use, the analogues are subject to comparable legacy effects.

Legacy effects of human land-use have substantial long-term economic (e.g. crop productivity, livestock capacity) and ecological (e.g., biodiversity, ecosystem functions) implications (Foley et al. 2005, Rhemtulla et al. 2007). Accordingly, ecologists and land managers are in need of an assessment of the legacy effects of both anthropogenic and environmental disturbance in sagebrush steppe landscapes. Studies exist that explore historical conditions and changes in Great Basin vegetation; however, these studies provide tools for studies of legacy effects more than they assess changes in biodiversity and resilience from historical sagebrush steppe communities. For example, Beiswenger (Beiswenger 1991) reconstructed Holocene climate and vegetation changes for the Great Basin, however pollen resolution is too coarse to look at community diversity.

Approximations of historical vegetation were made using relictual plant communities (Passey et al. 1982); however, Passey et al. offer only a snapshot in time of undisturbed communities rather than addressing change over time. Washington-Allen et al. (2006) combined GIS and archived remotely sensed imagery to assess long-term degradation of rangeland, but their study did not deal with the question of biodiversity and resilience. Tree-ring analyses were applied successfully by Ferguson (1964) to reconstruct fire histories in big sagebrush environments, but while this study looks at disturbance history, it is not concerned with overall community composition. Studies have experimentally shown impacts of grazing and herbivory in steppe and grassland systems (Coppock et al. 1983, Hobbs 1996, Adler and Lauenroth 2000, Adler et al. 2001), but they too did not evaluate managed disturbances or resilience. In grassland communities, Coffin et al. (1996) examined historical disturbance for vegetation

recovery. In short, we understand grassland community dynamics due to experiments and long-term data, and tools are available for retrospective studies in sagebrush steppe, but the long-term effects of disturbances in sagebrush steppe on diversity and resilience remain largely unexplored.

Literature Review

Legacy effects.-- Land-use legacies exist on today's landscape over an array of temporal scales and land-use types. Our study focuses on legacies of decades-old management, but substantial evidence exists of ancient land-use legacies, in both Europe and the Americas. Growth and expansion of the Roman Empire resulted in extreme reductions in forest cover over parts of Europe (Hermy and Verheyen 2007). As a result, forests in France exhibit floristic differences as much as 2,000 years after deforestation (Dupouey et al. 2002). The Mayan civilization built cities and intensively cultivated vast expanses of Central American forest ca. 1000 years ago (Turner 1974, Turner et al. 2003). Since the subsequent decline and disappearance of the Mayans, reforestation has occurred as expected. Today, forest reserves with deceptively natural forest vegetation exist. However, recent research (Beach 1998, Turner et al. 2003) has shown that ancient Mayan land-use left an enduring, 1000-year-old legacy on soils and vegetation. Near the same time period as the Mayans, the ancient Anasazi people inhabited portions of southern North America. The burgeoning Anasazi culture depended heavily on piñon pine as a seasonal food source and consequently over-harvested the seeds. Modern

expansion of piñon-juniper woodland is a legacy effect of this centuries old land-use (Swetnam et al. 1999).

Evidence of more recent legacies exists in forested systems, particularly in forests that have regrown following logging and agricultural conversion. Early European settlers of the Americas conducted extensive forest clearcutting frequently followed by cultivation. Some clearcut regions were harvested once then allowed to reforest. With the onset of the industrial era, many cultivated agriculture sites were abandoned and subsequently reforested. Research has shown that forest structure and diversity in these reforested sites differs from areas not subjected to the land-use practices of early settlers. In forests of the Great Lakes region, USA, Rhemtulla et al. (2009b) found that trees of medium- and large-diameter comprise a smaller proportion of the forests, and that the total area of late successional trees experienced a decline. Early successional tree species are more common than they were before Euroamerican impact. Similar legacy effects have been found in forests of northwestern Europe. Hermy and Verheyen (2007) investigated >100 year legacy effects in Belgian forests that developed on abandoned farmland and found differences in the understory composition of these so-called recent forests compared to ancient forests. In addition to legacies found in composition and structure, legacies of land-use are evident in ecosystem function and carbon dynamics as well (Foster et al. 2003, Flinn et al. 2005, Rhemtulla et al. 2009a).

Legacy effects of disturbance regimes and managed disturbance may be the most pervasive of land-use legacies, principally due to their extent. Altered fire regimes exist in parallel with human presence; it is implicit that nearly every continent and ecosystem

is impacted. In southern California, USA, altered fire regimes have increased the

abundance of dead woody material resulting in hotter, more widespread fires in chaparral

on the wildlife-urban interface (Franklin et al. 2005) Among other impacts, hotter fires

are more likely to destroy the seed-base while larger fires homogenize more of the

landscape, thereby providing greater opportunity for invasion. For nearly two decades,

Turner et al. have examined the long-term impacts of the 1988 Yellowstone fires

(Schoennagel et al. 2004, Smithwick et al. 2009). The Yellowstone fires resulted from a

combination of climatic fluctuation and fire suppression, and they burned hotter and more

extensively than fires of the typical disturbance regime. The fires themselves are

evidence of a disturbance legacy, and similarly, the 1988 fires have created their own

legacy effects on forest stand structure, biogeochemical cycling, and understory

composition (Schoennagel et al. 2004, Smithwick et al. 2009).

Legacy effects of managed disturbance in the sagebrush steppe have been the

focus of several research efforts in the Intermountain West region of North America. In

Idaho sagebrush steppe, Harniss and Murray (1973) used a long-term study to

demonstrate that sagebrush species responding to prescribed fire outcompete understory

grasses and forbs. A study by Watts and Wambolt (1996) investigated long-term recovery

of experimentally disturbed Wyoming big sagebrush (*Artemisia tridentata* ssp.

wyomingensis), and found that depending on treatment type, sagebrush cover recovered

within 10-18 years post-treatment. Both of these studies indicate legacies of increased

sagebrush in response to disturbance. Davies et al. (2009) published a study exploring

sagebrush steppe management techniques designed to emulate historic disturbance

regimes. They suggested that due to deviations from historic disturbance regimes, more low-severity disturbances may increase sagebrush steppe resilience. The legacy effects evident in the work of Davies et al. are of disturbance regimes altered beyond historic regimes and consequentially less resilient communities.

Alternate stable states.-- Sagebrush steppe vegetation dynamics exist as a result of a myriad of interacting factors such as soil, time, elevation, climatic trends, and anthropogenic and environmental disturbance. The current thinking is that sagebrush steppe and other semiarid systems are characterized by multiple equilibria (alternate stable states) and therefore operate under the influence of alternate stable state dynamics. Disturbance events may drive a sagebrush steppe community across a threshold to another stable state, depending on the resilience of the system. This interplay between multiple equilibria and disturbance dynamics is characterized by state-and-transition models (Laycock 1991, Stringham et al. 2003, Bestelmeyer et al. 2009). Within these models, resilience is considered a system's ability to recover from disturbances (Holling 1973, van der Maarel 1993); it is also characterized by the amount of disturbance a system is able to withstand before transitioning to another state (Gunderson 2000). Stable states change very slowly without anthropogenic influence (Paine et al. 1998, Gunderson 2000), but human influence changes the resilience of a system. Thus, both managed and natural disturbances may extirpate some species while simultaneously opening gaps for other species to invade (Paine et al. 1998).

Restoration ecologists and rangeland managers benefit from the use of state-and-transition models as management tools (Friedel 1991, Laycock 1991, Bestelmeyer et al.

2003, Stringham et al. 2003), which are designed to interrelate multiple stable states for many vegetation types (Laycock 1991). Thresholds and stable states in these models are assembled using classification and ordination of vegetation characteristics, taking into consideration soil type, seasonal conditions, other abiotic site factors, and management history (Friedel 1991). State-and-transition models depart from traditional successional models (Dyksterhuis 1949) in that they integrate nonlinear dynamics into the model. Multiple stable vegetation communities – 'states' – exist for any given site. Thresholds between sites can be crossed – 'transition' – via burning, overgrazing, and other forms of anthropogenic or environmental disturbance. With transition, environmental changes also occur, such as change in soil water and nutrient availability, thereby contributing to the inability of a site to return to its previous state. Once a threshold is crossed between stable states, considerable management intervention is required for transition to an alternate stable state (Friedel 1991, Bestelmeyer et al. 2004, McAdoo et al. 2004).

