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Overcoming an "irreversible" threshold: A 15-year fire experiment

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Abstract
A key pursuit in contemporary ecology is to differentiate regime shifts that are truly irreversible from those that are hysteretic. Many ecological regime shifts have been labeled as irreversible without exploring the full range of variability in stabilizing feedbacks that have the potential to drive an ecological regime shift back towards a desirable ecological regime. Removing fire from grasslands can drive a regime shift to juniper woodlands that cannot be reversed using typical fire frequency and intensity thresholds, and has thus been considered irreversible. This study uses a unique, long-term experimental fire landscape co-dominated by grassland and closed-canopy juniper woodland to determine whether extreme fire can shift a juniper woodland regime back to grassland dominance using aboveground herbaceous biomass as an indicator of regime identity. We use a space-for-time substitute to quantify herbaceous biomass following extreme fire in juniper woodland up to 15 years post-fire and compare these with (i) 15 years of adjacent grassland recovery post-fire,

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(ii) unburned closed-canopy juniper woodland reference sites and (iii) unburned grassland reference sites. Our results show grassland dominance rapidly emerges following fires that operate above typical fire intensity thresholds, indicating that grassland-juniper woodlands regimes are hysteretic rather than irreversible. One year following fire, total herbaceous biomass in burned juniper stands was comparable to grasslands sites, having increased from 5 ± 3 g m^{-2} to 142 ± 42 g m^{-2} (+2785 ± 812 percent). Herbaceous dominance in juniper stands continued to persist 15-years after initial treatment, reaching a maximum of 337 ± 42 g m^{-2} eight years post-fire. In juniper encroached grasslands, fires that operate above typical fire intensity thresholds can provide an effective method to reverse juniper woodland regime shifts. This has major implications for regions where juniper encroachment threatens rancher-based economies and grassland biodiversity and provides an example of how to operationalize resilience theory to disentangle irreversible thresholds from hysteretic system behavior.

Keywords: Threshold, Regime shift, Hysteresis, Disturbance, Woody plant encroachment, Invasion

1. Introduction

With increasing occurrence of ecological regime shifts across the globe (Rocha et al., 2015), reversing undesirable regime shifts to restore a past ecological regime is a primary objective for restoration (Standish et al., 2014; Wonkka et al., 2016). Yet, many regime shifts have been labeled as irreversible when the re-establishment of the initial regime's stabilizing feedbacks fail to restore the system to its past configuration (Briske et al., 2006; Crépin et al., 2012; D'Odorico et al., 2012; Kinzig et al., 2006; Pardini et al., 2010). For instance, removing low intensity fire from a grassland regime is associated with an ecological regime shift from grassland to woody plant dominance (Briggs et al., 2005; Engle et al., 2008). However, reintroduction of low intensity fire is unable to reverse this regime shift, leading to claims that the regime shift is irreversible (Twidwell et al., 2013b). Labeling a threshold as irreversible can greatly lower the perceived ecosystem service value of a given system, leading to de-prioritization of ecological restoration investments (Carpenter et al., 1999; Hobbs and Harris, 2001).

Past efforts to reintroduce stabilizing feedbacks of a fire-dependent ecological regime often focus on a limited range of variability in frequency and intensity (Twidwell et al., 2020). This can make it difficult to deduce whether regimes shifts are truly irreversible or simply

