

THE RELATIVE IMPORTANCE OF FIRE HISTORY, MANAGEMENT
TREATMENTS, BIOTIC, AND ABIOTIC FACTORS ON THE ABUNDANCE OF
KEY VEGETATIVE COMPONENTS IN AN ENDANGERED SAGEBRUSH-STEPPE
ECOSYSTEM

by

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Biotic and Abiotic Factors on the Abundance of Key Vegetative
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ABSTRACT

Dryland ecosystems are globally distributed and occupy nearly half of Earth's terrestrial surface. Drylands are particularly vulnerable to degradation and their restoration has become a global concern. Sagebrush-steppe ecosystems in the intermountain western United States have been subject to decades of active management efforts to address invasive species and restore plant communities, and can serve as a relevant case study to investigate dynamics between fire, invasive species, and management treatments in a representative dryland system. My objective was to determine the relative importance of fire history, management treatment history, abiotic, and biotic factors in relation to the abundance of key vegetative components in the Morley Nelson Snake River Birds of Prey National Conservation Area, a highly fire-prone and endangered sagebrush-steppe ecosystem. The vegetative components of interest included the non-native annual grass cheatgrass (*Bromus tectorum*), the native perennial bunchgrass Sandberg bluegrass (*Poa secunda*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), and biological soil crust. I performed multivariate model selection for each response variable in burned and unburned study areas.

My results indicate that within both burned and unburned areas, *B. tectorum* abundance was negatively associated with *P. secunda* and biological soil crust, highlighting the potential of shallow-rooted perennial grasses and soil crust to limit the abundance of *B. tectorum*. Post-fire management treatments were not included in best fit

models for *B. tectorum* abundance, confirming the findings of previous work on the limited success of post-fire treatments in warm and dry regions of the sagebrush-steppe ecosystem. *A. tridentata* ssp. *wyomingensis* exhibited a negative relationship with the distance to the nearest fire border in unburned areas, suggesting the role that fire edge effects may play in landscapes with unburned sagebrush. *P. secunda* appears to tolerate some level of fire, withstanding up to two repeat fire events. Conversely, *B. tectorum* reaches its highest abundance after three or more fires. Repeat fire is a significant threat to Wyoming big sagebrush-communities, but our results suggest that burned landscapes that still contain *P. secunda* and biological soil crust offer opportunities to explore the dynamics between *B. tectorum* and *P. secunda* and the restoration potential of *P. secunda*.

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LIST OF ABBREVIATIONS

ARTRW	<i>Artemisia tridentata</i> ssp. <i>wyomingensis</i>
BRTE	<i>Bromus tectorum</i>
BSC	Biological soil crust
POSE	<i>Poa secunda</i>
NCA	Morley Nelson Snake River Birds of Prey National Conservation Area
R&R	Resistance and Resilience
S&T	State and Transition

INTRODUCTION

Human activity has induced sweeping change to the structure, composition, and function of Earth's terrestrial ecosystems (Vitousek et al., 1997). The accelerating nature of these trends has prompted the emergence of global change research, which has enhanced our understanding of the factors driving these changes and their effects across regional and global scales (Vitousek, 1994). The prominent drivers of global change in terrestrial ecosystems include biological invasions, altered disturbance regimes, land use change, and climate change (Steffen et al., 2006). Earth's terrestrial ecosystems are highly diverse however, and exhibit variability in their vulnerability to global change drivers (Sala et al., 2000).

Dryland ecosystems, which encompass arid and semi-arid deserts, shrub lands, savannas, and grasslands, comprise nearly half of Earth's terrestrial surface and support the economic livelihoods of hundreds of millions of people (Reynolds et al., 2007). Dryland systems are vastly distributed and have been increasingly recognized for their roles in global net primary productivity and carbon dynamics (Poulter et al., 2014; Huang et al., 2016). As water-limited systems however, drylands are particularly vulnerable to global change drivers and resulting degradation (Sala et al., 2000; Svejcar and Kildisheva, 2017), which has motivated efforts to better understand dynamics within drylands systems and to devise strategies to prevent further losses (Huang et al., 2016;

Reynolds et al., 2007). In broader discussions of addressing degradation in dryland systems, scientists have proposed active management of the biotic components of dryland systems to enhance resilience to global change drivers and to prevent continued loss in ecological function and services (Aronson and Alexander, 2013; James et al., 2013; Maestre et al., 2016). Due to the complexity of both the ecological and social dimensions of drylands systems however, restoration will invariably require place-based approaches (Franklin et al., 2016). The sagebrush-steppe ecosystem in the western United States is a dryland system that has been heavily impacted by non-native annual grasses and altered fire regimes. It is also the subject of a large body of research on applied restoration. Thus, the sagebrush-steppe ecosystem provides an intriguing case study of the complexities involved in both management and restoration of dryland systems.

The Sagebrush-Steppe Ecosystem

The sagebrush-steppe is comprised of shrub and grass dominated communities that are broadly distributed across the interior western United States and Canada (Brooks and Chambers, 2011; West, 1983). Non-native annual grasses are of particular concern as they occupy significant portions of the sagebrush-steppe and both enhance and benefit from fire, leading to cycles of annual grass invasion and fire that have transformed diverse shrub dominated communities to invasive annual grass monocultures across a large portion of the sagebrush-steppe ecosystem (Balch et al., 2013; Whisenant, 1990). Fire and invasive annual grasses are key drivers of change in dryland systems across Earth's terrestrial systems, and are the primary drivers of ecological degradation in the sagebrush-steppe ecosystem (Brooks et al., 2004; D'Antonio and Vitousek, 1992; Svejcar

and Kildisheva, 2017). Fire, invasive species, and land conversion associated with human population growth have collectively destroyed roughly half of the sagebrush-steppe ecosystem since Euro-American settlement of the West (Knapp, 1996). These trends, including their interactive and cumulative effects, pose significant threats to an already dwindling ecosystem (Chambers and Wisdom, 2009; Knick et al., 2003).

The sagebrush-steppe ecosystem is the subject of a large body of applied research on active manipulation of biotic components, especially with regards to controlling invasive species and restoring native species in fire impacted areas (e.g., Baker, 2006; Davies et al., 2011; Svejcar et al., 2017). In addition, the sagebrush-steppe has been subject to a large-scale program of post-fire rehabilitation and restoration. The Bureau of Land Management has conducted extensive burned area recovery efforts through the use of post-fire treatments to prevent invasive weed dominance and to reestablish seeded species (Beyers, 2004). Over 5,000 seeding treatments have been implemented over millions of hectares of the sagebrush ecosystem in the last 75 years, potentially representing one of the largest vegetation manipulation efforts in the world (Pilliod et al., 2017). A majority of these post-fire seeding treatments are implemented under a federal rehabilitation program, the Emergency Stabilization and Burned Area Rehabilitation (often referred to as ESR) program (GAO, 2003).

There are two theoretical frameworks that have become integral to research and management in the sagebrush-steppe ecosystem. State and Transition (S&T) and Resistance and Resilience (R&R) have advanced our understanding of the effects of fire, invasive species, and livestock grazing on plant communities in the sagebrush-steppe. On

a fundamental level, S&T and R&R represent the kind of syntheses that scientists have identified are needed to understand the changes occurring in dryland systems across the Earth (Franklin et al., 2016; Maestre et al., 2016). A brief review of each of these frameworks will follow.

State and Transition

The State and Transition framework was proposed in the late 1980s to describe the “multi-equilibrial” nature of plant community dynamics in the sagebrush-steppe ecosystem (Westoby et al., 1989). Classic theories of ecological succession did not accurately portray the dynamics within sagebrush-steppe ecosystems, such as the observed non-linear changes in plant community composition and structure in response to disturbance and invasive weeds (Bestelmeyer et al., 2003). State and transition models were presented as a more accurate depiction of observed dynamics as they recognized the existence of multiple “states” that differed from climax communities in both their structure and composition (Westoby et al., 1989). “Transitions” were described as the mechanisms, such as land-use, disturbance, and climate, that alter biotic components and ecological processes to ultimately drive conversions to alternative “states” (Stringham et al., 2003). While “states” represent a proposed plant community that will not transition to an alternative state unless a certain boundary, often referred to as a threshold, is crossed (Stringham and Shaver, 2001). Thresholds represent factors that influence potential transitions between states such as management interventions, biotic interactions, and ecological processes (Stringham et al., 2003). Within a given state however, there exists a large potential for variation in species composition and community dynamics, which are

often referred to as “phases” (Stringham and Shaver, 2001). The S&T framework was embraced by the rangeland science community in the 1990s (Bestelmeyer et al., 2003) and became a key component of the Natural Resources Conservation Services Ecological Site Description (ESD) program (Stringham and Shaver, 2001). Within a given ESD, the possible states, phases, and potential transitions have been described for the dominant vegetation and soil types across the sagebrush-steppe. Importantly, each ESD identifies the historic plant community and contains additional information on soil conditions, climate, and management actions that may have particular influence on both states and potential transitions.

Resistance and Resilience

The R&R framework was originally informed by empirical testing of fire and invasive weed dynamics across the major climatic regimes and sagebrush plant community types in the sagebrush-steppe ecosystem (Brooks and Chambers, 2011; Chambers et al., 2014a, 2007). Within this framework, resistance is defined as the abiotic and biotic attributes of an ecosystem that limit growth of invading species (D’antonio and Thomsen, 2004) and resilience as the capacity of an ecosystem to maintain its structure and function when subjected to disturbance, most notably fire (Chambers et al., 2007). Resistance to invasion and resilience to fire are to be interpreted as innate characteristics of sagebrush-steppe plant communities (Pyke et al., 2015a). Areas of the sagebrush ecosystem are classified into low, moderate, and high resistance and resilience based primarily on temperature, precipitation, and soil moisture and soil temperature regimes (Chambers et al., 2014c). Researchers employing the framework have identified the key

biotic and abiotic determinants of resistance and resilience and have devised decision tools to support management actions across the sagebrush ecosystem (Pyke et al., 2015b).

Both S&T and R&R classify the dominant communities in the sagebrush-steppe into units that are meaningful to both scientists and managers. In S&T, the main management units are ecological sites and within R&R, management units are defined by low, medium, and high resistance and resilience. Both frameworks are intended to not only aid managers in determining the characteristics of given management units, but to help inform decision making by providing guidance on the appropriateness of management interventions (Chambers et al., 2014c, Miller et al., 2011). Both frameworks acknowledge that certain ecological sites and resistance and resilience zones are at high risk to fire and annual grass dominance (Bestelmeyer et al., 2003; Chambers et al., 2014a). In addition, researchers have acknowledged that both frameworks can help inform one another. For example, as inherent characteristics of given ecological sites, resistance and resilience can be used to determine how far a given state can be displaced from its equilibrium before transitioning to an alternative stable state (Stringham and Shaver, 2001). There are acknowledged limitations in the application of S&T and R&R however. One of the key gaps in the S&T framework are detailed descriptions of transitions and associated thresholds. Within ESDs for the various plant communities of the sagebrush-steppe, activities that can result in transitions such as overgrazing and wildfire are stated, but their attributes such as duration and intensity are not measured. In other words, these models have not quantified the processes underlying transitions (Bestelmeyer et al., 2003). Within the R&R framework, topographic and environmental

variability result in variability in the ecosystem attributes that influence site resistance to invasive annual grasses, which requires careful assessment of site conditions beyond the general categories of resistance and resilience (Miller et al., 2013).

Wyoming Big Sagebrush Communities

Wyoming big sagebrush communities are the most widespread plant community type in the sagebrush-steppe ecosystem and typically occupy regions with cool, wet winters, and dry, hot summers (Taylor et al., 2014). These climatic conditions are especially conducive to *B. tectorum* growth, survival, and reproduction (Bradford and Lauenroth, 2006; Bradley, 2009). *B. tectorum* invasion into Wyoming communities has been considerable and has led to shortened fire return intervals and a higher occurrence of large fire events (Balch et al., 2013; Brooks et al., 2004; Whisenant, 1990). Wyoming big sagebrush communities have lower overall productivity compared to other big sagebrush community types, which limits post-fire recovery (Beck et al., 2009; Shinneman and Baker, 2009; Shinneman and McIlroy, 2016). Thus, Wyoming big sagebrush exhibit inherently low resistance to invasive annual and grasses and low resilience to disturbance (Chambers et al., 2014a). As a result, Wyoming big sagebrush communities are also highly vulnerable to conversion to annual invaded states (Chambers et al., 2014b).

Both the Resistance and Resilience and State and Transition frameworks acknowledge the exceedingly difficult restoration context that low resistance and resilience Wyoming big sagebrush communities present. However, Wyoming big sagebrush landscapes vary widely in their degree of invasion, their disturbance history, and their management context. The Morley Nelson Snake River Birds of Prey National

Conservation Area (NCA) in southwestern Idaho is a low resistance and resilience landscape that has experienced high *B. tectorum* invasion, high fire activity, and in result, extensive conversion to invaded alternative states dominated by invasive annual grasses and forbs. It exhibits some of the highest fire frequencies recorded in the northern Great Basin and it has also been the site of over a hundred post-fire drill and aerial seedings since the mid 1950's (Bukowski and Baker, 2013).

The ecological site description for the dominant Wyoming big sagebrush community type in the NCA is “loamy 8-12 Wyoming big sagebrush/Bluebunch wheatgrass/Thurber’s needlegrass” (Fig. 1). The historical reference state in the corresponding state and transition model identifies Wyoming big sagebrush as the dominant overstory and two deep-rooted perennial bunchgrasses as the dominant understory: Bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) and Thurber’s needle grass (*Achnatherum thurberianum* (Piper) Barkworth). The model indicates that livestock grazing can reduce deep-rooted perennial bunchgrasses, resulting in a phase characterized by an increase Sandberg’s bluegrass (*Poa secunda* Presl), a shallow-rooted, native perennial bunchgrass. If livestock grazing that occurs across seasons and results in heavy utilization of native perennial bunchgrasses and fire occur, an ecological threshold may be crossed and the reference state can be converted to an alternative invaded state characterized by *P. secunda*, *B. tectorum*, and other annual invasive species. Once in this alternative stable state, management interventions such as seeding treatments can potentially convert invaded states into alternative seeded states, but return to the original historical reference state is considered unlikely. The model

acknowledges the potential of a fourth alternative stable state that may arise if extreme erosion and loss of soil resources occur. Thus, in Wyoming big sagebrush communities that have experienced a high degree of fire and livestock grazing, *B. tectorum* and *P. secunda* can become key species.