Research Questions

Our broad research objective was to explore the long-term effects of three disturbance types – use of herbicides, prescribed fires, and mechanical treatments – on sagebrush steppe plant communities. Central to this research was the incorporation of the legacy effects of disturbance, which, as the literature review above documents, are agents of transition between alternate stable states in state-and-transition models. Our specific questions were: (1) Does vegetation differ after disturbance? Here, we were interested in teasing out the effect of these treatments over time and the effects of the different

treatment types. (2) What are the characteristics of post-disturbance community composition over time? Here, we looked at quantitative and qualitative differences between native and non-native community composition in decadal time bins. And, (3) Are sagebrush steppe communities resilient to managed disturbance? Overall, we were interested in assessing legacy effects of managed disturbance on plant community diversity and composition, and in sagebrush steppe resilience to managed disturbance.

INTRODUCTION

Sagebrush steppe of the Intermountain West of North America has a legacy of altered plant community composition from over a century of anthropogenic influence co-mingled with its environmental history. Managed disturbances – including application of herbicides, controlled burns, and disking – have been applied on the shrubsteppe landscape since the mid-1900s (Harniss and Murray 1973, Stoddart et al. 1975, Holechek et al. 2004). The resilience of sagebrush steppe communities to such managed disturbance is also in question (Harniss and Murray 1973, Watts and Wambolt 1996, Davies et al. 2009, Wisdom and Chambers 2009) following decades of fire suppression and livestock grazing.

Resilience is defined as a system's ability to recover from disturbance (Holling 1973, van der Maarel 1993) and by the amount of disturbance a system is able to withstand before transitioning to another state (Gunderson 2000). Alternate stable state theory predicts that a disturbance of sufficient magnitude will propel a system across a threshold and from one stable state to another (Friedel 1991, Paine et al. 1998, Gunderson

2000, Scheffer et al. 2001). The lower a system's resilience, the smaller the magnitude of disturbance necessary to propel it across a threshold and into an alternate stable state. The threshold to an alternate stable state may be crossed either through a major disturbance, such as widespread wildfire, or by a novel perturbation to a non-resilient, previously-altered community (e.g., overfishing in an area affected by water pollution) (Paine et al. 1998). State-and-transition models employ an alternate stable state framework to predict state shifts, particularly in rangeland systems (Bestelmeyer et al. 2003, Stringham et al. 2003). In these models, state changes depend upon the resilience of the stable state and are bounded by thresholds between states (Friedel 1991). State-and-transition literature (Friedel 1991, Laycock 1991, Bestelmeyer et al. 2003, Stringham et al. 2003) proposes that once transition occurs, a reversal to the original state can only be accomplished through significant input of energy, typically by means of management intervention or restoration efforts.

Effects of land-use may persist on landscapes for decades to millennia (Dupouey et al. 2002, Foster et al. 2003, Hermy and Verheyen 2007, Rhemtulla and Mladenoff 2007). These legacy effects exist on today's landscape over an array of systems and land-use types. Our study focuses on legacies of decades-old management in the Intermountain West, where shrub-removal treatments have been a prevalent management practice since the mid-1900s (Harniss and Murray 1973, Stoddart et al. 1975, Holechek et al. 2004).

We investigated sagebrush steppe resilience to managed disturbance, and the legacy effects of managed disturbance on plant community diversity and composition.

Based on management objectives and invasion literature (Anderson and Inouye 2001, Keeley et al. 2003), we expected within-state phase changes and an increase in non-natives on disturbed versus reference sites. Proceeding from resilience theory (Paine et al. 1998, Scheffer et al. 2001) and a range of restoration literature (Johnson et al. 1996, Hemstrom et al. 2002, Olson and Whitson 2002, Rango et al. 2005, Seabloom 2007, Rau et al. 2008), we expected plant community diversity to show resilience to managed disturbance, characterized by a gradual return to baseline conditions.

We concentrated on three landscape-level shrub-removal disturbances (treatments): (i) herbicidal treatment either with Tebuthiuron or 2,4-dichlorophenoxyacetic acid (hereafter referred to as 'chemical'); (ii) fire; and (iii) mechanical, representing tractor-implemented treatments such as the Dixie harrow or Lawson pasture aerator. We evaluated these three types of managed disturbance as mechanisms of vegetation community change in the context of their long-term legacy effects. Other disturbance mechanisms, such as grazing history, drought, or insect outbreaks, did not fall within the scope of this study. In order to quantify long-term disturbance effects, it is necessary to have a working definition of disturbance. Similar to van der Maarel (1993), Pickett and White (1985), and Grime (1979), we define disturbance as a discrete event involving the destruction of plant biomass which changes resource and substrate availability, and the physical environment.

An abundance of research has evaluated the effects of shrub-removal treatments on biomass and metrics of productivity (Sturges 1993, Rau et al. 2008, Davies et al. 2009), soil properties (Sturges 1993, Berlow et al. 2003, Inouye 2006, Bechtold and

Inouye 2007), greater sage grouse habitat (Nelle et al. 2000, Crawford et al. 2004, Beck et al. 2009), and shrub cover (Watts and Wambolt 1996). The short-term effects of disturbances typical in rangelands are relatively well understood thanks to experiments (Hartnett et al. 1996, Knick and Rotenberry 1997), but the long-term effects of shrub removal have attracted less attention. Additionally, numerous studies have evaluated resilience/stability responses to disturbance in North America rangelands and applied alternate stable state theory in a variety of conservation settings (Collins and Barber 1986, Coffin and Lauenroth 1988, Coffin et al. 1996, Collins 2000, Davies et al. 2007). These previous efforts have typically focused on the response of dominant vegetation as measured by cover. Here, we focus on the long-term effects of these widespread managed disturbances on biodiversity and community composition.

The objective of our study was to quantify the long-term response of three managed disturbance types – chemical, fire and mechanical – on sagebrush steppe plant community composition, diversity, and resilience. Three key questions guided our research. (1) Does vegetation differ after disturbance compared to reference? Here, we are interested in teasing out the effect of these treatments over time and the effects of the different treatment types on current-day vegetation. (2) What are the characteristics of post-disturbance community composition over time? Here, we looked at quantitative and qualitative differences between native and non-native community composition in decadal bins over time. And, (3) Are sagebrush steppe communities resilient to managed disturbance? Our objective here was to assess whether managed disturbances caused within state shifts or transitions between alternate stable states.

METHODS

Study Area

Shrubsteppe and semidesert scrub are the dominant vegetation types of North America's Great Basin (ca. 584,000 km^2), and sagebrush steppe alone comprises at least 630,000 km^2 of the western United States (West and Young 2000). Historically, sagebrush steppe vegetation type constituted more of the semidesert vegetation than any other type (West 1983). These shrub-dominated regions of diverse flora and fauna are semi-natural systems, having been impacted for over a century by widespread livestock grazing and human use. Sagebrush steppe systems are characterized by low (50-90cm) annual precipitation, warm summers and cold winters, and moderately fertile soils (West 1983, West and Young 2000). This treeless, semiarid ecosystem has analogues worldwide with similar physiognomy and land-use. Global analogues include Eurasian cold-desert shrublands (Petrov 1972, Stoddart et al. 1975), Patagonian steppe (Adler et al. 2006), and Australian saltbush steppe (Stoddart et al. 1975).