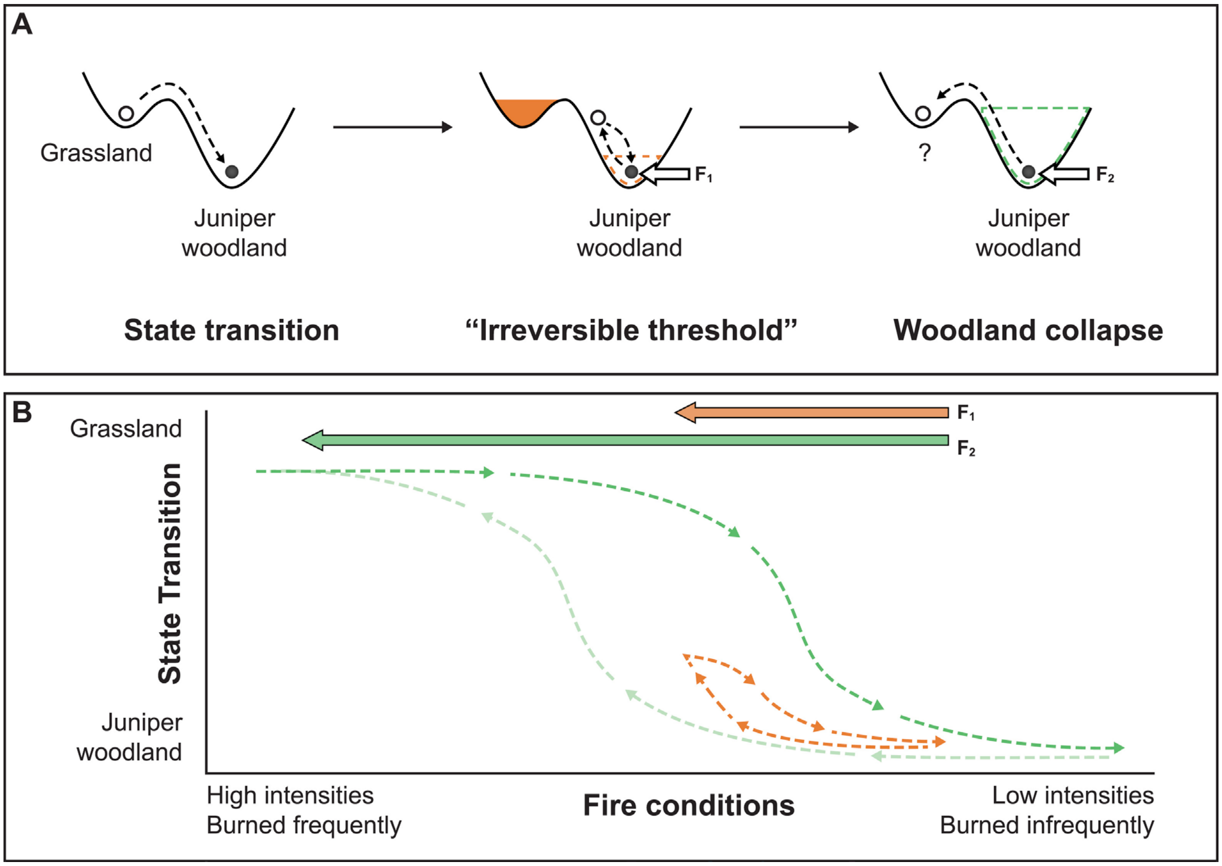

Fig. 1. Conceptual framework used to differentiate between state transitions that are truly irreversible versus those that are hysteretic in experimental restoration of grassland from an alternative juniper woodland state (adapted from Twidwell et al., 2020). Fire studies exploring a limited range of experimental fire conditions, such as those conditions that occurred prior to a transition, have the potential to misidentify a system as "irreversible" compared to studies testing for the occurrence of hysteretic system behavior using a broader array of experimental conditions (A). Distinguishing irreversibility from hysteresis requires scientific investigations that explore a greater range of experimental forcing (denoted as F) and the potential to overcome the resilience of the new juniper woodland state (B).

hysteretic (**Fig. 1**). A system with alternative ecological regimes is referred to as exhibiting some degree of hysteresis when the "path out" differs from the "path back" (Angeler and Allen, 2016; Holling, 1973). In contrast, an irreversible threshold assumes that there is no "path back" and a hysteretic loop does not exist (Folke et al., 2004; Scheffer and Carpenter, 2003). Hysteretic responses indicate that management need only explore a greater range of variability in stabilizing feedbacks to drive a regime shift to a past ecological regime. Thus, the full range of potential variability in the stabilizing feedbacks must be explored in order to distinguish irreversible versus hysteretic system behavior (Collins et al., 2021; Twidwell et al., 2020).

Grass-tree transitions have been hypothesized to be irreversible with fire alone in the Great Plains of North America (Ansley and Wiedemann, 2008; Briggs et al., 2002; Fuhlendorf et al., 1996). Studies that examined the reintroduction of low intensity fires consistent with historical fire return intervals in grasslands (e.g. every 3 years in tallgrass prairie) were not able to reverse the juniper woodland state (Engle and Kulbeth, 1992; Owensby et al., 1973). Multiple additional experiments show an inability to reverse juniper woodland with fire treatments in rangelands (Engle and Stritzke, 1995; Noel and Fowler, 2007; Ortmann et al., 2012), prompting the general "irreversibility hypothesis". The implication that a regime shift from grassland to juniper woodland is irreversible means that costly post-fire interventions, such as mechanical removal, are requisite for a return to the grassland regime (Twidwell et al., 2013a).

