Running head: Burn severity and ecosystem transformation

Title: Fuel connectivity, burn severity, and seedbank survivorship drive ecosystem transformation in a semi-arid shrubland.

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Open Reseach Statement: Data and code to recreate the analysis are freely available at https://www.github.com/admahood/seed-bank (DOI: https://doi.org/10.5281/zenodo.5293996).

Abstract

When multiple drivers interact to affect an ecosystem's function, ecosystem state changes can result. These state changes may be both precipitated and maintained by disturbances, but predicting whether the state change is fleeting or persistent requires an understanding of the mechanisms by which disturbance affects the alternative communities. In the sagebrush shrublands of the western United States, widespread annual grass invasion has increased fuel connectivity, which increases the size and spatial contiguity of fires, leading to post-fire monocultures of introduced annual grasses (IAG). The novel grassland state is persistent, and more likely to promote large fires than the shrubland it replaced. But the mechanisms by which pre-fire invasion and fire occurrence are linked to higher post-fire flammability are not fully understood.

We hypothesized that higher fuel connectivity would increase burn severity, which would then have differential effects on post-fire dispersal by causing seed bank survivorship to favor IAG. Subsequent seedbank composition dominated by IAG would lead to increased post-fire fuel connectivity. We found that pre-fire fuel connectivity did increase burn severity. We then used a Bayesian joint species distribution model to examine how burn severity affected the proportion of IAG in the seed bank, and found that higher burn severity had mostly positive effects on the occurrence of IAG and another non-native species, and mostly negative or neutral relationships with all other species. Finally, we found that the abundance of IAG seeds in the seedbank immediately post-fire had a positive effect on the fuel connectivity 3 years after fire, completing a positive feedback promoting IAG. These results demonstrate that the strength of the positive feedback is controlled by measurable characteristics of ecosystem structure, composition and disturbance, and each node in the loop is affected independently by multiple global change drivers. It is possible that these characteristics can be modeled to predict threshold behavior and inform management actions to mitigate the undesirable effects of the grass-fire cycle, perhaps via targeted restoration applications or

pre-fire fuel treatments.

Keywords: cheatgrass, sagebrush, grass-fire cycle, joint species distribution model, burn severity, fuel connectivity, *Bromus tectorum*, *Artemisia tridentata*

1. Introduction

Ecosystems around the world are being affected simultaneously by multiple facets of global change. For example, changes in land use can facilitate exotic plant invasions (Allan et al. 2015), which can alter ecosystem structure (Davies and Nafus 2013). Altered structure can change the likelihood of a disturbance, the properties of a disturbance and the capacity of the system to recover after a disturbance (Brooks et al. 2004). Global climate change can also directly affect the magnitude of disturbances (S. A. Parks and Abatzoglou 2020), and act as a demographic filter that influences how ecosystems recover after disturbances (Rother, Veblen, and Furman 2015; Davis et al. 2019) via impacts on adult plant survival and seed dispersal (Davis, Higuera, and Sala 2018; Eskelinen et al. 2020). The combined effects of global change forces on structure, function and disturbance can cascade and interact. For example, while burn severity (or the proportion of biomass burned (Keeley 2009)) is influenced by vegetation structure (Koontz et al. 2020; Sean A. Parks et al. 2018), it also increases with temperature and aridity (S. A. Parks and Abatzoglou 2020). These forces can ultimately lead to permanent compositional change, biodiversity losses and the loss of ecosystem services (Ratajczak et al. 2018; Mahood and Balch 2019; Mahood et al. 2022) due to internal, self-reinforcing mechanisms that arise from those structural and functional changes which then maintain an alternative stable state (Marten Scheffer and Carpenter 2003; Ratajczak et al. 2018).

There is a long history of univariate time series observations that show sudden state changes (Marten Scheffer and Carpenter 2003), and these have informed the development of theories that help us understand how systems of any type can change state suddenly, and exist in persistent alternative stable states (Marten Scheffer et al. 2015; Ratajczak et al. 2018). These theories typically represent the system's state with a single variable, of which the mean is observed to abruptly change in time or space (Marten Scheffer et al. 2015). Descriptive evidence of alternative stable states has been documented at broad scales in tropical ecosystems, where forests, savannas and grasslands are considered alternative stable states because they are floristically distinct (Aleman et al. 2020) and cluster around static values of woody cover (80, 30 and 0 percent) while occurring along overlapping ranges of precipitation (Hirota et al. 2011; Staver, Archibald, and Levin 2011). The forested state is has a self-reinforcing, positive feedback between evapotranspiration and tree cover (Staal et al. 2020), while the grassland and savanna states are maintained by feedbacks between grass flammability and fire occurrence (D'Antonio and Vitousek 1992; Staver, Archibald, and Levin 2011). Alternative stable states are believed to be widespread (M. Scheffer et al. 2001), but their existence is rarely proven at broader scales, with most demonstrative studies having been conducted in greenhouse and laboratory microcosm experiments (Schröder, Persson, and De Roos 2005). One of the reasons for this is that ecological systems are much more complex than a simple bivariate system with a single driver and a single response. There may be multiple drivers, and the state is the product of interactions between organisms and their immediate environment, as well as countless inter- and intraspecific interactions.

A central challenge in ecology in the 21st century is to move from describing how plant communities are affected by global change to the capacity to predict how species pools will assemble and persist in response to global change (Davis, Higuera, and Sala 2018; Keddy and Laughlin 2021). Prediction of community response to multi-faceted global change drivers is enhanced with a better understanding of the mechanisms that underlie community stability in the face of disturbances. A classic example of an ecosystem that appears to have disturbance-mediated alternative stable states, but whose stability mechanisms aren't well understood is the invasion of *Bromus tectorum* L. and other introduced annual grasses in the Great Basin of the western United States. Here, it is well described how the interaction of exotic plant invasions, fire (Balch et al. 2013) and grazing (Williamson et al. 2019) are associated with the degradation or loss of over half of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle & Young) ecosystems (Davies et al. 2011). In uninvaded areas, the space between shrubs is typically composed of bare ground covered in biological soil crust and caespitose perennial plants. The lack of fuel connectivity limits fire spread, and the pre-colonial fire regime was one of infrequent, patchy fires (Baker 2006; Bukowski and Baker 2013). Annual grass invasion increases fuel connectivity while decreasing fuel moisture (Davies and Nafus 2013), leading to increased fire size and frequency (Knapp 1996; Balch et al. 2013). After fire, the landscape is typically dominated by introduced annual grasses. But in order to understand how fire drives the persistence of the grassland state, we need to understand the demographic mechanisms by which fire impacts propagule dispersal and benefits the alternative state (Davis, Higuera, and Sala 2018). As with forested systems, propagule dispersal is a key filter through which species must pass in order to establish and persist in a post-fire landscape (Gill et al. 2022).

Petraitis and Latham (1999) posited that the maintenance of alternate species assemblages requires first a disturbance that removes the species from the initial assemblage and second the arrival of the species of the alternate assemblage. One understudied mechanism that may explain both for the *Artemisia*/*Bromus* system is the interaction between the species composition of the soil seed bank and burn severity. Because the invading species are annual, and most of the native plants are seed obligates, the seed is the key life history stage that fire must act upon to benefit the invading plants. Seeds and seedlings are particularly vulnerable to climate, competition and disturbance (Enright et al. 2015). Warmer and drier conditions simultaneously reduce recruitment, growth, and survival of seeds and seedlings (Enright et al. 2015; Schlaepfer, Lauenroth, and Bradford 2014), while also increasing burn severity (S. A. Parks and Abatzoglou 2020). In fire prone ecosystems, seed obligate species typically have life history strategies to cope with fires that burn at different severities (Maia et al. 2012; Wright, Latz, and Zuur 2016; Palmer, Denham, and Ooi 2018). Soil heating from fire affects the response of vegetation to fire (Gagnon et al. 2015), including the capacity of seeds to remain viable after fire (Humphrey and Schupp 2001). High severity fire can affect species that use the seedbank positively (Kimura and Tsuyuzaki 2011), negatively (Heydari et al. 2017), or have no effect (Lipoma, Funes, and Díaz 2018), depending on species-specific adaptations. Both the depth of the burn and fire temperature can affect subsequent recovery by seed germination (Morgan and Neuenschwander 1988; Schimmel and Granström 1996), as well as seed mortality and physical seed dormancy mechanisms (Liyanage and Ooi 2017).