Physical characteristics.-- Rich County, Utah, is centrally located within the distribution of sagebrush steppe of the western U.S. (Lowry et al. 2007) (FIG. 1). The area of Rich County is 2,808km^2 in size, 150 km^2 of which is water. Elevation ranges from 1,805 to 2,820m. The primary landcover type in Rich County is sagebrush steppe, which constitutes >75% of the county's landcover. Sagebrush steppe cover has a high to low elevational gradient from north to south, respectively. Mean annual minimum air temperature for the county is -5.4°C, mean annual maximum air temperature is 13.2°C,

mean annual precipitation is 27.7cm, and mean annual snowfall is 109.1cm (Utah

Climate Center http://climate.usurf.usu.edu/products/data.php). Higher elevation sites

experience slightly later seasonal thawing and marginally higher winter precipitation

levels. Soils of Rich County sagebrush steppe are typically aridisols (i.e. calcids) and

mollisols (i.e. aquolls, xerolls), but on occasion may also be inceptisols (i.e. xerepts) or

entisols (i.e. fluvents, orthents) (Soil Survey Staff 1999). Characteristics common to

most of these sagebrush steppe soils include limited soil moisture, xeric to aridic soil

moisture regime, and accumulation of carbonates, clay, and sometimes salts.
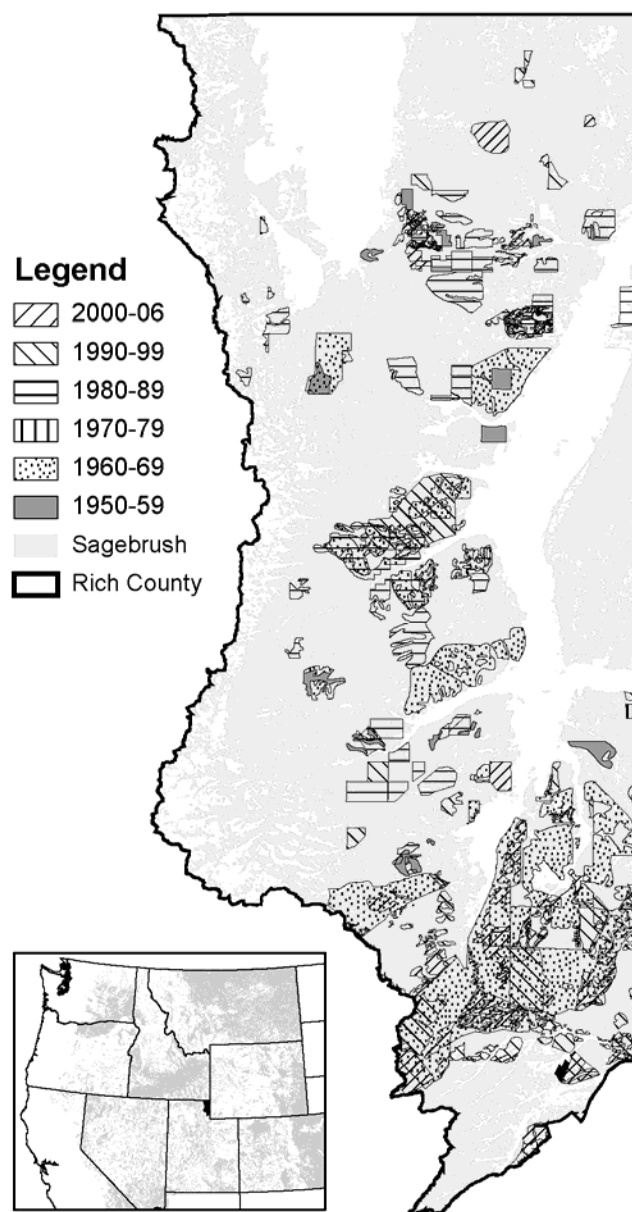
FIG. 1. Map of Rich County, Utah, USA study area. Main map shows outlined polygons (sampling sites) of the spatial and temporal distribution of historical shrub-removal. Inset map shows the western US with Rich County near the center of sagebrush steppe distribution.

Vegetation characteristics.-- The dominant *Artemisia* species include basin big sagebrush (*A. tridentata* ssp. *tridentata*), mountain big sagebrush (*A. tridentata* ssp. *vaseyana*), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) black sagebrush (*A. nova*), and low sagebrush (*A. arbuscula*). Each of the community types associated with these sagebrush species corresponds to somewhat different soil and environmental features (West et al. 1978, Young et al. 1985, Shumar and Anderson 1986, Jensen et al. 1988, Jensen et al. 1990). Typically, these community types are characterized by a dominant species of sagebrush and the associated abundant or distinctive understory vegetation (Passey et al. 1982, Jensen et al. 1988, Davies et al. 2007).

A. tridentata ssp. *tridentata* occurs at mid- to high-elevation sites (601 - 2,140m), on foothills, along drainages and in valley bottoms of the low to moderate precipitation zone. These sites are relatively warmer and wetter than sites associated with other sagebrush species. As distance from drainages increases, a pronounced decrease in shrub height becomes apparent in response to a moisture gradient (West et al. 1978, Barker and McKell 1983, Young et al. 1985). *A. tridentata* ssp. *wyomingensis* is found on mid-elevation sites (1,520 - 2,150m), on hilltops and flats in the low to moderate precipitation zone (Barker and McKell 1983, Young et al. 1985, Shumar and Anderson 1986). *A. tridentata* ssp. v*aseyana* is characterized by cool, wet, high elevation sites (West et al. 1978, Young et al. 1985). *A. nova* frequently occurs on sites of low precipitation (Jensen 1989). *A. arbuscula* is found on cold, dry sites of the higher mountains. *A. arbuscula* sites experience higher soil erosion loss than *A. tridentata* sites, probably due to less vegetation and litter ground cover (West et al. 1978, Jensen 1989).

Human disturbance history.-- Because the earliest settlers found the cultivation of crops unreliable, Rich County sagebrush steppe was historically used to graze livestock on the open-range (Parson 1996). By the 1950s, the region had been settled for nearly a century and the impacts of domestic livestock grazing had accumulated. Issues associated with fire-suppression and overgrazing, such as increased shrub cover and the spread of undesirable herbaceous vegetation, led to management intervention and widespread manipulation of vegetation implemented principally to maintain livestock grazing. Throughout the Intermountain West, land managers had begun to implement chemical and mechanical shrub-removal treatments. In the 1950s, these large-scale manipulations were introduced to Rich County, Utah. By the 1980s, ranchers and land-managers began to use controlled fires to manipulate sagebrush communities.

We developed a GIS map of historic treatments by compiling information gleaned via interviews with the local ranching community, aerial photos, and archived in private ranch and government agency repositories. Historically disturbed sites varied in size, treatment method and intensity depending on a number of factors. Certain landcover types were more likely to be manipulated than others, and certain shrub-removal types are more appropriate to a site than others depending on proximity to roads, slope, aspect, and soil characteristics. For example, sagebrush steppe sites near access roads and with little slope had a high likelihood of receiving mechanical treatment in the last 50 years. Consequently, management objectives and constraints particular to each landcover type and each shrub-removal type added variation to the matrix of disturbance history in Rich County, Utah. Treatment polygons ranged in size from 1 to 953 hectares. Our composite

map of chemical, fire, and mechanical disturbances, indicates that the greater part of Rich County's sagebrush steppe was altered at some point between 1950 and the present (FIG. 1). We selected sampling locations from a chronosequence of those sites treated between the 1950s and 2004.

Field Sampling

The Bear Lake region, which consists of Rich County and the adjoining mountains, contains nearly 700 plant species (Lott 2007), roughly 200 of which are sagebrush steppe species we identified over the course of this study. We gathered more than 2,600 plant specimens from a chronosequence of 70 managed disturbance sites and corresponding untreated reference sites. To reduce the impact of covariates on results, we selected reference sites from areas having no known treatment history, and falling within regions with the same landform classification (Lowry et al. 2007) as used to select disturbances. Reference sites experienced the same grazing regimes as treated sites, both historically and currently. Due to the non-random selection of sites for shrub management and the extent of treated sagebrush steppe, reference sites with physiognomic similarities to managed disturbance sites were difficult to locate. We opted to stratify the county into 3 sections and select one reference site from each section with similar landform to treatments. Our stratification and similar landform approach reduced covariate effects, homogenized site characteristics, and increased the likelihood of similarity between reference vegetation and pre-disturbance vegetation. Treated

sampling sites were randomly placed within disturbance polygons throughout Rich County.

From these sites, we created a cross-classified table of five decadal classes and three treatment factors (TABLE 1). Foster et al. (2003) observed that very complex legacies exist for sites of multiple management practices and that they may confound interpretation. Consequently, we sampled vegetation on sites where no known prior or subsequent treatments were conducted; thus, sites with multiple overlapping treatments were excluded due to the confounding effects of varying pre-treatment vegetation and land-use history.

