Research article

Woody plant reinvasion shortens the lifespan of grassland restoration treatments

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Highlights

- Woody plant reinvasion is rapid and greatly outpaces the initial invasion process.

- Restored grasslands are more vulnerable to transitioning back to woodland.

- Follow-up management is needed to extend the lifespan of restoration treatments.

- Management frameworks are needed that explicitly account for reinvasion.

Abstract

An important question in restoration ecology is whether restored ecological regimes are more vulnerable to transitions back to a degraded state. In woody-invaded grasslands, high-intensity fire can collapse woody plant communities and induce a shift back to a grass-dominated regime. Yet, legacies from woody-dominated regimes often persist and it remains unclear whether restored regimes are at heightened vulnerability to reinvasion. In this study, we utilize a 17-year history of fire-based restoration in Nebraska's Loess Canyons Experimental Landscape to determine whether restored grassland regimes experience faster rates of *Juniperus virginiana* (eastern redcedar) reinvasion compared to the initial invasion process in adjacent grasslands. In addition, we examine whether reinvasion and invasion patterns are clearly differentiated based on former ecotonal boundaries between grassland and woodland regimes. Our results show that *J. virginiana* reinvasion of restored grassland regimes outpaced the initial invasion process in adjacent grasslands, providing evidence that restored grassland regimes are more vulnerable to transitions back to woody dominance. *J. virginiana* seedlings established sooner and increased faster in density and cover during reinvasion compared to the initial invasion process. Seedlings established 1-year post-fire in restored grassland regimes compared to 14-years post-fire in adjacent grasslands that were >40m from the former grassland-woodland boundary. Reinvasion was initially easy to differentiate from invasion based on former ecotonal boundaries between grassland and woodland; however, reestablished juniper woodlands eventually began to expand into adjacent grasslands. Our findings demonstrate clear differences between reinvasion and invasion and highlight the need for management frameworks that explicitly account for reinvasion.
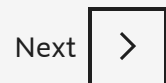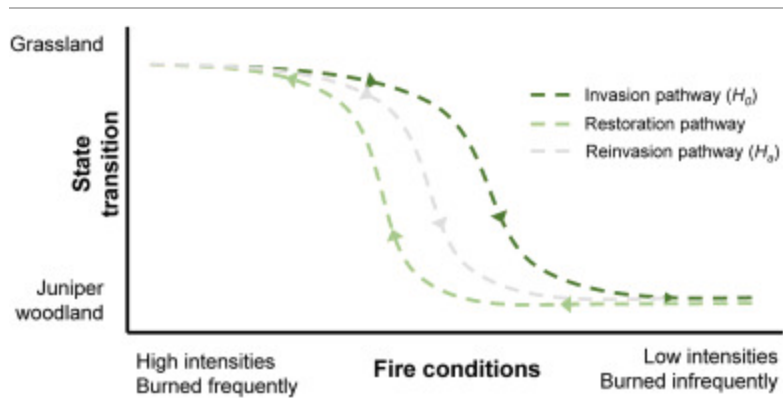
< Previous   Next >

Keywords

1. Introduction

With the global emphasis on ecosystem restoration, an important question is whether restored systems are more vulnerable to regime shifts back to a degraded state. Models of

hysteresis in restoration ecology consider degradation pathways, the 'path out', to differ from restoration pathways, the 'path back', but do not distinguish between subsequent paths out and back (Scheffer et al., 2001; Suding et al., 2004). This implies an expectation that restored regimes behave in a way that is like the initial regime, or that restored regimes are equally vulnerable to regime shifts. However, there is potential for hysteretic responses in systems that have undergone or are undergoing restoration, particularly when legacies of past invasions persist (Banks et al., 2018). Restoration practitioners are particularly interested in this because such history-dependent responses could mean that restored systems, or those undergoing restoration, are more vulnerable to transitions back to a degraded state and therefore require a different set of management conditions for their maintenance.

Grassland-woodland regime shifts are a classic example of alternative states in restoration ecology (Archer and Predick, 2014; Scheffer et al., 2001; Suding et al., 2004; Twidwell et al., 2013b; Wilcox et al., 2018) and provide an ideal system for examining whether restored regimes exhibit history-dependent responses. Grassland regimes are maintained through fire-vegetation feedbacks characterized by high fire occurrence and intensity, while, woodland regimes are maintained by low fire occurrence and intensity (Fig. 1) (Bond et al., 2005; Ratajczak et al., 2014; Twidwell et al., 2013b). Woody plant invasion initiates a destabilizing feedback, whereby increased woody plant abundance decreases herbaceous fuels, which decreases fire frequency and reinforces a transition to woody dominance (Langevelde et al., 2003; Twidwell et al., 2013a). This transition has been shown to be hysteretic, in that the initial path from a grassland to a woodland regime differs from that of woodland back to grassland (Bielski et al., 2021; Collins et al., 2021). In particular, more extreme fire conditions are needed to shift the woodland regime back to grassland dominance, relative to what is needed to maintain grassland regimes and prevent transitions to woody dominance (Bielski et al., 2021; Twidwell et al., 2020). However, no studies have looked for hysteresis in the context of reinvasion following restoration of a grassland regime.

Fig. 1. Conceptual framework used to differentiate between the initial invasion pathway, the 'path out', the restoration pathway, the 'path back', and the reinvasion pathway, the 'path back out' for grassland transitions to juniper woodland, adapted from (Twidwell et al., 2020; Bielski et al., 2021). We hypothesize that the reinvasion process of restored grassland regimes exhibits a hysteretic response (H_a) due to invasion legacies in the restored system. Hysteresis occurs in grassland-juniper woodland systems when the ecological state of the system cannot be predicted by fire conditions alone but requires additional knowledge of the system's recent history.

