CONCEPTS & SYNTHESIS

EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales

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Abstract. Regime shifts are difficult-to-reverse transitions that occur when an ecosystem reorganizes around a new set of self-reinforcing feedbacks. Regime shifts are predicted to occur when the intensity of some exogenous driver variable, such as temperature, annual harvest rate, or nutrient addition rate, gradually approaches and crosses a threshold value, initiating a transition to an alternative state. However, many driver variables now change rapidly as presses or pulses, not gradually, requiring new conceptual frameworks for understanding and predicting regime shifts. We argue that identifying and controlling regime shifts in response to presses and pulses will require a greater focus on the duration, not just the intensity, of changes in driver variables. In ecosystems with slower dynamics, transitions to an alternative state can take years to decades and as a result, a driver press with an intensity capable of resulting in a regime shift over long time spans may fail to cause a regime shift when applied for shorter durations. We illustrate these ideas using simulations of local-scale alternative stable state models and preliminary evidence from long-term grazing and eutrophication experiments. The simulations also suggest that small changes in the duration of driver presses or pulses can determine whether an ecosystem recovers to its original state. These insights may extend to larger scales. In spatially extended simulations that included patchiness, spatial heterogeneity, and spatial connectivity, all patches recovered to their original state after shorter presses. However, once press duration exceeded a threshold, growing proportions of the landscape shifted to an alternative state as press duration increased. We observed similar patchy transitions in a catchment-scale experiment that reinstated frequent fires approximately halfway through a regime shift from grassland to shrubland, initiated by fire suppression. In both the local- and larger-scale models, the threshold duration needed to elicit regime shifts decreased as press intensity increased or when factors counteracting regime shifts weakened. These multiple lines of evidence suggest that conceptualizing regime shifts as an interactive function of the intensity and duration of driver changes will increase understanding of the varying effects of driver presses, pulses, and cycles on ecosystem dynamics.

Key words: alternative stable states; bistability; catastrophic shifts; critical transitions; extreme events; invasive species; non-equilibrium; resilience; restoration; tipping points; transience.

Introduction

Regime shifts occur when an ecosystem reorganizes around a new set of self-reinforcing feedbacks in an alternative state (Holling 1973, Noy-Meir 1975, May 1977, Walker et al. 1981). Regime shifts can be difficult to reverse and often have major effects on biodiversity and ecosystem goods and services (Folke et al. 2004). Prominent examples of regime shifts include transitions between rainforest and flammable savanna (Hoffman et al. 2012), semiarid grasslands and desert shrublands (Walker et al. 1981, D'Odorico et al. 2012), clear and

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turbid freshwater lakes (Scheffer et al. 2001), and coral and macro-algal dominance (Mumby et al. 2007). The growing pace and extent of global environmental change could potentially force regime shifts at local to global scales (Barnosky et al. 2012). Therefore, it is critical to understand what changes in ecosystem drivers are likely to result in regime shifts.

Regime shifts, sometimes referred to as “state shifts, “state transitions,” or “catastrophic shifts,” typically result when the intensity of exogenous drivers exceeds a threshold value, making the current state no longer stable and initiating a transition to an alternative state (Fig. 1A, B; Scheffer et al. 2001, Bestelmeyer et al. 2011). However, it is increasingly apparent that many ecosystems take several years to decades to transition between states (deMenocal et al. 2000, Holling 2001, Mumby 2009, Fukami and Nakajima 2011, Hughes et al. 2013, Ratajczak et al. 2014*b*, Bozec and Mumby 2015). In these instances, we argue that (1) the reversibility of ecosystem transitions could hinge upon the duration of change in drivers as much, or more than the change in press intensity, and (2) that the press duration needed to trigger a regime shift is partially a function of pulse/press intensity and endogenous ecological characteristics, such as growth rate, life span, or spatial properties.

Many anthropogenic pressures on ecosystems have increased rapidly over the last century, from nitrogen deposition to stocking rate of livestock, fire suppression, and atmospheric CO_2 concentrations (Vitousek et al. 1998, Steffen et al. 2015). These pressures often change rapidly or abruptly and then are sustained as an extended “press” on the ecosystem (Fig. 1; Smith et al. 2009, Collins et al. 2011, Hughes et al. 2013). However, many of these changes in driver variables, especially those controlled at local and regional scales, could be reversed for economic or environmental reasons, resulting in global change presses or pulses that differ in their duration (Fig. 1). Climate change projections also forecast more extreme weather events, which will likely alter the intensity and duration of precipitation and temperature anomalies (Jentsch et al. 2007). Moreover, numerous climate drivers, such as seasonality, the El Niño Southern Oscillation, and solar insolation, follow cycles that vary in intensity (amplitude) and duration (wavelength; Hays et al. 1976, Stenseth et al. 2003, Schwinning and Sala 2004, Knapp et al. 2015, Honglin et al. 2016). Consumer abundance is frequently pulsed or cyclical as well, including pest outbreak cycles (Ludwig et al. 1978), disease epidemics (Prins and Van Der Jeugd 1993), and following regular migratory patterns (Holdo et al. 2009).