An additional biotic component that is critically important to the ecological integrity of the sagebrush-steppe, and drylands more broadly, are biological soil crusts (Belnap et al., 2001a). Biological soil crusts are a key component of the soil substrate and are a community of mosses, lichens, cyanobacteria and fungi that influence water filtration, nitrogen fixation, and plant germination and growth (Belnap et al., 2001b). There is some experimental evidence that biological soil crusts can limit the germination and growth of *B. tectorum* (Deines et al., 2007; Serpe et al., 2006). In addition, several observational studies have documented negative relationships between biological soil crust and *B. tectorum* abundance across the sagebrush ecosystem (Gelbard & Belnap, 2003; Peterson, 2013; Reisner et al., 2013; Shinneman & Baker, 2009). Despite their importance, the state and transition model for the dominant Wyoming big sagebrush community type does not address how biological soil crusts are influenced by livestock grazing and fire, or how they may change between phases and states.

Research Objectives

Both State and Transition and Resistance and Resilience frameworks focus on the transformative effects of fire and invasive annual grasses in the sagebrush-steppe ecosystem, but the vast majority of applied research on plant community responses to fire evaluates the effects of single fire events (Condon et al., 2011; Knutson et al., 2014). The

effects of multiple fires on vegetation are less understood (Miller et al. 2013). The fire and management history of the NCA offer the opportunity to investigate how frequent fire and management treatments may influence vegetation in degraded Wyoming big sagebrush steppe communities. The primary objective of this study is to determine if fire history and management treatments have influenced the key biotic components of a highly fire-prone Wyoming big sagebrush community. Fire and management history will be evaluated alongside additional abiotic, biotic, and spatial factors to determine their relative importance on *B. tectorum*, *P. secunda*, *A. tridentata* ssp. *wyomingensis*, and biological soil crust.

METHODS

Study Site

This study area is located within the 243,000 ha Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) (43° N, 116°W) (Fig. 2). The NCA is located within the Snake River Plain ecoregion and receives approximately 200 mm of precipitation annually primarily between November and March (Fig. 3). The NCA is characterized by loess derived soils and has relatively flat topography with the exception of a few isolated buttes. The NCA is bordered by the Snake River canyon on its western and southern boundary, and agricultural and suburban areas on its northern boundary (Fig. 4). The Bureau of Land Management manages the NCA under a multiple use framework, and permits grazing, recreation, wildlife viewing, and scientific research (Knick and Rotenberry, 1997). Because of its importance to nesting raptors, the NCA attracts diverse research on fire and fuel dynamics, wildlife population dynamics, restoration ecology, and human-wildlife interactions.

Prior to European settlement, plant communities at the NCA consisted primarily of Wyoming big sagebrush, while winterfat (*Krasheninnikovia lanata* (Pursh) A. Meeuse & Smit) and salt desert shrub communities (*Atriplex* spp.) comprised a lesser component. The NCA experienced heavy and prolonged grazing by cattle and sheep during the early 1900s (Yensen, 1982), leading to the depletion of the native herbaceous understory and

the spread of *B. tectorum* (USDI, 2008). The NCA has experienced a significant increase in fire size and fire frequency in the last century, with particularly large fire seasons in the early 1980s, 1995, and 1996 (USDI, 2008). The cumulative impacts of fire and annual grass invasion have converted over half of the NCA's native shrub communities to non-native communities dominated by *B. tectorum* and increasingly, by secondary weeds such as Russian thistle (*Salsola kali* L.) and annual mustards (*Descurainia* spp., *Sisymbrium* spp) (USDI, 2008). The remaining Wyoming big sagebrush habitat is highly fragmented and at risk conversion to *B. tectorum* (Knick and Rotenberry, 1997). As a federally managed entity, the NCA has received nearly 100 post-fire seeding treatments since the late 1950s. Prior to 1990, these treatments consisted of plowing and seeding, but since the early 1990s, treatments have consisted of fall seedings with rangeland drills and/or fall or spring aerial seedings (USDI, 2008).

Experimental Design

This study utilized field data from a previously conducted study carried out by the U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center (USGS FRESC) (Shinneman et al., 2015). The USGS FRESC study utilized the USGS Land Treatment Digital Library (Pilliod and Welty, 2013) to create spatial layers of both fire and post-fire treatment history spanning 1957-2014. These layers were then used to stratify sampling locations across three categories of fire and treatment history: (1) previously burned areas that received BLM post-fire emergency stabilization and rehabilitation treatments with native and non-native species using aerial, drill, or both aerial and drill methods (i.e. treated), (2) previously burned areas from 1957-present with

no record of post-fire treatments (i.e. burned), (3) areas that have no record of fire from 1957-2014 (i.e. unburned). Treated areas that burned multiple times were included only if they were treated after the most recent fire. The USGS established 98 field plots in 2012 and conducted sampling between May and August (Fig. 5). This study utilized field data collected in 2012, which was the first year of a three-year study. The precipitation in 2012 was most similar to the long-term average for the region (Fig. 3, Table 1). Field plots consisted of 98 randomly assigned 1-hectare plots across unburned, burned, and treated strata and thus captured differences in fire and treatment history.

Within each 1-ha plot, nine, evenly spaced subplots were established 25 m apart. At each subplot center, a 1x1 m quadrat frame was placed and a nadir oriented photo was taken 2 m above each quadrat. Photos were analyzed with SamplePoint software to derive percent canopy cover of all present species as well as the soil surface (litter, bare mineral soil, rock, and biological soil) for each subplot (Booth et al., 2006). Percent cover was averaged over the nine subplots, resulting in plot-level cover for individual species and the soil surface. Plot-level cover for plant functional groups was determined by combining the cover of all individual species in a given functional group, e.g., native perennial bunchgrasses, non-native seeded perennial bunchgrasses, etc. Plot-level canopy cover was used for both predictor and response variables.

Predictor Variables

A spatial layer of all fires from 1957-2014 compiled from the USGS Land Treatment Digital Library (LTDL) was used to derive several fire variables for each field plot. The LTDL contains digitized fire polygons and ancillary information such as fire

year, which was compiled into a spatial database in ArcGIS. If a fire record existed in LTDL, it was assumed that the entire polygon represented burned area. From 1957-2014, 58% of the NCA has burned (Fig. 6). However, this burned area consists of a fire gradient of 1-8 fires (Fig. 7). This fire gradient layer was used to create a spatial layer of fire frequency categories (Fig. 8). In addition, a spatial layer of year since last fire was used to create spatial layer of fire recentness (Fig. 9). Using these spatial layers, fire history variables were derived for each plot (Table 2). Roughly 20% of the NCA has received post-fire rehabilitation treatments in the form of drill or aerial seedings from 1957-2014 (Fig. 10, Fig. 11). This layer was used to derive treatment type for each plot (Table 2). Several spatial variables including nearest fire border, nearest road, and nearest allotment boundary were derived for each field. Using proximity tools in ArcGIS, the perpendicular distance in meters from the plot center to the nearest fire border, road, and allotment were determined (Table 2). Two key abiotic variables, mean elevation and soil type, were derived in ArcGIS (Table 2). Three native perennial plant functional groups were included as biotic predictor variables to evaluate the influence of present day-vegetation on each response variable (Table 3, Table 4b). In addition, each response variable contained the other response variables as predictors, e.g. models for *B. tectorum* included *P. secunda*, *A. tridentata* ssp. *wyomingensis*, and biological soil crust as predictors.

Data Analysis

Multiple linear regression was used to evaluate the relative importance of biotic, abiotic, disturbance, and management factors in relation to the abundance of each of the

four response variables: *B. tectorum* (BRTE), *P. secunda* (POSE), *A. tridentata* ssp. *wyomingensis* (ARTRW), and biological soil crust (BSC). Each response variable consisted of plot level percent canopy cover that was log transformed to improve normality and meet model assumptions. Separate submodels for each response variable were developed for unburned and burned plots (Table 5). For each of the four response variables in both burned and unburned submodels, model selection was employed using a forward stepwise approach based on corrected Aikie Information Criteria (AICc) (Mazerolle, 2011). Factors were added iteratively and AICc was calculated and compared until the addition of factors no longer reduced AICc values. Interactions between predictors were not included in model selection. Final models represent the most parsimonious models with significant main effects. If the final model contained multiple factors, each factor was dropped individually to assess its relative importance based on the observed change in AICc value. Factors were considered to have high, moderate, or low importance if the change in AICc was greater than 10, between 10 and 2, or less than 2 (Bansal and Sheley, 2016). All analysis was performed using R computer software (R Core Team, 2014).

RESULTS

Unburned

B. tectorum

In unburned areas, the best fit model contained several biotic factors as well as one spatial factor (Table 6). Cover of *B. tectorum* decreased with increasing cover of *P. secunda*, native shrubs, and biological soil crust and with increasing distance from the nearest allotment boundary. Removal of *P. secunda* and biological soil crust from the best fit model resulted in a larger change in AICc compared to the removal of native shrubs and nearest allotment, indicating stronger relationships between *B. tectorum* and *P. secunda* and *B. tectorum* and biological soil crust. Other spatial factors such as nearest road and nearest fire border were not present in the final best fit model. With an adjusted R^2 of .78, the best fit model in unburned areas explained a relatively large proportion of the variability in *B. tectorum* cover within unburned plots.

P. secunda

In unburned areas, the best fit model for *P. secunda* displayed a strong, negative relationship with BRTE cover (Table 6). Additional spatial, biotic, and abiotic factors were not included in the best fit model. The best fit model explained 61% of the variability in *P. secunda* cover within unburned plots.

Biological soil crust

In unburned areas, the best fit model for biological soil crust contained cover of *A. tridentata* ssp. *wyomingensis* and distance to the nearest allotment boundary and displayed positive relationships with both (Table 6). Biological soil crust cover increased with increasing Wyoming big sagebrush cover and as the distance to the nearest allotment boundary increased. The best fit model did not contain other biotic, abiotic, and spatial factors. Roughly 50% of the variability in biological soil crust within field plots was explained by Wyoming big sagebrush cover and proximity to allotment boundaries.

A. tridentata ssp. *wyomingensis*

In unburned areas, the best fit model for *A. tridentata* ssp. *wyomingensis* contained the distance to the nearest fire border and cover of *B. tectorum* (Table 6). Cover of *A. tridentata* ssp. *wyomingensis* increased as the distance away from the nearest fire border increased and as the cover of *B. tectorum* decreased. Removal of these two predictors resulted in smaller relative change in AICc scores. The best fit model explained 27% of the variability of *A. tridentata* ssp. *wyomingensis* cover within unburned plots.

Burned

B. tectorum

In burned areas, the best fit model contained only a subset of the originally hypothesized relevant factors (Table 6). As in unburned areas, *B. tectorum* exhibited strong, negative relationships with *P. secunda* and biological soil crust, with these two factors alone explaining 70% of the variability in BRTE cover. Other factors such as fire

history and management treatments were not included in the best fit model. Figures 12-15 display the cover each response variable in relation to fire and treatment history. Cover of *B. tectorum* was similar between burned and untreated and burned and treated plots, although burned plots displayed greater cover than unburned plots (Fig. 12a). Cover of *B. tectorum* was similar in plots that burned one or two times, but cover of *B. tectorum* in plots that burned three to five times since 1957 were dominated by *B. tectorum* (Fig 13a). *B. tectorum* cover did not differ across categories of fire recentness (Fig 14a), or across treatment categories (Fig 15a).

P. secunda

In burned areas, the best fit model contained only a subset of the originally hypothesized relevant factors (Table 6). As in unburned plots, *P. secunda* negative relationship with *B. tectorum* cover, but categories of times burned were also included in the best fit model. These two factors explained 64% of the variability in *P. secunda* cover in burned plots. Cover of *P. secunda* did not differ greatly across unburned, burned and untreated, and burned and treated plots (Fig 12b). However, cover of *P. secunda* did differ across categories of times burned, with plots that burned three to five times containing much less *P. secunda* cover compared to plots that burned once or twice (Fig 13b). Within treated areas, *P. secunda* cover was lowest in areas that received drill seeding treatments and a combination of drill and aerial treatments (Fig. 15b).

A. tridentata ssp. wyomingensis

Model selection did not produce a best fit model for *A. tridentata ssp. wyomingensis* in burned plots, likely due to the low or absent *A. tridentata ssp.*

wyomingensis cover in burned plots (Fig. 12c). *A. tridentata* ssp. *wyomingensis* cover was very low or absent in plots regardless of number of times burned (Fig. 13c), or years since the last fire (Fig 14c).

Biological soil crust

In burned areas, the best fit model for biological soil crust contained non-sagebrush native shrubs and *B. tectorum* (Table 6). As in unburned plots, biological soil crust displayed a positive relationship with native shrubs in burned plots. In addition, biological soil crust displayed a negative relationship with *B. tectorum*. The best fit model for biological soil crust in burned areas explained slightly more of the variability in biological soil rust cover (68%) than in unburned areas. In general, biological soil crust cover was lower in burned plots than in unburned plots (Fig. 12d), but there were no strong distinctions in biological soil crust cover across categories of times burned (Fig. 13d), fire recentness (Fig. 14d), or across management treatments (Fig. 14d).

DISCUSSION

Relative Importance of Fire, Management Treatments, Spatial, and Biotic Factors

This study assessed the relative importance of fire and management treatments in Wyoming big sagebrush landscapes. Factors related to each of these processes were included in model selection for each response variable, but proved to be unimportant in most cases for explaining percent canopy cover of each response variable. Rather, present day vegetative components explained most of the variation in the abundance of our chosen response variables.