In addition to size and frequency, exotic plant invasions can alter fire temperature (Brooks et al. 2004; R. O. Jones et al. 2015) and burn severity. While in many cases fires that burn at higher temperatures will also consume more biomass, grass fires may not always have such a relationship. Direct measurements have shown that *B. tectorum* burns at low temperatures (Beckstead et al. 2011; Germino, Chambers, and Brown 2016), but because it also increases horizontal fuel connectivity (Davies and Nafus 2013), it leads to more contiguously burned areas and therefore higher burn severity, despite lower fire temperatures. In order for an annual like *B. tectorum* it to benefit from fire (Balch et al. 2013; Mahood and Balch 2019), it would need enough viable seeds in the post-fire landscape to achieve a fitness benefit and become well-represented in the post-fire plant assemblage (Bond and Midgley 1995). If the fire is patchy, this can happen through post-fire seed dispersal, and *B. tectorum* seeds have been shown to have increased dispersal distances after fire (Monty, Brown, and Johnston 2013). Without unburned patches, seeds must survive the fire. If the increase in fuel connectivity caused by *B. tectorum* increases the severity of fire, it stands to reason that burn severity would then influence the community composition of the post-fire seed bank in a way that facilitates the post-fire dominance of *B. tectorum*. In other words, an area with high burn severity should have a lower occurrence of viable seeds of native species, and a higher occurrence of the seeds of fire-tolerant introduced annual plants. This would lead to the dominance of introduced annual grasses and would result in higher fuel connectivity, closing the positive feedback loop. Plants that are not adapted to frequent fire would be less likely to produce seeds that are adapted to surviving fire, or dispersal mechanisms to take advantage of the resources available immediately after fire (Keeley et al. 2011). To our knowledge, despite several studies on the relationship between fire occurrence and the seed bank in this system (Young and Evans 1975; Hassan and West 1986; Humphrey and Schupp 2001; Boudell, Link, and Johansen 2002; Barga and Leger 2018), no studies to date have examined the effect of burn severity on the seed bank.

Here, we collected soil cores from 14 locations along the perimeter of a large fire (the Hot Pot fire, ~50,000 ha) immediately after it was extinguished, in northern Nevada in July 2016. Because it burned a large area in only three days, we could sample a broad area while being reasonably certain that the climatic conditions during the fire were similar at all sites. Because we collected our samples immediately after the fire was extinguished, we felt confident that the seed bank samples did not contain seeds deposited by post-fire dispersal. We put the samples in cold storage and germinated the seeds from those cores in a greenhouse the following spring. In spring 2017 and fall 2019 we collected information on vegetation structure and diversity at each location. We hypothesized that (H1) Pre-fire fuel connectivity would be positively related to burn severity; (H2) burn severity would increase the occurrence probability of introduced annual species in the seed bank and reduce the occurrence probability of native species. Alternatively, (H2a) increased fuel connectivity brought on by the invasion of annual grasses may have already depleted the diversity of the soil seed bank before the fire occurred; (H3) the abundance of post-fire *B. tectorum* seeds in the seedbank would be positively related to post-fire fuel connectivity. In addition, because in our study system post-fire sites are floristically distinct from the pre-fire state (Mahood and Balch 2019), typically with near monocultures of *B. tectorum*, we hypothesized that (H4) high post-fire fuel connectivity of those near-monocultures would result in lower aboveground species diversity due to competitive exclusion of native plants.

2. Methods

2.1 Study Area

The study was conducted in north-central Nevada the day after a large fire (the Hot Pot Fire) was extinguished (Appendix S1, Fig. S1). The Hot Pot Fire burned just over 50,000 hectares in less than a week. The pre-fire landcover was predominantly *B. tectorum* and Wyoming big sagebrush plant communities. The fire occurred after the early season plants, including *B. tectorum* and *Poa secunda* J. Presl, the most abundant native understory species, had gone to seed, and before the late season species, including Wyoming big sagebrush, had produced flowers. Thus we were able to isolate the effect of the fire without any confounding effects of post-fire seed dispersal, while achieving a broad spatial extent. The sites we sampled ranged from 1,397 to 1,607 meters in elevation.

2.2 Seed Bank Sampling

In early July 2016, we collected samples of the soil seed bank at fourteen locations the day after the Hot Pot fire was contained. Each site was located at the perimeter of the fire where it was clearly delineated by a bulldozer line or in one case a narrow dirt road. Eleven sites were mature sagebrush communities with no history of fire since at least 1984. Three plots had previously burned in 1984 according to the Monitoring Trends in Burn Severity (MTBS) fire history (Eidenshink et al. 2007) and had high cover of *B. tectorum*, but still had scattered sagebrush cover. We used a metal stake to mark paired burned and unburned sampling locations on each side of the perimeter, 10 m from the nearest evidence of anthropogenic disturbance (i.e. bulldozer effects, footprints) associated with active fire suppression along the perimeter. Within 3 m of each marker, we extracted twelve, 6 cm deep, 5 cm diameter, soil cores. Seeds of sagebrush generally do not fall far (<30 m) from their parent plants in this system (Shinneman and McIlroy 2016), and so they are not uniformly distributed (Boudell, Link, and Johansen 2002). In addition, seeds from *B. tectorum* (Young and Evans 1975) and *Artemisia* have different germination rates based on the micro-site they find themselves in (i.e. under a shrub or in the bare ground between shrubs, Eckert et al. 1986). To account for these potentially confounding effects, we placed half of the core locations under shrubs, and half in shrub interspaces. In the burned areas, it was obvious where shrubs had been located. Even when they were completely incinerated, their imprint remained on the soil surface (Bechtold and Inouye 2007; Germino et al. 2018). To examine the effect of seed depth, we divided each soil core into 0-2 cm and 2-6 cm depths. Litter was aggregated with the 0-2 cm samples. Samples were then placed in cold storage (~2 deg C) for 3 months (Meyer, Monsen, and Mcarthur 2013). At all sites, to be sure that we were at a site where sagebrush germination could occur we checked for first year germinants on the unburned side (we found them at all sites), and to ensure that there were no confounding effects of post-fire seed dispersal, we determined whether or not the sagebrush were flowering (they were not flowering at all sites), and recorded species occupancy for all aboveground plant species.

We followed the methodology of Ter Heert et al. (1996) to germinate the seeds. Each sample was run through 0.2 mm sieve, and spread in a 3-5 mm layer over the top of 1 - 4 pots. These pots were filled 3 cm deep with potting soil, topped by a thin layer of sand. Pots were watered as needed to stay at field capacity. Every week emerging germinants were identified, counted and removed. Most of the germination occurred within 6 weeks, and after 8 weeks we ended the germination assay.

2.3 Post-Fire Vegetation Sampling

We sampled the aboveground fuel structure and plant diversity in May 2017, the growing season immediately after the fire and again in September 2019. At each location, we established 50m transects starting at the boundary of the burned and unburned sides of the perimeter, running perpendicular to the fire perimeter, and marked the transect ends with rebar. In order to characterize aboveground plant diversity, we measured the occupancy and abundance of all plant species by measuring cover of every species in 0.1 m^2 quadrats spaced every 5 m along each transect. In order to characterize fuel structure, we used the line intercept method to measure shrub cover (coarse fuels) and herbaceous plant cover (fine fuels) along the transect, and summed those measurements to get total vegetation cover (TVC). Both live and dead plants were included in these measurements.

2.4 Estimating Burn Severity with Landsat 8 OLI

We downloaded the “fire bundle” of the Hot Pot fire from www.mtbs.gov. This included cloud-free Landsat 8 scenes collected before the Hot Pot fire, and already calculated layers of the Differenced Normalized Burn Ratio (dNBR, J. D. Miller et al. 2009). Because our sites were generally within 10 meters of the burn perimeter, The pixels directly intersecting the plot locations were likely to be mixed pixels (i.e. containing burned and unburned ground). To minimize this effect, we extracted all the dNBR values within a 120 meter buffer of each seed bank plot for pixels whose centroids fell inside of the fire perimeter and calculated the mean.

2.5 Statistical Analysis

Our statistical analysis centered around trying to understand each component of the positive feedback loop posited by the 4 hypotheses described above. In order to understand how pre-fire fuel connectivity influenced burn severity (H1), we used total vegetation cover (TVC) from two separate data sources as a proxy for fuel connectivity, and created separate linear models with TVC as the predictor variable and burn severity (dNBR, J. D. Miller et al. 2009) as the response variable. With the field data we collected, we created an ordinary least squares (OLS) linear model with burn severity as the dependent variable and TVC (defined as shrub cover plus herbaceous plant cover from the unburned side of the paired plots), elevation and aspect as independent variables.

We were concerned that because our data were collected at the edge of the fire, the burn severity calculated at each point may have included partially burned pixels. So, as a supplement, we examined the same relationship by creating a model of TVC using Landsat Thematic Mapper (TM) surface reflectance data using TVC from the Bureau of Land Management's Assessment, Inventory and Monitoring dataset (AIM, U.S. Department of Interior 2018). The AIM dataset contained 813 sampling locations within the Central Basin and Range ecoregion (Commission for Environmental Cooperation 2006) that were visited by BLM field crews between 2011 and 2015. They were mostly sampled once but there were some repeats, for 1,117 total measurements. For each of these points, we extracted the surface reflectance values of each Landsat band for the sampling year near peak biomass using a cloud-free scene from May or early June. Then, we used those surface reflectance values to calculate various vegetation indexes (Appendix S1: Table S1), including the Green Normalized Differenced Vegetation Index (Green NDVI, Equation 1), and Normalized Differenced Senesced Vegetation Index (NDSVI, Equation 2). We used these indexes to create generalized linear model of TVC with a beta distribution. For this and all linear models, we started with the largest possible model and used backwards selection following the methodology of Zuur et al. (2009). We used the final reduced model to create a layer of predicted TVC for the study area for the pre-fire scene, and extracted both our predictions of TVC and dNBR of the fire from 1000 regularly-spaced points within the fire perimeter. Finally, to quantify the effect of TVC on burn severity, we created an OLS linear model with our modeled TVC and its second-order polynomial as predictor variables and burn severity as the response variable.