There are several factors that could potentially drive a more rapid reinvasion pathway compared to the initial invasion process. During the invasion process in grasslands, increased abundance of woody plants alters ecosystem structure (Norris et al., 2001), species composition (Andersen and Steidl, 2019; Linneman and Palmer, 2006; Ratajczak et al., 2012), carbon and nitrogen cycling (McKinley and Blair, 2008), hydrological processes (Wilcox et al., 2022; Zou et al., 2018), soil microbial communities (Liang et al., 2017; Utaile et al., 2021; Zhao et al., 2022), and plant-soil feedbacks (Bennion and Ward, 2022). Following woody plant removal and recovery of herbaceous plants, some of these properties are expected to remain as invasion legacies that have potential to compromise restored grassland regimes, potentially leading to an accelerated reinvasion process. Similar to how information and material legacies assist in the recovery of ecosystems following disturbance (Franklin and MacMahon, 2000; Holling and Gunderson, 2002; Johnstone et al., 2016; Roberts et al., 2019), invasion legacies have been attributed to rapid reinvasion following initial control or eradication of an invasive species (Banks et al., 2018). In restored sagebrush steppe communities for example, *Juniperus occidentalis* quickly reinvaded from seed and seedlings left behind from juniper cutting treatments (Bates et al., 2005). Similar examples can be found in the mixed-grass prairie (Fogarty et al., 2021; Wonkka et al., 2016), alpine meadows (Halpern and Antos, 2021; Kremer et al., 2014), and oak savannas (Brudvig and

Asbjornsen, 2007). However, aside from anecdotal evidence that woody plant reinvasion follows a more rapid path, no direct comparisons with the initial invasion process have been made.

In this study, we examine whether grassland regimes restored from woody plant dominance experience a faster reinvasion process by *Juniperus virginiana* (eastern redcedar) relative to the initial invasion of nearby grasslands (Fig. 1). *J. virginiana* is a prolific native invader in North America's central Great Plains (Nackley et al., 2017; Simberloff et al., 2012). Human-mediated fire exclusion and widespread cultivation in grasslands have removed the natural barriers to this fire-sensitive species' proliferation and allowed *J. virginiana* to spread and dominate in grassland environments (Briggs et al., 2005; Engle et al., 2008). The Loess Canyons Experimental Landscape, located in the central Great Plains, has an extensive 17-year history of using prescribed fire to restore grasslands from *J. virginiana* dominance and provides a unique setting to compare invasion and reinvasion pathways. This landscape is co-dominated by grassland and juniper-woodland regimes (Fogarty et al., 2020). Since 2002, a series of fire treatments have been implemented as part of a regional effort to collapse juniper woodlands and restore grassland dominance (Bielski et al., 2021). This has resulted in a complex landscape where juniper woodland, grassland, and sites at various stages of (re)invasion are intermixed within a broader grassland matrix (Fig. 2). Previous research has documented juniper reinvasion following woodland collapse in this landscape and others (Ansley et al., 2006; Bates et al., 2005; Fogarty et al., 2021), but it remains unclear whether and how invasion and reinvasion pathways differ. Managers are especially interested in the potential for a distinct reinvasion pathway because this has direct implications on how to manage landscapes undergoing restoration.

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Fig. 2. Various stages of woody plant (re)invasion in the Loess Canyons Experimental Landscape, Nebraska, USA. Photo by Erin McCready.

We answer the following questions: 1) Are restored grassland regimes more vulnerable to transitions back to a juniper woodland regime (evidenced by faster rates of reinvasion following fire-induced woodland collapse), and if so, how does reinvasion compare with the initial invasion process? 2) Are patterns of juniper reinvasion vs invasion easily delineated on the landscape based on the location of past grassland-woodland boundaries? We answer these questions using a space-for-time substitution to quantify the rate of juniper reinvasion and invasion 17 years after high-intensity prescribed fires were used to collapse juniper woodlands embedded within a grassland ladndscape. In addition, we characterize unburned juniper woodland and unburned grassland sites to represent undisturbed conditions for woodland and grassland regimes. We hypothesize that reinvasion will occur at a faster rate compared to the initial invasion process in adjacent grasslands, evidenced by earlier seedling establishment, greater juniper densities, and earlier onset of exponential increases in juniper cover (Fig. 1). Regarding spatial patterns of (re)invasion, we hypothesize that juniper reinvasion and invasion will be clearly delineated based on past regime boundaries.

2. Methods

2.1. Study system

This study was conducted in the Loess Canyons Experimental Landscape located in central Nebraska, USA (Fig. 3). The Loess Canyons Experimental Landscape consists of a collection of privately-owned properties where high-intensity prescribed fire treatments are used as part of a regional effort to address *J. virginiana* invasion. This landscape encompasses a nearly contiguous 74,569 ha where scientists have partnered with prescribed burn associations (PBAs) and conservation practitioners to address land management challenges. Native vegetation communities are characterized by mixed-grass prairie. Little bluestem (*Schizachyrium scoparium*), sideoats grama (*Bouteloua curtipendula*), plains muhly (*Muhlenbergia cuspidata*), and Fendler threeawn (*Aristida purpurea* var. *longiseta*) are dominant grasses with subdominant species including big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), composite dropseed (*Sporobolus compositus* var. *compositus*), and sand dropseed (*Sporobolus cryptandrus*). Common forbs include dotted blazing star (*Liatris punctata*), white prairie clover (Dalea candida), and upright prairie coneflower (*Ratibida columnifera*). Soapweed yucca (*Yucca glauca*) is the most common shrub. Annual vegetation productivity ranges from 1121–3363 kg per ha (USDA-NRCS, 2019).