Influences on the Abundance of *B. tectorum*

In the best-fit model for *B. tectorum* in burned plots, fire recentness, fire frequency, and management treatments were not present in the final best fit model. There were minimal differences in the cover of *B. tectorum* across categories of fire frequency (Fig. 13a), fire recentness (Fig. 13b), and management treatments (Fig. 13c). Reducing the abundance of invasive annual grasses is a primary objective of post-fire rehabilitation, but the majority of post-fire management efforts have had little to no impact on invasive abundance (Pyke et al., 2013), particularly in Wyoming big sagebrush communities in warmer and drier portions of the sagebrush-steppe ecosystem (Knutson et al., 2014). Rather, biotic factors were found in the best-fit models for *B. tectorum* in burned and unburned plots. In the best-fit model for *B. tectorum* in both burned and unburned plots,

P. secunda and biological soil crust displayed strong, negative relationships with the cover of *B. tectorum*. *P. secunda* is the most common native perennial bunchgrass present within the NCA (Quinney, 1999), and other studies have observed high relative abundance of *P. secunda* in degraded Wyoming big sagebrush communities (Davies et al., 2015; Davies and Svejcar, 2008). There is ample evidence that native perennial bunchgrasses contribute to site resistance to invasive annual grasses by limiting both the amount of space and resources available to *B. tectorum* (Chambers et al., 2007; Chambers et al., 2014a). Reisner et al. (2013) demonstrated however, that sites with deep-rooted perennial bunchgrasses that contained *P. secunda* and biological soil crust in interspaces exhibited particularly high resistance to invasive grasses. Historic overgrazing at the NCA has depleted much of the deep-rooted perennial bunchgrass community however (Quinney, 1999; Yensen, 1982). Our results suggest that both *P. secunda* and biological soil continue to be important influences on *B. tectorum* even within highly altered Wyoming big sagebrush communities. From this data alone it is difficult to discern which mechanisms may underlie the negative relationship between *P. secunda* and *B. tectorum*, but our results suggest that *P. secunda* can persist in highly invaded environments, while there is growing evidence that *P. secunda* can limit *B. tectorum* under certain conditions.

***B. tectorum* and *P. secunda* Dynamics**

The competitive abilities of *B. tectorum* compared to native perennial bunchgrasses in the seedling stage are well established; *B. tectorum* displays fast root growth (Arredondo et al., 1998) and can rapidly consume soil moisture and outcompete native perennial grass seedlings (Kulmatiski et al., 2006a, Mangla et al., 2011; Schantz et al.,

2015). Recent research on trait differences in *P. secunda* populations from invaded areas versus non-invaded areas indicate that *P. secunda* from invaded areas may possess traits that enable growth and reproduction even under competitive pressure from *B. tectorum*. Populations of *P. secunda* from invaded areas exhibit earlier timing of flowering and reproduction and appear to maintain root growth rates in the presence of *B. tectorum* (Baughman et al., 2016; Goergen et al., 2011; Johnson et al., 2015; Monaco et al., 2005). Researchers have suggested that these traits are the result of local adaptation of *P. secunda* to high competitive pressure (Goergen et al., 2011; Kulpa and Leger, 2013). Perhaps one of *P. secunda*'s most important traits is that it engages in several reproductive modes including outcrossing, selfing, and apomixis (Kellogg, 1987). However, it is thought that reproduction via apomixis is common, resulting in high levels of apomictic seed production in native populations (Kelley et al., 2009). Reproduction via apomixis entails asexual production of seeds, and permits species to reproduce even at low density, which may explain how *P. secunda* can persist in invaded environments like the NCA. Collectively, these traits explain how *P. secunda* can co-exist with *B. tectorum*, but other studies have noted that dense populations of *P. secunda* may limit *B. tectorum* germination and growth and even exclude *B. tectorum* (Bates and Davies, 2014; Davies et al. 2012). Our results indicate that burned study plots that contained 30% cover of *P. secunda* contained very little to no *B. tectorum*. Chambers et al., (2014b) found that 20% total cover of *P. secunda* and deep-rooted perennial bunchgrasses was necessary to limit *B. tectorum* in a similar Wyoming big sagebrush site, suggesting that *P. secunda* may

need to maintain even higher density to exclude *B. tectorum* if other perennial bunchgrass species are absent.

Over the course of this study, we observed sites within the NCA that were dominated by *P. secunda*, suggesting that *P. secunda* can become a cover type under certain conditions. Davies et al. (2012) described a *P. secunda* phase in a Wyoming big sagebrush landscape with a similar disturbance history to the NCA. They described two phases, one dominated by *Poa secunda* and one dominated by *B. tectorum* and observed that the *B. tectorum* phase was replaced by *P. secunda* over a seven year period that experienced one fire. The authors suggested that post-fire herbicide treatments may have reduced *B. tectorum* growth, opening a window for an increase in *P. secunda*. Longer-term observations, like the aforementioned study by Davies et al. (2012), allows researchers to describe changes in abundance over time and to identify causal factors. In our study, we are unable to offer insights on temporal dynamics between *B. tectorum* and *P. secunda*, however our results suggest that very high abundances of *P. secunda* can exclude *B. tectorum* at smaller spatial scales. Although we are unable to describe the dynamics and longevity of existing populations of *P. secunda* at the NCA, our results do shed light on how *P. secunda* responds to repeat fire.

Fire and Disturbance Effects on *B. tectorum* and *P. secunda*

The best fit model for *P. secunda* in burned areas contained categories of fire frequency as a predictor. Plots that burned one or times did not differ greatly in *P. secunda* abundance, but plots that burned 3-5 times from 1957-2014 contained significantly less *P. secunda*. The S&T model acknowledges that fire is a key factor

driving the transition from State 1 to State 2 (T1), but it does not quantify this threshold (Fig. 1). These results suggest however that three fires can remove *P. secunda* from burned areas. Though it is unclear what may explain this dynamic, it is possible that the combination of repeated disturbance and high competitive pressure from *B. tectorum* overwhelms the ability of *P. secunda* to maintain growth and reprod. These results suggest however that three fires can reduce or remove populations of *P. secunda*. Though it is unclear what may explain this dynamic, it is possible that the combination of repeated disturbance and high competitive pressure can negatively impact populations of *P. secunda* over time. Though *P. secunda* possesses traits that allow established populations to persist in invaded environments, *B. tectorum* can rapidly deplete soil moisture following fire and negatively impact the soil water status and productivity of established perennial species (Melgoza et al., 1990). Thus, the influence of repeated fire and high competition may overwhelm the ability of *P. secunda* to maintain growth and reproduction. Although fire frequency was not a significant factor in the best fit model for *B. tectorum*, the range in *B. tectorum* cover in plots that experienced 1-2 fires versus plots that burned 3 or more times was far greater (Fig. 13a). In plots that burned three or more times, *B. tectorum* was greater than 60% in all sampled plots. These results indicate that three or more fires are likely to result in high *B. tectorum* dominance, whereas 1 or 2 fires can result in a range in both *B. tectorum* and *P. secunda* abundance. Thus, our results offer insights into transitions as well as the resulting states in fire-prone Wyoming big sagebrush communities and indicate that *P. secunda* and biological soil

crust are key biotic factors in alternative states, suggesting a more nuanced interpretation of State 2 within the S&T model.

An intriguing trend was the lower cover of *P. secunda* in plots that received drill seeding treatments (Fig. 15b). *P. secunda* was less abundant in plots that were drill seeded versus plots that were aerially treated or untreated following fire. Rangeland drills have been used extensively for post-fire rehabilitation in the sagebrush-steppe for decades (James and Svejcar, 2010). Conventional rangeland drills employ rotating disks to till the soil surface. The disturbance associated with tilling increases resource availability and can favor the establishment of species that respond quickly to higher resource availability such as *B. tectorum* (Beckstead and Augspurger, 2004; Doerr et al., 1984; Kulmatiski et al., 2006b). Tilling can also bury the seeds of *B. tectorum* further favoring its establishment. One study noted that *B. tectorum* seeds sown at 9mm exhibited 100x greater emergence compared to those sown on bare soil (Chambers and MacMahon, 1994), indicating that even minimal soil disturbance can enhance *B. tectorum* establishment. Rangeland drills can also damage residual native species and/or fail to establish seeded species, enhancing resources and space and resulting in greater post-treatment establishment of *B. tectorum* (Kulpa et al., 2012; Ratzlaff and Anderson, 1995). Ott et al., (2016) found that residual populations of *P. secunda* were damaged by conventional rangeland drills compared to minimum till drills, which suggests that under certain conditions, rangeland drills can negatively impact residual native species. However, site conditions such as elevation and precipitation likely influence outcomes associated with rangeland drills. Rangeland drill treatments are more likely to be

successful and minimize invasive species in sites with greater moisture availability (Knutson et al., 2014). Given the potential for negative outcomes in certain contexts, researchers have recently recommended the cautious use of rangeland drills in low resistance and resilience areas where residual native species and biological soil crust remain intact after fire, or in areas where post-fire erosion potential is high (Germino, 2016). Despite the widespread use of rangeland drills, there are few studies that have assessed the direct and indirect effects of rangeland drills on residual vegetation, soils, and biological soil crust across environmental gradients in the sagebrush-steppe ecosystem (Miller et al., 2013). Though our results are observational in nature, the lower abundance of *P. secunda* in drill-seeded areas suggests that past use of conventional rangeland drills may have reduced *P. secunda* populations in drill seeded portions of the NCA. However, it is likely that drill-seeding interacts with climatic conditions and grazing to influence seeding outcomes, which limits our ability to interpret our results.

Influences on the Abundance of Biological Soil Crust

The best-fit model for biological soil crust in burned areas did not contain fire or management factors. A complicating factor is that biological soil crust communities may take 125 years to recover from disturbances associated with historic overgrazing (Belnap et al., 2001b). Since livestock grazing has persisted over time at the NCA, it is likely that fire and management treatments included in this study (since the late 1950s) are not the primary influences on biological soil crust cover at the NCA. Furthermore, determining the effects of grazing on biological soil crusts has proven difficult across the sagebrush-steppe due to not only the high prevalence of grazing, but to the potentially long-lasting

legacy of grazing disturbance (Jones and Carter, 2016). Livestock grazing has occurred virtually across the entire sagebrush-steppe ecosystem (West, 1999), which also makes it difficult to disentangle the effects of fire separate from the effects of grazing (Condon, 2016). We did include distance to the nearest allotment as a potential proxy for the influence of grazing, where further distances from allotment boundaries may correlate to less grazing use. The distance to the nearest allotment boundary was found in the best fit model for *B. tectorum* in unburned plots, where *B. tectorum* and distance to the nearest allotment displayed a negative relationship. Thus, as distance to the nearest allotment boundary increases, the abundance of *B. tectorum* tends to decrease at the NCA.

Whether or not this is due to directly to livestock use is unclear however. Allotment boundaries are often aligned with roads and fence-lines, and there is clear evidence that disturbance associated with spatial boundaries such as roads and powerlines can increase *B. tectorum* abundance and damage biological soil crusts (Bradley and Mustard, 2006; Gelbard and Belnap, 2003). However the legacy of historic overgrazing at the NCA complicates the ability to draw inferences on the interaction between spatial factors and species abundances.

***P. secunda* and Restoration**

P. secunda is one of the most important native bunchgrasses in the sagebrush-steppe ecosystem, but it is often a minor component of post-fire rehabilitation seed mixes because it produces less biomass for livestock grazing compared to deep-rooted perennial bunchgrasses (Pilliod et al., 2017). However, there has been growing interest in developing native plant materials that can establish and persist in drier and more variable

sites (Shaw and Jensen, 2014). Similarly, researchers have suggested that species that are more tolerant of fire and competitive pressure (such as *P. secunda*) may be more appropriate choices for restoration in areas that are disturbance-prone (Leger and Baughman, 2015; Uselman et al., 2014). The State and Transition model for the Wyoming big sagebrush communities at the NCA cautions that once the reference state crosses a threshold to an invaded state, a return to the historic reference state is unlikely, even with active restoration. However, there is growing interest in the role that *P. secunda* could play in restoring native species to degraded landscapes. There is limited research on best practices for targeted restoration in native microsites, but at least one study suggests that native sites that dominated by early-season grasses may be suitable for plantings of sagebrush seedlings, potentially because they exert less competitive pressure on sagebrush seedling establishment and growth (McAdoo et al., 2013). A closely related question is whether or not land management agencies should establish more *P. secunda* in post-fire contexts. The use of *P. secunda* cultivars in post-fire rehabilitation increased at the NCA and across the sagebrush-steppe starting in the early 2000s (Pilliod et al., 2017), but only a handful of treatments at the NCA have included *P. secunda* in drill mixes and none of our treated plots were located in those treatments. *P. secunda* is almost exclusively included as a minor component in post-fire rehabilitation seed mixes (Pilliod et al., 2017), and there has been limited experimentation seeding application rates of *P. secunda* in restoration contexts. Though there are presently opportunities to leverage populations of *P. secunda* to restore native species, we lack a complete understanding of dynamics between *P. secunda* and *B. tectorum* over time and

in variable conditions. We recommend research to investigate longer-term dynamics between *P. secunda* and *B. tectorum* in landscapes where they co-occur.

Resistance and Resilience Looking Forward

The R&R framework recommends prioritizing restoration investments in landscapes where success is more likely (Chambers et al., 2014c). If this were strictly followed, landscapes like the NCA would likely not be considered ideal sites for restoration investments because of the high interannual variability in precipitation and the oftentimes inadequate levels of precipitation needed for seeded species establishment (Brabec et al., 2015; Ott et al., 2016). If we ignore areas like the NCA, however, we risk ongoing degradation that may impact the sagebrush-steppe ecosystem more broadly. Low resistance and resilience areas like the NCA can serve as fire ignition sites, placing adjacent higher elevation areas at greater risk of fire and invasion (Balch et al., 2013). Projected climate change may also increase the risk of invasion and fire into adjacent landscapes, resulting in greater potential synergy between invasive annual grasses and fire activity across elevation gradients in the sagebrush-steppe ecosystem (Abatzoglou and Kolden, 2011; Barbero et al., 2015; Compagnoni and Adler, 2014). Thus, decreasing our investments in invasive species control and restoration in areas like the NCA may have implications for the ecological integrity of the sagebrush-steppe ecosystem as a whole. However, establishing seeded species and meeting restoration objectives will continue to be a challenging endeavor in landscapes with limited and variable precipitation (Hardegree et al., 2016; James et al., 2011). Our results suggest that populations of *P. secunda* can persist in otherwise degraded Wyoming big sagebrush

landscapes, and may provide managers with leverage to enhance the restoration of native species restoration. The S&T and R&R frameworks provide an important foundation for understanding the challenges to restoration in low resistance and resilience areas like the NCA, but establishing seeded species and controlling invasive species in areas like the NCA should continue to be a priority of the research and management community (Chambers et al., 2009; Svejcar et al., 2017).