We used a variation on the Whittaker plot (Shmida 1984, Stohlgren et al. 1995) to quantify plant community composition. Our sampling unit was composed of one 15m × 35m quadrat randomly oriented on a systematic grid within each treatment polygon. We compiled plant inventories for each site and collected voucher specimens of each plant species present at each site. All voucher specimens were keyed to species level with

TABLE 1. Sample sizes stratified by decades since disturbance.

	41-50yrs	31-40yrs	21-30yrs	11-20yrs	1-10yrs	Total
Chemical	4	1	6	7	2	20
Fire	0	0	2	3	7	12
Mechanical	12	3	3	4	13	35
Total	16	4	11	14	22	67

consultation from the Utah State University Intermountain Herbarium. We identified 17

grass species, 75 forb species, and 16 shrub species across all sample sites. Species

present and respective endemism are given in APPENDIX A.

Analysis

We used five community diversity metrics to compare plant species diversity

among managed disturbance types on reference and disturbed sites. We calculated alpha

diversity using species richness, Shannon diversity, and Simpson diversity (Krebs 1999);

and we calculated beta diversity between reference and disturbed vegetation using

Jaccard similarity and Simpson dissimilarity (Krebs 1999). These analyses included

presence/absence and abundance data from 70 treatment and reference sites. Time since

disturbance was our factor of interest, so we conducted a factorial analysis of covariance

(ANCOVA) using time since treatment as the only covariate. ANCOVA can be used to

assess the influence of a covariate, e.g. time, by controlling for the variation associated

with it. We used ANCOVA to test whether there were differences in diversity on three

managed disturbance types over time. Analyses were designed to compare community

TABLE 2. AIC scores for linear and nonlinear model comparison.

	Species Richness	Shannon Diversity	Simpson Diversity	Jaccard Similarity	Simpson Dissimilarity
Linear	488.0	82.9	-198.7	-157.4	277.7
Nonlinear	489.9	84.5	-197.9	-155.4	279.7

composition of reference vegetation to post-disturbance vegetation through time. We

tested the null hypothesis that time since treatment would have no effect on plant

community diversity. Significant slope and gaps between treatments would indicate

change in diversity over time and differences between treatment types, whereas, little or

no slope without gaps between treatments would indicate no change in diversity over

time and no differences in diversity between treatment types. We examined linear and

non-linear models (see TABLE 2) both with and without an interaction between

disturbance type and time since disturbance. Program R was used for all statistical

analyses (R Development Core Team 2009).

RESULTS

Time-Treatment Effects

We selected a linear ANCOVA model without an interaction in order to afford the

simplest, best-fit model owing to the principle of parsimony. FIGURES 2a-c show

bivariate plots of ANCOVA for alpha diversity across time since disturbance, and FIGS.

3a-b show ANCOVA plots of beta diversity. Disturbance effects were apparent for all

response variables (FIGS. 2a-c and 3a-b, TABLES 3 and 4). There were differences in

treatment types through time; however, the effect of time was not significant for any of

the response metrics (TABLES 3 and 4). Chemical managed disturbances consistently had

significant p-values across all diversity response metrics (TABLES 3 and 4). Chemical

sites were also the sites consisting of highest plant diversity regardless of the diversity
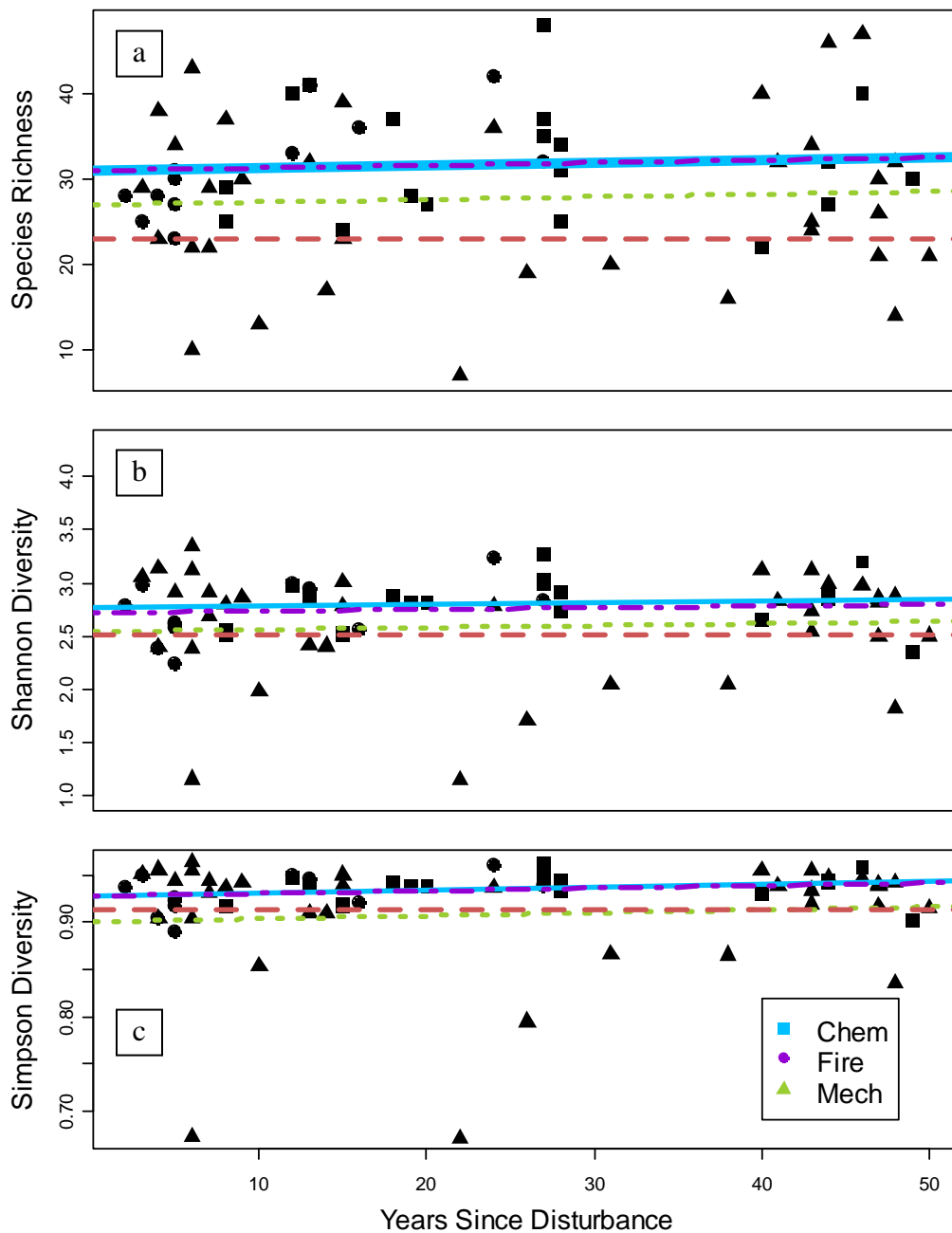
FIG. 2. ANCOVA plots for alpha diversity metrics – (a) species richness, (b) Shannon diversity, and (c) Simpson diversity – over time since disturbance. Regression lines as follows: solid line for chemical, dotdash for fire, dotted for mechanical, and dashed for reference.
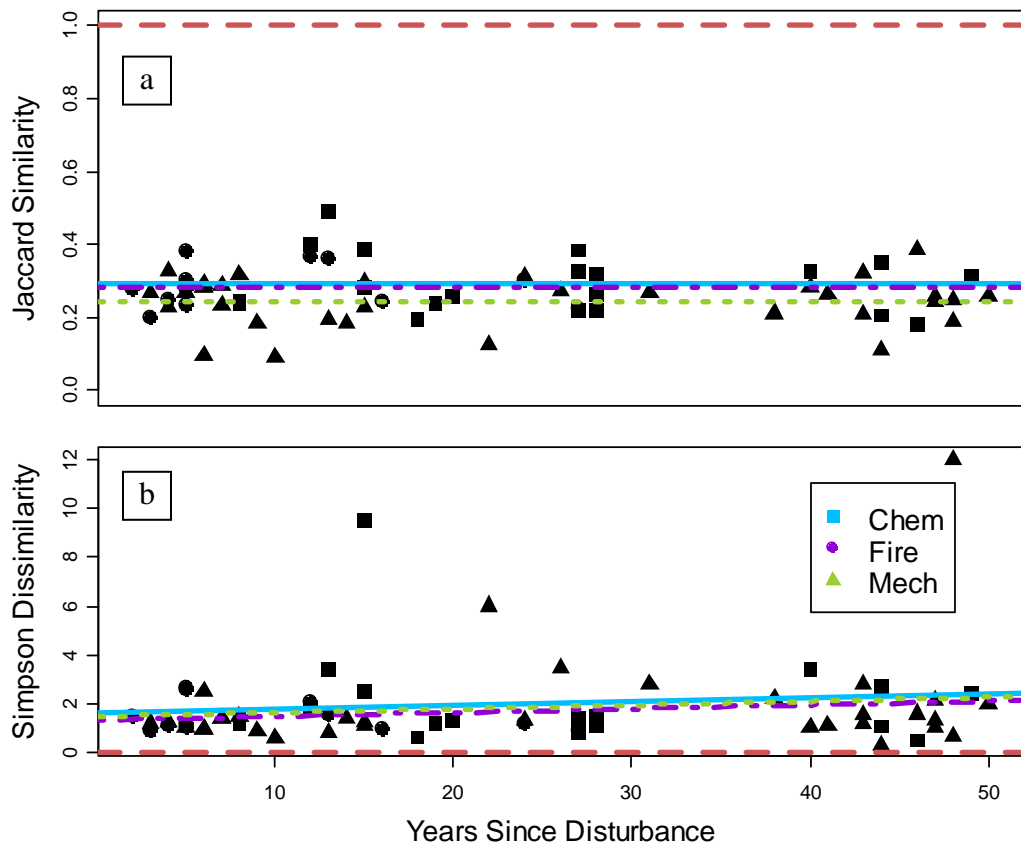
FIG. 3. ANCOVA plots for beta diversity metrics – (a) Jaccard similarity and (b) Simpson dissimilarity – over time since disturbance. Regression lines as follows: solid line for chemical, dotdash for fire, dotted for mechanical, and dashed for reference.