Topography in the region consists of steep loess hills and canyons (20–60% slope) with elevation ranging from 781 to 989 m above sea level. Soils are dominated by the Coly series and consist of very deep, well drained soils formed in loess (Soil Survey Staff). The climate is temperate with a mean annual temperature of 9.5 °C, monthly averages ranging from −3.4-23.4 °C, and a mean annual precipitation of 542 mm based on 30-year normals (1991–2020) (PRISM Climate Group, https://prism.oregonstate.edu)https://prism.oregonstate.edu ↗.
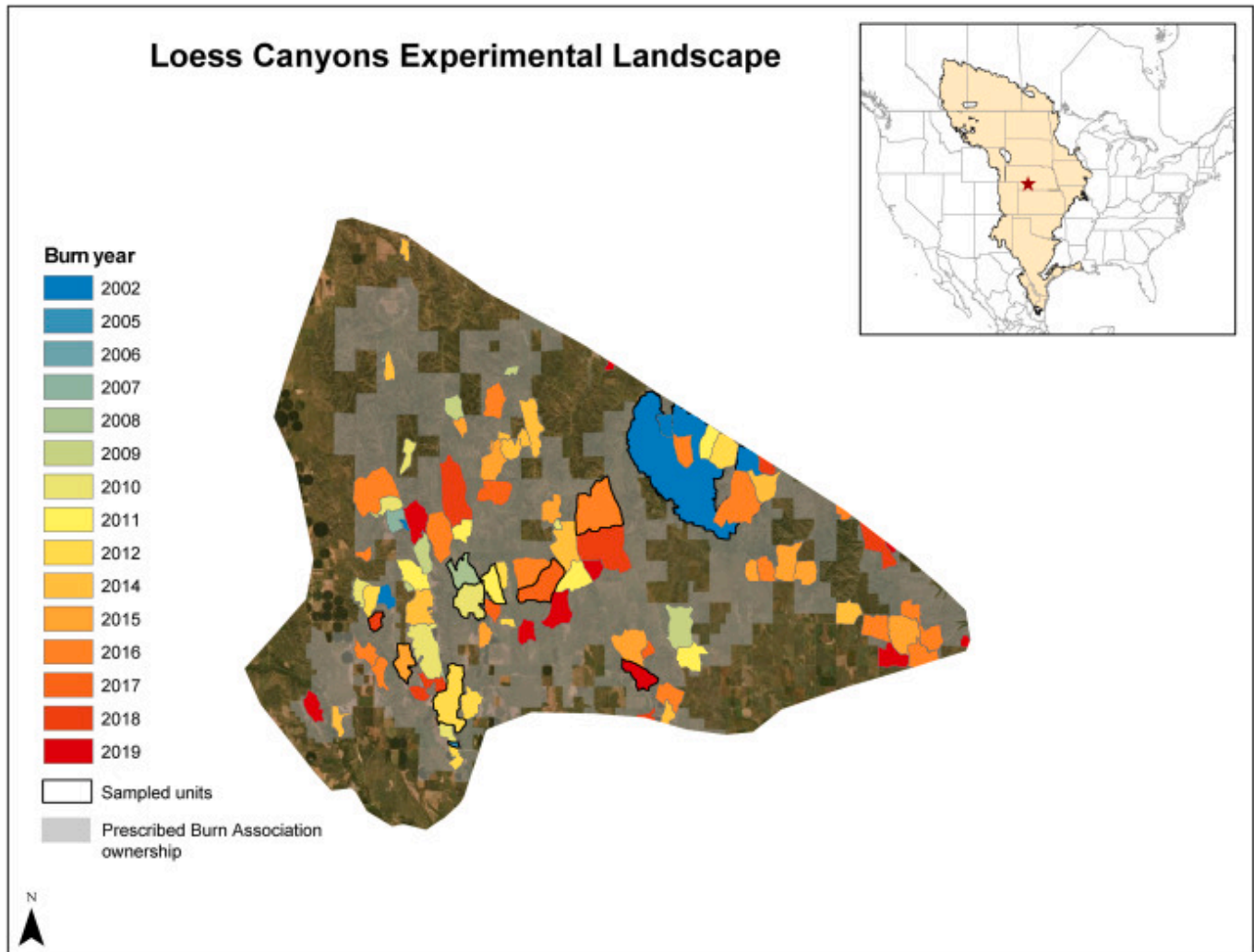
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Fig. 3. Seventeen-year fire history in the Loess Canyons Experimental Landscape (shaded gray) located in the Loess Canyons ecoregion of Nebraska, USA. Inset map shows the study site location (star) within North America's Great Plains grassland biome (in tan).

An estimated fire return interval of 6–10 years limited the distribution of *J. virginiana* in the Loess Canyons landscape prior to European settlement (Guyette et al., 2012). *J. virginiana* is a fire-sensitive, obligate seeder that is native to the Great Plains region. Prior to European settlement, frequent fires maintained *J. virginiana* as a rare species that was restricted to

rocky outcrops and steep riparian slopes where fire was infrequent (Twidwell et al., 2013). Human-mediated fire exclusion following European settlement has allowed *J. virginiana* to escape this natural barrier and consequently spread and dominate previously uninhabitable prairie ecosystems. Management efforts in the Loess Canyons Experimental Landscape seek to restore fire as a natural barrier to *J. virginiana's* proliferation.

