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Refining thresholds in coupled fire–vegetation models to improve management of encroaching woody plants in grasslands

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Summary

1. Restoration priorities are typically established without quantitative information on how to overcome the thresholds that preclude successful restoration of desirable ecosystem properties and services. We seek to demonstrate that quantifying ecological thresholds and incorporating them into management-oriented frameworks provide a more comprehensive perspective on how the threshold concept can be applied to achieve restoration goals.

2. As an example, restoration actions have been largely unsuccessful when based on prevailing ecological knowledge of fire-based thresholds in nonresprouting *Juniperus* woodland. We build on previous threshold-based research and link well-established models from applied fire physics with a widely applied ecological positive feedback model of woody plant encroachment to introduce a more comprehensive understanding of the mechanism influencing fire intensity and juniper mortality.

3. Our coupling of physical and ecological fire models revealed a critical knowledge gap, a lack of a quantitative estimate on the critical surface fire intensity required to cause mortality of *Juniperus ashei* trees, which limits the linking of scientific knowledge from these two disciplines.

4. To quantify the relationship between fire intensity and *J. ashei* mortality, we input data from a previous experiment into Byram's fireline intensity model. This critical surface fire intensity–mortality threshold was estimated to be $I_s > 160$ kJ m^{-1} s^{-1}. This value establishes a specific threshold that managers should target when attempting to use restoration to collapse *J. ashei* woodlands.

5. *Synthesis and applications*. For scientific information associated with the threshold concept to be useful to practitioners, specific information is needed that demonstrates how to use restoration activities to overcome thresholds and collapse the current, degraded state in favour of a more desired ecological state. With this in mind, we present a broadly applicable decision support model within a state and transition framework that identifies the ecological states where the surface fire intensity–mortality threshold is most likely to meet restoration objectives and provides examples of how fuel properties that drive fire intensity should be targeted in restoration to surpass this threshold.

Key-words: fire intensity, fire physics, fire trap, grassland, juniper, positive feedback, regime shifts, resilience, restoration ecology, state and transition model

Introduction

The threshold concept challenges scientists to identify and characterize abrupt changes associated with the dynamic nature of ecological systems (see Table 1 for definitions on threshold and other terms). This in turn provides resource managers with critical information on how to successfully promote ecosystem services desired by humans. To this end, the threshold concept has become a centre piece for bridging applied ecology research and

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Table 1. Glossary of terms and modelling equations

Terms	Definition
Threshold terms	
Threshold[1,2]	1. The point at which a relatively small change in a driver causes large responses in a system 2. The point at which there is an abrupt change in a quality, property or phenomenon in a system 3. A boundary separating alternative stable states in a system
State-and-transition model (STM)[3]	Qualitative or quantitative models that characterize the occurrence of potential alternative stables states and the transitions between states for a given site
Positive ecological feedback	Causal processes that accelerate the system away from the reference state or condition.
Negative ecological feedback	Causal processes that reinforce the trajectory of the system towards the reference state or condition.
Fire trap	A fire-induced bottleneck where resprouting woody plants are kept small and prevented from reaching their full potential (see also Oskar–Gulliver hypothesis[4])
Fine fuel load – fire threshold	A threshold model used to describe woody encroached grasslands and savannas that states a critical amount of fine fuel is required for fire to meet restoration objectives (Fig. 1b)
Surface fire intensity – mortality threshold	The critical surface fire intensity required for mortality (kJ m^{-1} s^{-1})
Fire terms[5,6,7]	
Fine fuel loading (w)	The mass of fuels (typically <6 mm) per unit area of the fuel bed (i.e. herbaceous biomass)
Low fuel heat content (h)	The heat of a material produced by combustion
Bulk density (ρ_b)	The amount of oven dry fuel per unit volume of the fuel bed
Effective heating number (ε)	The proportion of a fuel particle that is heated to preignition upon the onset of flaming combustion
Fireline intensity (I)	The rate of heat release per unit time per unit length of the flaming fire front
Rate of fire spread (r)	Rate of spread of the flaming fire front
Heat of preignition (Q_{ig})	The amount of heat per unit mass required for ignition
Reaction intensity (I_r)	The total rate of heat release per unit area of the fire front
Reaction velocity (Γ)	The rate and completeness of fuel consumption
Optimum reaction velocity (Γ')	The reaction velocity that would exist if the fuel were free of moisture and contained minerals at the same reaction concentration as α-cellulose
Fuel moisture content (m_f)	The amount of moisture in fuel expressed as a percentage on a dry weight basis
Foliage moisture content (FMC)	The amount of moisture in tree or shrub foliage expressed as a percentage on a dry weight basis
Moisture of extinction (m_x)	The moisture content of the fuel at which point fire will not spread.
Moisture damping coefficient (η_m)	A ratio accounting for the decrease in reaction intensity caused by the combustion of fuels that originally contained moisture
Mineral damping coefficient (η_s)	A factor that modifies reaction intensity as a function of the silica-free ash content
Modelling equations	Equation
J. virginiana cover – fine fuel load relationship	$w = -45{\cdot}56C_{JUVI} + 4727{\cdot}9$ eqn 1
Fireline intensity	$I = whr$ eqn 2
Rate of fire spread	$r = \frac{I_r \xi f(\varpi, \varsigma)}{\rho_b \varepsilon Q_{ig}}$ eqn 3
Heat of preignition	$Q_{ig} = 581 + 2594m_f$ eqn 4
Reaction intensity	$I_r = wh\Gamma$ eqn 5
Reaction velocity	$\Gamma = \Gamma' \eta_m \eta_s$ eqn 6
Mineral damping coefficient	$\eta_m = 1 - 2{\cdot}59\frac{m_f}{m_x} + 5{\cdot}11\left(\frac{m_f}{m_x}\right)^2 - 3{\cdot}52\left(\frac{m_f}{m_x}\right)^3$ eqn 7
Surface fire intensity – *Juniperus* mortality threshold	$I_s > 160\,\text{kJ m}^{-1}\text{s}^{-1}$ if $\text{FMC}_{juas} < 80\%$ eqn 8

Definitions are from [1]Groffman *et al.* 2006; [2]Briske, Fuhlendorf & Smeins 2003; [3]Westoby, Walker & Noy-Meir 1989; [4]Bond & Van Wilgen 1996; [5]Rothermel 1972; [6]Albini 1976; [7]Pyne, Andrews & Laven 1996.