CONCLUSION

The scientific community has elevated degradation in drylands ecosystems to an issue of societal concern (Svejcar and Kildisheva, 2017). The sagebrush-steppe ecosystem is reflective of the key processes impacting dryland systems including altered disturbance regimes, invasive species, and habitat degradation. Scientists have encouraged those involved in drylands restoration to identify and enhance biotic components that are important for ecological integrity (Bestelmeyer et al., 2015; Franklin et al., 2016; Maestre et al., 2016). In the sagebrush-steppe ecosystem, researchers have stressed the importance of native perennial bunchgrasses for limiting invasive annual grasses (Briske et al., 2015; Chambers et al., 2007, 2014a, 2014b; Davies et al., 2011; Reisner et al., 2013). Though it has received less research and management attention over the years, *P. secunda* is an important native perennial bunchgrass in degraded environments and merits more research to understand its potential role in maintaining and enhancing ecological integrity in landscapes that are prone to invasive annual grasses and fire.

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TABLES

Table 1. 2012 monthly precipitation (mm) for the BOP NCA compared to the 100-year monthly average (1910-2010). A positive difference value indicates months where 2012 precipitation was above the 100-year monthly average, and a negative difference indicates months where 2012 precipitation was below the 100-year monthly average. Data derived from PRISM climate group, Oregon State University.

Monthly Precipitation	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Yearly Total
2012 (mm)	45.68	6.74	34.85	22.66	13.18	1.75	3.45	0.97	0.79	19.02	9.89	7.41	166.39
100-year Average (mm)	24.76	17.42	19.85	21.31	24.31	19.67	5.31	5.88	10.40	16.08	24.75	21.01	210.75
Difference (mm)	20.92	-10.68	15	1.35	-11.13	-17.92	-1.86	-4.91	-9.61	-2.94	-14.86	-13.6	-44.36

Table 2. Predictor variables used in model selection.

Category	Variable	Variable Type	Categories/Range
Fire History	Times burned	Continuous	1, 2, 3+ (fires) *3+ refers to 3-5 fires
	Times burned	Categorical	1, 2, 3+ (fires) *3+ refers to 3-5 fires
	Fire recentness	Continuous	0-57 (years)
	Fire recentness	Categorical	0-10, 11-20, >21 (years)
Management	Treatment Type	Categorical	Aerial, Aerial & Ground, Ground
Spatial	Nearest fire	Continuous	25-3305 (m)
	Nearest road	Continuous	163-1914 (m)
	Nearest allotment	Continuous	376-7496 (m)
Abiotic	Elevation	Continuous	Ranges form 870-1100 (m)
	Soil Type	Categorical	Calcerous, Claypan, Loamy, Sandy/Stony
Biotic	Native Perennial Bunchgrass (minus <i>P. secunda</i>)	Continuous	Cover ranges from 0-10%
	Native Shrub (minus <i>A. tridentata ssp. Wyomingensis</i>)	Continuous	Cover ranges from 0-20%
	Non-Native Seeded Perennial Bunchgrass	Continuous	Cover ranges from 0-15%

Table 3. Species included in biotic predictor variables.

Native Perennial Bunchgrass	Native Shrub (Non-Sagebrush)	Non-Native Seeded Perennial Bunchgrass
Big squirreltail (<i>Elymus multisetus</i>)	Bud sagebrush (<i>Picrothamnus desertorum</i>)	Crested Wheatgrass (<i>Agropyron cristatum</i>)
Indian ricegrass (<i>Achnatherum hymenoides</i>)	Winterfat (<i>Krascheninnikovia lanata</i>)	Russian wildrye (<i>Psathyrostachys junceus</i>)
Thurber's needlegrass (<i>Achnatherum thurberianum</i>)	Rubber (gray) rabbitbrush (<i>Ericameria nauseosa</i>)	
Thickspike wheatgrass (<i>Elymus lanceolatus</i>)	Silver sagebrush (<i>Artemisia cana</i>)	
Needle and thread grass (<i>Hesperostipa comata</i>)	Fourwing saltbush (<i>Atriplex canescens</i>)	
Basin wildrye (<i>Leymus cinereus</i>)	Shadscale saltbush (<i>Atriplex confertifolia</i>)	
Bluebunch wheatgrass (<i>Pseudoroegneria spicata</i>)	Yellow rabbitbrush (<i>Chrysothamnus viscidiflorus</i>)	
Squirreltail (<i>Elymus elymoides</i>)	Greasewood (<i>Sarcobatus vermiculatus</i>) Spiny hopsage (<i>Grayia spinosa</i>)	

Table 4. Minimum, median, and maximum % cover values for biotic response and predictor variables. Unburned n=39, Burned n=59, Treated n=30.

Response Variables												
Plot Type	<u>BRTE</u>			<u>POSE</u>			<u>ARTRW</u>			<u>BSC</u>		
	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.	Min.	Med.	Max.
Unburned	0.00	27.89	96.30	0.00	14.06	43.05	0.00	11.66	46.87	0.00	4.461	18.40
Burned	0.00	55.60	94.29	0.00	11.80	51.30	0.00	1.10	22.46	0.00	1.79	12.06
Treated	0.00	57.64	93.65	0.00	9.61	38.82	0.00	1.01	17.39	0.00	2.20	12.76

Predictor Variables										
Plot Type	<u>Native PG</u>			<u>Native Shrub</u>			<u>Non-Native Seeded PG</u>			
	Min.	Med.	Min.	Min.	Min.	Max.	Min.	Med.	Max.	
Unburned	0.00	0.32	0.00	0.00	0.00	46.87	0.00	3.43	21.13	
Burned	0.00	0.60	0.00	0.00	0.00	22.79	0.00	0.73	6.17	
Treated	0.00	0.48	0.00	0.00	0.00	18.28	0.00	0.78	5.14	

Table 5. Sample size and predictors used in unburned and burned submodels. Abiotic and spatial factors were identical for each submodel type. Unburned submodels did not contain fire and management predictors while burned submodels contained both fire and management factors as predictors.

Submodel	Sample Size	Predictor Variables				
		Biotic	Abiotic	Spatial	Fire	Management
Unburned	n=39	Native perennial bunchgrass, Native non-sagebrush shrub, Non-native seeded perennial bunchgrass	Mean elevation, Soil type	Nearest fire, road, allotment	-	-
Burned	n=59	Native perennial bunchgrass, Native non-sagebrush shrub, Non-native seeded perennial bunchgrass	Mean elevation, Soil type	Nearest fire, road, allotment	Times Burned, Fire Recentness (continuous and categorical)	Treatment type

Table 6. Multiple Linear Regression Model Results. Model terms in italics represent <2 change in AICc when removed; model terms in bold represent >10 change in AICc when removed. BRTE: *Bromus tectorum*, POSE: *Poa secunda*, ARTRW: *Artemisia tridentata* ssp. *wyomingensis*, BSC: biological soil crust, Native Shrub: all non-ARTRW native shrub species. Model terms with a negative relationship are denoted with (-), positively related terms have no symbol following.

Submodel	Response Variable	Best Fit Model	Adjusted R ²	AICc	K
Unburned	BRTE	POSE (-), BSC (-), ARTRW (-), <i>Nearest allotment (-)</i>	.78	-113.9	5
	POSE	BRTE (-)	.61	-237.3	2
	BSC	BRTE (-), ARTRW	.49	-221.4	3
	ARTRW	<i>Nearest fire, BRTE (-)</i>	.27	-68.2	3
Burned	BRTE	POSE (-), BSC (-)	.70	-170.0	3
	POSE	BRTE (-), <i>Times burned categories</i>	.64	-239.0	5
	BSC	Native Shrub, BRTE (-)	.65	-402.4	3
	ARTW	no model	-	-	-

FIGURES

Loamy 8-12 Wyoming big sagebrush/Bluebunch wheatgrass State and Transition Model

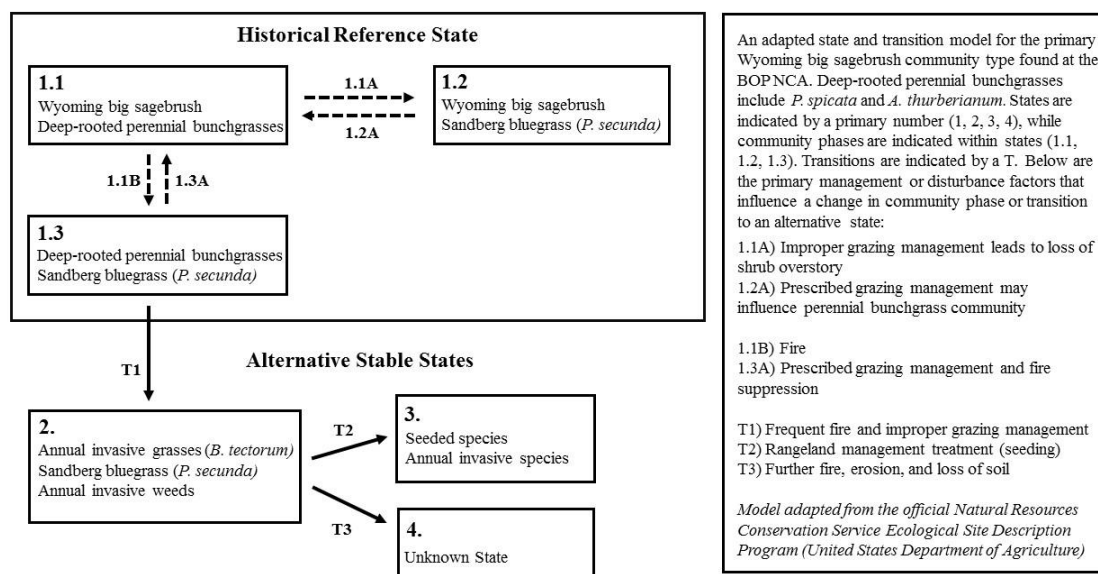


Figure 1. Natural Resource Conservation Service ecological site and state and transition model for the Wyoming big sagebrush communities found at the NCA (NRCS, n.d.).

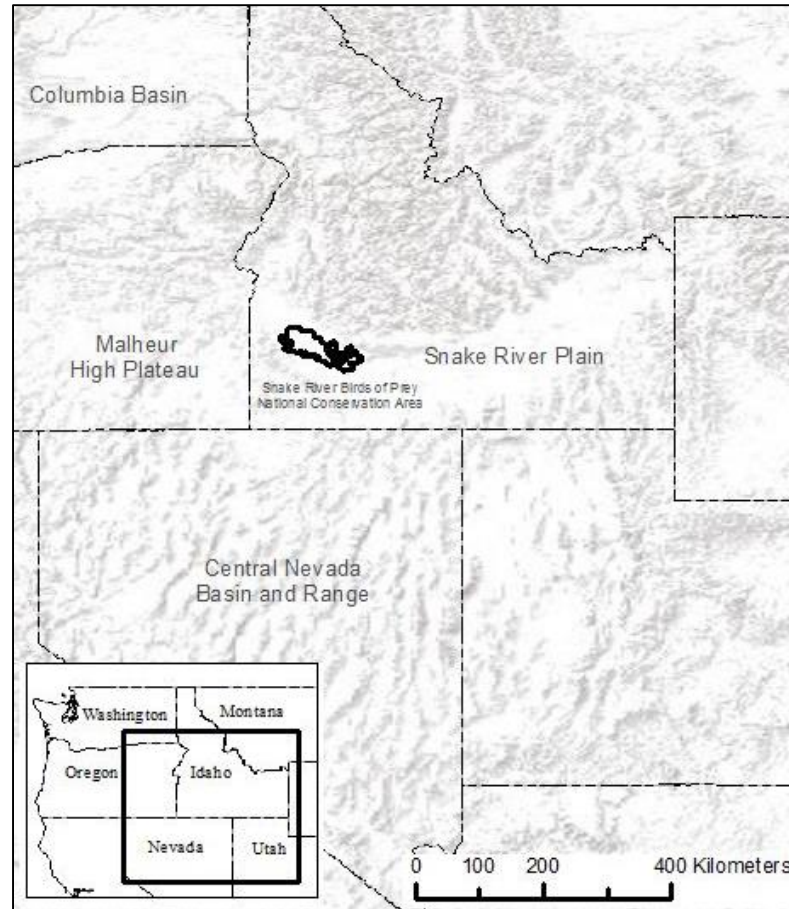


Figure 2. Study site. The Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) is located in southwestern Idaho and resides on the western portion of the Snake River Plain ecoregion.

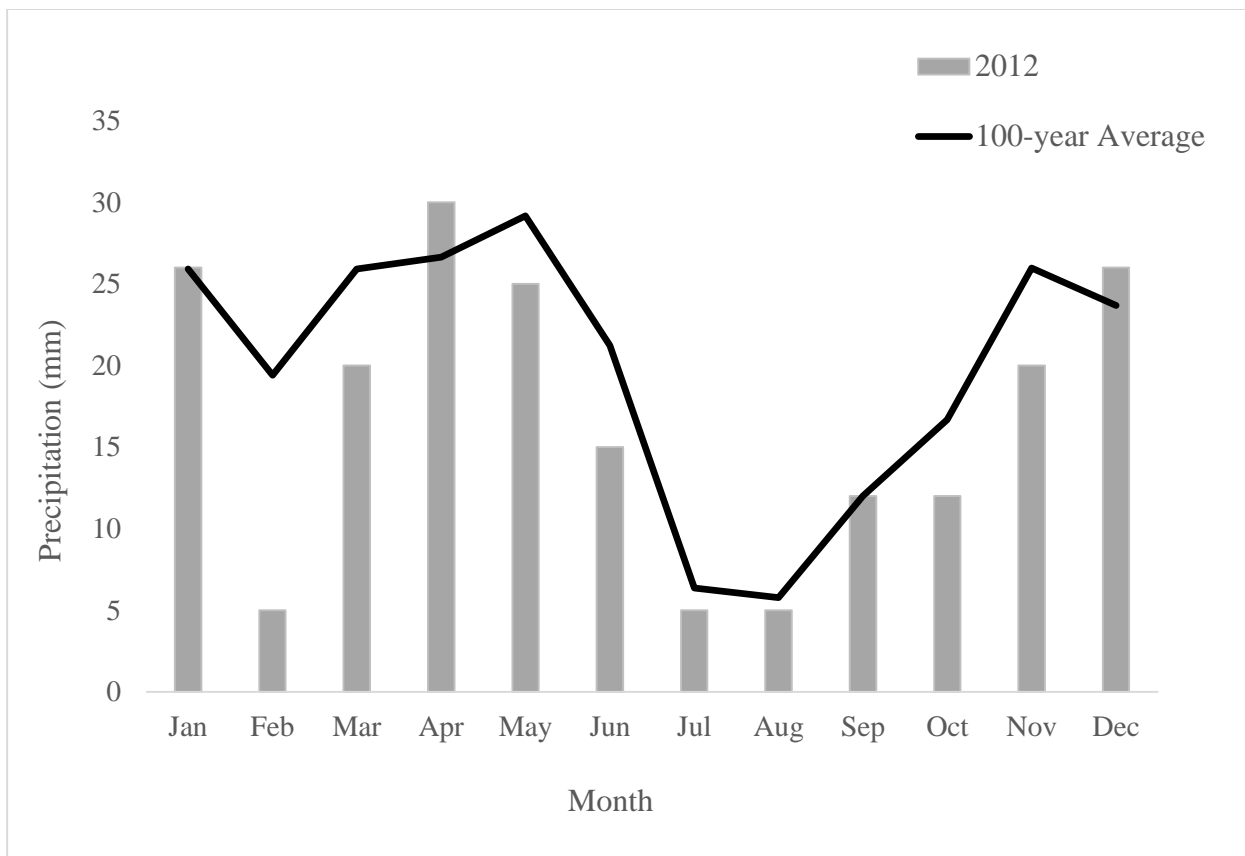


Figure 3. Monthly precipitation (mm) in 2012.