It is possible that the "irreversible" threshold in grassland-juniper woodland regime shifts represents sociopolitical constraints on management rather than a purely ecological threshold (Twidwell et al., 2020). A positive feedback loop limits the accumulation of biomass following a grassland to juniper woodland regime shift, limiting the occurrence and intensity of surface fires. However, fires that operate above typical fire intensity ranges used in management can surpass critical tree mortality thresholds, driving tree cover reduction (Smit et al., 2016; Twidwell et al., 2013b; Williams et al., 1999). It is unclear if and how grassland productivity emerges following these extreme fire events. Consistent with seeding programs in the western United States following extreme fire (fires that exhibit rapid and erratic changes in fire behavior and cause rapid and sudden changes in the structure and function of ecological systems; Twidwell et al., 2016), costly seeding interventions (e.g. over $37.5 M spent in 2017 (USDI BLM, 2018); in juniper woodlands following stand-consuming fire are implemented due to concerns over lack of grassland resurgence (Fernández et al., 2012; Grant-Hoffman et al., 2018). Large-scale assessments of the impacts of wildfire on grasslands in the Great Plains indicate rapid recovery of herbaceous cover following fire (Donovan et al., 2020); however, links between grassland and herbaceous biomass recovery following extreme fire in the juniper woodland state have yet to be investigated.

In this study, we assess whether the grassland-juniper woodland regime shift is irreversible or hysteretic by tracking herbaceous resurgence following stand-consuming extreme fire in juniper woodlands. We utilize a unique experimental landscape in the Loess Canyons of Nebraska that is co-dominated by grassland and closed-canopy juniper woodlands. A series of extreme fires in juniper woodlands have been implemented across the landscape for the last 15 years targeting high density juniper stands. We used a space-for-time substitution to quantify herbaceous resurgence following extreme fire in the juniper woodland state. We compare these estimates to herbaceous biomass measures from burned grassland sites adjacent to burned juniper woodlands, along with unburned closed-canopy juniper woodland and unburned grassland sites (to represent undisturbed site conditions within each ecological regime). We expect one of the following three potential outcomes: (1) grasslands re-emerge following extreme fire in juniper woodland matching adjacent grassland biomass and indicating hysteretic system behavior, (2) juniper woodlands rapidly re-establish dominance following extreme fire, indicating a potential irreversible threshold and long-term absence of herbaceous biomass similar to unburned juniper woodlands, or (3) a novel ecological state emerges that was not present previously (e.g. a shift in functional group dominance), indicating a potential irreversible threshold.

2. Methods

2.1. Study site

The Loess Canyons Experimental Fire Landscape is a unique, long-term ecoregion-level fire experiment where a series of extreme fire events have been applied nearly every year, for the last 15 years (Table S1; **Fig. 2**). This 72,843 ha experimental landscape resulted from a partnership between private land stewards in the Loess Canyon Rangeland Alliance (LCRA) and the Institute of Agriculture and Natural Resources at the University of Nebraska. The LCRA is a prescribed burn cooperative (Twidwell et al., 2013c) operating as a coalition of