Prescribed fire treatments in the Loess Canyons Experimental Landscape are implemented by rancher-led prescribed burn associations and target conditions necessary to collapse juniper woodlands. Prescribed burn associations are community-based coalitions where members pool resources and coordinate fire management across a network of properties (Twidwell et al., 2013b; Weir et al., 2016). The Loess Canyons Experimental Landscape consists of two prescribed burn associations, the Loess Canyons Rangeland Alliance operating in the western portion of the experimental landscape since 2002 and the Central Platte Rangeland Alliance operating in the eastern portion of the landscape since 2011. Based on a reconstruction of prescribed fire history with prescribed burn associations, a total of 124 fire treatments were implemented from 2002 to 2019, totaling 34,752 ha. Prescribed fire treatments are typically implemented in the spring and target weather and fuel conditions necessary to overcome juniper mortality thresholds (sensu Twidwell et al., 2013a). Desired fuel conditions are often achieved by stuffing cut juniper trees around the perimeter of juniper woodlands (locally referred to as *cut and stuff*; Crockford et al., 2017). Collapsed juniper woodland regimes are then allowed to reorganize without immediate intervention. Recovery of herbaceous plants typically occurs within 1 year of the prescribed fire and does not include reseeding (Bielski et al., 2021). As a result of these fire-based restoration efforts, grasslands in the Loess Canyons Experimental Landscape capture a wide range of time-since-fire and provide a long-term experimental setting to compare reinvasion and invasion dynamics.

2.2. Sampling and analysis

We used a space-for-time substitute to characterize *J. virginiana* (re)invasion 17 years following high-intensity prescribed fire. Eleven high severity fire treatments were selected for this study that ranged in size from 28-6464 ha. Fire treatments all had a similar effect on vegetation and consumed above-ground herbaceous biomass in grasslands and collapsed the juniper woodland regime (100% tree mortality within a patch) (Bielski et al., 2021). Sites used in this study did not receive further intervention (e.g., reseeding, or post-fire management of woody plants). The selected sites represented the full range of time-since-fire history in the Loess Canyons Experimental Landscape and ranged from 3 months to 17 years.

At each site, we sampled *J. virginiana* reinvasion and invasion of restored grassland regimes (collapsed woodland patches) and adjacent grasslands, respectively (Fig. 4). Sites were selected within individual fire treatments based on the following criteria: 1) prior to fire-based restoration treatments, woodland patches were dominated by mature *J. virginiana* (the final stage of invasion) and adjacent grassland patches were dominated by grasses and forbs with a low density of juvenile *J. virginiana* (the incipient stage of invasion); 2) a single fire treatment collapsed the juniper woodland patch (100% tree mortality within a patch) and consumed herbaceous biomass in adjacent grasslands; 3) grassland plant dominance recovered in the collapsed woodland patch and adjacent grassland following fire (Bielski et al., 2021); and 4) collapsed woodland patches and adjacent grasslands were each at least 30-m in diameter. We used a combination of remotely sensed imagery and field observations to confirm these criteria. For example, pre- and post-fire conditions were initially examined using imagery archives from Google Earth Pro and were then confirmed in the field based on the presence of burned *J. virginiana* skeletons. In addition to sampling burned sites, we also selected three unburned grassland and woodland patches to establish a reference point for undisturbed conditions for both grassland and woodland regimes.
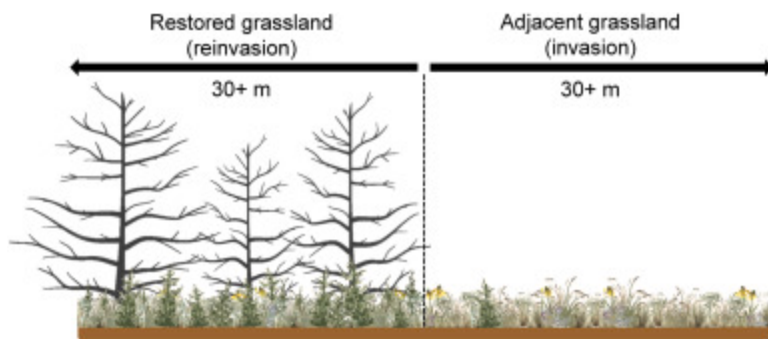
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Fig. 4. Schematic diagram of sites used to characterize juniper reinvasion of restored grassland regimes and invasion of adjacent grasslands following high-intensity fire treatments. Fire treatments collapsed juniper woodland regimes (100% tree mortality) and consumed herbaceous biomass in adjacent grasslands. Herbaceous biomass rapidly reestablished within collapsed woodland patches to conditions similar to adjacent grasslands.

J. virginiana (re)invasion metrics were sampled across 11 restored grassland regimes, 11 adjacent grasslands, 3 unburned woodlands, and 3 unburned adjacent grasslands. The 11 restored grassland regimes and adjacent grasslands were burned in one of the following years: 2002, 2005, 2008, 2010–2012, and 2015–2019. Sampling occurred in 5 x 5-m plots

centered along a transect that extended from the restored grassland regime into the adjacent grassland. Transects were terminated in the adjacent grassland when a maximum distance from restored grassland regimes was reached (considering the location of other restored grasslands) or when the end of a hillside was reached. Thus, transect length was variable between sites but contained a minimum of 6, 5 x 5-m plots in each patch type. We used the line intercept method with a minimum gap size of 0.1 m (i.e., canopy gaps <0.1 m were not recorded) to measure *J. virginiana* cover (Bonham, 2013). The line intercept method is well-suited for measuring cover at various stages of the invasion process, ranging from seedlings to mature trees. At sites with mature trees, a sighting pole was used to measure canopy gaps along the transect tape (Bonham, 2013). Density was determined for each plot based on the number of *J. virginiana* rooted within the plot. Seedlings obstructed by vegetation were detected by closely searching within the herbaceous layer within 1-m of ground level. *J. virginiana* height was measured to the nearest centimeter using a telescoping measuring pole. Field sampling occurred in July of 2019 and sampling effort was consistent across all sites.