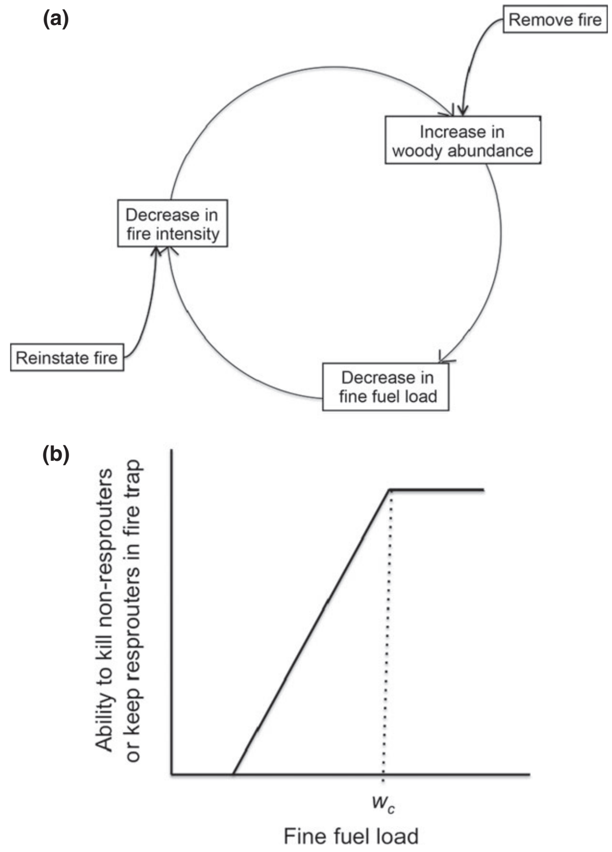

Fig. 1. (a) The ecological positive feedback among woody plant abundance, fine fuel load, and fire intensity is triggered by removing fire and promotes the establishment and encroachment of woody plants. Increasing woody plant abundances reduces fine fuel load and thereby decreases fire intensity, which reinforces the stability of the developing woody plant dominated state and reduces the potential for fire-induced mortality when it is reintroduced (model adapted from van Langevelde *et al.* 2003). (b) According to the fine fuel load–fire threshold model, the removal of fire and the onset of the positive feedback mechanism reduces fine fuel loading beneath a critical threshold (w_c), thereby preventing fire from killing non-resprouting trees or keeping resprouting species within the fire trap.

natural resource management (Hobbs & Norton 1996), resulting in the emergence of numerous threshold-based frameworks meant to guide management actions across various ecological disciplines (Suding, Gross & Houseman 2004). State-and-transition models (STMs) are threshold-based frameworks that have become the central focus of applied ecologists in rangelands and are being widely applied by agencies to guide management actions in the United States (Briske, Fuhlendorf & Smeins 2003, 2005) and internationally (Westoby, Walker & Noy-Meir 1989; Letnic & Dickman 2010). Unfortunately, most thresholds in STMs are poorly characterized (Bestelmeyer 2006), and it has been particularly challenging to quantitatively link thresholds to the feedback mechanisms that drive state transitions. Most often, thresholds are characterized as a function of abrupt changes in the patterning of structural properties over time or due to changing environmental conditions (Briske, Fuhlendorf & Smeins 2005). As an example, thresholds associated with cover, biomass, reflectance or vegetation composition dominate STMs in rangeland ecology (Bestelmeyer 2006). In contrast, thresholds associated with the rates, frequencies or intensities of ecological or physical processes are poorly developed. Our inability to quantify and incorporate thresholds associated with natural processes into STMs therefore represents a sizeable knowledge gap that we believe is critically limiting the scientific impact and application of the threshold concept in management and restoration (*sensu* Milner-Gulland *et al.* 2012).