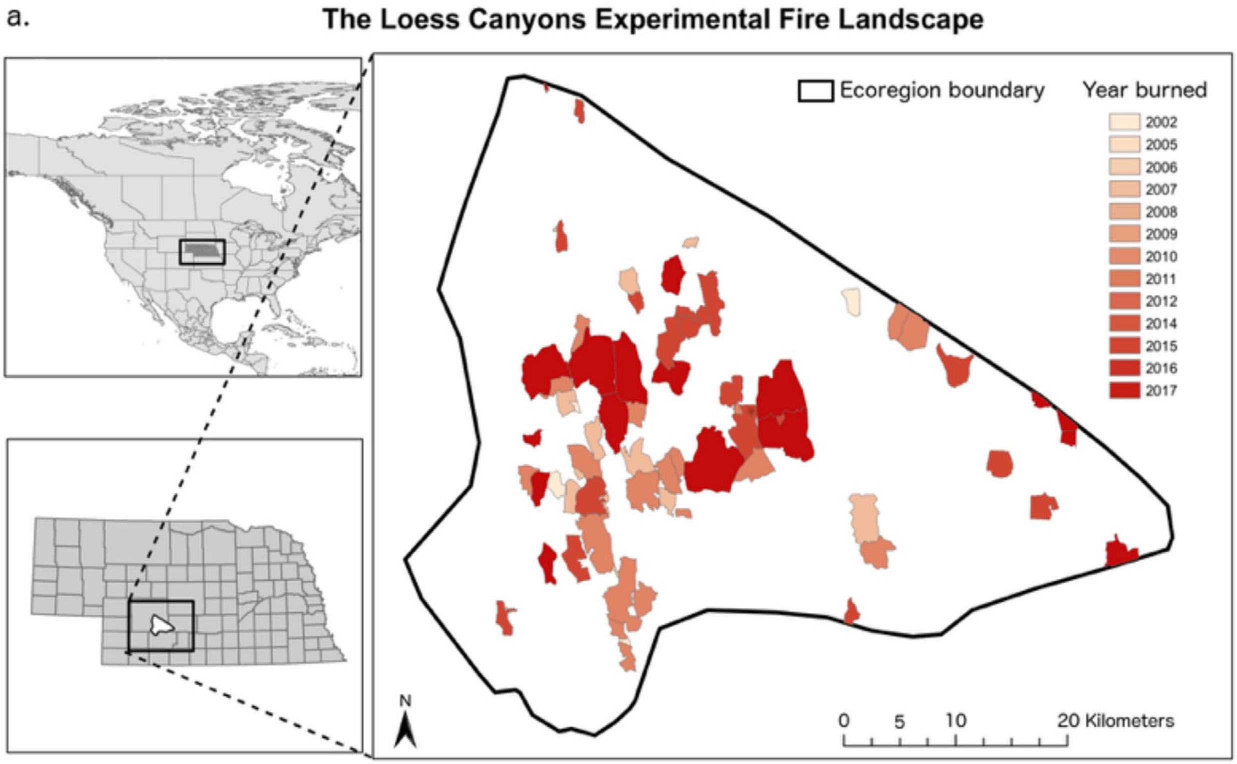

Fig. 2. The Loess Canyons Experimental Fire Landscape with maps of 15-years of extreme fire treatments.

landowners with a shared goal of restoring fire to the Loess Canyons ecoregion. Fuels are manipulated and weather conditions are targeted to consistently implement fires capable of operating above known juniper mortality thresholds (Twidwell et al., 2013b), offering a unique opportunity to investigate the complex adaptive responses to the implementation of extreme fires (Figure S1) as a fundamental driver of large-scale ecosystem change.

The Loess Canyons ecoregion is located in southcentral Nebraska, USA and spans 121,405 ha. The ecoregion has been identified among conservation groups as one of the state's most biologically unique landscapes, supporting at-risk species including the previously Federally Endangered American burying beetle (Walker Jr and Hoback, 2007), at-risk ecological communities, and a broad array of common species (Schneider et al., 2012). This ecoregion consists of steep loess hills and canyons dominated by mixed-grass prairie and scattered cropland. Eastern redcedar (*Juniperus virginiana* L.) has encroached throughout the ecoregion and transformed 19.6% of the Loess Canyons from perennial grassland dominance to juniper woodland (Roberts et al., 2018). Reductions in aboveground herbaceous biomass following a shift from grassland to closed-canopy juniper woodland in the Loess Canyon Experimental Fire Landscape are similar to those observed in previous studies (Briggs et al., 2002; Fuhlendorf et al., 2008). Elevation ranges from 781 to 989 m above sea level. Precipitation in this region is unimodal with an average annual precipitation of 550 mm. Mean annual temperature is 9.8 °C with monthly average temperatures ranging from −11.1 °C in January to 31.8 °C in July (Arguez et al., 2012).

2.2. Sampling and analysis

Because extreme fires were applied during different years across the Loess Canyons landscape, a space-for-time substitute was implemented to quantify aboveground herbaceous biomass response following extreme fire in the juniper woodland state. Twenty burn units were selected (Table S1) ranging from 0 to 15 years since extreme prescribed fire treatments (Fig. 2).