We quantified the rate of reinvasion and invasion to determine whether restored grassland regimes exhibited a history-dependent, reinvasion response (Fig. 1). (Re)invasion rates were quantified based on relationships between *J. virginiana* density, cover, and height (response variables) and time since fire (independent variable). Response variables were calculated as patch-level averages using 5 x 5-m plots sampled within restored grassland regimes and adjacent grassland patches. We used a candidate set of four regression models (and a null model) to determine whether a linear, logarithmic (ln[x+1]), second-order, or third-order polynomial trend described the relationship between (re)invasion response variables and time since fire. These models contrasted three hypotheses related to the (re)invasion process. Specifically, 1) that (re)invasion variables (i.e., density, cover, and height) increase over time by a constant amount (linear trend), 2) that they increase at a constant rate (logarithmic trend), or 3) that reinvasion variables change along more complex curvilinear trends characterized by different rates of change over time (polynomial trend). A logarithmic transformation (ln[y+1]) was used for *J. virginiana* density in restored grassland regimes and cover in adjacent grasslands to meet normality and heteroscedasticity assumptions. Akaike's information criterion corrected for small sample sizes (AIC_c) was used to identify top models based on the lowest ΔAIC_c value (Burnham and Anderson, 2002). Because, AIC is a relative measure of support, we used R^2 values as a measure of the top model's fit.

We quantified (re)invasion variables along sampling transects that spanned the former grassland-woodland ecotonal boundary to assess spatial patterns of (re)invasion.

Specifically, we examined whether rates of juniper invasion in grasslands were greater near the former woodland boundary compared to areas farther from the boundary. This was done using linear bivariate interpolation, conducted with the 'interp' function in R package 'akima' (Akima and Gebhardt, 2022). This method of bivariate interpolation takes an irregular grid of x, y, and z points and generates a contour surface of z values based on the ACM 751 algorithm (Renka, 1996). In this case, transects represented the x-axis (space), with 5 x 5-m plots represented as individual grid cells; time since fire represented the y-axis, with years represented as individual grid cells, and (re)invasion variables (density and cover, each separately) represented the z-axis. Transects were standardized based on distance to the former grassland-woodland boundary. This x, y, z grid was then imposed on a 100 x 100cell grid where reinvasion variables were interpolated across space (x dimension) and time since fire (y dimension). The resultant contour surface provides a spatiotemporal heat map of invasion and reinvasion 17 years following fire.

3. Results

3.1. Rates of juniper reinvasion and invasion

Post-fire increases in *J. virginiana* occurred faster in restored grassland regimes undergoing reinvasion, compared to adjacent grasslands undergoing the initial invasion process. In restored grassland regimes, seedlings established 1 year following fire, compared to 4 years before the first seedlings were observed in adjacent grasslands with the same time-since-fire history. Density increased in restored grassland regimes and adjacent grasslands along two significantly different trajectories (based on non-overlapping 95% confidence intervals; Fig. 5). In restored grassland regimes, increases in density followed a logarithmic trend (R^2=0.70) (Table 1, Table 2), were highly variable (as evidenced by a wide 95% confidence interval), and rapid. Density in restored grassland regimes reached levels similar to that of unburned woodlands (1486–4133 trees ha^{-1}) within 4–11 years and continued to increase beyond the range found in unburned woodlands. In adjacent grasslands, density increased following a polynomial trend (R^2=0.92) (Table 1, Table 2) and was relatively low and stable, with steady increases in density starting 11-years post-fire. *J. virginiana* density in adjacent grasslands reached similar levels to that of unburned grasslands 17 years post-fire but did not obtain densities found in unburned woodlands.
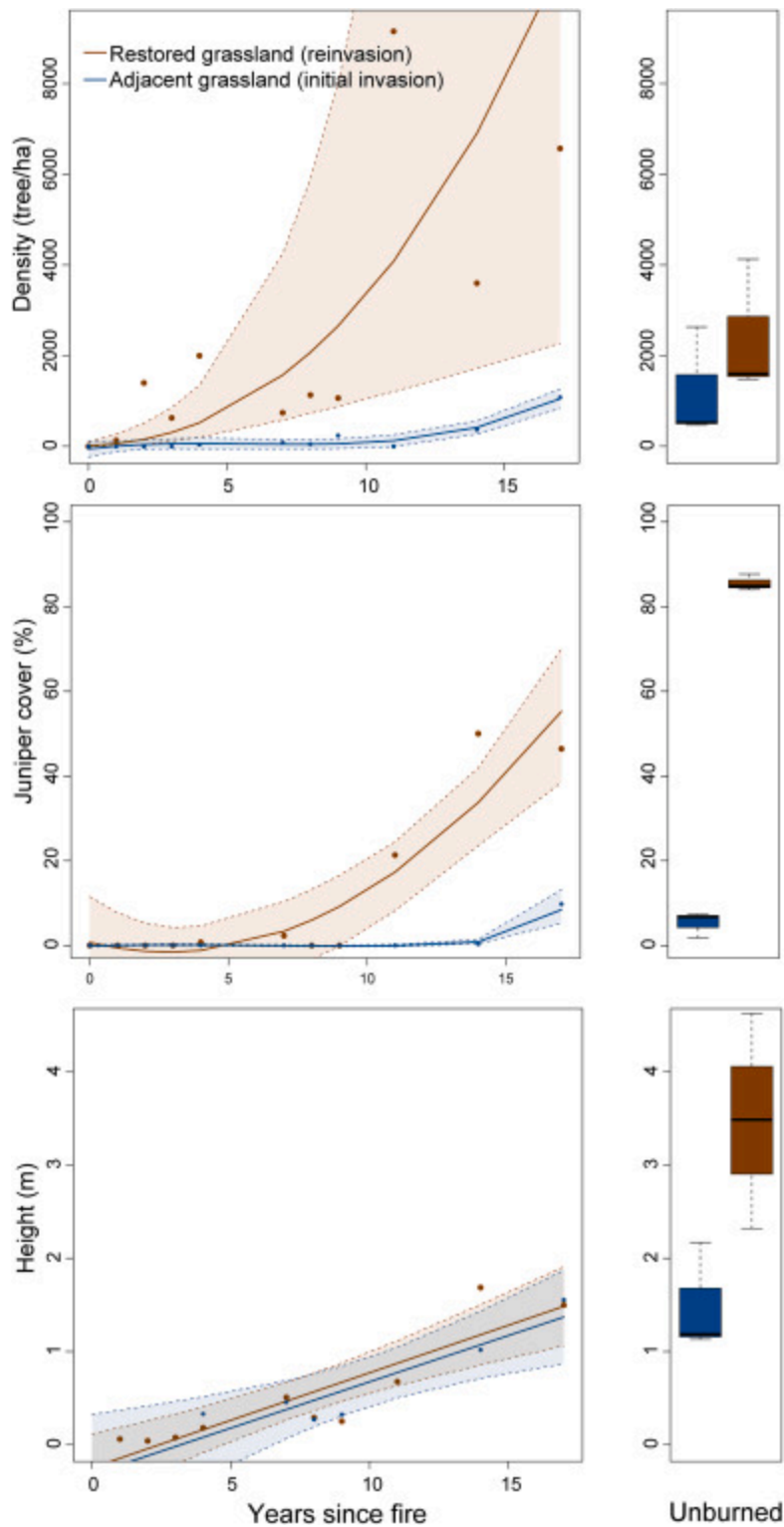
Fig. 5. Relationships between *Juniperus virginiana* density (top), cover (middle), and height (bottom) and years since fire in restored grassland regimes and adjacent grasslands (left panels), relative to unburned grassland and woodland patches (right panels) which provide