Efforts to understand ecological thresholds have focused on identifying abrupt changes in the properties or phenomena of an ecosystem as a result of ecological feedbacks (Briske, Fuhlendorf & Smeins 2006; Groffman *et al.* 2006; Bestelmeyer *et al.* 2011). For example, in fire-dependent grasslands and savannas where woody plant cover has increased (e.g. African semi-arid savanna, Sankaran *et al.* 2005; Australian tropics, Brook & Bowman 2006; North American mesic grasslands, Briggs *et al.* 2005; South American subtropical savanna, Adamoli *et al.* 1990), fire thresholds are associated with a positive feedback mechanism that promotes further woodland progression (Fig. 1a; van Langevelde *et al.* 2003). The removal of fire from grass-dominated ecosystems triggers the positive feedback mechanism and provides a suitable environment for woody plant establishment (Higgins, Bond & Trollope 2000; Briggs, Knapp & Brock 2002b; Bond 2008; Taylor *et al.* 2012). An increase in the abundance of woody plants reduces grass biomass (herbaceous fine fuel load), which lowers fire intensity (Trollope 1984; Kaufmann, Cummings & Ward 1994; Fuhlendorf, Smeins & Grant 1996; Scholes & Archer 1997). Less intense fires are unable to cause enough damage to kill mature nonresprouting trees (Engle, Stritzke & Claypool 1988; Briggs, Hoch & Johnson 2002a; Twidwell *et al.* 2009) or to keep resprouting woody plants within the 'fire trap' (Higgins, Bond & Trollope 2000; Govender, Trollope & Van Wilgen 2006; Higgins *et al.* 2007; Bond 2008). Eventually, a stable woody plant community is reached at the point when the reintroduction of fire is largely incapable of restoring the grassland or savanna community that occurred prior to the removal of fire (Fuhlendorf, Smeins & Grant 1996; Briske, Fuhlendorf & Smeins 2006). Numerous studies have attributed the ineffectiveness of fire in controlling juniper to low fine fuel loading (Wink & Wright 1973; Engle & Kulbeth 1992; Fuhlendorf, Smeins & Grant 1996; Briggs, Hoch & Johnson 2002a; van Langevelde *et al.* 2003; Briggs *et al.* 2005; Fuhlendorf *et al.* 2008). As a result, many managers have adopted a fuel load–fire threshold model that assumes a critical minimum amount of fine fuel is essential if fire is to contribute to restoration of grasslands or savannas with encroaching woody plants (Fig. 1b; Wright & Bailey 1982; USDA-NRCS 2011).

Consider the application of the fuel load–fire threshold on restoration plans and actions within nonresprouting

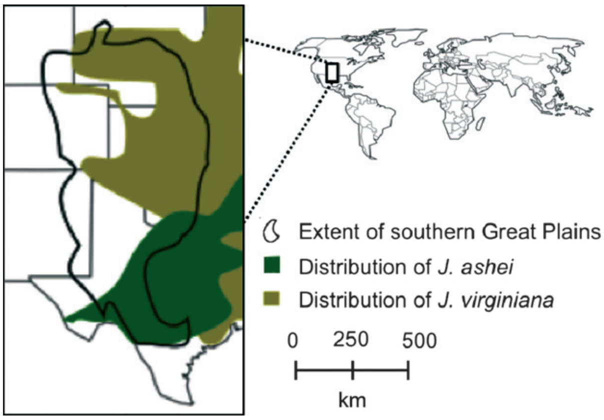

Fig. 2. Map of the distribution of *Juniperus ashei* and *J. virginiana* in the southern Great Plains, USA. Plant distributions are compiled from the USDA Plants Database. The boundary for the southern half of the Great Plains is based on Trimble (1980).

Juniperus woodlands of the southern Great Plains (Fig. 2). *Juniperus* species like Ashe juniper *J. ashei* and Eastern redcedar *J. virginiana* are native trees that are sensitive to fire-induced mortality because of their inability to resprout. However, long-term exclusion of fire has allowed these species to rapidly encroach into grasslands throughout the Great Plains (Briggs, Hoch & Johnson 2002a; Taylor *et al*. 2012). While many STMs developed for managers suggest fire can reverse the grassland to juniper woodland transformation (USDA-NRCS 2011), experimental evidence suggests that prescribed fire rarely kills large juniper trees (Table 2). An increase in the distribution of juniper lowers the potential for fire-induced mortality by reducing fine fuel loading and fire intensity (e.g. Fig. 1a; Bryant, Launchbaugh & Koerth 1983; Engle, Stritzke & Claypool 1988) below the hypothesized critical threshold required to completely scorch and kill *Juniperus* trees ($w_c \geq 3000$ kg ha^{-1} in Fig. 1b, Engle & Kulbeth 1992). In fuel-limited grasslands, the seemingly obvious means of increasing herbaceous biomass and surpassing this fine fuel load threshold is to remove grazers (Briggs *et al*. 2005; Fuhlendorf *et al*. 2008). However, the lack of fine fuel may be a function of the displacement of herbaceous biomass by the encroachment and maturation of *Juniperus* trees, which can be independent of grazing animals (e.g. Fig. 1a). Removing grazers is therefore not going to increase fine fuel loading in most high-density *Juniperus* stands where grasses have been largely displaced by woody encroachment (Fuhlendorf *et al*. 2008). Even in grasslands that have not undergone complete conversion to woodland, the removal of grazers is most likely to increase fine fuel loading in areas where grass already exists (in the interspaces among patches of juniper trees) rather than at the scale necessary for fire to kill mature trees using traditional fire prescriptions (underneath juniper crowns; Twidwell *et al*. 2009). Increasing fine fuel loading is therefore likely to be effective only in highly productive areas where *Juniperus* encroachment has yet to fully displace herbaceous surface fuels (e.g. Briggs *et al*. 2005 in tallgrass prairie). This has contributed to speculation that the transition from grassland to *Juniperus* woodland may be irreversible using fire alone (Fuhlendorf, Smeins & Grant 1996; Briggs, Hoch & Johnson 2002a; Ansley & Wiedemann 2008).

Implicating that an irreversible threshold has been crossed can have severe negative impacts on the perceived value of ecosystems and the services they provide (Carpenter, Ludwig & Brock 1999; MA 2005). In these cases, it behoves scientists to thoroughly assess the assumptions and knowledge gaps surrounding the potential reversibility of degraded ecological states. In *Juniperus* woodlands, an alternative approach to the fuel load–fire threshold model is to target environmental conditions that are independent of the feedbacks causing limitations in fine fuel load but are important drivers of fire intensity and *Juniperus* mortality. Twidwell *et al*. (2009) showed burning in low fine fuel moisture conditions caused 100% mortality of *J. ashei* (Fig. 3a), whereas burning in similar fine fuel load levels in high fine fuel moisture conditions killed only 29% of trees (Fig. 3b). The inability of the fuel load –fire threshold model to account for mortality events driven by variability in other factors demonstrates the need for a more comprehensive understanding of the complex relationships between fuels, fire behaviour and fire-induced mortality of *Juniperus* trees.