TABLE 3. ANCOVA summary statistics for alpha diversity response variables.

Resp:	Species Richness				Shannon Diversity				Simpson Diversity			
	Est	SE	T	P	Est	SE	t	P	Est	SE	t	P
Chem	31.0	2.72	11.36	*<0.01*	2.76	0.13	20.80	*<0.01*	0.93	0.02	57.21	*<0.01*
Fire	0.02	3.43	0.01	1.00	-0.05	0.17	-0.29	0.77	<0.01	0.02	-0.08	0.93
Mech	-3.94	2.48	-1.59	0.12	-0.21	0.12	-1.74	*0.09*	-0.03	0.01	-1.88	*0.06*
Time	0.03	0.07	0.42	0.67	<0.01	<0.01	0.49	0.63	<0.01	<0.01	0.68	0.50
Model p-value	0.36				0.33				0.22			
Adj R^2	<0.01				<0.01				0.02			
Resid SE	8.84 on 63 DOF				0.43 on 63 DOF				0.05 on 63 DOF			

TABLE 4. ANCOVA summary statistics for beta diversity response variables.

Resp:	Jaccard Similarity				Simpson Dissimilarity			
	Est	SE	t	P	Est	SE	t	P
Chem	<0.01	<0.01	13.25	*<0.01*	1.64	0.57	02.89	*<0.01*
Fire	<0.01	<0.01	-0.27	0.79	-0.30	0.71	-0.42	0.67
Mech	<0.01	<0.01	-2.32	*0.02*	-0.15	0.52	-0.29	0.78
Time	<0.01	<0.01	-0.03	0.97	0.02	0.02	1.02	0.31
Model p-value	0.11				0.64			
Adj R^2	0.05				-0.02			
Resid SE	0.07 on 63 DOF				1.84 on 63 DOF			

metric. ANCOVA results for species richness (FIG. 2a) show reference sites as having the lowest richness. Shannon diversity ANCOVA (FIG. 2b) indicated that mechanical sites had a moderately significant effect on diversity ($p = 0.08$), and trajectory of change was non-significant. Again, reference sites had the lowest diversity. Simpson diversity analysis (FIG. 2c), we showed mechanical sites as the sites of lowest diversity, with reference site diversity nearly as low. Mechanical disturbances also showed a moderately significant effect on biodiversity ($p = 0.06$). For Jaccard similarity ANCOVA (FIG. 3a), we observed significant differences between reference vegetation and chemically treated sites ($p \ll 0.01$) and mechanically treated sites ($p = 0.05$). Fire sites did not differ significantly from reference sites for this metric ($p = 0.85$). For Simpson's dissimilarity ANCOVA (FIG. 3b), we found significant differences between chemically treated sites and reference vegetation ($p \ll 0.01$). Fire and mechanical sites did not differ significantly from reference for either of the beta diversity metrics (see TABLE 4). Descriptive statistics for all metrics over time since disturbance are given in APPENDIX B.

Plant Community Composition Effects

To assess the contribution of non-native plants to increased diversity on disturbed sites, we conducted further comparative analyses of native vs. non-native community composition over time. FIGURES 4a-c depict changes in the relative proportion of native versus non-native vegetation classes on each of the three disturbance types – chemical, fire, and mechanical. Reference conditions are included on the left of barplot clusters for
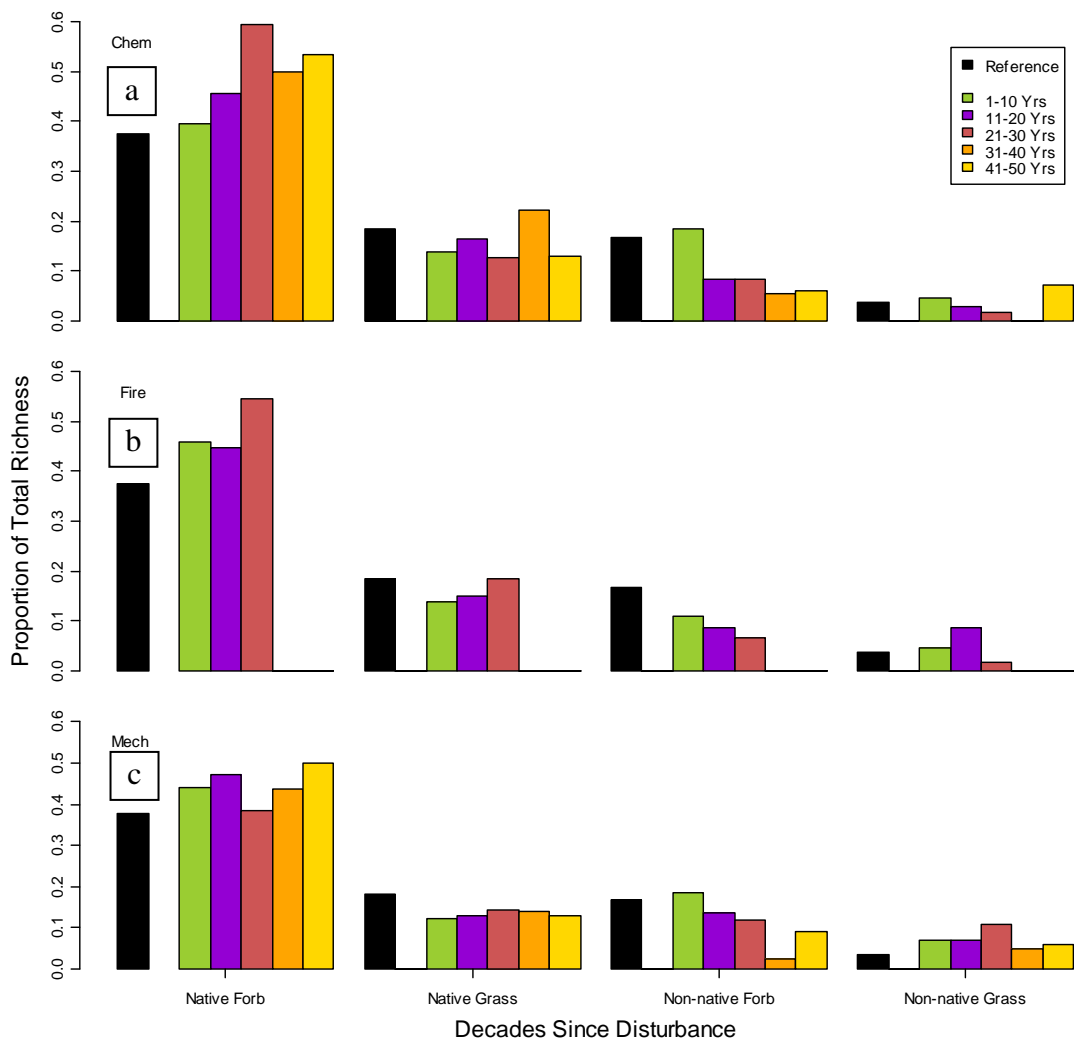
FIG. 4. Barplots showing the trend in proportion of total richness for native versus non-native plant species present on (a) chemical, (b) fire, and (c) mechanical sites over time since disturbance. Reference conditions are shown at the left of each functional group cluster for comparison.