a point of reference for longer time-since-fire trajectories in the Loess Canyons Experimental Landscape, Nebraska, USA.

Table 1. Equations for top models used to describe relationships between *Juniperus virginiana* (re)invasion variables (density, cover, and height) and years since fire in mixed-grass prairie in the Loess Canyons Experimental Landscape, Nebraska, USA.

Response variable	Model equations
Density (tree/ha)	
Reinvasion	$y = \exp[2.4684 + 2.3527 \cdot \ln\{x+1\}] - 1$
Initial invasion	$y = -56.2216 + 72.7074x - 13.6735x^2 + 0.7780x^3$
Cover (%)	
Reinvasion	$y = 0.7194 - 1.60896x + 0.28333x^2$
Initial invasion	$y = \exp[-0.1430768 + 0.1947002x + -0.0423911x^2 + 0.0023056x^3] - 1$
Height (m)	
Reinvasion	$y = -0.24744 + 0.1019x$
Initial invasion	$y = -0.31786 + 0.09927x$

Table 2. Model selection results for models used to describe relationships between *Juniperus virginiana* (re)invasion variables (density, cover, and height) with years since fire in mixed-grass prairie in the Loess Canyons Experimental Landscape, Nebraska, USA.

Model	K[a]	ΔAIC_c[b]	ωi[c]
Density			
Reinvasion			
Logarithmic	3	0.0	0.96
Linear	3	7.1	0.03
Second-order polynomial	4	9.3	0.01
Null	2	10.3	0.01
Third-order polynomial	5	11.9	<0.01

Model	K[a]	ΔAIC_c[b]	ωi[c]
Initial invasion			
Third-order polynomial	5	0.0	0.69
Second-order polynomial	4	1.7	0.30
Linear	3	8.5	0.01
Logarithmic	3	14.0	<0.01
Null	2	14.7	<0.01
Cover			
Reinvasion			
Second-order polynomial	4	0.0	0.80
Linear	3	3.5	0.14
Third-order polynomial	5	5.3	0.06
Logarithmic	3	11.1	<0.01
Null	2	13.4	<0.01
Initial invasion			
Third-order polynomial	5	0.0	0.98
Second-order polynomial	4	8.1	0.02
Linear	3	15.4	<0.01
Null	2	17.7	<0.01
Logarithmic	3	19.1	<0.01
Height			
Reinvasion			
Linear	3	0.0	0.76
Second-order polynomial	4	2.6	0.21
Logarithmic	3	6.8	0.03
Third-order polynomial	5	10.2	<0.01
Null	2	12.5	<0.01

Model	K^a	ΔAIC_c^b	ωi^c
Initial invasion			
Linear	3	0.0	0.58
Null	2	1.1	0.34
Logarithmic	3	4.1	0.08
Second-order polynomial	4	18.9	<0.01
Third-order polynomial	5	∞	<0.01

a

    Number of parameters in the model.