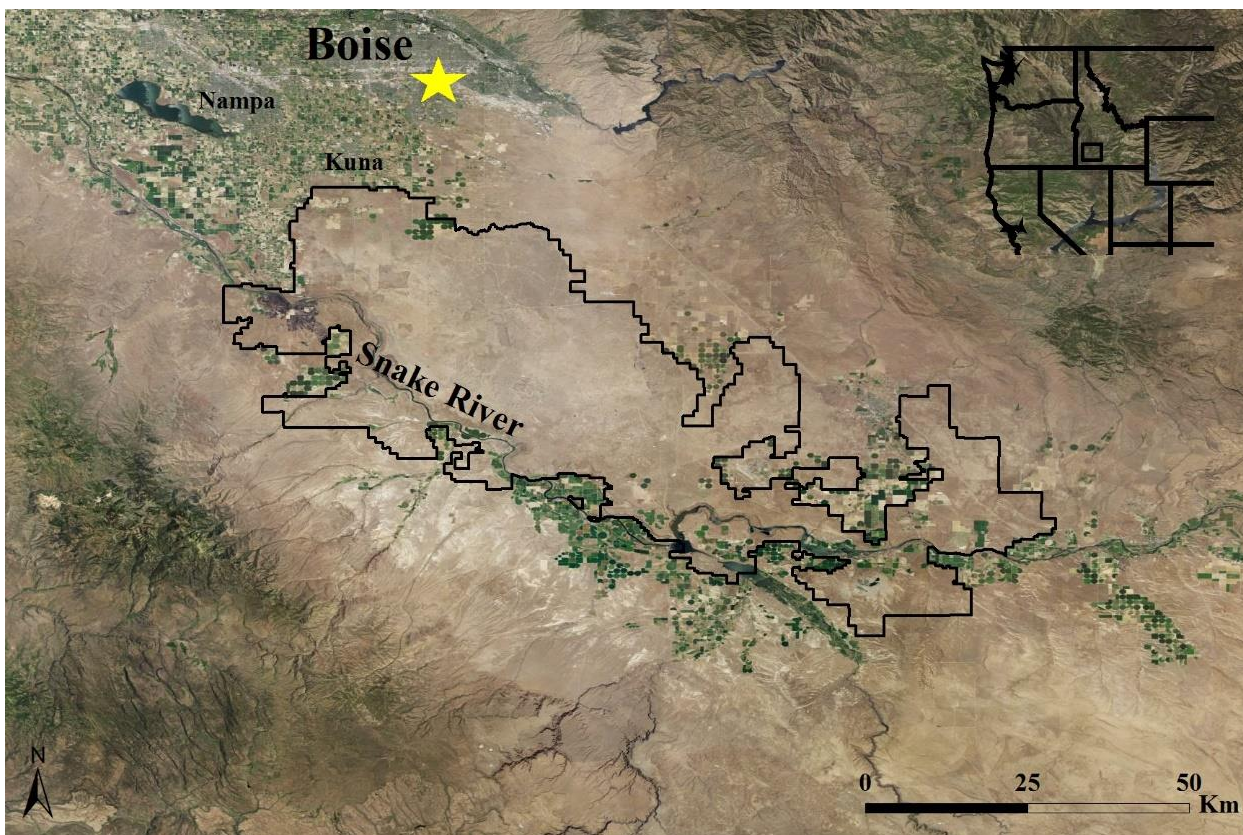


Figure 4. Study site in relation to southwestern Idaho's urban, suburban, and agricultural areas. The Snake River forms much of the southern boundary of the NCA. Irrigated agriculture borders the southern and southeastern boundary, as well as the northeastern boundary. Base imagery acquired from the US Department of Agriculture's National Agriculture Imagery Program.

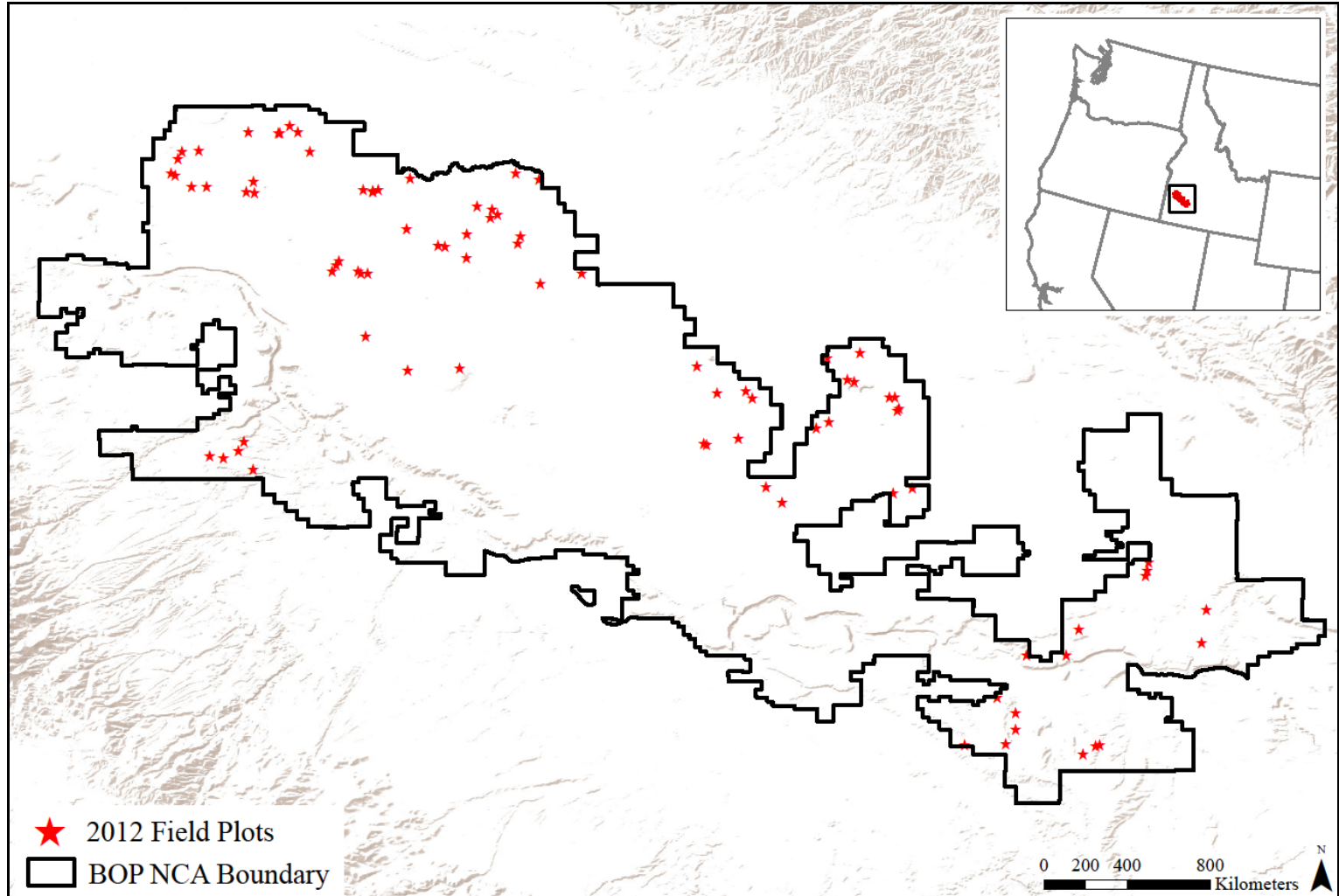


Figure 5. 2012 field plot locations within the NCA, (n=98).

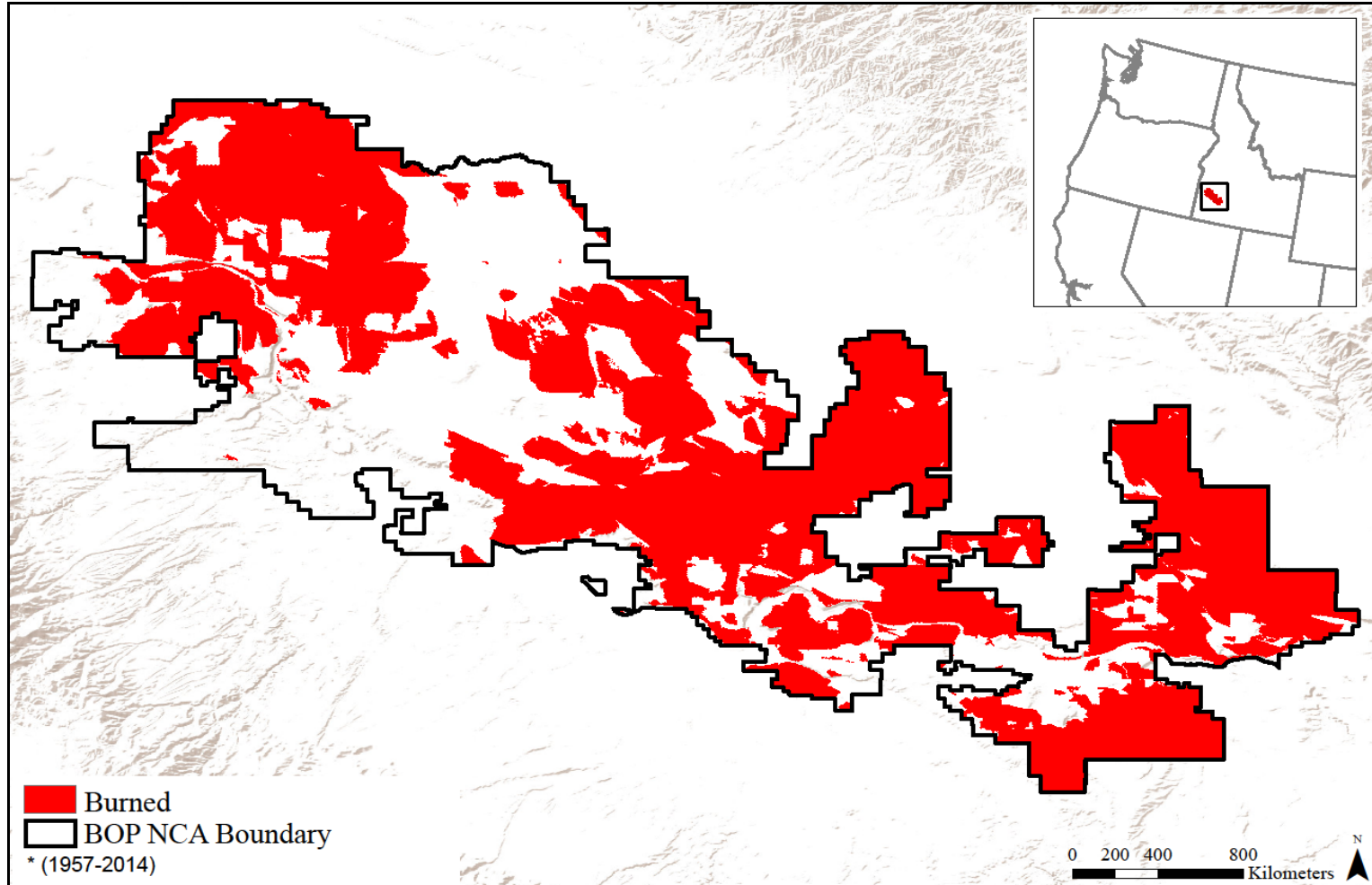


Figure 6. Burn history of the NCA from 1957-2014. Nearly 60% of the NCA burned within this timeframe. This figure depicts areas that have burned one to multiple times within this time frame.