comparison. A temporal trend of increasing native forb and decreasing non-native forb richness is plain across all three treatment types and relative to reference, over all bins of time. Native forb richness is consistently higher than reference, and non-native forb richness is consistently lower than reference. All treatment types also show increased native forb richness with increasing time since treatment. Trends in grasses differed from forbs. On average, native grass richness is lower than on reference sites, particularly on mechanically treated sites. Non-native grass richness is higher than reference conditions on treated sites of all types, particularly on mechanically treated sites. Native grass richness is lower than reference site richness, with the exception of 31-40 year old chemically treated sites. There is no perceptible trend in native shrub species richness, and no non-native shrubs are present. Overall, the greatest contribution to increased richness on disturbed sites is made by native forbs. Non-native grasses, on average, make the second largest contribution to increased richness, but this trend is less temporally consistent.

DISCUSSION

We hypothesized that the relationship between time since disturbance and diversity would have the response curve characteristic of returning to baseline reference conditions. This curve would indicate that plant communities were on a return trajectory to a prior state. We also expected plant community diversity to show resilience to managed disturbance, expecting treatments to cause within-state shifts rather than state to alternate stable state transition. Instead we found that once disturbed, the legacy effect of

these managed disturbances is one of a persistent change in plant community composition and diversity over time periods of up to 50 years. Our observed plant communities give very little indication of a return to prior state reference conditions after treatment.

The vegetation recovery trajectory – if there is one – is difficult to interpret, whether we employ a multiple stable state framework or a linear successional framework. The lack of a return to an earlier state implies that sagebrush steppe plant communities are not resilient to chemical, fire or mechanical treatments. Paine et al. (1998) introduced a model of disturbance wherein a 'major' disturbance was superimposed on an already altered community. Their model results led to a community no longer resilient in its altered state; instead, disturbance resulted in a permanently altered community that was ultimately unable to rebound to its pre-disturbance state. Given that our sagebrush steppe plant communities have undergone over a century of fire suppression and prolonged intensive grazing by domestic herbivores, these communities may parallel the maintained altered state proposed by Paine et al. It is possible that sagebrush steppe communities lack resilience in their already altered (i.e., grazed, altered fire regime) state, and thus are permanently changed by subsequent chemical, fire, and mechanical disturbances. If so, sagebrush steppe community stability was weakened by the presence of fire suppression and a grazing regime different than the pattern under which they evolved. Then, once subjected to a novel managed disturbance, community diversity was affected irreparably. This being the case, our results corroborate the effects of the Paine et al. (1998) model of multiple superimposed disturbances.

Our second objective was to assess the contribution of non-native plants to overall diversity following disturbance. We expected within-state changes and higher numbers of introduced species across disturbance types and time. We expected the increase to largely be due to the role of non-native species. Our expectations of non-native grass contribution were met since the mean proportional richness was higher across all disturbance types than on reference sites. Similarly, the proportion of native grass richness was lower, on average, than at reference sites. However, native forb richness was higher than reference over all time periods and across all disturbance types. Non-native forb richness was the approximate inverse of native forb richness, in that non-native forb richness decreased over time. The increase in native forbs and non-native grasses could be accounted for by a number of factors. It is possible that managed disturbance released the seed bank and previously inaccessible resources, thereby allowing the plant diversity to increase. The native forbs may have filled the space previously occupied by shrubs or by native perennial grasses. It is also possible that the native forbs are more resilient to disturbance, and that non-native grasses are either resilient or introduced at the time of disturbance. When native non-native contributions are compared with our ANCOVA results, however, it seems most likely that the compound effect (*sensu* Paine et al. 1998) of post-settlement anthropogenic influence followed by a novel disturbance type left a legacy of permanently altered community composition. In this case, a legacy effect of these novel managed disturbances appears to be an increase in overall plant species diversity, and a landscape whose composition is irreversibly altered. A threshold was crossed with the application of chemical, fire, and

mechanical managed disturbance types, and the system – now less resilient due to ongoing anthropogenic influence - shifted to an alternate stable state that included increased native forb and non-native grass biodiversity.

Results that contrast with our findings regarding the resilience response of sagebrush steppe to managed disturbance (Harniss and Murray 1973, Watts and Wambolt 1996, Davies et al. 2009, Wisdom and Chambers 2009) may be rectified in context of findings from forest ecology literature. Hermy et al. (1999), for example, demonstrated that understory composition and relative abundances in European forest subjected to anthropogenic disturbance remained altered long after tree canopy cover was restored. Additionally, Foster et al. (2003) described the dynamics of forest canopy cover relative to ecosystem structure and function. Despite tree canopy recovery that followed disturbance, soil structure and lake sediments reflected persisting legacies. Presumably, plant species diversity remained altered due to the persisting legacy evident in ecosystem structure and function. If we apply these lessons from forest ecology to sagebrush steppe dynamics, it is plausible that while sagebrush cover recovered from disturbance, as found in the studies cited above, diversity did not return to pre-disturbance conditions but remained irreversibly altered.

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APPENDICES

APPENDIX A. Plant species endemism and presence by disturbance type.

Scientific Name		chem	fire	mech	ref
Achillea millefolium L.	native	+	+	+	+
Achnatherum hymenoides Roemer & Schultes (Barkworth)	native	+	+	+	-
Achnatherum lettermanii (Vasey) Barkworth	native	+	+	+	+
Achnatherum nelsonii (Scribn.) Barkworth ssp. Nelsonii	native	+	-	+	-
Agastache urticifolia (Bentham) Kuntze	native	+	-	+	-
Agoseris glauca (Pursh) Rafinesque	native	+	+	+	-
Agropyron cristatum (L.) Gaertner	non-native	+	+	+	+
Allium acuminatum Hooker	native	+	+	+	-
Alyssum alyssoides (L.) L.	non-native	-	+	+	-
Alyssum desertorum Stapf	non-native	+	+	+	+
Amelanchier alnifolia (Nuttall) Nuttall	native	-	-	+	-
Amelanchier utahensis Koehne	native	+	+	+	-
Antennaria dimorpha (Nuttall) Torrey & Gray	native	+	+	+	+
Antennaria microphylla Rydberg	native	+	+	+	+
Arabis holboellii Hormemann var. pinetorum (Tidestrom) Rollins	native	+	+	+	-
Arenaria congesta Nuttall in Torrey & Gray var. congesta	native	-	+	+	-
Artemisia arbuscula Nuttall	native	+	-	+	-
Artemisia ludoviciana Nuttall var. ludoviciana	native	-	+	+	-
Artemisia nova A. Nelson var. nova	native	+	+	+	+
Artemisia tridentata Nuttall	native	+	+	+	+
Artemisia tripartita Rydb.	native	+	+	+	-
Astragalus agrestis Douglas ex G. Don	native	+	-	+	-
Astragalus convallarius Greene var. convallarius	native	+	+	+	+
Astragalus falcatus Lamarck	native	-	-	+	-
Astragalus jejunus S. Watson var. jejunus	native	-	-	+	-
Astragalus lentiginosus Douglas ex Hooker var. chartaceus M.E. Jones	native	+	+	+	+
Astragalus miser Douglas ex Hooker var. tenuifolius (Nuttall) Barneby	native	+	+	+	+
Astragalus purshii Douglas ex Hooker var. glareosus (Douglas) Barneby	native	+	-	+	-
Astragalus tenellus Pursh	native	+	-	-	-
Astragalus utahensis (Torrey) Torrey & Gray	native	+	+	+	+
Atriplex argentea Nutt.	native	+	+	+	-
Atriplex canescens (Pursh) Nuttall var. canescens	native	-	-	+	-
Atriplex confertifolia (Torrey & Fremont) S. Watson	native	-	+	+	-
Atriplex corrugata S. Watson	native	-	-	+	-
Atriplex falcata (M.E. Jones) Standl.	native	+	+	+	-
Balsamorhiza sagittata (Pursh) Nuttall	native	+	+	+	+
Bassia prostrata (L.) A. J. Scott	non-native	-	+	+	-
Bromus arvensis L.	non-native	-	-	+	-
Bromus carinatus Hooker & Arnot	non-native	+	+	+	-