In landscapes co-dominated by grassland and juniper woodland regimes, extreme fire is capable of surpassing the fireline intensity-juniper mortality threshold, causing 100% juniper mortality (Twidwell et al., 2013b). Accordingly, areas within burn units (all co-dominated by grassland and juniper woodland) that experienced extreme fire were characterized by 100% juniper mortality with little to no crown foliage and tree skeletons following fire. One burned juniper woodland stand was randomly selected within each burn unit for biomass sampling. Juniper woodland stands were defined as closed-canopy stands ≥30 m in diameter. To limit variability among burn units, we avoided selecting juniper woodland stands in canyon bottoms or canyons tops and focused on patches that occurred on physically accessible slopes of similar topography.

Twenty burned grassland sites (≥30 m diameter) adjacent to each burned juniper stand were selected to track grassland re-emergence following fire. Five unburned closed-canopy juniper woodland stands and 5 unburned grassland sites were also selected to determine baseline herbaceous biomass across undisturbed grassland and juniper woodland regimes. Unburned grassland sites served as a proxy for aboveground herbaceous biomass prior to the transformation of grassland to closed-canopy juniper woodland. Unburned, closed-canopy juniper woodland stands served as a proxy for pre-existing juniper woodland conditions.

Aboveground herbaceous biomass of graminoid and forb functional groups were harvested underneath each burned juniper woodland stand, unburned juniper woodland stand, unburned grassland, and burned grassland sites (50 sites) using 10 randomly placed 0.1 m^2 plots (total of 500 plots). To avoid edge effects and to ensure representative biomass samples, sampling was not conducted within the outermost 1 m of each juniper stand and grassland site. All sampling occurred in 2017 during June and July. Samples were separated into functional groups (graminoid and forb) and dried in a drying oven at 70°C. Dry weights were recorded per functional group.

Mean total herbaceous biomass, mean total forb biomass, and mean total graminoid biomass in both burned juniper woodland and adjacent burned grassland sites within each burn unit were calculated. Thereafter, means relative to time-since-fire to identify temporal trends in herbaceous response to fire were plotted. Non-parametric local regression (loess) smoothing curves were used to visualize trends in biomass relative to time-since-fire. Mean total biomass in burned juniper woodland sites were compared to unburned juniper woodland and grassland reference sites to determine whether post-fire herbaceous biomass was more similar to one ecological regime or another. We also compared the relative mean total biomass of forbs versus total graminoids in order to detect shifts in herbaceous functional group dominance.

3. Results

Mean total herbaceous biomass in juniper woodlands burned with extreme fire was consistently higher than unburned juniper woodlands (**Fig. 3**; $t = -15.415$, $p < 0.0001$), whereas burned and unburned grassland sites were similar (Fig. 3; $t = -1.4916$, $p = 0.137$). One-year post-fire, mean herbaceous biomass had reached levels similar to that recorded in burned and unburned grassland sites. Total herbaceous

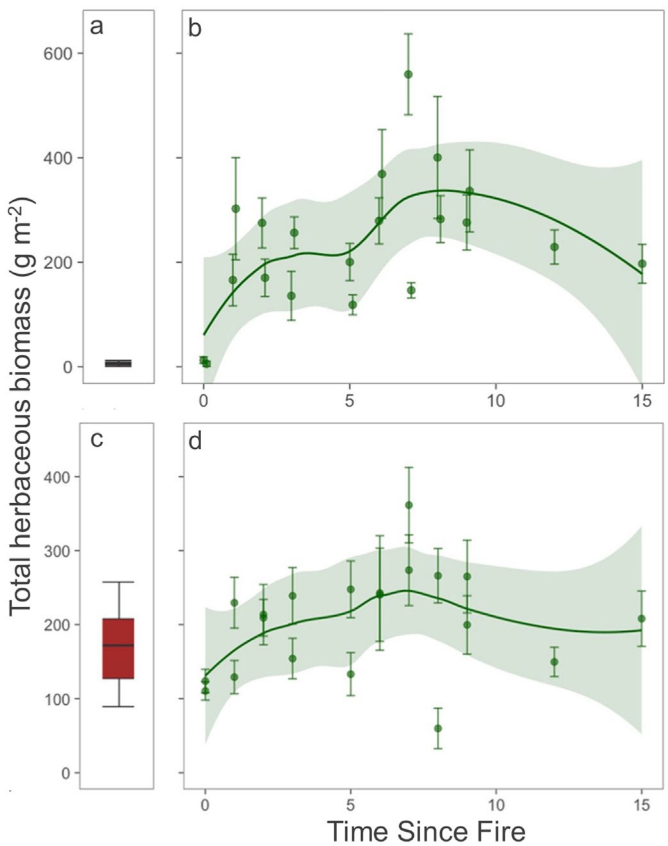

Fig. 3. Total aboveground herbaceous biomass in (a) unburned juniper woodland (b) burned juniper woodland multiple years post-fire, (c) unburned grassland, and (d) burned grassland multiple years post-fire. Error bars represent standard error. A loess smoothing model was used to assist with trend visualization. Light green shading represents 95% confidence intervals of the model.