In this study, we demonstrate how a more mechanistic interpretation of the fire process can improve restoration actions in woody encroached grasslands. First, we couple well-established models from applied fire physics and fire ecology to provide a more comprehensive perspective than the fuel load–fire threshold model on how different environmental factors influence fire intensity to drive mortality of *Juniperus* trees. To date, managers working in these systems have not had access to models that link the physical process of fire to the ecological feedbacks associated with woody encroachment. They have instead relied on incomplete models that attempt to derive fire effects on vegetation from a single variable, fine fuel load (e.g. Fuhlendorf, Smeins & Grant 1996; Fuhlendorf *et al*. 2008), leading to inconsistent restoration outcomes (Table 2). Next, while coupling physical and ecological fire models, we reveal a critical knowledge gap that may prevent the linking of scientific information from these two disciplines. Specifically, we lack a quantitative estimate of the surface fire intensity required to cause high mortality in large *J. ashei* trees. To quantify this threshold, we use data from a previous experiment (Twidwell *et al*. 2009) in a simple fire intensity model (Byram 1959). Lastly, we input the information developed from this study into a fire-driven STM to demonstrate how quantifying thresholds associated with the restoration process can directly link science and practice by providing managers with specific information to target when conducting restoration treatments.

Table 2. Summary of the general lack of control and mortality of mature nonresprouting juniper trees (>1·8 m tall) in previous grassland fire research in the Great Plains

References	Tree height (m)	Treatment	Fine fuel load (kg ha^{-1})*	% control[†]	% mortality
Dalrymple (1969)	<0·6		550–1160		100
	0·6–1·8				77
	>1·8				27
Buehring, Santelmann & Elwell (1971)[‡]	<0·45		n.r.	96	99
	0·45–0·9			83	88
	0·9–1·8			63	65
Owensby *et al.* (1973)	<0·6		n.r.	89	72
	0·6–1·8			83	48
	>1·8			39	20
Wink & Wright (1973)	<1·8		768–3568		99
Engle & Stritzke (1995)	<1·5	Summer	8800	71	52
		Winter	8700	92	87
	1·5–2·5	Summer		54	41
		Winter		81	62
	2·5–5·0	Summer		39	27
		Winter		30	0
Ortmann *et al.* (1998)	<1·0		1080–3620		88
	1·0–2·0				60
	2·0–3·0				35
	>3·0				10
Briggs, Hoch & Johnson (2002a)[‡]	<1·5	Grazed	2490		50
		Ungrazed	3740		100
	1·5–2·5	Grazed			20
		Ungrazed			90
	2·5–3·0	Grazed			10
		Ungrazed			85
Noel & Fowler (2007)[‡]	<0·5		n.r.	40	70
	0·5–1·0			30	40
	1·0–1·5			25	30
	1·5–2·0			20	25
	>2·0			5	10
Twidwell *et al.* (2009)	1·0–4·5	High FFM	980–3365		29
		Low FFM	1068–4062		100

FFM, fine fuel moisture; n.r., not reported.
*The range is reported except when only the mean was given (as shown by a single value).
[†]% control is defined as the percentage of trees that exhibit obvious effects from treatment (e.g. scorch and dead branches) (definition adapted from Owensby *et al.* 1973).
[‡]values are approximated from a figure in the publication; In Buehring, Santelmann & Elwell (1971), values are averaged across two sites; per cent control represents trees exhibiting scorch within 1 month of each burn; per cent mortality represents effects 1 year after burn. In Noel & Fowler (2007), per cent control represents the proportion of trees killed by fire compared with the proportion of trees killed in unburned areas.

Materials and methods

COUPLING PHYSICAL AND ECOLOGICAL FIRE MODELS

Model Background

To establish a mechanism that ultimately results in fire-induced mortality of *J. ashei* trees, we developed a unique model that connects previous, well-established research from applied fire physics with a simple positive feedback model that is well established in fire ecology (Fig. 1a; Fuhlendorf, Smeins & Grant 1996; van Langevelde *et al.* 2003; Briske, Fuhlendorf & Smeins 2006). Two physics-based fire models were used in this exercise. We started with Byram's fireline intensity model (Byram 1959) and ended with Albini's adjustment of Rothermel's rate of fire spread model (Rothermel 1972; Albini 1976). These two fire models are among the most widely applied models in fire science and management in the United States (Pyne, Andrews & Laven 1996). Byram's fireline intensity model depicts the rate of heat released by the flaming fire front and is typically used to characterize fire intensity for ecological applications (Johnson 1992). Rothermel's rate of fire spread model characterizes the heat flux produced from the flaming fire front that is available to unburned fuel relative to the heat required for ignition of the unburned fuel. Rothermel's rate of fire spread model is described as a semi-physical model, because it empirically solved Frandsen's fire spread equation (Frandsen 1973) based on the principle of conservation of energy. The rationale for using Rothermel's model in this exercise was that it was developed to calculate rate of fire spread using variables that could be known *a priori* and measured in the field (Rothermel 1972; Johnson 1992). This provides restoration managers the opportunity to use fuel and weather factors that can be determined *a priori* to predict and target conditions that have the potential to increase fire intensity in prescribed fires meant for