Bromus inermis Leysser	non-native	-	-	+	-
Bromus tectorum L.	non-native	+	+	+	+
Calochortus nuttallii Torrey & Gray	native	+	+	+	+
Carduus nutans L.	non-native	+	-	-	-
Carex douglasii F. Boott	native	+	+	+	-
Carex micoptera Mackenzie	native	-	-	+	-
Carex vallicola Dewey	native	-	-	+	-
Castilleja chromosa A. Nelson	native	+	+	+	-
Castilleja flava S. Watson var. flava	native	+	+	-	-
Castilleja linariifolia Bentham	native	+	+	+	-
Ceratocephala testiculatus (Crantz) Bess.	non-native	+	+	+	+
Chaenactis douglasii (Hooker) Hooker & Arnot	native	+	+	+	+
Chrysothamnus viscidiflorus (Hooker) Nuttall	native	+	+	+	+
Cirsium arvense (L.) Scopoli	non-native	+	+	+	-
Cirsium calcareum (M.E. Jones) Woot. & Standl.	native	+	+	-	+
Cirsium subniveum Rydberg	native	+	+	+	-
Cirsium undulatum (Nuttall) Sprengel var. undulatum	native	+	-	+	+
Collinsia parviflora Douglas ex Lindley	native	+	-	+	-
Collomia linearis Nuttall	native	-	-	+	-
Comandra umbellata (L.) Nuttall ssp. pallida (A. DC.) Piehl	native	+	+	+	-
Conium maculatum L.	non-native	+	-	+	-
Cordylanthus ramosus Nuttall ex Bentham	native	+	+	+	-
Crepis acuminata Nuttall	native	+	+	+	-
Crepis occidentalis Nuttall	native	-	-	+	-
Cryptantha caespitosa (A. Nelson) Payson	native	+	+	+	-
Cryptantha flavoculata (A. Nelson) Payson	native	+	-	+	-
Cryptantha gracilis Osterhout	native	-	-	+	-
Cryptantha sericea (A. Gray) Payson	native	+	+	+	-
Cymopterus longipes S. Watson	native	+	-	+	-
Cynoglossum officinale L.	non-native	-	-	+	-
Dactylis glomerata L.	non-native	-	-	+	-
Delphinium nuttallianum Pritzel ex Walpers	native	+	-	+	-
Delphinium occidentale (S. Watson) S. Watson	native	+	-	-	-
Descurainia incana (Bernhardi ex Fischer & C.A. Meyer) Dorn	native	+	+	+	-
Descurainia pinnata (Walter) Britton ssp. Nelsonii (Rydb.) Detling	native	+	+	+	-
Descurainia sophia (L.) Webb ex Prantl	non-native	+	-	+	-
Elymus elymoides (Rafinesque) Swezey	native	+	+	+	+
Ericameria nauseosa (Pall. ex Pursh) G.L. Nesom & Baird	native	+	+	+	+
Erigeron compositus Pursh	native	-	+	-	-
Erigeron eatonii A. Gray	native	+	+	+	-
Erigeron engelmannii A. Nelson	native	+	+	+	+
Erigeron glabellus Nuttall	native	+	+	-	+
Eriogonum brevicaule Nuttall var. brevicaule	native	+	-	+	-

Eriogonum caespitosum Nuttall	native	+	-	+	+
Eriogonum cernuum Nuttall	native	-	-	+	-
Eriogonum heracleoides Nuttall	native	+	-	+	-
Eriogonum microthecum Nuttall var. laxiflorum Hooker	native	+	+	+	+
Eriogonum ovalifolium Nuttall	native	+	+	+	+
Eriogonum umbellatum Torrey var. majus Hooker	native	+	+	+	+
Erysimum asperum (Nuttall) DC.	native	-	-	+	-
Erysimum repandum L.	non-native	-	+	-	-
Festuca idahoensis Elmer ssp. Idahoensis	native	-	-	+	-
Fritillaria atropurpurea Nuttall	native	+	-	+	-
Geranium viscosissimum Fischer & Meyer ex C.A. Meyer	native	+	+	+	-
Geum aleppicum Jacq.	native	-	+	+	-
Geum macrophyllum Willdenow var. perincisum (Rydberg) Raup	native	-	+	-	-
Gutierrezia sarothrae (Pursh) Britton & Rusby	native	-	+	+	-
Hackelia floribunda (Lehmann) I.M. Johnston	native	+	+	+	-
Hackelia patens (Nuttall) I.M. Johnston var. patens	native	-	+	-	-
Halogeton glomeratus (Bieberstein) C.A. Meyer	non-native	-	-	+	-
Helianthus annuus L.	native	-	+	-	-
Hesperostipa comata (Trinius & Ruprecht) Barkworth	native	+	+	+	-
Heuchera rubescens Torrey var. rubescens	native	-	+	-	-
Holosteum umbellatum L.	non-native	+	+	+	+
Hordeum jubatum L.	native	+	-	+	-
Ipomopsis aggregata (Pursh) V. Grant var. aggregata	native	+	+	+	+
Ipomopsis congesta (Hooker) V. Grant var. congesta	native	-	-	+	-
Juncus arcticus Willdenow	native	-	-	+	-
Juniperus osteosperma (Torrey) Little	native	-	+	-	-
Koeleria macrantha (Ledebour) Schultes	native	+	-	+	+
Krascheninnikovia lanata (Pursh) Meeuse & Smit	native	+	+	+	+
Lappula occidentalis (S. Watson) E.L. Greene	native	+	+	+	-
Leymus cinereus Scribner & Merrill	native	-	+	+	+
Leymus salinus (M.E. Jones) A. Love	native	-	+	+	-
Linanthus pungens (Torr.) J.M. Porter & L.A. Johnson	native	-	-	+	-
Linum lewisii Pursh var. lewisii	native	+	+	+	-
Lithospermum ruderale Dougl. ex Lehm.	native	+	+	+	-
Lomatium graveolens (S. Watson) Dorn & Hartman var. graveolens	native	+	+	+	-
Lupinus argenteus Pursh ssp. Rubricaulis (Greene) Hess & D. Dunn	native	+	-	+	-
Lupinus caudatus Kellogg ssp. caudatus	native	-	+	-	-
Lupinus parviflorus Nutt. Ex Hook. & Arn. ssp. Parviflorus	native	-	-	+	-
Lupinus sericeus Pursh ssp. sericeus	native	+	+	+	-
Machaeranthera canescens (Pursh) Gray	native	+	+	+	-