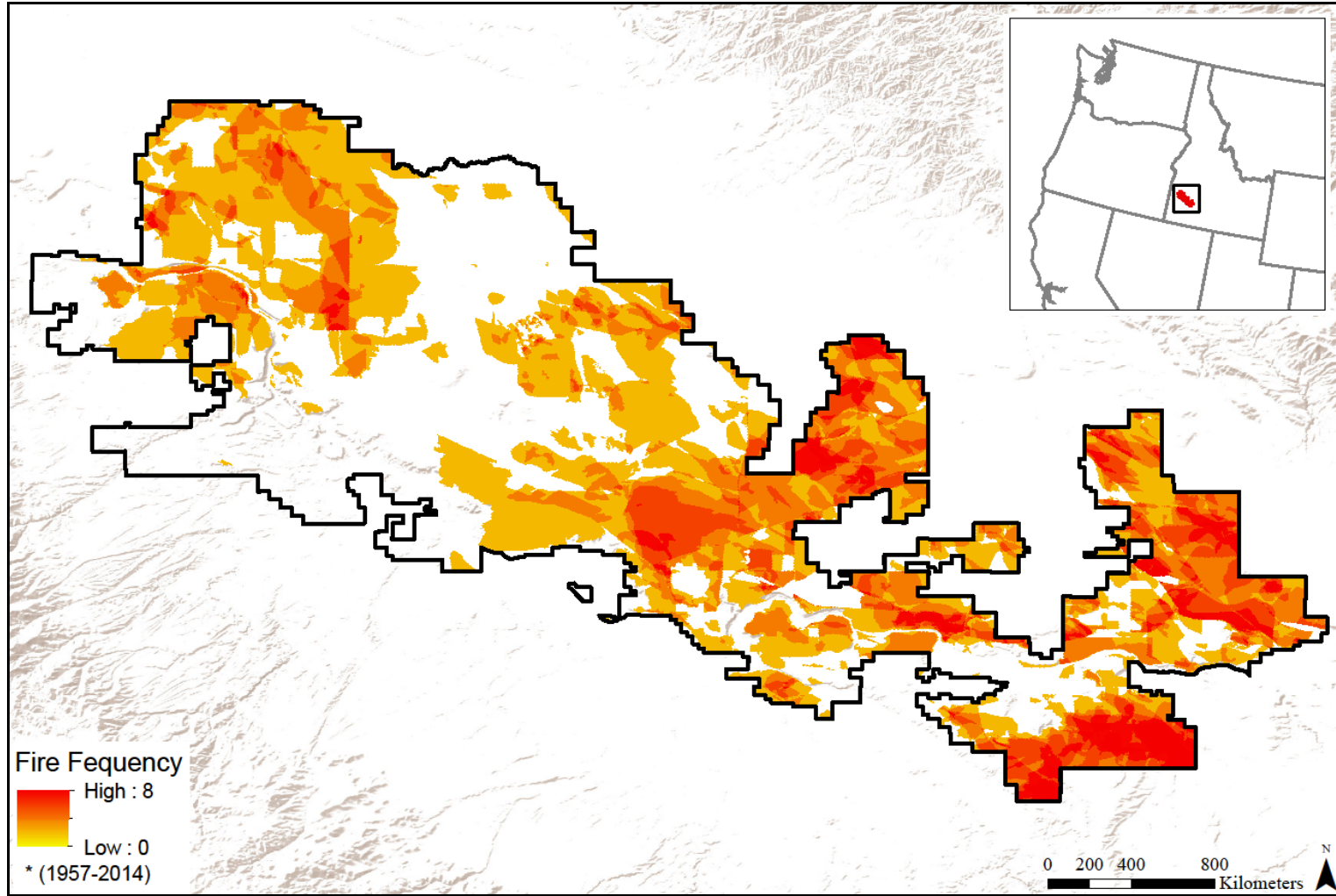


Figure 7. Fire gradient at the NCA from 1957-2014. The western and southwestern portion of the NCA have experienced especially high fire activity.

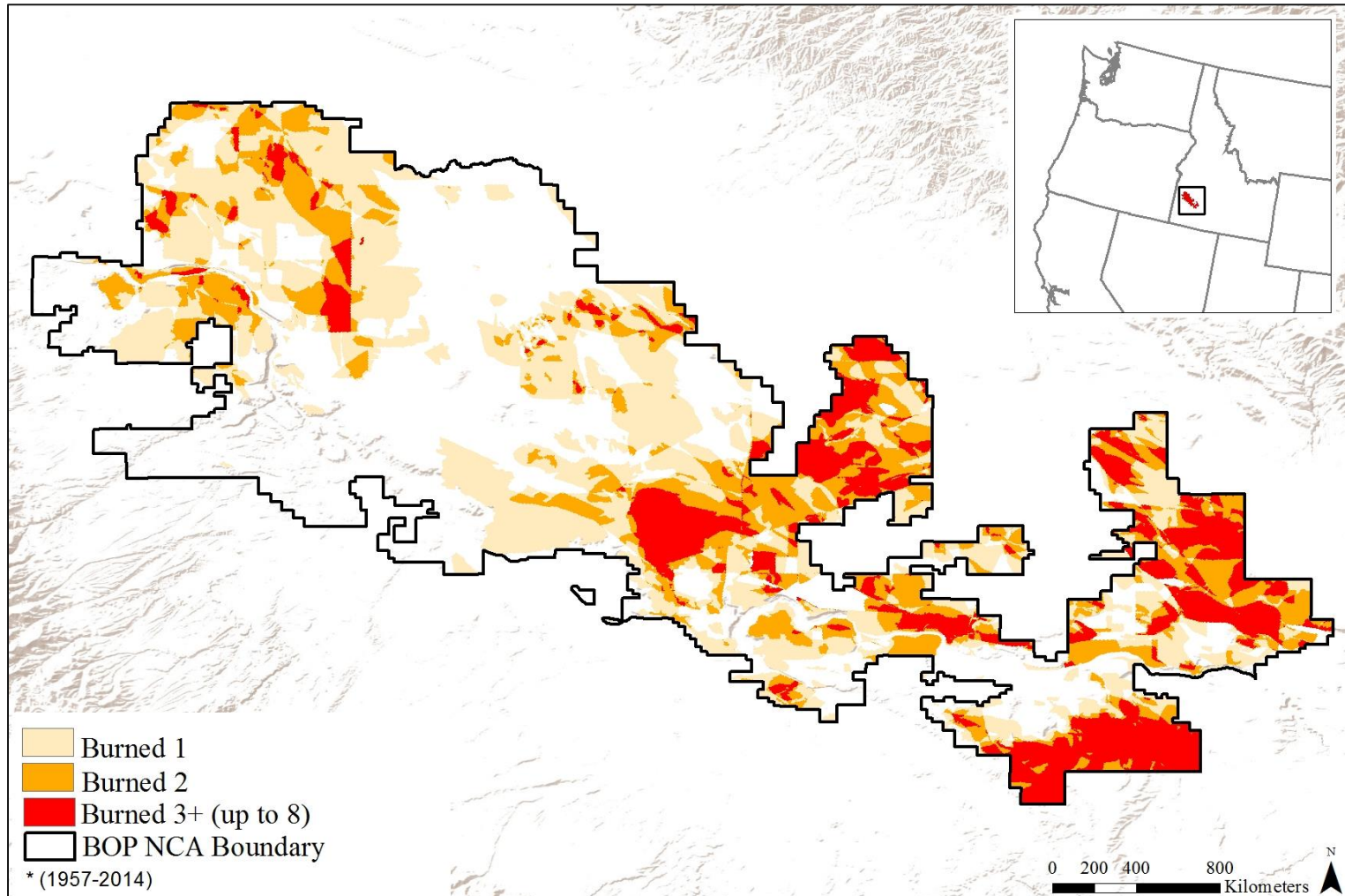


Figure 8. Fire frequency categories at the NCA.

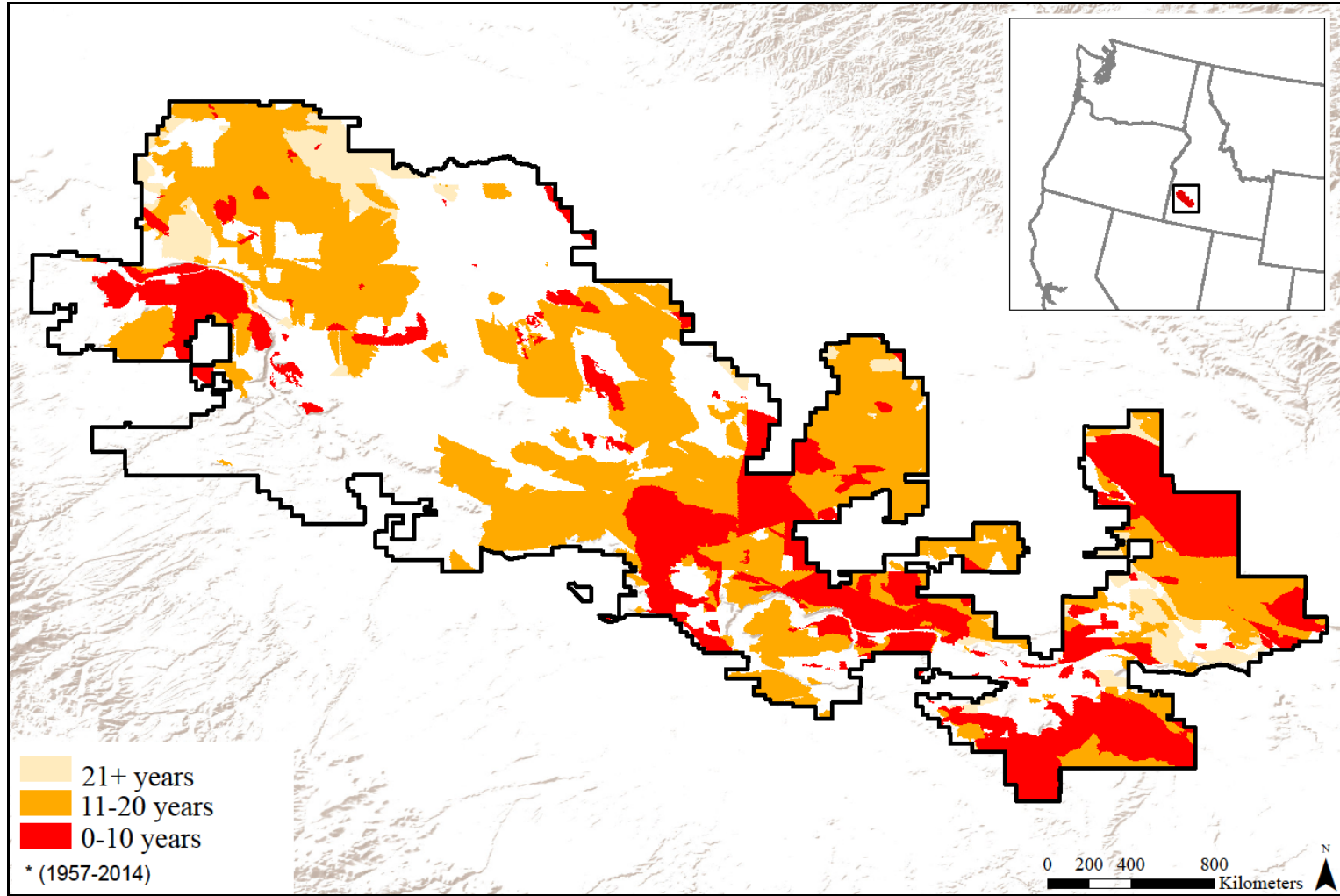


Figure 9. Categories of years since the last fire at the NCA. Most of the burned area was burned between 11-20 years ago, while fires in the last decade make up the next largest category.

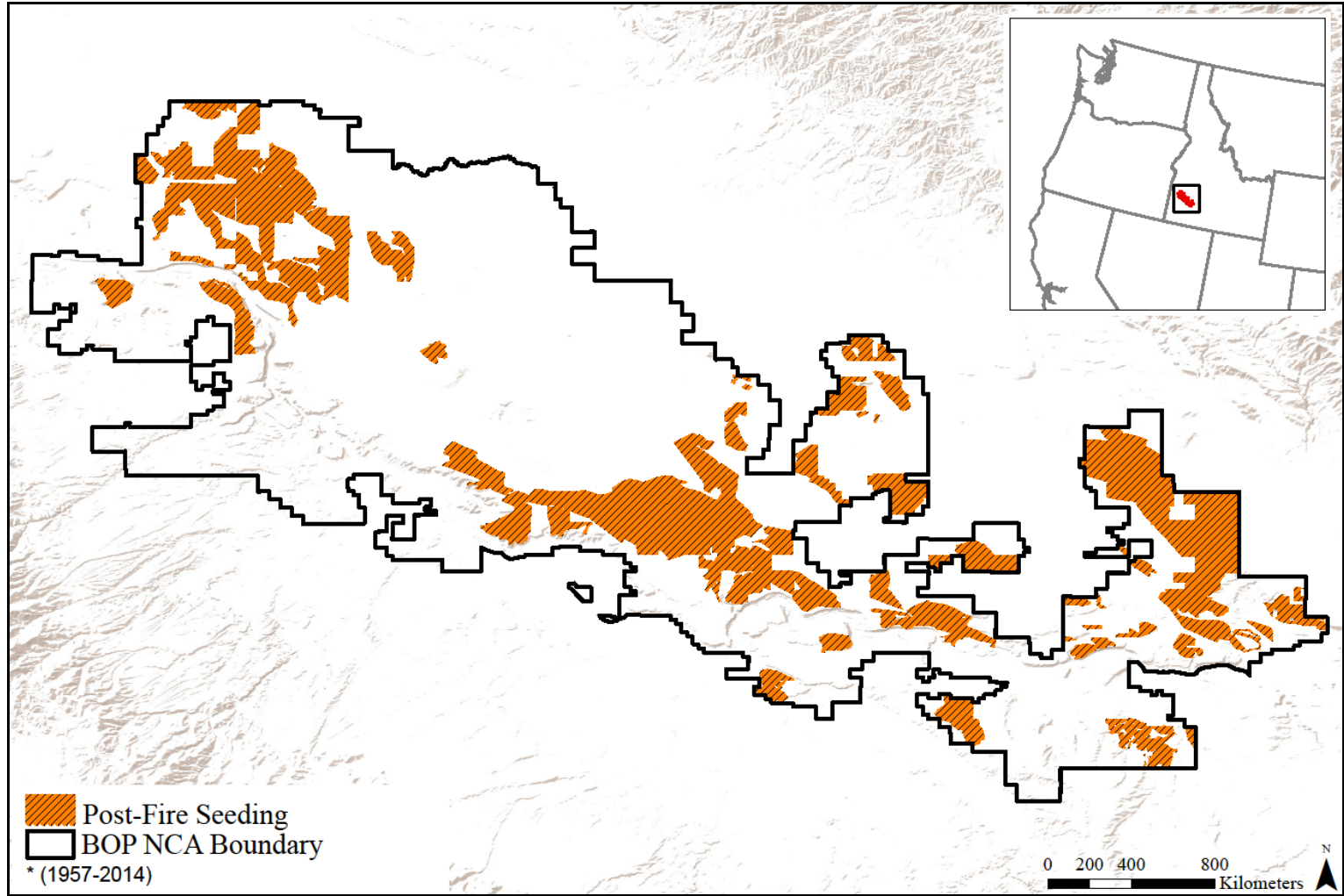


Figure 10. All post-fire seeding treatments conducted at the NCA from 1957-2014. The shaded areas represent Bureau of Land Management drill and/or aerial seeding treatments.