Equation 1: $Green\ NDVI = \frac{NIR - Green}{NIR + Green}$

Equation 2: $NDSVI = \frac{SWIR_1 - Red}{SWIR_1 + Red}$

To examine how burn severity affected the community composition of the seed bank (H2), we created a joint species distribution model (JSDM) in a Bayesian framework (Tikhonov et al. 2020) for the occurrence of all species germinated from the seed bank that were found at more than one location. We created four Markov Chain Monte Carlo (MCMC) chains, each consisting of 150,000 iterations. We discarded the first 50,000 iterations for each chain and then recorded every 100th for a total of 1,000 posterior samples per chain, and 4,000 total. We assessed model convergence using the effective sample size and the potential scale reduction factor (Gelman, Rubin, et al. 1992). We used the model to predict the probability of occurrence of germinable seeds of a given species along a gradient of burn severity. We included burn severity, elevation, aspect, pre-fire seedbank diversity and soil depth as independent variables.

To account for the possibility of H2a as a confounding factor, we included the Shannon-Weaver diversity index (Shannon and Weaver 1949) in the paired, unburned seed bank samples as one of the predictor variables in our JSDM. We also created OLS models with the unburned species richness and Shannon-Weaver diversity index predicted by prefire fuel connectivity, with the expectation that pre-fire fuel connectivity would have had a negative effect on the prefire seedbank diversity. To examine how community composition and burn severity then affected subsequent fuel connectivity (H3), we created OLS models with fuel connectivity three years post-fire as the dependent variable, and burn severity, seed counts for *B. tectorum*, *P. secunda* and other species, elevation, aspect, depth, and alpha diversity as independent variables. To examine how the resulting fuel connectivity was related to biodiversity (H4), we used the diversity data and connectivity data that we collected in 2019 to create a Poisson GLM with number of species encountered aboveground at each plot location as the dependent variable, as well as an OLS linear model with the Shannon-Weaver index (Shannon and Weaver 1949) as a dependent variable. We used fuel connectivity, elevation, and aspect as independent variables.

All analyses were done in R (R Core Team 2020). Data and code to recreate the analysis are freely available at https://www.github.com/admahood/seed-bank (DOI available after acceptance) and the Dryad data repository (url given after acceptance).

3. Results

We found support for each hypothesized component of the positive feedback loop. For H1, the most parsimonious model for our *in situ* observations had only TVC as the predictor, which had a weak positive relationship with burn severity ($\beta = 2.4$, $p = 0.083$, $R^2 = 0.27$, Figure 1a, Appendix 1: Table S2). For our remotely sensed analysis, our most parsimonious model of TVC explained 35% of the variation and had Green NDVI, NDSVI and their interaction as predictors (Appendix S1: Table S2). Our model of dNBR using the predicted TVC within the fire perimeter as a predictor of dNBR explained 42% of the variation and the relationship between TVC and burn severity was positive and significant ($p \ll 0.01$, Figure 1a, Appendix S1: Table S2).

The vast majority of seeds that germinated in the greenhouse were the two most common grass species, *P secunda* and *B. tectorum* (Appendix S1: Table S3). Eight dicot species were found in more than one location, and these 10 prevalent species are those that were used in our JSDM. Burned plots had an average of 34 ± 32 total seeds in the top 2 cm, and 12 ± 14 in the bottom 4 cm. Unburned plots had an average of 299 ± 170 in the top 2 cm and 59 ± 29 in the bottom 4 cm (Appendix S1: Fig. S2). For H2, the JSDM converged well (Appendix S1: Fig S3). Gelman diagnostics were all very close to 1 and the effective sample size centered on 4,000, which indicated good model convergence. Elevation had the strongest effects on individual species occurrence and explained the most variance on average (36%). Burn severity explained 23% of the variance on average and was supported at the 95% level for 5 species. For the introduced species, the predictions along a gradient of burn severity were positive for *B. tectorum*, *Sisymbrium altissimum* L. and *Lepidium perfoliatum* L., and negative for *Ceratocephala testiculata* and *Alyssum desertorum* Stapf. For native species, the effect of burn severity on occurrence was positive for *A. tridentata*, but the mean prediction never rose above 50%. It was neutral for *P. secunda* and negative for the remaining species. Testing H2a revealed a positive relationship between pre-fire aboveground species diversity and pre-fire fuel connectivity, and so we felt it was reasonable to rule out pre-fire fuel connectivity as a confounding factor for H2.

For H3, we found that, after accounting for elevation, pre-fire aboveground richness, and the number of *P. secunda* seeds, the number of *B. tectorum* seeds in the post-fire seedbank was positively associated with the fuel connectivity in 2019 (β = 0.54, p = 0.01, Adj R^2 = 0.75,Figure 1c, Appendix S1: Table S2). For H4 the most parsimonious model (Adj R^2 = 0.89, Appendix S1: Table S2) had elevation, aspect, fuel connectivity and an interaction between elevation and fuel connectivity as predictors of aboveground Shannon-Weaver alpha diversity. Fuel connectivity was negatively associated with Shannon-Weaver diversity (β = -0.28, p=0.004, Figure 1d).

4. Discussion

Here we document the mechanisms by which changes in ecosystem structure brought on by invasion can lead to cascading effects on ecosystem function and composition via changes in the disturbance regime. It has already been shown that *B. tectorum* invasion increases fire frequency (Balch et al. 2013), and is indicative of a grass-fire cycle. However, an understanding of the positive feedback mechanisms that link *B. tectorum* invasion success to fire occurrence is required to infer the long-term persistence of such a cycle. The interaction between burn severity and seed bank composition documented here may explain that link. Prior work has shown that annual grass invasion increases fuel connectivity by filling in shrub interspaces with a contiguous bed of fine fuels (Davies and Nafus 2013). This change in the spatial distribution of fine fuels has been associated with larger and more frequent fires (Balch et al. 2013). Here, we found higher fuel connectivity (via TVC) increased burn severity (H1, Figure 1a). Higher burn severity was associated with an increased occurrence of introduced annuals in the seedbank and a decreased occurrence of native plants (H2, Figure 1b). Finally, greater abundance of *B. tectorum* seeds in the post-fire seedbank resulted in higher post-fire fuel connectivity (H3, Figure 1c). In addition, we found evidence that high post-fire fuel connectivity was associated with lower aboveground diversity (H4, Figure 1d). This suggests that during inter-fire intervals, there may be additional mechanisms (e.g. competition, altered ecohydrology) maintaining the post-fire, annual grass-dominated species assemblage.

The difference in species composition before and after fire explains an apparent contradiction in results between H2a (positive relationship between pre-fire fuel connectivity and diversity) and H4 (negative relationship between post-fire fuel connectivity and diversity). Most plot locations had mature canopies of native shrubs with the inter-shrub space occupied mostly by native bunchgrasses and forbs, with no fire occurrence since 1984. Even in locations with high annual grass cover between shrubs, shrubs provide ecosystem structural heterogeneity and islands of fertility (Doescher, Miller, and Winward 1984; Bechtold and Inouye 2007), and perennial natives that may have been established before invasion have deep roots established that allow for the avoidance of competition for water with shallow-rooted annuals (Gibbens and Lenz 2001; Ottaviani et al. 2020). This may provide enough niche compartmentalization to allow native plants to persist in spite of the invasion. Three years after fire, almost all of the plots were dominated by introduced annuals, and lacked any structural heterogeneity. Thus native plants may have been be able to persist via niche compartmentalization after the initial invasion, but fire burned away most of the seeds (Appendix S1, Fig. S1) and removed all of the structural benefits, and microclimatic refugia that shrub cover provides. In this clean slate post-fire environment, the altered species composition of the seedbank and superior post-fire dispersal of *B. tectorum* (Monty, Brown, and Johnston 2013) allow the process of interspecific competition to be dominant (Schlaepfer, Lauenroth, and Bradford 2014).