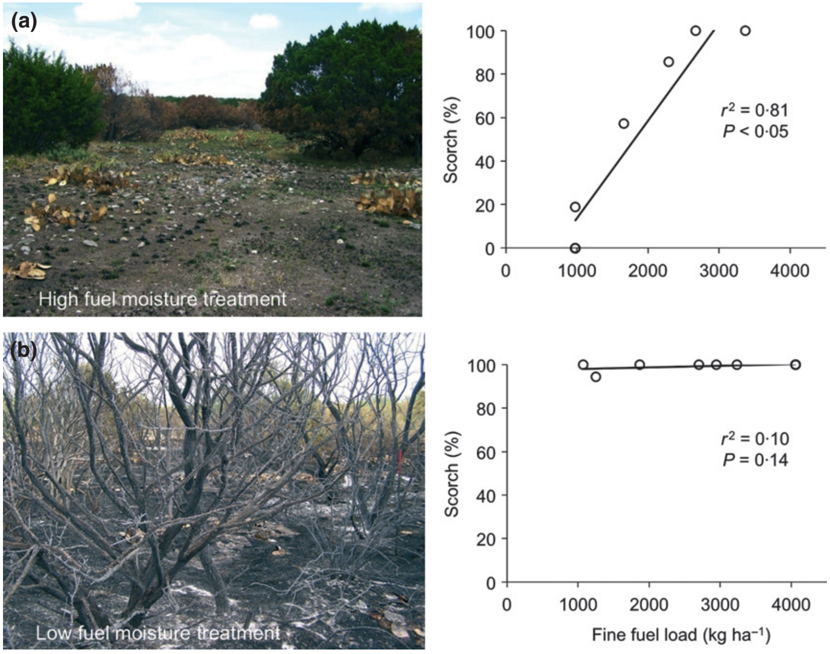

Fig. 3. Fires conducted in (a) high fine fuel moistures caused low levels of *Juniperus* crown scorch and mortality compared to fires conducted in (b) low fine fuel moistures in a previous experiment with similar amounts of fine fuel (all juniper trees with $\geq 85\%$ crown scorch were killed in this previous study; figure adapted from Twidwell *et al.* 2009). Targeting differences in fine fuel moisture conditions when fine fuel load is similar fails to support broad application of the fuel load–fire threshold model and demonstrates the need for a more comprehensive understanding of fire dynamics in *Juniperus* encroached grasslands.

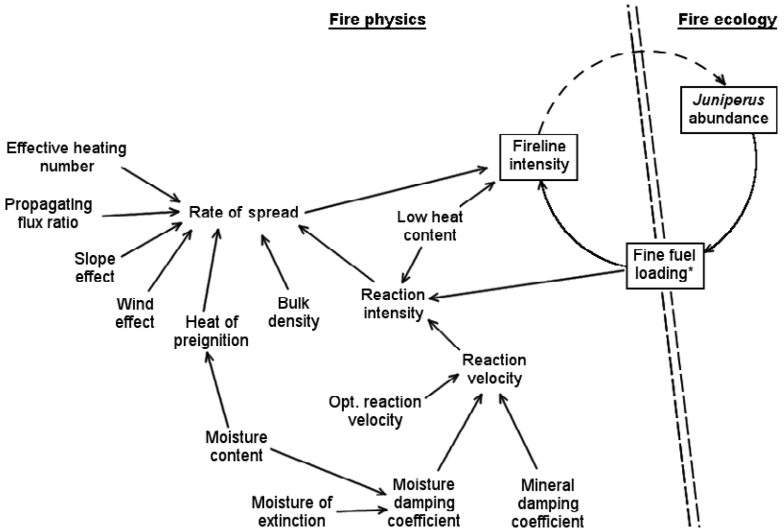

Fig. 4. Illustration of a model that characterizes the mechanism influencing surface fire-induced mortality of non-resprouting *Juniperus* trees. The model links scientific knowledge of a semi-physical model from fire physics with a positive feedback model from fire ecology. Solid arrows connecting variables depict mathematical functions described in the text. Dashed arrows depict relationships that had not been quantified prior to this study. For ease of illustration, we do not expand the model to include all potential mathematical relationships beyond those shown here, especially for factors that are constants (e.g. mineral damping coefficient). For example, bulk density is a function of fuel loading and fuel depth (additional information such as this can be derived from Rothermel 1972; Albini 1976; Wilson 1980, and many other sources). *Note:* *our model assumes all available fine fuel is consumed completely by the fire. The actual term used in Byram's fireline intensity equation is the amount of fuel consumed by the flaming fire front (w), which is a proportion of net fuel loading (see text).

restoration. To ease interpretation, we present the outcome of this exercise as a diagram that combines the mathematical relationships featured in the fire physics models with the positive feedback mechanism for *Juniperus* woodlands (Fig. 4).

Model Description

We started with the generalized ecological positive feedback model that promotes woody plant encroachment and made it specific to *J. ashei* woodlands. Increasing abundance of *Juniperus* trees decreases fine fuel loading. This relationship has been described *in situ* as a function of *J. virginiana* canopy cover (eqn 1; Limb *et al.* 2010):

$$w = -45{\cdot}56C_{JUVI} + 4727{\cdot}9 \quad \text{eqn 1}$$

where w is fine fuel load (kg ha^{-1}) and C_{JUVI} is percentage canopy cover of *J. virginiana*. We use eqn 1 to parameterize our model, because it is the simplest relationship for this exposition. However, users of the model should also consider relationships developed in previous modelling efforts and note the slight differences in the rates of fine fuel load displacement as a function of *J. virginiana* and *J. ashei* encroachment (Fuhlendorf, Smeins & Grant 1996, Fuhlendorf *et al.* 2008).