biomass in juniper stands increased from 5 ± 3 g m^{-2} to 142 ± 42 g m^{-2} (+2785% ± 812) one year after fire (Fig. 3). Herbaceous dominance persisted after fire treatment, reaching a maximum of 337 ± 42 g m^{-2} eight years after extreme fire (an increase of 6625% ± 828 compared to unburned juniper stands).

Graminoids dominated both burned and unburned grassland sites across all times since fire, whereas forb abundance was consistently low in both burned and unburned grasslands (**Fig. 4**b, d). In contrast, graminoid and forb biomass differed between burned and unburned juniper stands (Fig. 4a, c). Increased forb biomass immediately following fire was owed to juniper mortality (Fig. 4c). Total forb biomass

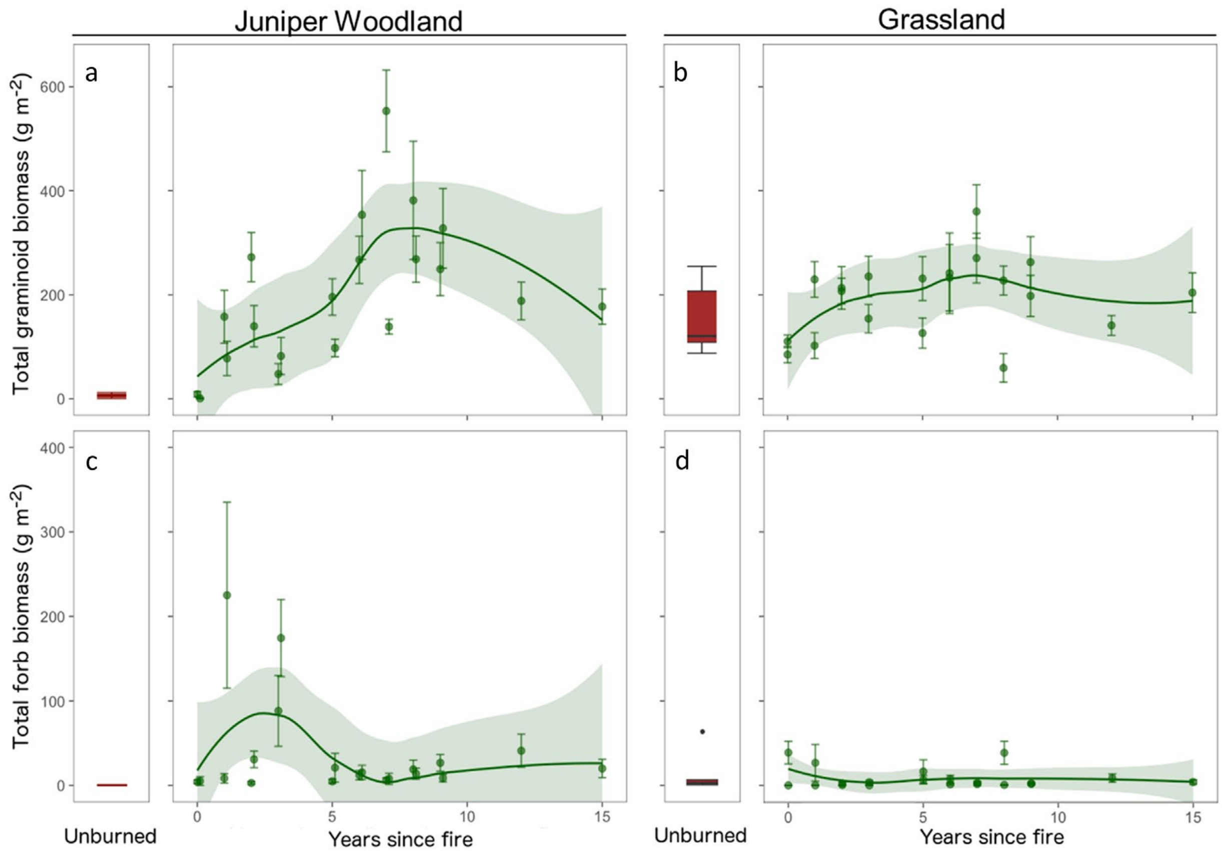

Fig. 4. Aboveground graminoid biomass and total forb biomass in juniper woodland and grassland sites. Each point represents the average total biomass collected within an individual burn unit. A loess smoothing model was used to assist with trend visualization. Error bars represent standard error. Light green shading represents 95% confidence intervals deduced from the model.

peaked one-year post-fire (225.07 ± 348.07 g m^{-2}) but was replaced by graminoid biomass three years following fire, resembling reference grassland conditions (Fig. 4a, c).

4. Discussion

Grassland-juniper woodland regime shifts are hysteretic rather than irreversible, based on measures of aboveground productivity as an indicator of regime identity. Our study shows the capacity for grassland dominance to emerge rapidly following the occurrence of fires that operate outside of typical prescribed fire constraints (for prescribed fire constraints, refer to Twidwell et al., 2016b; Weir, 2009). The regime shift from grassland to juniper woodland was hypothesized to be irreversible following the reintroduction of relatively low intensity fires consistent with historical fire return intervals (Ansley and Wiedemann, 2008; Briggs et al., 2002; Fuhlendorf et al., 1996). Manipulation of fire frequency alone has yet to restore productivity in grasslands following conversion to woody plant dominance in North American prairies (Ratajczak et al., 2014). However, introducing a greater range of variability in fire intensity has consistently resulted in a shift from juniper woodland to grassland in various locales of the Great Plains (Twidwell et al., 2009, 2013c, 2019) and may provide opportunities elsewhere (e.g. Govender et al., 2006; Murphy et al., 2015) to distinguish between regime shifts that are hysteretic versus actually irreversible with fire alone.