b

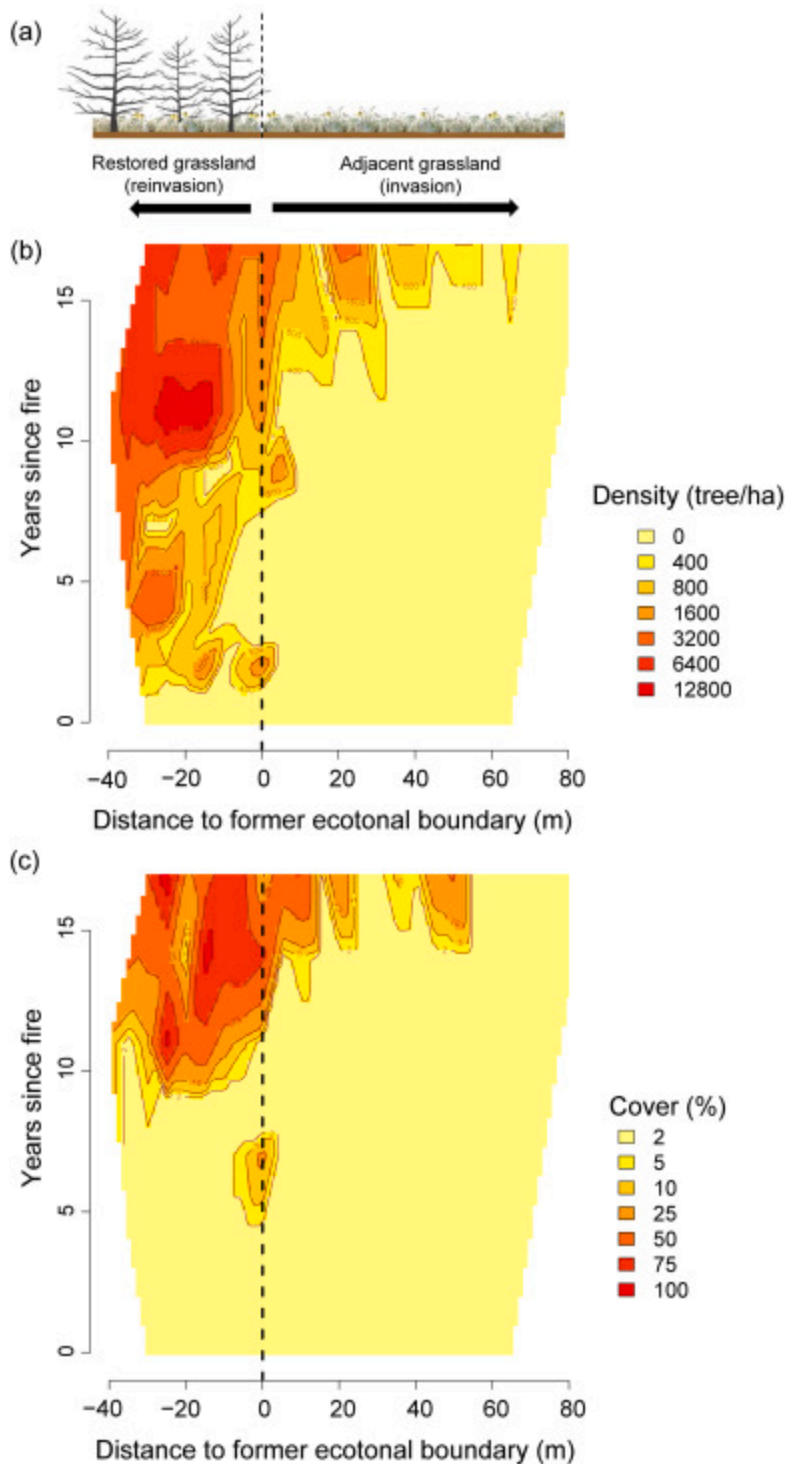   Difference in AICc value between model and the most strongly supported model.

c

    AICc Weight - relative strength of support for model.

Increases in *J. virginiana* cover were significantly different between restored grassland regimes undergoing reinvasion and adjacent grasslands undergoing the initial invasion process (as evidenced by non-overlapping 95% confidence intervals; Fig. 5). Cover increased faster in restored grassland regimes compared to adjacent grasslands (Fig. 5). In restored grassland regimes, increases occurred along a polynomial trend (R^2=0.84) (Table 1, Table 2), in which cover was initially stable and then began to increase rapidly 7-years post-fire. Seventeen-years post-fire, predicted *J. virginiana* cover was 55.2% (95% CI=39.4–71.0%), compared to 84.0–87.7% in unburned woodlands. In contrast to what was observed in restored grassland regimes, cover remained low and stable in adjacent grasslands for the first 14 years post-fire, with notable increases in cover observed 17 years post-fire (R^2=0.94; see Table 1 for model equations). Seventeen-years post-fire, predicted cover was 2.2% (95% CI=1.8–2.7%) in adjacent grasslands, within the range found in unburned grasslands but well below that of reinvaded grasslands and unburned woodlands. Increases in mean *J. virginiana* height were not significantly different between restored grassland regimes and adjacent grasslands (as evidenced by overlapping 95% confidence intervals; Fig. 5). Mean *J. virginiana* height within both restored grassland regimes and adjacent grasslands increased along a linear trajectory (R^2=0.79 and 0.80, respectively). Seventeen-years post-fire, mean

tree height was 1.5 and 1.4m in restored grassland regimes and adjacent grasslands, respectively.

3.2. Spatial patterns of juniper reinvasion and invasion

Initially, *J. virginiana* reinvasion and invasion was easily distinguishable based on the former grassland-woodland ecotonal boundary (Fig. 6); however, over time this became less distinct as the juniper woodland reestablished and expanded into adjacent grasslands. Initial increases in *J. virginiana* occurred almost immediately and ubiquitously in the restored grassland regime. However, in adjacent grasslands increases in *J. virginiana* occurred slower and distance to the former grassland-woodland boundary influenced invasion patterns in addition to time since fire (Fig. 6). Post-fire increases in *J. virginiana* occurred earlier in grassland areas that were close to the former grassland-woodland boundary, compared to areas farther from the boundary. Seedlings first established 1-year post-fire in restored grassland regimes, 4 years post-fire in burned grasslands ≤40m from the former woodland edge, and 14 years post-fire in burned grasslands >40m from the former woodland edge. Increases in cover followed the same general pattern but lagged behind that of density (Fig. 6).

(a)

Restored grassland (reinvasion) ← → Adjacent grassland (invasion)

(b)

Years since fire

Density (tree/ha)
- 0
- 400
- 800
- 1600
- 3200
- 6400
- 12800

Distance to former ecotonal boundary (m)

(c)

Years since fire

Cover (%)
- 2
- 5
- 10
- 25
- 50
- 75
- 100

Distance to former ecotonal boundary (m)

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Fig. 6. Reinvasion and invasion within restored grassland regimes and adjacent grasslands following fire in the Loess Canyons Experimental Landscape. Top illustration (a) depicts the former ecotonal boundary separating woodland and grassland regimes. Heat maps show (re)invasion variables, density (b) and cover (c), interpolated across the former ecotonal boundary (x axis) and years since fire (y-axis).