Contrasts among forests and shrublands as it pertains to remote sensing

Burn severity metrics like dNBR were conceived of in the context of forested ecosystems, and calibrated using the composite burn index (Key and Benson 1999), tree mortality, and percent change in tree canopy cover (J. D. Miller et al. 2009). It is unclear how well these metrics carry over to shrubland systems. We recorded qualitative observations of burn severity while we were sampling, mainly to ensure that we sampled a range of severities, and the dNBR we used appears to correspond with our observations. In areas where the space between shrubs was well-connected by fine fuels (Figure 2 a-c) the dNBR was higher, and the shrubs had completely burned throughout the root system, leaving only a hole in the ground filled with ashes as evidence of their prior presence. In these areas the entirety of the soil surface—underneath shrub canopy and in canopy interspaces—was consumed by fire, and there was little evidence of remaining litter or biological soil crust. Areas with lower fuel connectivity had lower dNBR (Figure 2 d-f). Here, shrubs were usually consumed only to the stumps, and sometimes left standing and charred, destined for mortality. In these areas the soil surface often still had biological soil crust, partially consumed litter (R. O. Jones et al. 2015) and unconsumed annual and perennial grass bases. The manual severity classification provided by MTBS had exclusively low and medium severity, but our observations of essentially complete consumption of plant and litter tissues and very few unburned patches suggested that these should have been mostly medium and high severity. This discrepancy was not unexpected, as the ordinal burn severity classifications produced by MTBS are known to be of limited use for research (Kolden, Smith, and Abatzoglou 2015).

Spectral reflectance has long been used to characterize ecosystem structure, including wildfire fuels. Unique signatures of remotely-sensed spectral reflectance are typically matched to categorical fuel classifications (CFCs), which describe the physiognomy of vegetation and its potential to support various fire behavior (Ottmar et al. 2007). While different CFCs can provide a general understanding of fuel amount and connectivity, recent efforts using data with finer spatial and spectral resolution may improve fuel classification with more continuous, multi-dimensional measurements (Stavros et al. 2018). The continuous measure of NDVI in western U.S. coniferous forests is a proxy for live fuel biomass, which likely explains its positive association with wildfire severity (Sean A. Parks et al. 2018; Koontz et al. 2020). NDVI also correlates with vegetation cover in these forested systems, and so greater crown connectivity may also explain the NDVI/severity relationship at local scales. When using a more direct NDVI-derived measure of vegetation connectivity in Sierra Nevada yellow pine/mixed-conifer, Koontz et al. (2020) found that greater variability in forest structure, implying fuel discontinuity decreased the probability of high-severity fire. Here, we arrived at a combination of NDVI and NDSVI to describe the fuel connectivity of the annual grass invaded Great Basin sagebrush community to better reflect key differences in the physiognomies of forest and arid shrublands. In sagebrush shrublands, the fuel that contributes to large wildfires is a mixture of evergreen shrubs interspersed with herbaceous plants that remain green for only a portion of the growing season, and then become dry and straw-colored. Thus, both the live and dead fuel need to be taken into account in remote measurements of fuel connectivity for this system.

Management implications

These results demonstrate that the strength of the grass-fire cycle in this system is controlled by measurable fire properties and ecosystem structural components. Land managers may be able to increase their chances of restoration success by using existing methods or developing novel ones that manipulate these components to weaken or even break the positive feedback cycle. This work provides further evidence that the post-fire annual grassland is a system where the degraded state represents an alternative species assemblage from that of the restoration target. Because the propagules of the original assemblage are no longer present, methods that rely on natural succession may not be sufficient (Suding, Gross, and Houseman 2004). Estimating burn severity using satellite imagery may help land managers identify areas with a greater likelihood of successful seeding. Our results highlight the importance of prioritizing the preservation of existing native shrub cover and in particular policies that encourage land managers to maximize the preservation of unburned patches within the fire perimeter during the suppression of wildfires in this system (Steenvoorden et al. 2019), as these are the primary sources of native propagules.

Livestock grazing can reduce fuel connectivity in uninvaded sagebrush (Davies et al. 2010). At the same time, livestock grazing can decrease the resistance to invasion by *B. tectorum* via negative effects on biological soil crust (BSC) (Chambers et al. 2014; Condon and Pyke 2018), and can reduce the survival of *Artemisia* seedlings that are not protected by shrub canopies (Owens and Norton 1992). In wet years, targeted grazing at already invaded sites may reduce fuel connectivity and alleviate fire risk. Post-fire grazing may help reduce *B. tectorum* cover, but it may also exacerbate the problem by introducing cheatgrass in uninvaded sites (Williamson et al. 2019) or increasing the already superior post-fire dispersal of *B. tectorum* seeds (Monty, Brown, and Johnston 2013). We suggest management approaches that are specifically tailored each year to the conditions of a given site, and targeting grazing only in already invaded areas to reduce *B. tectorum* cover where it may aid in native plant restoration.

Herbaceous cover in these dryland systems has high interannual variability (Mahood et al. 2022). Because the components of ecosystem structure and disturbance severity in positive feedback cycle described here are continuous mechanistic variables, it may be possible to develop theoretical models (*sensu* (Ludwig, Jones, and Holling 1978)) to estimate the threshold of vegetation cover that will lead to high burn severity. These can then be applied in conjunction with near real time fuel loading forecasts (M. O. Jones et al. 2021) to identify areas that are vulnerable to high severity fire, which can be used by land managers to take preemptive measures in high value areas.

Global implications

Understanding how different facets of global change create multiple mechanisms that act in concert to drive ecosystem transformation will provide important insights about ecosystem change on a global scale. Ecological systems are much more complex than a simple bivariate system with a single driver and a single response. The system studied here has at least four external processes that may influence the positive feedback loop we documented. First, land use change in the form of the introduction of livestock grazing facilitates invasion (Ponzetti, Mccune, and Pyke 2007; Williamson et al. 2019). Second, the introduction of exotic grasses increases fuel connectivity (Davies and Nafus 2013), which we document affects burn severity. Third, increasing temperatures due to climate change both increase burn severity (S. A. Parks and Abatzoglou 2020) while simultaneously decreasing seed viability and seedling survival (Schlaepfer, Lauenroth, and Bradford 2014; Enright et al. 2015). Fourth, CO_2 enrichment may preferentially enhance biomass (i.e. higher fuel connectivity) and seed production of annual grass species (Smith et al. 2000; Nagel et al. 2004), strengthening the fuel connectivity to burn severity to seed composition feedback loop. All four of these external drivers are globally ubiquitous consequences of global change.

The "state" the ecosystem is the product of countless endogenous interactions. The grass-fire cycle studied here is reinforced through providing fitness benefits to the introduced annual grasses via at least three redundant processes. First, we document how it changes the composition of the seedbank. Second, introduced annual grasses competitively exclude native plants. Third, the dominance of introduced annual grasses initiates ecohydrological feedbacks to create a warmer, drier microclimate (Turnbull et al. 2012; Wilcox et al. 2012). It is possible that some of these feedbacks are idiosyncratic to the system being studied, while others may reflect fundamental properties of ecosystem function that change when a system is converted from being dominated by deep-rooted woody plants to being dominated by annual herbaceous plants (Kitzberger et al. 2016). At least 13 grass species initiate self-reinforcing feedbacks with fire in the U.S. alone (Fusco et al. 2019; Tortorelli, Krawchuk, and Kerns 2020). There are likely many more worldwide, beyond documented cases in Australia (G. Miller et al. 2010; Setterfield et al. 2010), Brazil (Rossi et al. 2014) and South Africa (Milton 2004). The conversion of forests and shrublands to grasslands may have consequences relevant to the global carbon cycle, especially when ecosystems dominated by deep-rooted plants that store carbon belowground are replaced by shallow-rooted ecosystems that lose carbon to grazers and fire Mahood et al. (2022).

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References

Aleman, J. C., A. Fayolle, C. Favier, A. C. Staver, K. G. Dexter, C. M. Ryan, A. F. Azihou, et al. 2020. "Floristic Evidence for Alternative Biome States in Tropical Africa." *Proceedings of the National Academy of Sciences* 117 (45): 28183–90. https://doi.org/10.1073/pnas.2011515117.

Allan, Eric, Pete Manning, Fabian Alt, Julia Binkenstein, Stefan Blaser, Nico Blüthgen, Stefan Böhm, et al. 2015. "Land Use Intensification Alters Ecosystem Multifunctionality via Loss of Biodiversity and Changes to Functional Composition." *Ecology Letters* 18 (8): 834–43. https://doi.org/10.1111/ele.12469.

Baker, William L. 2006. "Fire and restoration of sagebrush ecosystems." *Wildlife Society Bulletin* 34 (1): 177–85. https://doi.org/10.2193/0091-7648(2006)34%5B177:farose%5D2.0.co;2.

Balch, Jennifer K., Bethany A. Bradley, Carla M. D'Antonio, and José Gómez-Dans. 2013. "Introduced annual grass increases regional fire activity across the arid western USA

(1980-2009).” *Global Change Biology* 19 (1): 173–83. https://doi.org/10.1111/gcb.12046.

Barga, Sarah, and Elizabeth A. Leger. 2018. “Shrub cover and fire history predict seed bank composition in Great Basin shrublands.” *Journal of Arid Environments* 154 (November 2017): 40–50. https://doi.org/10.1016/j.jaridenv.2018.03.004.

Bechtold, H. A., and R. S. Inouye. 2007. “Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal.” *Journal of Arid Environments* 71 (1): 122–32. https://doi.org/10.1016/j.jaridenv.2007.02.004.

Beckstead, Julie, Laura E. Street, Susan E. Meyer, and Phil S. Allen. 2011. “Fire effects on the cheatgrass seed bank pathogen Pyrenophora semeniperda.” *Rangeland Ecology and Management* 64 (2): 148–57. https://doi.org/10.2111/REM-D-10-00052.1.