Humans have greatly reduced the historic range of variability in disturbance regimes in an effort to reduce uncertainty and increase stability in natural systems (Archibald, 2016; Holling and Meffe, 1996; Twidwell et al., 2020). Thus, a mismatch between contemporary variability in disturbance regimes and historic ranges of variability can lead to misconceived irreversible thresholds. A challenge for ecosystem managers, researchers, and policymakers is identifying the magnitude and type of disturbance required to overcome the resilience of an undesired state (Palmer et al., 2016). In systems with alternative stable states, inducing a “path back” to the original state may require a completely different type or magnitude of disturbance that goes beyond that which occurred during the “path out” (Angeler and Allen, 2016; Holling, 1973; Suding and Hobbs, 2009). Experimental design should consider the full range of variability in stabilizing feedbacks and identify the potential to induce a “path back” following an undesired regime shift. Identifying thresholds that exhibit hysteresis rather than irreversibility may require long-term monitoring and re-establishing historic ranges of variability in disturbances over time and space (Bestelmeyer et al., 2011; Briske et al., 2010).

In this study, the rapid re-emergence of herbaceous vegetation following fire and reduction in juniper was owed in part to the availability of native grassland propagules and seed availability in grassland adjacent to burned juniper stands (Allen et al., 2016). In such cases, post-fire seeding treatments are likely unnecessary in the absence of exotic invasive herbaceous species. Our results echo previous studies that indicate that proposed post-fire seeding expenditures (Hardegree et al., 2016; Pyke et al., 2013) may be unnecessary (Arterburn et al., 2018; Donovan et al., 2020). However, without the reintroduction of critical grassland feedbacks through follow-up management (e.g. repeat fires or mechanical removal) in burned juniper stands, those areas are likely to return to juniper woodland due to the availability of nearby propagule sources (Donovan et al., 2018).

No evidence was found to support the emergence of a novel herbaceous ecological regime (e.g. forb dominance) following extreme fire in juniper woodland. A novel ecosystem occurs when the composition and/or function of an ecosystem differs from those that prevailed historically and is capable of self-organizing and persisting without intensive human intervention (Hobbs et al., 2013; Mascaro et al., 2013). On the contrary, many novel ecosystems are likely to be the result of the simplification of disturbance regimes and the removal of extreme events (Holling and Meffe, 1996; Twidwell et al., 2016a).