The effect of fuel loading on fire intensity is straightforward (Fig. 4). Lower fuel loading decreases the amount of fuel available for combustion. Everything else being constant a reduction in fine fuel loading decreases fireline intensity by decreasing the amount of fuel consumed by the fire. This is shown in Byram's fireline intensity model (1959):

$$I = whr \qquad \text{eqn 2}$$

Factors influence fire intensity via w, the weight of fuel consumed by the fire per unit area (kg m^{-2}) and r, rate of fire spread (m s^{-1}). The third term in the equation, h, is the low fuel heat content that varies so little among different fuel types (van Wagner 1972) it is assumed constant at 18 260 kJ kg^{-1}.

Using only the ecological positive feedback model, predicting fireline intensity is a direct function of fuel loading; however, physical fire models show a considerably more complex mechanism (Fig. 4). Increased complexity in predicting fire intensity arises in how factors such as slope, wind speed and fuel moisture influence fire intensity through the rate of spread term (Fig. 4). This is evident in Rothermel's model:

$$r = \frac{I_r \xi f(\varpi, \varsigma)}{\rho_b \varepsilon Q_{ig}} \qquad \text{eqn 3}$$

where I_r is reaction intensity, ξ is the propagating flux ratio, $f(\varpi, \varsigma)$ is a function-describing wind (ϖ) and slope (ς) effects, ρ_b is bulk density, ε is the effective heating number, and Q_{ig} is the heat of preignition. Wind speed and slope effects occur in the numerator of Rothermel's rate of fire spread equation (eqn 3), wherein higher wind speeds and greater slopes increase fire intensity (eqn 2) by increasing rate of fire spread (eqn 3; see Rothermel 1972, 1983 for more information).

Fuel moisture (m_f) influences rate of fire spread (eqn 3) through two pathways (Fig. 4). Both pathways alter rate of fire spread in the same direction, causing rate of fire spread to decrease when fuel moisture increases and to increase when fuel moisture decreases. First, higher fuel moistures increase the heat of preignition (Q_{ig}), or the energy per unit mass required for ignition:

$$Q_{ig} = 581 + 2594 m_f \qquad \text{eqn 4}$$

Second, higher fuel moistures reduce reaction intensity (I_r) by lowering reaction velocity (Γ), or the rate and completeness of fuel consumption, below its maximum potential (Γ') by lowering the moisture damping coefficient (η_m):

$$I_r = wh\Gamma \qquad \text{eqn 5}$$

$$\Gamma = \Gamma' \eta_m \eta_s \qquad \text{eqn 6}$$

$$\eta_m = 1 - 2{\cdot}59 \frac{m_f}{m_x} + 5{\cdot}11 \left(\frac{m_f}{m_x}\right)^2 - 3{\cdot}52 \left(\frac{m_f}{m_x}\right)^3 \qquad \text{eqn 7}$$

where η_s is the mineral damping coefficient and m_x is the fuel moisture of extinction (other terms have been defined previously and are presented in Table 1).

At this point, we have met our objective of providing a more comprehensive perspective of the mechanism driving fire-induced mortality of *J. ashei* and have identified numerous other variables, besides fine fuel load, that can be targeted by restoration practitioners with the intent of increasing fire intensity. Importantly, the physics submodel presented here can account for mortality events of mature *Juniperus* trees that are driven by variability in factors other than fine fuel load (e.g. Twidwell *et al.* 2009).We therefore stop our presentation of Rothermel's rate of fire spread model at this point even though several additional parameters would need to be included to operationalize the model (for more details see Rothermel 1972; Albini 1976; and Wilson 1980; also see Pyne, Andrews & Laven 1996 for an excellent review).

This leads us to the linking of the physical and ecological models and how fire intensity influences *J. ashei* abundance. Unfortunately, the fire intensity required to kill mature *J. ashei* trees has yet to be quantified. This represents the only critical knowledge gap in the model (Fig. 4; dashed arrow) and prevents the direct coupling of models from fire physics and fire ecology. This knowledge gap is addressed in the next section.

QUANTIFYING A CRITICAL FIRE INTENSITY–MORTALITY THRESHOLD

Here, we expand upon our findings from a previous field experiment (Twidwell *et al.* 2009) and input the necessary data into Byram's fireline intensity equation (eqn 2; Byram 1959) to develop a quantitative estimate of the critical fire intensity released by the surface fuel bed at the scale relevant to crown scorch and mortality of individual juniper trees. Specific details on the study site, experimental design, fire treatments and sampling protocol are given in the study described by Twidwell *et al.* (2009). Revisiting Byram's fireline intensity equation (eqn 2) and how terms were measured in Twidwell *et al.* (2009):

$$I = whr \qquad \text{eqn 2}$$

where w is the fine fuel load (kg m^{-2}) measured underneath individual juniper crowns and assumes complete combustion of the surface fuel bed, h is the low fuel heat content and is constant (h = 18 260 kJ kg^{-1}), and r is the rate of fire spread measured at 10 m intervals about each individual juniper crown (the closest scale of measurement we could consistently measure rate of spread under and around juniper trees; m s^{-1}).