Bond, William J., and Jeremy J. Midgley. 1995. “Kill Thy Neighbour: An Individualistic Argument for the Evolution of Flammability.” *Oikos* 73 (1): 79. https://doi.org/10.2307/3545728.

Boudell, JA, SO Link, and JR Johansen. 2002. “Effect of soil microtopography on seed bank distribution in the shrub-steppe.” *Western North American Naturalist* 62 (1): 14–24. https://doi.org/10.2307/41717153.

Brooks, Matthew L., Carla M. D’Antonio, David M. Richardson, James B. Grace, Jon E. Keeley, Joseph M. DiTomaso, Richard J. Hobbs, Mike Pellant, and David Pyke. 2004. “Effects of Invasive Alien Plants on Fire Regimes.” *BioScience* 54 (7): 677–88.

Bukowski, Beth, and William L. Baker. 2013. “Historical fire regimes, reconstructed from land-survey data, led to complexity and fluctuation in sagebrush landscapes.” *Ecological Applications* 23 (3): 546–64.

Chambers, Jeanne C., Bethany A. Bradley, Cynthia S. Brown, Carla M. D’Antonio, Matthew J. Germino, James B. Grace, Stuart P. Hardegree, Richard F. Miller, and David A. Pyke. 2014. “Resilience to Stress and Disturbance, and Resistance to Bromus Tectorum L. Invasion in Cold Desert Shrublands of Western North America.” *Ecosystems* 17 (2): 360–75. https://doi.org/10.1007/s10021-013-9725-5.

Commission for Environmental Cooperation. 2006. "Ecological regions of North America – Levels I, II, and III: Montreal, Quebec, Canada, Commission for Environmental Cooperation, scale 1:10,000,000." https://www.epa.gov/eco-research/ecoregions-north-america.

Condon, Lea A., and David A. Pyke. 2018. "Fire and Grazing Influence Site Resistance to Bromus tectorum Through Their Effects on Shrub, Bunchgrass and Biocrust Communities in the Great Basin (USA)." *Ecosystems* 21 (7): 1416–31. https://doi.org/10.1007/s10021-018-0230-8.

D'Antonio, Carla M., and Peter M. Vitousek. 1992. "Biological invasions by exotic grasses, the grass/fire cycle, and global change." *Annual Review of Ecological Systems* 23: 63–87.

Davies, Kirk W., Jonathan D. Bates, Tony J. Svejcar, and Chad S. Boyd. 2010. "Effects of long-term livestock grazing on fuel characteristics in rangelands: An example from the sagebrush steppe." *Rangeland Ecology and Management* 63 (6): 662–69. https://doi.org/10.2111/REM-D-10-00006.1.

Davies, Kirk W., Chad S. Boyd, Jeffrey L. Beck, Jon D. Bates, Tony J. Svejcar, and Michael A. Gregg. 2011. "Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities." *Biological Conservation* 144 (11): 2573–84. https://doi.org/10.1016/j.biocon.2011.07.016.

Davies, Kirk W., and Aleta M. Nafus. 2013. "Exotic annual grass invasion alters fuel amounts, continuity and moisture content." *International Journal of Wildland Fire* 22 (3): 353–58. https://doi.org/10.1071/WF11161.

Davis, Kimberley T., Solomon Z. Dobrowski, Philip E. Higuera, Zachary A. Holden, Thomas T. Veblen, Monica T. Rother, Sean A. Parks, Anna Sala, and Marco P. Maneta. 2019. "Wildfires and Climate Change Push Low-Elevation Forests Across a Critical Climate Threshold for Tree Regeneration." *Proceedings of the National Academy of Sciences*, 201815107. https://doi.org/10.1073/pnas.1815107116.

Davis, Kimberley T., Philip E. Higuera, and Anna Sala. 2018. "Anticipating Fire-mediated Impacts of Climate Change Using a Demographic Framework." Edited by Charles Fox.

Functional Ecology 32 (7): 1729–45. https://doi.org/10.1111/1365-2435.13132.

Doescher, Paul S., Richard F. Miller, and Alma H. Winward. 1984. "Soil Chemical Patterns under Eastern Oregon Plant Communities Dominated by Big Sagebrush." https://doi.org/10.2136/sssaj1984.03615995004800030038x.

Eckert, Richard E., Frederick F. Peterson, Michael S. Meurisse, and L. Stephens. 1986. "Effects of Soil-Surface Morphology on Emergence and Survival of Seedlings in Big Sagebrush Communities." *Journal of Range Management* 39 (5): 414–20. http://www.jstor.org/stable/3899441.

Eidenshink, Jeff, Brian Schwind, Ken Brewer, Zhi-liang Zhu, Brad Quayle, and Stephen Howard. 2007. "A Project for Monitoring Trends in Burn Severity." *Fire Ecology* 3 (1): 3–21. https://doi.org/10.4996/fireecology.0301003.

Enright, Neal J., Joseph B. Fontaine, David M. J. S. Bowman, Ross A. Bradstock, and Richard J. Williams. 2015. "Interval Squeeze: Altered Fire Regimes and Demographic Responses Interact to Threaten Woody Species Persistence as Climate Changes." *Frontiers in Ecology and the Environment* 13 (5): 265–72. https://doi.org/10.1890/140231.

Eskelinen, Anu, Kelly Gravuer, W Stanley Harpole, Susan Harrison, Risto Virtanen, and Yann Hautier. 2020. "Resource-enhancing Global Changes Drive a Whole-ecosystem Shift to Faster Cycling but Decrease Diversity." *Ecology* 101 (12). https://doi.org/10.1002/ecy.3178.

Fusco, Emily J., John T. Finn, Jennifer K. Balch, R. Chelsea Nagy, and Bethany A. Bradley. 2019. "Invasive Grasses Increase Fire Occurrence and Frequency Across US Ecoregions." *Proceedings of the National Academy of Sciences* 116 (47): 23594–99. https://doi.org/10.1073/pnas.1908253116.

Gagnon, Paul R., Heather A. Passmore, Matthew Slocum, Jonathan A. Myers, Kyle E. Harms, William J. Platt, and C. E. Timothy Paine. 2015. "Fuels and fires influence vegetation via above- and belowground pathways in a high-diversity plant community." *Journal of Ecology* 103 (4): 1009–19. https://doi.org/10.1111/1365-2745.12421.

Gelman, Andrew, Donald B Rubin, et al. 1992. “Inference from Iterative Simulation Using Multiple Sequences.” *Statistical Science* 7 (4): 457–72.

Germino, Matthew J., David M. Barnard, Bill E. Davidson, Robert S. Arkle, David S. Pilliod, Matthew R. Fisk, and Cara Applestein. 2018. “Thresholds and hotspots for shrub restoration following a heterogeneous megafire.” *Landscape Ecology* 33 (7): 1177–94. https://doi.org/10.1007/s10980-018-0662-8.

Germino, Matthew J., Jeanne C. Chambers, and Cynthia S. Brown. 2016. *Exotic Brome-Grasses in Arid and Semiarid Ecosystems of the Western US Causes, Consequences, and Management Implications*. http://www.springer.com/series/412.

Gibbens, Robert P., and James M. Lenz. 2001. “Root systems of some Chihuahuan Desert plants.” *Journal of Arid Environments* 49: 221–63.

Gill, Nathan S, Monica G Turner, Carissa D Brown, Sydney I Glassman, Sandra L Haire, Winslow D Hansen, Elizabeth R Pansing, Samuel B St Clair, and Diana F Tomback. 2022. “Limitations to Propagule Dispersal Will Constrain Postfire Recovery of Plants and Fungi in Western Coniferous Forests.” *BioScience*, January, biab139. https://doi.org/10.1093/biosci/biab139.

Hassan, M. A., and N. E. West. 1986. “Dynamics of Soil Seed Pools in Burned and Unburned Sagebrush Semi-Deserts.” *Ecology* 67 (1): 269–72.

Heerdt, G. N. J. Ter, G. L. Verweij, R. M. Bekker, and J. P. Bakker. 1996. “An Improved Method for Seed-Bank Analysis: Seedling Emergence After Removing the Soil by Sieving.” *Functional Ecology* 10 (1): 144. https://doi.org/10.2307/2390273.

Heydari, Mehdi, Reza Omidipour, Mehdi Abedi, and Carol Baskin. 2017. “Effects of fire disturbance on alpha and beta diversity and on beta diversity components of soil seed banks and aboveground vegetation.” *Plant Ecology and Evolution* 150 (3): 247–56. https://doi.org/10.5091/plecevo.2017.1344.

Hirota, Marina, Milena Holmgren, Egbert H. Van Nes, and Marten Scheffer. 2011. “Global resilience of tropical forest and savanna to critical transitions.” *Science* 334 (6053): 232–

35. https://doi.org/10.1126/science.1210657.

Humphrey, L David, and Eugene W Schupp. 2001. “Seed banks of Bromus tectorum-dominated communities in the Great Basin.” *Western North American Naturalist* 61 (1): 85–92. https://doi.org/10.2307/41717080.