This study demonstrates how to operationalize resilience theory for grassland restoration (Fig. 1). A conversion of grassland to woodland is associated with detrimental responses associated with an array of complex social and ecological drivers in grassland systems (Archer et al., 2017; Wilcox et al., 2018). Based on our expectations, this long-term experimental fire landscape revealed the capacity for grassland dominance to rapidly re-emerge following fires operating above juniper mortality thresholds, indicating that grasslands in transition to juniper dominance exhibit hysteresis rather than an irreversible threshold. Similar investigations elsewhere in the world may shed new light into fire's role as a driver of complex vegetation change and the potential for ecological restoration to navigate alternative ecological states. Future research efforts should aim to move past heuristic threshold models and instead strive to explore the full range of potential variability in system drivers across spatial and temporal scales before ruling out hysteretic regime shifts.

Author contributions Christine H. Bielski, Conceptualization, Data curation; Methodology, Formal analysis, Writing – original draft, Writing – review & editing, Rheinhardt Scholtz, Writing – review & editing, Victoria M. Donovan, Writing – review & editing, Craig R. Allen, Writing – original draft, Funding acquisition; Dirac Twidwell, Writing – review & editing, Conceptualization, Data curation; Methodology, Formal analysis, Funding acquisition; Writing – original draft

Declaration of competing interest The authors declare no competing interests.

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Appendix A. Supplementary data Supplementary data to this article follows the References.

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Supplementary Material

Tables

Table S1. Summary of extreme fires conducted in the Loess Canyons Experimental Fire Landscape. Figure S1 shows an example of extreme fire behavior conducted by the LCRA.

Year	Total No. of extreme fires	Total acres burned	Average fire size
2002	4	1,643	411
2005	1	66	66
2006	2	2,176	1,088
2007	1	474	474
2008	4	1,154	289
2009	6	3,262	544
2010	7	4,993	713
2011	5	4,155	831
2012	6	4,027	671
2014	12	7,666	639
2015	5	3,832	766
2016	9	11,101	1,233
2017	5	4,004	801
Total	67	48,554	656

Figures

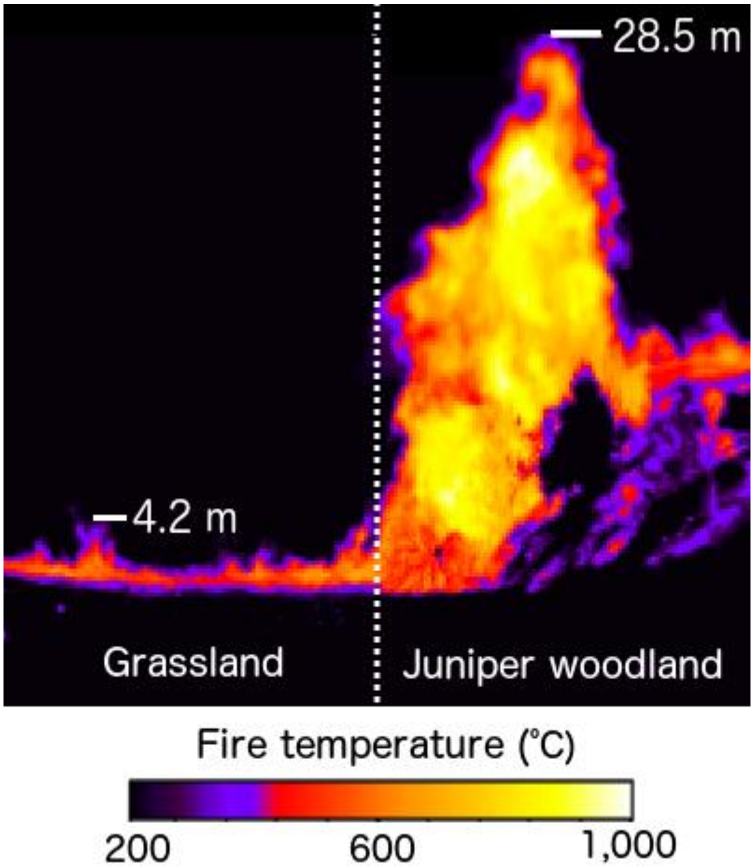

Figure S1. Visualization of an extreme fire treatment showing differences in flame lengths and fire temperatures in a grassland fire vs. a juniper woodland fire.