Plotting the fireline intensity underneath each *Juniperus* tree with the crown scorch observed for that tree revealed the critical surface fire intensity required to overcome a threshold that limits juniper mortality. The critical surface fire intensity–juniper mortality threshold was estimated to be 160 kJ m^{-1} s^{-1} (Fig. 5). When the fire intensity under juniper crowns exceeded this value, all juniper trees were completely scorched and killed (Fig. 5), irrespective of fire treatment or tree height (max height = 4·5 m in this study; data not shown). These data may appear counter-intuitive because the surface fire intensity value is low. A video is presented in the online supporting information that demonstrates how these threshold values indeed depict the surface fire intensity and flame length required for complete scorch and mortality of individual juniper trees (Appendix S1, Supporting Information). Furthermore, the critical fire intensity threshold value characterized in this study (Fig. 5) corresponds with well-established predictions of the fire intensity required for crown combustion when the foliage of conifer trees is at ground level (van Wagner 1977). As evident in the video, foliage of *J. ashei* trees are typically on or near the ground due to its shrub-like growth form and short boles.

The surface fire intensity–mortality threshold of *J. ashei* (I_s > 160 kJ m^{-1} s^{-1}) is contingent on a couple of factors. First, this value represents the intensity of surface fires produced by the combustion of herbaceous surface fuels located directly under the crown of each juniper tree and ignores intensities produced from other fuel sources. Second, this threshold value may be dependent upon factors driving juniper flammability. *J. ashei* flammability is influenced by differences in various intrinsic properties (Owens *et al.* 1998), but the key factor is believed to be foliage moisture content (FMC; Bryant, Launchbaugh & Koerth 1983). The hypothesized moisture content threshold required for combustion of *J. ashei* trees is $\leq$80% (Britton, Wester & Racher 2007) but has not been tested empirically. In our previous field experiment, juniper FMC was as low as 42% and averaged 72 ± 4% for the two fire treatments (Twidwell *et al.* 2009). It is therefore uncertain whether researchers and restoration practitioners will achieve the levels of juniper mortality observed in the study described by Twidwell *et al.* (2009), if fires are conducted when FMC is above the threshold required for crown combustion or if fires occur during periods when crowns are less susceptible to scorch. This potential contingency is given below:

$$I_s > 160\,\text{kJ m}^{-1}\text{s}^{-1} \text{ if } \quad FMC_{juas} < 80\% \qquad \text{eqn 8}$$

Discussion

The new physical-ecological fire model developed in this study provides a more comprehensive understanding of the fire process in *Juniperus* woodlands by (i) identifying and linking key physical and ecological models relevant to fire in *J. ashei* woodlands, (ii) evaluating the models for key assumptions or knowledge gaps that need to be improved or quantified, and (iii) quantifying the key knowledge gap: the critical surface fire intensity–juniper mortality threshold. This model (Fig. 4) is easily transferable to fire ecologists in other surface fire-dominated ecosystems by replacing the functions used to parameterize the juniper-specific ecological feedback model with relationships from their own ecosystems. Applications of such models include, but are not limited to, improving landscape simulations, enhancing our understanding of the ecological implications of spatial and temporal changes in physical fuel properties, or providing a scientific basis for restoration actions. Additionally, the model presented here can be modified to include physical fire models that are less dependent than Rothermel's model on empiricism (e.g. Navier–Stokes equations) or expanded to include meteorological models or more complex ecological models that incorporate plant community succession, plant ecophysiological relationships, interactions with alternate disturbance agents, among other dynamics. Nevertheless, even with increased scientific understanding of the complex mechanism driving fire effects, such models are unlikely to be applied unless the information is input into frameworks or models that are used by managers (Milner-Gulland *et al.* 2012).

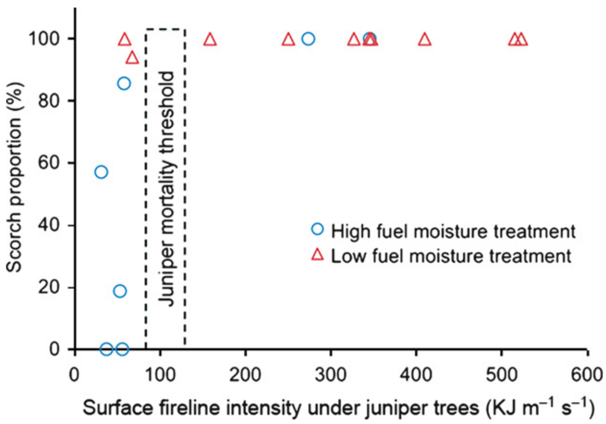

Fig. 5. The critical surface fire intensity threshold required for complete scorch and mortality of mature *Juniperus ashei* trees. Circles and triangles correspond to the treatments conducted by Twidwell *et al.* (2009) and data presented in Fig. 3.

By incorporating our findings into a fire-driven state and transition model that characterizes the grassland to woodland transition, we are able to identify the ecological states where the surface fire intensity–mortality threshold is most likely to meet restoration objectives and the properties from the model that should be targeted in restoration to surpass this threshold (Table 3). The benefit of this approach is that it allows managers to operationalize our model without demanding that they understand the entirety of surface fuel fire models. In the early stages of degradation, when juniper encroachment is beginning to lower fine fuel accumulation, the critical surface fire intensity–juniper mortality threshold can be surpassed through intervention that increases fine fuel load (Table 3, State 2). It is at this state that understanding the fuel load–fire threshold (Fig. 1b) can be useful in restoration (Table 3, State 2). In more degraded states (Table 3, States 3–4), however, restoration efforts that focus solely on increasing fine fuel load will be unsuccessful because sufficient degradation has occurred to produce a state that is highly resilient to management efforts aimed at reversing the effects of the positive ecological feedback loop. In contrast, attempts to surpass the surface fire intensity–mortality threshold via properties that are independent from the ecological positive feedback mechanism (e.g. fine fuel moisture) will continue to produce the desired results (Table 3, State 3). Only when degradation is sufficient to preclude the occurrence of surface fires will the surface fire intensity–mortality threshold quantified here no longer apply. At this point, it is necessary for scientists to develop a mechanistic understanding of alternate restoration processes, such as crown fires, that occur in a given state and can be targeted by restoration practitioners (Table 3, State 4). Hence, the key to restoration success with fire requires an understanding of how the physical process of fire functions in different stable states and how the properties that drive the process can be targeted in restoration to collapse an undesirable state. For this to occur, additional research is needed that takes the surface fire intensity–mortality threshold quantified in this study, identifies how interactions between the physical and ecological properties that influence the process can produce values above the