Machaeranthera grindelioides (Nuttall) Shinners var. grindelioides	native	+	-	+	-
Mahonia repens (Lindley) G. Don	native	+	+	+	-
Medicago sativa L.	non-native	+	+	+	-
Melica bulbosa Geyer ex Porter & Coulter	native	-	-	+	-
Mertensia oblongifolia (Nuttall) G. Don	native	+	-	+	-
Navarretia breweri (A. Gray) Greene	native	+	-	+	-
Oenothera caespitosa Nuttall ssp. caespitosa	native	+	-	-	-
Oenothera pallida Lindley ssp. pallida	native	-	-	+	-
Onobrychis viciifolia Scopoli	non-native	+	+	+	-
Opuntia polyacantha Haworth var. polyacantha	native	+	+	+	+
Orobanche fasciculata Nuttall	native	+	-	-	-
Orthocarpus luteus Nuttall	native	+	+	+	-
Packera multilobatus (Torrey & Gray ex. A. Gray) W.A.Weber & A. Löve	native	-	+	+	-
Pascopyrum smithii (Rydberg) A. Love	native	+	+	+	+
Penstemon caespitosus Nutt. ex Gray var. caespitosus	native	-	-	+	-
Penstemon cyananthus Hooker var. cyananthus	native	-	+	+	-
Penstemon humilis Nuttal ex A. Gray	native	+	+	+	-
Penstemon procerus Douglas ex Graham	native	-	-	+	-
Penstemon radicosus A. Nelson	native	+	+	+	-
Penstemon rydbergii A. Nelson	native	+	+	+	-
Phlox hoodii Richardson ssp. canescens (Torrey & Gray) Wherry	native	+	+	+	+
Phlox longifolia Nuttall	native	+	+	+	+
Poa bulbosa L.	non-native	+	-	-	-
Poa fendleriana (Steudel) Vasey	native	+	+	+	-
Poa pratensis L.	non-native	+	+	+	-
Poa secunda J. Presl	native	+	+	+	+
Polygonum aviculare L.	non-native	+	+	-	+
Polygonum douglasii E.L. Greene ssp. douglasii	non-native	-	+	-	-
Polygonum polygaloides Wall. Ex Meisn. Ssp. kelloggii (Greene) J.C. Hickman	native	+	-	-	-
Potentilla pectinisecta Rydb.	native	+	-	+	-
Potentilla pulcherrima Lehmann	native	-	-	+	-
Prunus virginiana L. var. melanocarpa (A. Nelson) Sargent	native	-	-	+	-
Pseudoroegneria spicata (Pursh) A. Love ssp. Spicata	native	+	+	+	+
Purshia tridentata (Pursh) DC.	native	+	+	+	-
Ribes cereum Douglas	native	-	-	+	-
Rosa woodsii Lindley var. ultramontana (S. Watson) Jepson	native	-	+	-	-
Rumex acetosella L.	native	+	-	-	-
Sanguisorba minor Scopoli	non-native	-	-	+	-
Sedum lanceolatum Torrey	native	-	+	+	-
Senecio canus Hooker	native	-	-	+	-
Senecio integerrimus Nuttall	native	+	+	+	-

Sidalcea oregana (Nuttall ex Torr. & Gray) A. Gray ssp oregana var. oregana	native	-	+	-	-
Silene drummondii Hook. var. drummondii	native	+	+	-	-
Sisymbrium altissimum L.	non-native	-	+	+	+
Sphaeralcea coccinea (Nuttall) Rydberg	native	+	+	+	-
Sphaeralcea grossulariifolia (Hook. & Arn.) Rydb.	native	-	-	+	-
Sphaeralcea munroana (Douglas ex Lindl.) Spach ex Gray	native	+	+	+	+
Stenotus acaulis (Nuttall) A. Gray	native	+	+	+	-
Symphoricarpos oreophilus A. Gray var. utahensis Rydberg	native	+	+	+	-
Taraxacum officinale Weber ex F.H. Wiggers	native	+	+	+	-
Tetradymia canescens DC.	native	+	+	+	+
Thinopyrum intermedium (Host) Barkworth & D.R. Dewey	non-native	-	+	+	-
Tragopogon dubius Scopoli	non-native	+	+	+	-
Trifolium gymnocarpon Nuttall	native	+	+	+	-
Verbascum thapsus L.	non-native	-	-	+	-
Veronica biloba L.	non-native	+	-	-	-
Viola nuttallii Pursh	native	+	-	+	-
Viola purpurea Kellogg ssp. venosa (S. Watson) M.S. Baker & J. C. Clausen	native	-	-	+	-
Zigadenus paniculatus (Nuttall) S. Watson	native	+	+	+	+

APPENDIX B. Descriptive statistics for chemical, fire, mechanical, and reference sites.

Time binned into decades since disturbance.

Response/Time:	Chemical			Fire			Mechanical			Reference			All		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
Species Richness															
All	31.8	7.01	20	31.33	5.91	12	27.83	10.32	35	23	2.65	3	29.36	8.78	70
1-10	27.00	2.83	2	27.43	2.76	7	28.69	10.46	13	NA	NA	NA	28.14	8.10	22
>10-20	31.57	7.50	7	36.67	4.04	3	27.75	9.71	4	NA	NA	NA	31.57	7.79	14
>20-30	35.00	7.62	6	37.00	7.07	2	20.67	14.57	3	NA	NA	NA	31.45	11.18	11
>30-40	22.00	NA	1	NA	NA	0	25.33	12.86	3	NA	NA	NA	24.50	10.63	4
>40-50	32.25	5.56	4	NA	NA	0	29.33	9.81	12	NA	NA	NA	30.06	8.86	16
Shannon Diversity															
All	2.81	0.24	20	2.73	0.28	12	2.60	0.54	35	2.51	0.25	3	2.68	0.43	70
1-10	2.54	0.03	2	2.60	0.24	7	2.67	0.58	13	NA	NA	NA	2.64	0.46	22
>10-20	2.77	0.18	7	2.84	0.23	3	2.66	0.29	4	NA	NA	NA	2.75	0.22	14
>20-30	2.95	0.20	6	3.03	0.28	2	1.88	0.83	3	NA	NA	NA	2.67	0.65	11
>30-40	2.65	NA	1	NA	NA	0	2.41	0.62	3	NA	NA	NA	2.48	0.52	4
>40-50	2.83	0.35	4	NA	NA	0	2.71	0.35	12	NA	NA	NA	2.74	0.34	16
Simpson Diversity															
All	0.94	0.02	20	0.93	0.02	12	0.91	0.07	35	0.91	0.02	3	0.92	0.05	70
1-10	0.92	<0.01	2	0.92	0.02	7	0.91	0.08	13	NA	NA	NA	0.92	0.06	22
>10-20	0.93	0.01	7	0.94	0.02	3	0.93	0.02	4	NA	NA	NA	0.93	0.01	14
>20-30	0.95	0.01	6	0.95	0.02	2	0.80	0.13	3	NA	NA	NA	0.91	0.09	11
>30-40	0.93	NA	1	NA	NA	0	0.90	0.05	3	NA	NA	NA	0.90	0.05	4
>40-50	0.94	0.03	4	NA	NA	0	0.93	0.03	12	NA	NA	NA	0.93	0.03	16
Jaccard Similarity															
All	0.29	0.08	20	0.29	0.06	12	0.25	0.07	35	NA	NA	3	0.27	0.07	70
1-10	0.24	0.01	2	0.27	0.06	7	0.24	0.07	13	NA	NA	NA	0.25	0.07	22
>10-20	0.32	0.11	7	0.32	0.07	3	0.23	0.05	4	NA	NA	NA	0.29	0.09	14
>20-30	0.29	0.07	6	0.26	0.05	2	0.24	0.10	3	NA	NA	NA	0.27	0.07	11
>30-40	0.33	NA	1	NA	NA	0	0.25	0.04	3	NA	NA	NA	0.27	0.05	4
>40-50	0.26	0.08	4	NA	NA	0	0.26	0.07	12	NA	NA	NA	0.26	0.07	16
Simpson Dissimilarity															
All	2.04	1.94	20	1.49	0.63	12	1.88	2.04	35	NA	NA	3	1.86	1.82	70
1-10	1.28	0.16	2	1.59	0.74	7	1.24	0.45	13	NA	NA	NA	1.35	0.55	22
>10-20	2.91	3.04	7	1.56	0.55	3	1.16	0.27	4	NA	NA	NA	2.12	2.24	14
>20-30	1.28	0.27	6	1.06	0.18	2	3.62	2.32	3	NA	NA	NA	1.88	1.54	11
>30-40	3.40	NA	1	NA	NA	0	2.02	0.88	3	NA	NA	NA	2.36	1.00	4
>40-50	1.68	1.06	4	NA	NA	0	2.33	3.12	12	NA	NA	NA	2.17	2.73	16