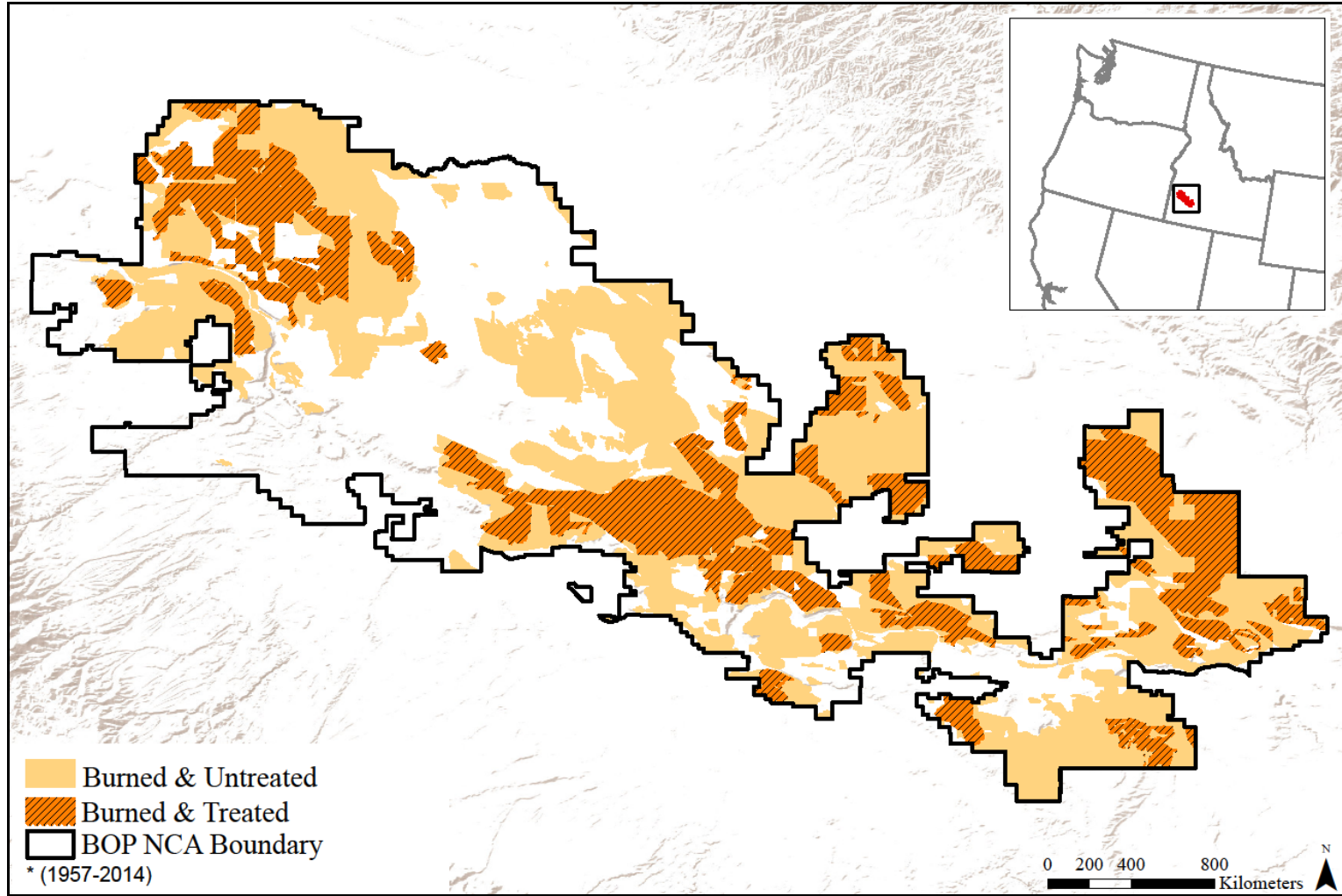


Figure 11. Burned and Treated versus Burned and Untreated areas of the NCA from 1957-2014.

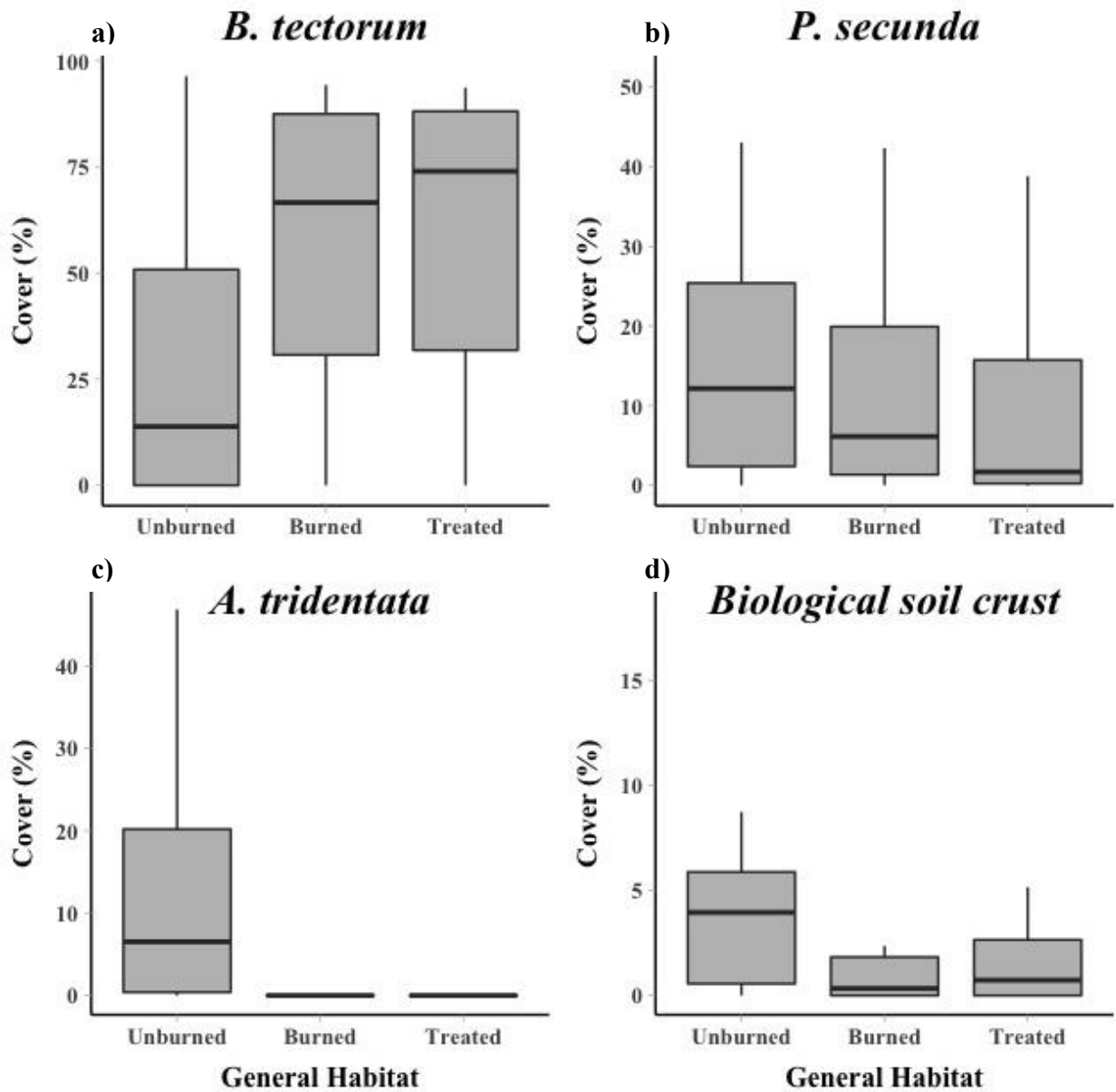


Figure 12. General fire and treatment history (1957-2014) for each response variable. Unburned= unburned; Burned=burned and untreated, Treated= burned and treated. Median represented by solid, middle line. Upper and lower whiskers extend to the largest and smallest values that are no further than 1.5 * inter-quartile range. Outliers beyond that range have been removed.

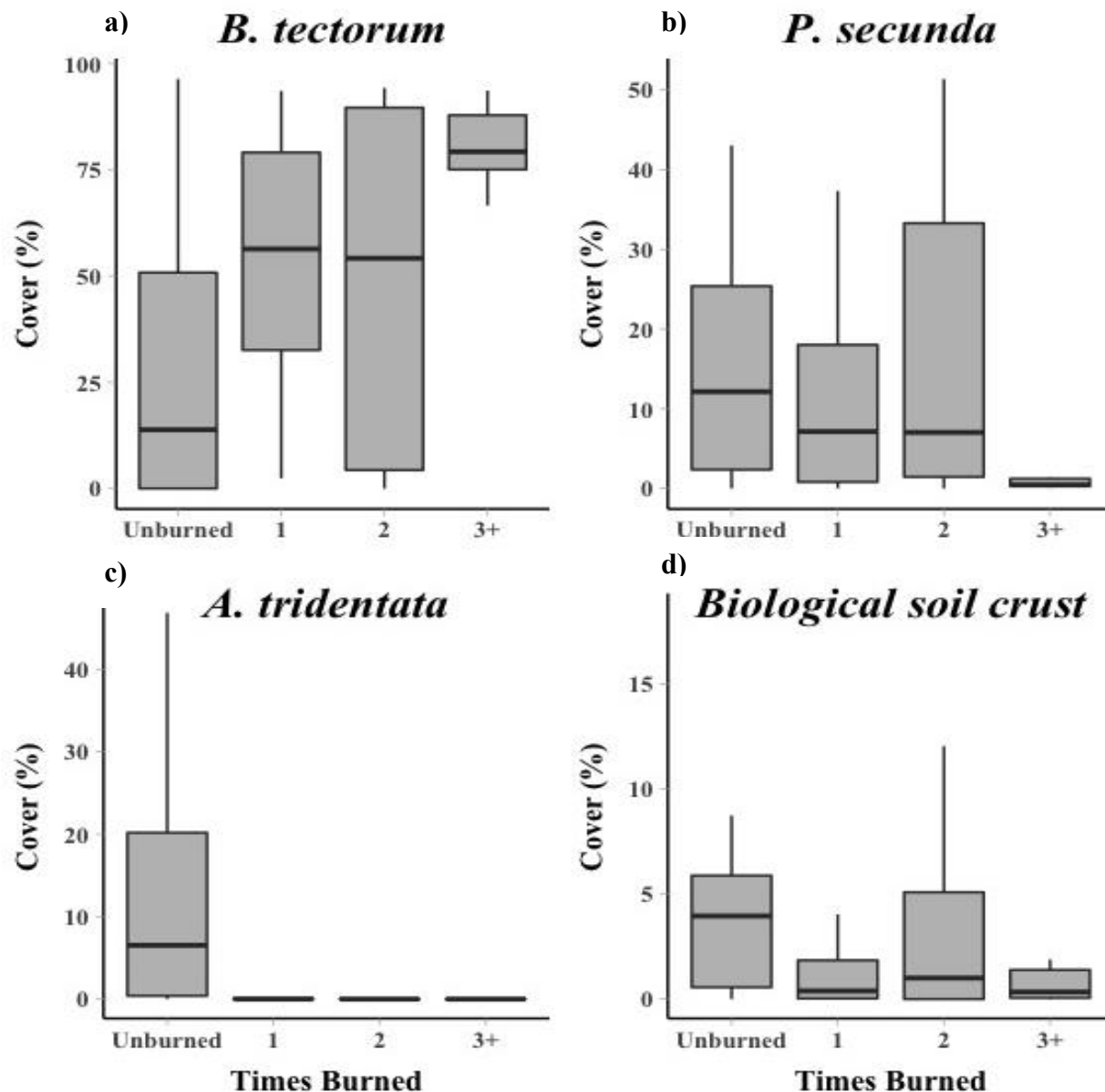


Figure 13. Categories of times burned (1957-2014) for each response variable. Unburned=unburned; 1=burned once; 2=burned twice; 3+=burned three to five times. Median represented by solid, middle line. Upper and lower whiskers extend to the largest and smallest values that are no further than $1.5 \times$ inter-quartile range. Outliers beyond that range have been removed.

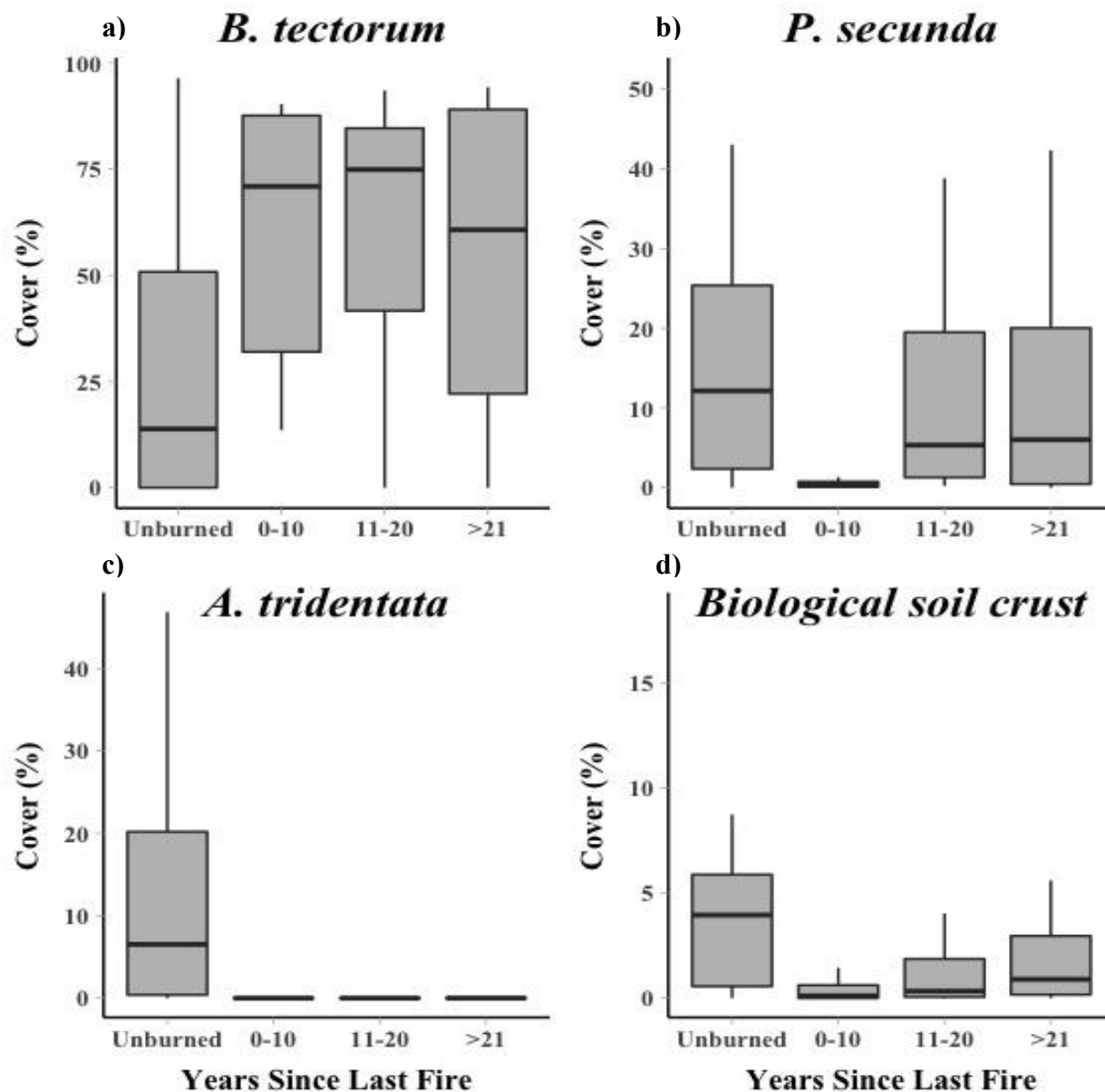


Figure 14. Categories of years since last fire (1957-2014) for each response variable. Median represented by solid, middle line. Upper and lower whiskers extend to the largest and smallest values that are no further than $1.5 \times$ inter-quartile range. Outliers beyond that range have been removed.