Jones, Matthew O., Nathaniel P. Robinson, David E. Naugle, Jeremy D. Maestas, Matthew C. Reeves, Robert W. Lankston, and Brady W. Allred. 2021. “Annual and 16-Day Rangeland Production Estimates for the Western United States.” *Rangeland Ecology & Management* 77 (July): 112–17. https://doi.org/10.1016/j.rama.2021.04.003.

Jones, Rachel O., Jeanne C. Chambers, David I. Board, Dale W. Johnson, and Robert R. Blank. 2015. “The role of resource limitation in restoration of sagebrush ecosystems dominated by cheatgrass (Bromus tectorum).” *Ecosphere* 6 (7): 1–21.

Keddy, Paul A, and Daniel C Laughlin. 2021. *A Framework for Community Ecology: Species Pools, Filters and Traits.* Cambridge University Press.

Keeley, Jon E. 2009. “Fire intensity, fire severity and burn severity: A brief review and suggested usage.” *International Journal of Wildland Fire* 18 (1): 116–26. https://doi.org/10.1071/WF07049.

Keeley, Jon E., Juli G. Pausas, Philip W. Rundel, William J. Bond, and Ross A. Bradstock. 2011. “Fire as an evolutionary pressure shaping plant traits.” *Trends in Plant Science* 16 (8): 406–11. https://doi.org/10.1016/j.tplants.2011.04.002.

Kerns, Becky K., Claire Tortorelli, Michelle A. Day, Ty Nietupski, Ana M. G. Barros, John B. Kim, and Meg A. Krawchuk. 2020. “Invasive grasses: A new perfect storm for forested ecosystems?” *Forest Ecology and Management* 463 (November 2019): 117985. https://doi.org/10.1016/j.foreco.2020.117985.

Key, Carl H, and Nathan C Benson. 1999. “The Composite Burn Index (CBI): Field Rating of Burn Severity.” *USGS, NRMSC Research,[online] Available: Http://Nrmsc. Usgs. Gov/Research/Cbi. Htm [3/14/2006].*

Kimura, Hideo, and Shiro Tsuyuzaki. 2011. “Fire severity affects vegetation and seed bank in a wetland." *Applied Vegetation Science* 14 (3): 350–57. https://doi.org/10.1111/j.1654-109X.2011.01126.x.

Kitzberger, Thomas, G. L. W. Perry, J. Paritsis, J. H. Gowda, A. J. Tepley, A. Holz, and T. T. Veblen. 2016. "Fire–vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand." *New Zealand Journal of Botany* 54 (2): 247–72. https://doi.org/10.1080/0028825X.2016.1151903.

Knapp, Paul A. 1996. "Cheatgrass (Bromus tectorum L) dominance in the Great Basin Desert." *Global Environmental Change* 6 (1): 37–52. https://doi.org/10.1016/0959-3780(95)00112-3.

Kolden, Crystal A, Alistair M S Smith, and John T. Abatzoglou. 2015. "Limitations and utilisation of Monitoring Trends in Burn Severity products for assessing wildfire severity in the USA." *International Journal of Wildland Fire* 24: 1023–28.

Koontz, Michael J, Malcolm P North, Chhaya M Werner, Stephen E Fick, and Andrew M Latimer. 2020. "Local Forest Structure Variability Increases Resilience to Wildfire in Dry Western US Coniferous Forests." *Ecology Letters* 23 (3): 483–94.

Lipoma, M. Lucrecia, Guillermo Funes, and Sandra Díaz. 2018. "Fire effects on the soil seed bank and post-fire resilience of a semi-arid shrubland in central Argentina." *Austral Ecology* 43 (1): 46–55. https://doi.org/10.1111/aec.12533.

Liyanage, Ganesha S., and Mark K. J. Ooi. 2017. "Do dormancy-breaking temperature thresholds change as seeds age in the soil seed bank?" *Seed Science Research* 27 (1): 1–11. https://doi.org/10.1017/S0960258516000271.

Ludwig, D., D. D. Jones, and C. S. Holling. 1978. "Qualitative Analysis of Insect Outbreak Systems: The Spruce Budworm and Forest." *The Journal of Animal Ecology* 47 (1): 315. https://doi.org/10.2307/3939.

Mahood, Adam L., and Jennifer K. Balch. 2019. "Repeated fires reduce plant diversity in low-elevation Wyoming big sagebrush ecosystems (1984 – 2014)." *Ecosphere* 10 (2):

e02591. https://doi.org/10.1002/ecs2.2591.

Mahood, Adam L., Rachel O. Jones, David I. Board, Jennifer K. Balch, and Jeanne C. Chambers. 2022. “Interannual Climate Variability Mediates Changes in Carbon and Nitrogen Pools Caused by Annual Grass Invasion in a Semiarid Shrubland.” *Global Change Biology* 28 (1): 267–84. https://doi.org/10.1111/gcb.15921.

Maia, P., J. G. Pausas, V. Arcenegui, C. Guerrero, A. Pérez-Bejarano, J. Mataix-Solera, M. E. T. Varela, I. Fernandes, E. T. Pedrosa, and J. J. Keizer. 2012. “Wildfire effects on the soil seed bank of a maritime pine stand - The importance of fire severity.” *Geoderma* 191: 80–88. https://doi.org/10.1016/j.geoderma.2012.02.001.

Meyer, Susan E, Stephen B Monsen, and E Durant Mcarthur. 2013. “Germination Response of Artemisia tridentata (Asteraceae) to Light and Chill: Patterns of Between-Population Variation.” *Botanical Gazette* 151 (2): 176–83.

Miller, Georgia, Margaret Friedel, Paul Adam, and Vanessa Chewings. 2010. “Ecological impacts of buffel grass (Cenchrus ciliaris L.) invasion in central Australia does field evidence support a fire-invasion feedback?” *The Rangeland Journal* 32 (4): 353–65. https://doi.org/10.1071/RJ09076.

Miller, Jay D., Eric E. Knapp, Carl H. Key, Carl N. Skinner, Clint J. Isbell, R. Max Creasy, and Joseph W. Sherlock. 2009. “Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA.” *Remote Sensing of Environment* 113 (3): 645–56. https://doi.org/10.1016/j.rse.2008.11.009.

Milton, Sue J. 2004. “Grasses as invasive alien plants in South Africa.” *South African Journal of Science* 100 (1-2): 69–75.

Monty, Arnaud, Cynthia S. Brown, and Danielle B. Johnston. 2013. “Fire promotes downy brome (Bromus tectorum L.) seed dispersal.” *Biological Invasions* 15 (5): 1113–23. https://doi.org/10.1007/s10530-012-0355-1.

Morgan, P., and L. F. Neuenschwander. 1988. “Seed-Bank Contributions to Regeneration of Shrub Species After Clear-Cutting and Burning." *Canadian Journal of Botany* 66 (1): 169–72. https://doi.org/10.1139/b88-026.

Nagel, Jennifer M., Travis E. Huxman, Kevin L. Griffin, and Stanley D. Smith. 2004. "CO2 enrichment reduces the energetic cost of biomass construction in an invasive desert grass." *Ecology* 85 (1): 100–106. https://doi.org/10.1890/02-3005.

Ottaviani, Gianluigi, Rafael Molina-Venegas, Tristan Charles-Dominique, Stefano Chelli, Giandiego Campetella, Roberto Canullo, and Jitka Klimešová. 2020. "The Neglected Belowground Dimension of Plant Dominance." *Trends in Ecology and Evolution* 35 (9): 763–66. https://doi.org/10.1016/j.tree.2020.06.006.

Ottmar, Roger D, David V Sandberg, Cynthia L Riccardi, and Susan J Prichard. 2007. "An Overview of the Fuel Characteristic Classification System—Quantifying, Classifying, and Creating Fuelbeds for Resource Planning." *Canadian Journal of Forest Research* 37 (12): 2383–93.

Owens, M. K., and B. E. Norton. 1992. "Interactions of Grazing and Plant Protection on Basin Big Sagebrush (Artemisia tridentata ssp . tridentata) Seedling Survival." *Journal of Range Management* 45 (3): 257–62. http://www.jstor.org/stable/4002974.

Palmer, Harrison D., Andrew J. Denham, and Mark K. J. Ooi. 2018. "Fire severity drives variation in post-fire recruitment and residual seed bank size of Acacia species." *Plant Ecology* 219 (5): 527–37. https://doi.org/10.1007/s11258-018-0815-5.

Parks, S. A., and J. T. Abatzoglou. 2020. "Warmer and Drier Fire Seasons Contribute to Increases in Area Burned at High Severity in Western US Forests From 1985 to 2017." *Geophysical Research Letters* 47 (22). https://doi.org/10.1029/2020GL089858.

Parks, Sean A., Lisa M. Holsinger, Morgan A. Voss, Rachel A. Loehman, and Nathaniel P. Robinson. 2018. "Mean composite fire severity metrics computed with google earth engine offer improved accuracy and expanded mapping potential." *Remote Sensing* 10 (6): 1–15. https://doi.org/10.3390/rs10060879.