4. Discussion

Restored grassland regimes were more vulnerable to shifts back to a juniper woodland regime compared to grasslands experiencing the initial woody invasion process. Our results show that this process was driven by high levels of *J. virginiana* reestablishment following woodland collapse, as opposed to increased growth rates which we found no evidence of. *J. virginiana* reestablished at high densities almost immediately after woodland collapse, which led to an earlier onset of the exponential growth phase. This is an important finding for differentiating between the initial invasion process (the 'path out') and the reinvasion process (the 'path back out'). The onset of exponential growth signifies strong destabilizing feedbacks whereby increases in woody plant abundance quickly narrows the range of fire conditions needed to reverse woody-plant invasion (Bielski et al., 2021; Twidwell et al., 2013a, 2016b). During the initial invasion process, low-intensity fires on a 10-15-year return interval may be sufficient to reverse woody-plant invasion and maintain grassland dominance. Yet, these same fire conditions are unlikely to reverse the rapid reinvasion process and prevent a transition to juniper dominance. Instead, more frequent and/or intense fire conditions are required to reverse reinvasion and maintain grassland dominance (Twidwell et al., 2016a). While previous research has shown distinct trajectories for invasion and restoration pathways (Bielski et al., 2021; Collins et al., 2021), our results show evidence of a distinct reinvasion pathway characterized by a more rapid trajectory from grassland to woody dominance (Fig. 1).

Our finding of a more rapid reinvasion process suggests that legacies from past woodland regimes can compromise grasslands undergoing restoration and make them more vulnerable to woodland transitions. *J. virginiana* is a non-resprouting, fire sensitive species, yet soil seed banks, burned tree skeletons, and plant-soil feedbacks are a few examples of invasion legacies that may increase a site's overall risk of transitioning back to a woodland regime. For example, standing dead trees serve as avian perches and are likely to increase avian seed deposition (Prather et al., 2017); fire treatments may leave behind juniper seeds in the soil seed bank; and soil microbial communities altered during the initial invasion process (Liang et al., 2017; Utaile et al., 2021; Zhao et al., 2022) may increase rates of seed germination and seedling survival (Bennion and Ward, 2022). Bates et al. (2005, 2006) demonstrate how juvenile juniper, left behind from tree cutting treatments, lead to faster rates of reinvasion that shorten the lifespan of restoration investments. Similar examples are found from a growing literature on reinvasion, which identifies the reinvasion process as distinct from the initial invasion due to potential changes in the invader, the invaded environment, and species interactions (Banks et al., 2018). In other words, a system's history of invasion and remaining legacies drive ecological differences between reinvasion and

invasion. We suspect that the magnitude of difference between juniper invasion and reinvasion is dependent upon the extent and type of these invasion legacies. Future research is needed to better understand the mechanisms driving faster rates of reinvasion, their persistence over time, and how to contend with them from a management perspective.

Our results also provide insight on the spatial patterns of reinvasion and how legacies of past woody regimes influence invasion patterns in nearby grasslands. Our findings show an initial sharp contrast between restored grassland regimes and adjacent grasslands. High levels of *J. virginiana* reestablishment occurred in restored grassland regimes compared to adjacent grasslands, indicating major differences in seed occurrence and/or seedling establishment between patches undergoing reinvasion vs invasion. However, as juniper woodlands recovered and matured, they expanded into adjacent grasslands. Expansion was characterized by a high density of recruitment near the grassland-woodland boundary and was consistent with patterns of recruitment around a seed source (Fogarty et al., 2022; Holthuijzen et al., 1987; Holthuijzen and Sharik, 1985). Further, the observed delay of increased *J. virginiana* density in adjacent grasslands was consistent with the timeline for seed production by reestablished *J. virginiana* (Fogarty et al., 2021). These patterns suggest that invasion in surrounding grasslands was driven by reestablished seed sources in recovered woodlands. Thus, reinvasion not only compromises sites undergoing restoration but also compromises surrounding grasslands by increasing propagule pressure.

4.1. Implications for ecosystem management

There are two main implications based on our finding that restored grassland regimes are more vulnerable to transitions back to woody dominance. First, evidence of a rapid reinvasion pathway underscores the importance of proactive management that avoids woodland transitions in grasslands. Relatively slow rates of tree establishment during the initial invasion process can be managed with less intensive treatments compared to reinvasion. Post-fire establishment of *J. virginiana* occurred up to 13 years later in grasslands compared to restoration sites experiencing reinvasion. Hence, fire treatments focused on grassland maintenance have relatively long lifespans for woody plant control and reduce future management needs associated with reinvasion (Roberts et al., 2018; Twidwell et al., 2021). The second implication is that integrated management frameworks are needed that explicitly account for reinvasion and the potential for history-dependent responses in systems undergoing restoration. Reinvasion is different from invasion and grasslands undergoing restoration require follow-up management to extend and sustain the lifespan of initial restoration treatments. Frameworks for follow-up management should be developed based on the life cycle of targeted woody plants, with the goal of preventing demographic

transitions to mature, seed-bearing trees. For instance, frequent fire in grasslands and savannas creates a recruitment trap that prevents saplings from reaching adult size classes (Bond, 2008). Follow-up management can similarly be used to prevent the reestablishment of seed-bearing trees and should be considered upfront in the planning process as part of integrated grassland restoration plans.

CRediT authorship contribution statement

Dillon T. Fogarty: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Michele Beadle:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Data curation, Conceptualization. **Craig R. Allen:** Writing – review & editing, Visualization, Project administration, Funding acquisition. **Christine Bielski:** Writing – review & editing, Conceptualization. **Dirac Twidwell:** Writing – review & editing, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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