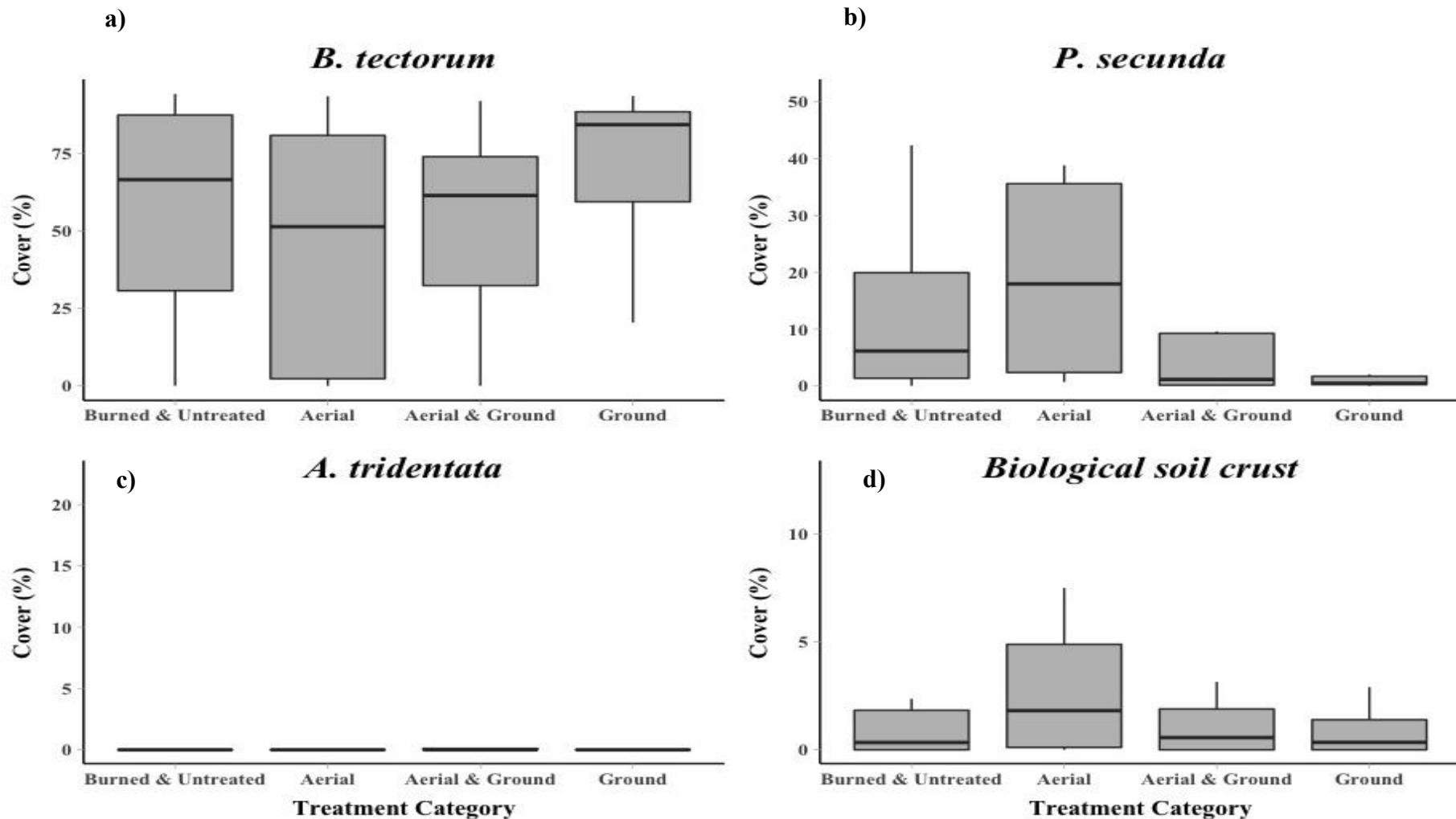


Figure 15. Treatment type (1957-2014) for each response variable. Burned & Untreated included as a reference. Median represented by solid, middle line. Upper and lower whiskers extend to the largest and smallest values that are no further than 1.5 * inter-quartile range. Outliers beyond that range have been removed.

APPENDIX A

2013 Results

Introduction

Although data from 2013 was available, only 2012 was included in the primary analysis. The same model selection on response variables in unburned and burned plots was conducted on plots that were sampled in 2013 (n=105). In general, the models produced by the AICc model selection had less predictive power than the models produced in 2012. The adjusted R^2 values for 2013 models were relatively low compared to the 2012 models, indicating that terms present in the best fit models exhibited weaker relationships with respective response variables. It is unclear why the fit of 2013 models was poorer compared to 2012 models, but one possible explanation is that growing season precipitation in 2013 was lower than in 2012 (particularly in February and March), which resulted in less herbaceous cover of *B. tectorum* and *P. secunda* (see Appendix B). Lower median values and range in canopy cover of herbaceous species may have explain the poorer fit of models. Although 2013 models were less predictive than 2012 models, the terms included in the best fit models for 2013 were similar to 2012, particularly with regards to *B. tectorum* and *P. secunda* in burned areas. *P. secunda* was found in the best-fit model for *B. tectorum* in burned and unburned plots. So although the abundances of herbaceous components were less in 2013 compared to 2012, the relationships remained the same.

2013 Model Selection Results

Figure A1. Multiple Linear Regression Model Results. Model terms in italics represent <2 change in AICc when removed; model terms in bold represent >10 change in AICc when removed. BRTE: *Bromus tectorum*, POSE: *Poa secunda*, Model terms with a negative relationship are denoted with (-), positively related terms have no symbol following.

Submodel	Response Variable	Best Fit Model	Adjusted R ²	AICc	K
Unburned	BRTE	<i>POSE (-), Nearest allotment (-), Nearest fire border (-), Native shrub (-)</i>	.50	-96.9	5
	POSE	<i>BRTE (-), Nearest road (-)</i>	.16	-137.4	3
	BSC	<i>BRTE (-)</i>	.15	-228.6	2
	ARTRW	<i>BRTE (-)</i>	.10	-56.4	2
Burned	BRTE	POSE (-), Times burned categories	.38	-145.8	5
	POSE	BRTE (-), Times burned categories	.29	-279.1	5
	BSC	<i>Native perennial grass, Nearest fire border</i>	.13	-499.5	3
	ARTW	no model	-	-	-

APPENDIX B

Interannual Variability in Precipitation and Abundance of Herbaceous Vegetation

Introduction

There were 57 plots that were sampled in 2012, 2013, and 2014. 2012 was selected for analysis because the amount and timing of precipitation most resembled the 100-year precipitation average. 2013 was much drier in February and March, whereas 2014 exhibited the driest growing season from February to April. The variability in precipitation, particularly during the growing season, appears to have influenced herbaceous cover in resampled plots. *B. tectorum* exhibited a 56% decline in canopy cover from 2012-2014, whereas *P. secunda* exhibited a nearly 40% decline in canopy cover in resampled plots.

Differences in Precipitation and Percent Canopy Cover 2012-2014

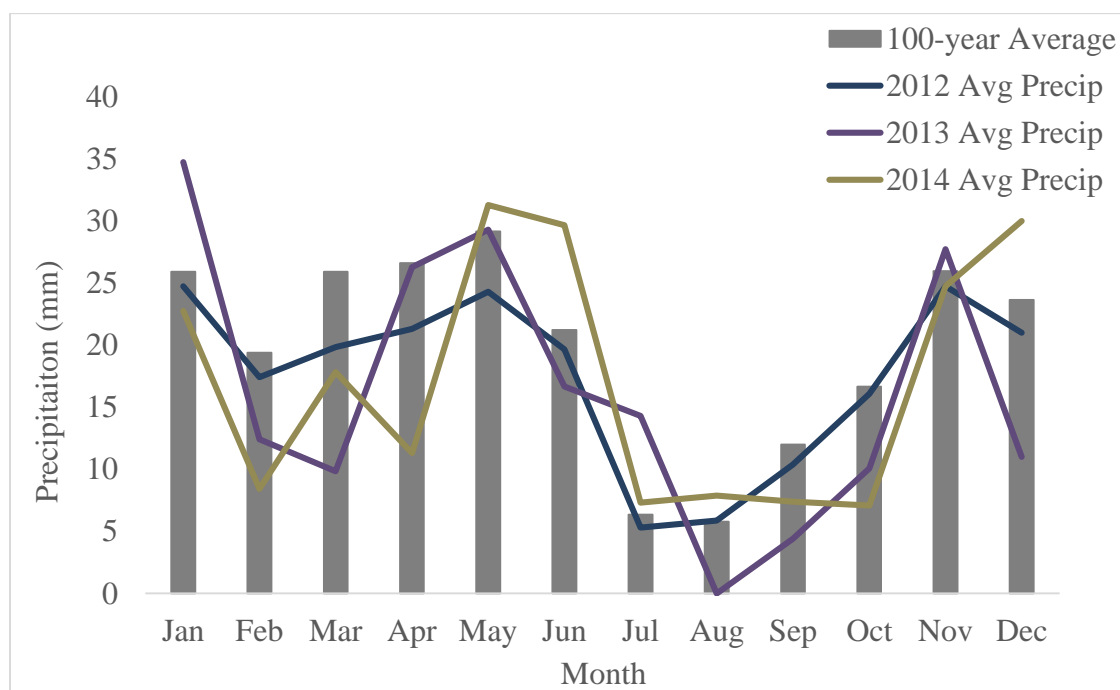


Figure B1. Monthly precipitation for 2012, 2013, and 2014 compared to the 100-year average precipitation.

Table B1. Average percent canopy cover of response variables in resampled plots (n=57), including the change in percent canopy cover between 2012 and 2014.

	2012	2013	2014	Percent Change (2012-2014)
BRTE	38.4	33.3	16.6	-56.6
POSE	14.7	10.5	8.9	-39.4
BSC	3.0	3.2	3.6	19.5
ARTRW	7.8	8.7	6.5	-16.1

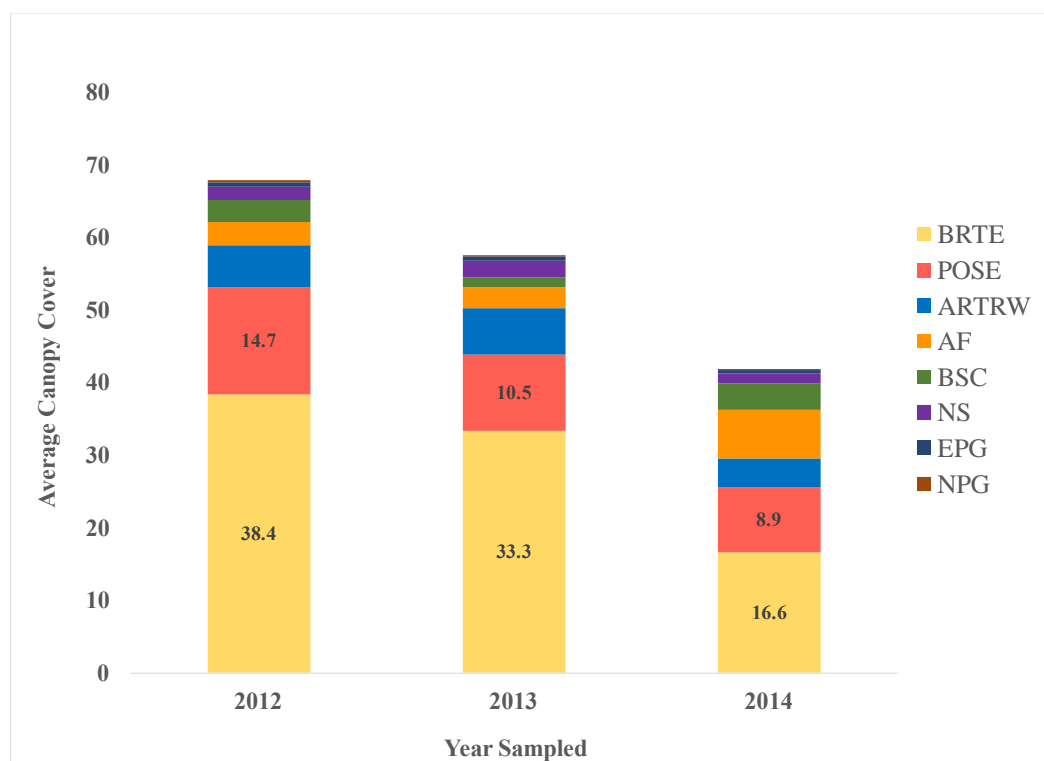


Figure B2. Average percent canopy cover of the major species and functional groups within plots were repeatedly sampled from 2012-2014 (n=57). Species and functional group acronyms: BRTE=*Bromus tectorum*, POSE=*Poa secunda*, ARTRW=*Artemisia tridentata* ssp. *wyomingensis*, AF=total annual exotic forb, BSC=biological soil crust, NS=total native shrub (non-sagebrush), EPG=total exotic perennial grass, NPG=total native perennial grass (non-*P. secunda*).