Petraitis, Peter S., and Roger Earl Latham. 1999. "The importance of scale in testing the origins of alternative community states.” *Ecology* 80 (2): 429–42. https://doi.org/10.1890/0012-9658(1999)080%5B0429:TIOSIT%5D2.0.CO;2.

Ponzetti, J. M., B. Mccune, and David A. Pyke. 2007. “Biotic Soil Crusts in Relation to Topography, Cheatgrass and Fire in the Columbia Basin, Washington.” *The Bryologist* 110 (4): 706–22. https://doi.org/10.1639/0007-2745(2007)110%5B706:BSCIRT%5D2.0.CO;2.

R Core Team. 2020. *R: A Language and Environment for Statistical Computing.* Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Ratajczak, Zak, Stephen R. Carpenter, Anthony R. Ives, Christopher J. Kucharik, Tanjona Ramiadantsoa, M. Allison Stegner, John W. Williams, Jien Zhang, and Monica G. Turner. 2018. “Abrupt Change in Ecological Systems: Inference and Diagnosis.” *Trends in Ecology and Evolution* 33 (7): 513–26. https://doi.org/10.1016/j.tree.2018.04.013.

Rossi, Rafael Drumond, Carlos Romero Martins, Pedro Lage Viana, Evandro Luís Rodrigues, and José Eugênio Côrtes Figueira. 2014. “Impact of invasion by molasses grass (Melinis minutiflora P. Beauv.) on native species and on fires in areas of campo-cerrado in Brazil.” *Acta Botanica Brasilica* 28 (4): 631–37. https://doi.org/10.1590/0102-33062014abb3390.

Rother, Monica T., Thomas T. Veblen, and Luke G. Furman. 2015. “A Field Experiment Informs Expected Patterns of Conifer Regeneration After Disturbance Under Changing Climate Conditions.” *Canadian Journal of Forest Research* 45 (11): 1607–16. https://doi.org/10.1139/cjfr-2015-0033.

Scheffer, Marten, and Stephen R. Carpenter. 2003. “Catastrophic Regime Shifts in Ecosystems: Linking Theory to Observation.” *Trends in Ecology & Evolution* 18 (12): 648–56. https://doi.org/10.1016/j.tree.2003.09.002.

Scheffer, Marten, Stephen R. Carpenter, Vasilis Dakos, and Egbert H. van Nes. 2015. “Generic Indicators of Ecological Resilience: Inferring the Chance of a Critical Transition.” *Annual Review of Ecology, Evolution, and Systematics* 46 (1): 145–67. https://doi.org/10.1146/annurev-ecolsys-112414-054242.

Scheffer, M, S Carpenter, JA Foley, C Folke, and B Walker. 2001. "Catastrophic Shifts in Ecosystems." *Nature* 413: 591–96.

Schimmel, Johnny, and Anders Granström. 1996. "Fire Severity and Vegetation Response in the Boreal Swedish Forest." *Ecology* 77 (5): 1436–50.

Schlaepfer, Daniel R., William K. Lauenroth, and John B. Bradford. 2014. "Natural Regeneration Processes in Big Sagebrush (Artemisia tridentata)." *Rangeland Ecology & Management* 67 (4): 344–57. https://doi.org/10.2111/REM-D-13-00079.1.

Schröder, Arne, Lennart Persson, and André M. De Roos. 2005. "Direct Experimental Evidence for Alternative Stable States: A Review." *Oikos* 110 (1): 3–19. https://doi.org/10.1111/j.0030-1299.2005.13962.x.

Setterfield, Samantha A., Natalie A. Rossiter-Rachor, Lindsay B. Hutley, Michael M. Douglas, and Richard J. Williams. 2010. "Turning up the heat: The impacts of Andropogon gayanus (gamba grass) invasion on fire behaviour in northern Australian savannas." *Diversity and Distributions* 16 (5): 854–61. https://doi.org/10.1111/j.1472-4642.2010.00688.x.

Shannon, CE, and W Weaver. 1949. "The Mathematical Theory of Communication. University of Illinois Press, Urbana-Champaign, Illinois, USA, 117 p."

Shinneman, Douglas J., and Susan K. McIlroy. 2016. "Identifying key climate and environmental factors affecting rates of post-fire big sagebrush (Artemisia tridentata) recovery in the northern Columbia Basin, USA." *International Journal of Wildland Fire* 25: 933–45. https://doi.org/10.1071/WF16013.

Smith, Stanley D., Travis E. Huxman, Stephen F. Zitzer, Therese N. Charlet, David C. Housman, James S. Coleman, Lynn K. Fenstermaker, Jeffrey R. Seemann, and Robert S. Nowak. 2000. "Elevated CO2 increases productivity and invasive species success in an arid ecosystem." *Nature* 408 (6808): 79–82. https://doi.org/10.1038/35040544.

Staal, Arie, Ingo Fetzer, Lan Wang-Erlandsson, Joyce H. C. Bosmans, Stefan C. Dekker, Egbert H. van Nes, Johan Rockström, and Obbe A. Tuinenburg. 2020. "Hysteresis of tropical forests in the 21st century.” *Nature Communications* 11 (1): 1–8. https://doi.org/10.1038/s41467-020-18728-7.

Staver, A. Carla, Sally Archibald, and Simon A. Levin. 2011. “The global extent and determinants of savanna and forest as alternative biome states.” *Science* 334 (6053): 230–32. https://doi.org/10.1126/science.1210465.

Stavros, E. Natasha, Janice Coen, Birgit Peterson, Harshvardhan Singh, Kama Kennedy, Carlos Ramirez, and David Schimel. 2018. “Use of Imaging Spectroscopy and LIDAR to Characterize Fuels for Fire Behavior Prediction.” *Remote Sensing Applications: Society and Environment* 11: 41–50. https://doi.org/https://doi.org/10.1016/j.rsase.2018.04.010.

Steenvoorden, Jasper, Arjan J. H. Meddens, Anthony J. Martinez, Lee J. Foster, and W. Daniel Kissling. 2019. “The potential importance of unburned islands as refugia for the persistence of wildlife species in fire-prone ecosystems.” *Ecology and Evolution* 9 (15): 8800–8812. https://doi.org/10.1002/ece3.5432.

Suding, Katharine N., Katherine L. Gross, and Gregory R. Houseman. 2004. “Alternative states and positive feedbacks in restoration ecology.” *Trends in Ecology & Evolution* 19 (1): 46–53. https://doi.org/10.1016/j.tree.2003.10.005.

Tikhonov, Gleb, Otso Ovaskainen, Jari Oksanen, Melinda de Jonge, Oystein Opedal, and Tad Dallas. 2020. *Hmsc: Hierarchical Model of Species Communities*. https://CRAN.R-project.org/package=Hmsc.

Tortorelli, Claire M., Meg A. Krawchuk, and Becky K. Kerns. 2020. “Expanding the invasion footprint: Ventenata dubia and relationships to wildfire, environment, and plant communities in the Blue Mountains of the Inland Northwest, USA.” *Applied Vegetation Science*, no. May: 1–13. https://doi.org/10.1111/avsc.12511.

Turnbull, Laura, Bradford P. Wilcox, J. Benlap, S. Ravi, P. D’Odorico, D. Childers, W. Gwenzi, et al. 2012. “Understanding the role of ecohydrological feedbacks in ecosystem state change in drylands.” *Ecohydrology* 5: 174–83. https://doi.org/10.1002/eco.

U.S. Department of Interior, Bureau of Land Management (BLM). 2018. “BLM AIM TerrADat TerrestrialAIM point.” BLM National Operations Center: BLM. https://gis.blm.gov/AIMdownload/layerpackages/BLM_AIM_Terrestrial.lpk.

Wilcox, Bradford P., Laura Turnbull, Michael H. Young, C. Jason Williams, Sujith Ravi, Mark S. Seyfried, David R. Bowling, et al. 2012. “Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts Bradford.” *Ecohydrology* 5: 160–73. https://doi.org/10.1002/eco.247.

Williamson, Matthew A., Erica Fleishman, Ralph C. Mac Nally, Jeanne C. Chambers, Bethany A. Bradley, David S. Dobkin, David I. Board, et al. 2019. “Fire, livestock grazing, topography, and precipitation affect occurrence and prevalence of cheatgrass (Bromus tectorum) in the central Great Basin, USA.” *Biological Invasions* 22 (2): 663–80. https://doi.org/10.1007/s10530-019-02120-8.

Wright, Boyd R., Peter K. Latz, and A. F. Zuur. 2016. “Fire severity mediates seedling recruitment patterns in slender mulga (Acacia aptaneura), a fire-sensitive Australian desert shrub with heat-stimulated germination.” *Plant Ecology* 217 (6): 789–800. https://doi.org/10.1007/s11258-015-0550-0.

Young, James A ., and Raymond A . Evans. 1975. “Germinability of Seed Reserves in a Big Sagebrush Community.” *Weed Science* 23 (5): 358–64. http://www.jstor.org/stable/4042337.