Table 3. A generalized fire-based restoration framework that places quantitative scientific knowledge into a state-and-transition model (STM) to establish management priorities and guide on-the-ground restoration actions. States are differentiated from one another based on the degradation of fuel properties and fire processes that drive state transitions. Because successful restoration activities are dependent on the functioning of the processes that drive transitions between states, restoration practitioners can use the model developed in this study along with this framework to target conditions that overcome the surface fire intensity–mortality threshold (I_s) needed to transition to a more desirable state

State classification	Alternative states in a fire-driven STM	State description	Restoration priority to overcome threshold	Consequences of crossing threshold	Value required to overcome threshold	Example of restoration action
State 1: desired state	Grassland 	State is intact; desired functioning of the state is maintained through negative feedbacks.	None; the state is maintained through negative feedback process.	–	–	None; the state is maintained with frequently occurring surface fires.
State 2: early degraded state	*Juniperus* savanna 	Drivers trigger a feedback switch from negative to positive, resulting in alterations in an ecological property that is important to the restoration process.	Restore the ecological property that is altered or target other ecological properties that are important to the process.	Fine fuel load has been reduced by *Juniperus* encroachment but can be increased with management intervention	$I_s > 160$ kJ m^{-1} s^{-1} Given: Surface fires; $FMC_{JUAS} < 80\%$	Remove grazers to increase fine fuel load and increase surface fire intensity above the mortality threshold.
State 3: moderately degraded state	*Juniperus* woodland 	Positive feedback mechanism leads to a state that is highly resilient to management; efforts to increase the ecological property that has been altered are unsuccessful.	Target ecological properties that are important to the process but independent of the positive feedback mechanism.	Fine fuel load cannot be increased to sufficient levels with management, but adequate fine fuel exists to carry surface fires.	$I_s > 160$ kJ m^{-1} s^{-1} Given: Surface fires; $FMC_{JUAS} < 80\%$	Target low fine fuel moisture conditions to increase surface fire intensity above the mortality threshold.
State 4: heavily degraded State	*Juniperus* closed-canopy 	Continuation of the positive feedback mechanism leads to a highly stable state that does not support the occurrence of the ecological process that maintained the desired, intact state.	Target alternate biological pathways that can disrupt the positive feedback mechanism.	Fine fuel load is not sufficient to support surface fires. Fire can still occur as ground fires through juniper foliar duff and crown fires through juniper crowns.	Unknown	Target environmental conditions that lead to sustained crown fires.

quantified threshold and provides practitioners with specific values that should be targeted given the current level of degradation in their system.

If scientists are to meet the demands of society and have greater impact in applied ecology (Milner-Gulland *et al.* 2012), it is critical to develop ways to directly and quantitatively couple scientific knowledge from disparate disciplines. Because disciplinary boundaries exist, ecological restoration has largely targeted environmental properties that are explained in ecological models (e.g. ecological positive feedback models; Fig. 1a) and ignored well-documented pathways from other disciplines that are important contributors to the overall mechanism that governs system dynamics (e.g. coupled physical-ecological fire model; Fig. 4). It is not explicitly clear why the disconnection between disciplines occurs, although there has been considerable discussion of this issue in fire (Johnson & Miyanishi 2001), restoration and conservation (Hobbs *et al.* 2011) and for ecology in general (Miller *et al.* 2008). As shown in this study, a factor contributing to our inability to link scientific knowledge in disparate disciplines is the occurrence of critical knowledge gaps resulting from the lack of quantification of thresholds in applied ecology. To our point, few attempts have been made to quantify thresholds associated with the rates and frequencies of ecological and physical processes and to incorporate them into STMs (but see Lopez *et al.* 2011). Instead, transitions between states are largely conceptually derived (Suding & Hobbs 2009) and based on expert opinion (Czembor *et al.* 2011). The lack of quantification makes state transitions in STMs impossible to test experimentally and difficult to refine or improve. In contrast, quantitative thresholds are easily testable. Using this study as an example, our working hypothesis is that the critical surface fire intensity required for *J. ashei* mortality is >160 kJ m^{-1} s^{-1} given that fire intensity measurements are measured or estimated at the appropriate spatial scale (Twidwell *et al.* 2009) and FMC is $\leq 80\%$ (the hypothesized FMC required for crown combustion, Britton, Wester & Racher 2007). Additional experimentation can evaluate the assumptions surrounding this threshold, refine this information or reject it entirely, establish more precise threshold values and identify different or more realistic mechanisms that can be used by resource managers for restoration. Quantifying and testing thresholds in this manner has the potential to remove much of the speculation associated with carrying out restoration activities and prevent the establishment of techniques that offer false promise and unrealistic expectations, which has plagued restoration ecology in practice (see Hobbs *et al.* 2011). Moreover, such an approach not only allows applied ecology research to be linked to research in other scientific disciplines (e.g. Fig. 4), it also allows scientific information to be readily updated within management-oriented models (e.g. Table 3) as scientific knowledge expands, leading to more rapid adoption of experimental research in resource management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Video of a fire that exceeded the surface fire intensity–mortality threshold of an individual juniper tree.