Zuur, A. F., E. N. Leno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer. https://doi.org/10.1007/978-0-387-87458-6.

Figure Captions

Figure 1. On the left side of (a), burn severity (dNBR) as predicted by total vegetation cover (TVC; the sum of live and dead, shrub and herbaceous cover). On the right, burn severity is predicted by modelled TVC. Panel b shows the modelled occurrence of germinable seeds for all species found at more than one location along a gradient of burn severity, after accounting for soil depth, aspect, elevation and pre-fire diversity. Black line is the mean prediction, each colored line represents one posterior sample. In (c), fuel connectivity three years post-fire is modelled by seedbank composition, elevation and pre-fire aboveground species richness. In (d) shannon-Weaver diversity index of the aboveground, post-fire community composition, was negatively affected by fuel connectivity after accounting for elevation. For a, c and d, lines are the fitted partial effects, points are the partial residuals, and dotted lines are the 95% confidence intervals. $p < 0.05$ for black lines, $p > 0.05$ for grey lines.

Figure 2. Visual illustration of the relationship between fuel connectivity and burn severity. On the left, panel a shows the intershrub space invaded by annual grasses. The photo in panel b was taken in the exact same place two weeks later, days after all of the biomass was consumed by the fire. Panel C is a closeup of the soil surface, showing in more detail how the litter was also almost completely consumed by the fire. On the right, the photos in panels d and e were on opposite sides of a fire line in an area that had minimal annual grass invasion over a broad area, and thus lower fuel connectivity. Note the remaining plants and stumps in panel e and the presence of only partially consumed litter in panel f.

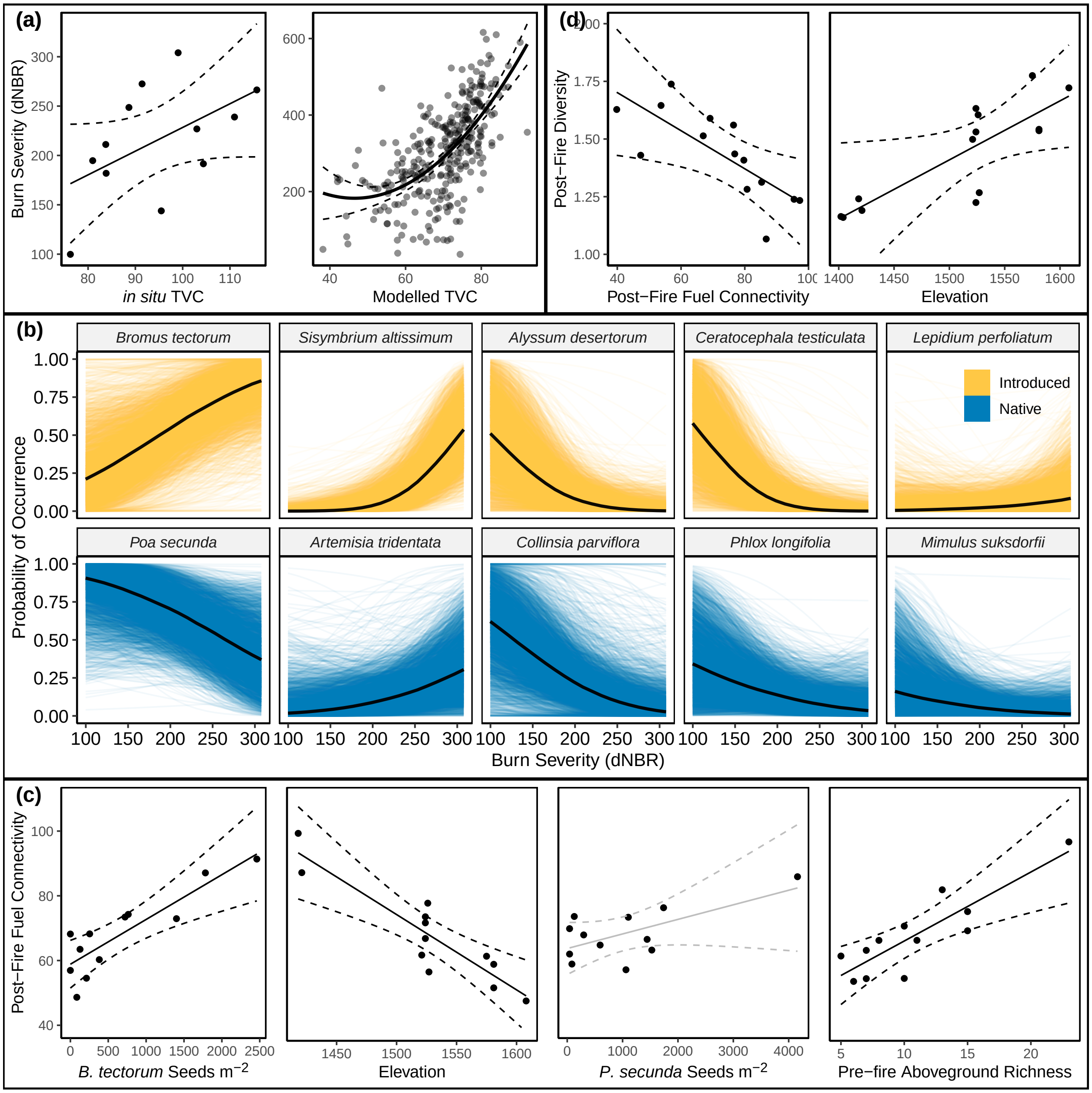
(a)
Burn Severity (dNBR)
100
150
200
250
300
80
90
100
110
in situ TVC
200
400
600
40
60
80
Modelled TVC
(d)
Post−Fire Diversity
1.00
1.25
1.50
1.75
2.00
40
60
80
100
Post−Fire Fuel Connectivity
1400
1450
1500
1550
1600
Elevation
(b)
Bromus tectorum
Sisymbrium altissimum
Alyssum desertorum
Ceratocephala testiculata
Lepidium perfoliatum
Poa secunda
Artemisia tridentata
Collinsia parviflora
Phlox longifolia
Mimulus suksdorfii
Introduced
Native
Probability of Occurrence
0.00
0.25
0.50
0.75
1.00
100
150
200
250
300
Burn Severity (dNBR)
(c)
Post−Fire Fuel Connectivity
40
60
80
100
0
500
1000
1500
2000
2500
B. tectorum Seeds m^{-2}
1450
1500
1550
1600
Elevation
0
1000
2000
3000
4000
P. secunda Seeds m^{-2}
5
10
15
20
Pre−fire Aboveground Richness

Figure 1: .

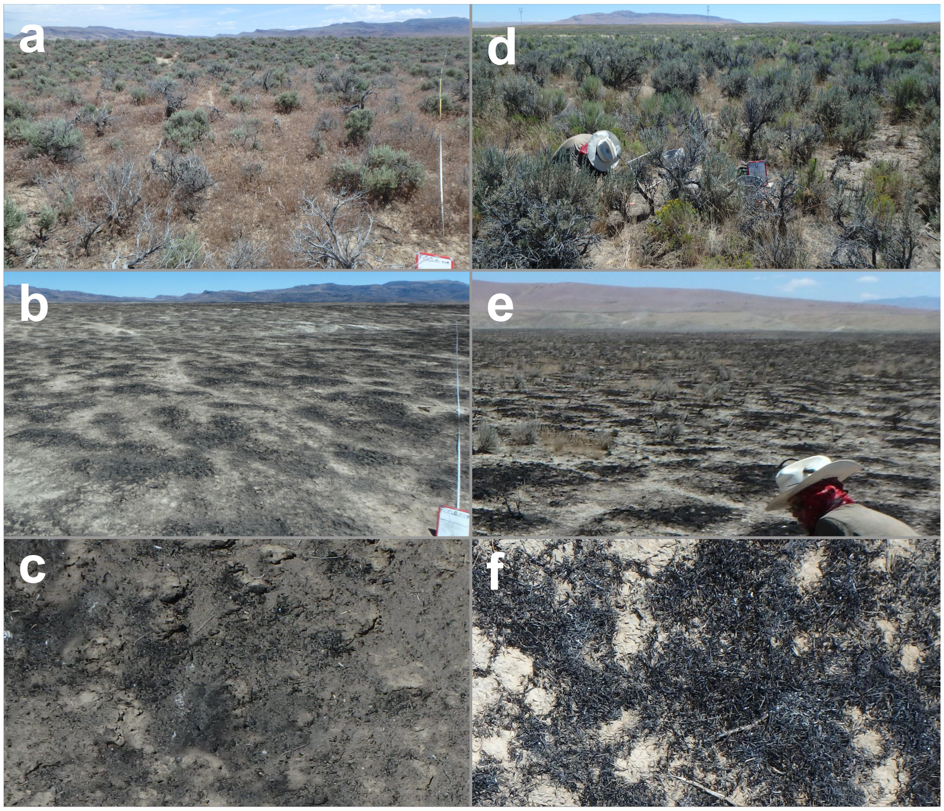

Figure 2: .