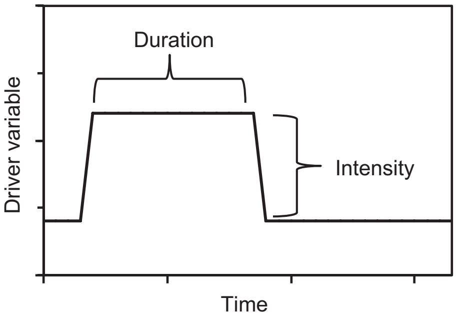

Fig. 1. Illustration of press with finite duration. We use “block function” presses, defined by a pre/post press driver variable value, press duration, and press intensity. Throughout the manuscript the term “driver press” is frequently used to refer to this type of change in driver variable over time. Note that shorter versions of such presses are similar to pulses. Cyclic variation in driver variables over time bears some resemblance to this type of press as well, with intensity roughly corresponding to amplitude, and duration to wavelength.

Yet differing characteristics of driver press/pulses, such as their duration, have rarely been considered as a determinant of whether or not a regime shift occurs. Instead, most theoretical work on thresholds and regime shifts has focused on long-term equilibria in modeling exercises where driver variables change slowly over time and the system remains close to equilibrium (e.g., Wissel 1984, van Nes and Scheffer 2007, but see Schmitz 2004, Fukami and Nakajima 2011, Hughes et al. 2013). In empirical research, repeatable experimental regime shifts have primarily been completed in systems that respond very quickly to changing conditions (e.g., Chase 2003, Carpenter et al. 2011), where the role of press duration is necessarily small. However, extending this assumption widely is not necessarily justified because many regime shifts tend to occur over longer periods of time (Hughes et al. 2013). Indeed, long-term experiments in terrestrial systems have typically taken at least 5–10 years to yield large changes in ecosystem state (Smith et al. 2015) that might constitute a regime shift (Bestelmeyer et al. 2011). As a result of this focus on gradual changes in driver variable, current conceptual frameworks are poorly equipped to predict which combinations of press/pulse characteristics have a greater chance of resulting in regime shifts.

Here we address the response to rapid changes in driver variables that are sustained for finite durations, rather than gradual sustained driver changes or near-equilibrium changes in state. This approach has rarely been applied to alternative state models previously (e.g., Scheffer et al. 2008, Hughes et al. 2013), despite the pervasiveness of driver presses in ecological experiments and areas impacted by global change (Jentsch et al. 2007, Smith et al. 2009, Collins et al. 2011). We used simulations of a foundational model of systems with alternative states (Noy-Meir 1975, May 1977) and three long-term experiments to investigate the ecosystem dynamics resulting from changes in driver variables applied as abrupt driver presses (Fig. 1). In both the experiments and models, these multi-year presses had intensities that exceed the threshold needed to initiate a transition towards an alternative state, based on past research of driver–response relationships (Bestelmeyer et al. 2011, Isbell et al. 2013, Ratajczak et al. 2014*a*). If changes in ecosystem state prove to be easily reversed after one of these external presses, it suggests that the duration of a driver press might have been insufficient to force a regime shift. In simulations, we were also able to assess how the effect of duration may vary as a function of press intensity and inherent characteristics, such as variation in vegetation growth rates. We also investigated the impacts of stochastic events, spatial context, and model generality. The analysis of spatial context used a spatially extended model to assess whether observations from the local-scale model apply at larger (e.g., watershed) scales that include patchy and heterogeneous spatial structure, and connectivity between patches. Using a spatially extended model also allowed us to assess how several proposed "resilience indicators" changed in response to press drivers (e.g., Scheffer et al. 2012). We conclude with a synthesis of these multiple approaches, along with a broader discussion of factors that should lead to slower transitions between states, and therefore, a greater role for press duration in ecological regime shifts.

THEORETICAL EVIDENCE

Modeling studies have demonstrated that it can take several time steps for some ecosystems to converge on an alternative state (e.g., Noy-Meir 1975, May 1977, van Geest et al. 2007, Blackwood et al. 2012) and that ecosystems can sometimes recover after being beyond a bifurcation for a short period of time (Hughes et al. 2013). However, even in these few instances where driver pulses have been considered in models with alternative stable states, the focus has been either solely on pulse intensity or duration (e.g., van Geest et al. 2007, Scheffer et al. 2008, Guttal and Jayaprakash 2009, Hughes et al. 2013). Our theoretical approach differs in that it explicitly addresses both how the duration *and* intensity of a press driver may determine whether a regime shift will occur, as well as the potential for press duration to exhibit threshold-like dynamics with the eventual ecosystem state. We also identify endogenous conditions that are likely to determine the combinations of press duration and intensity needed to force a regime shift. Uniquely, we include a spatially extended model to assess responses to press drivers in larger, more complex ecosystems.

In keeping with past work, we relate shifts between states with reference to unstable states and the long-term equilibria of a system. When the relationship between stable equilibria and ecosystem driver(s) exhibits a fold bifurcation, regime shifts between alternative states (or "attractors") are typically attributed to crossing one of two thresholds (Fig. 2A; Scheffer et al. 2001): ecosystem drivers may change (generally slowly) until they cross a bifurcation point, making the current state unstable and initiating the transition toward the alternative attractor (or state). Once this type of regime shift occurs the ecosystem will exhibit "hysteresis," a form of path dependency where the driver variable needs to cross a second bifurcation point for the ecosystem to return of its original state (Fig. 2A). Alternatively, an event can directly alter the ecosystem state (i.e., its state variable), pushing it across a critical threshold, corresponding to the unstable equilibrium (or "ridge") that separates alternative attractors (Fig. 2C).

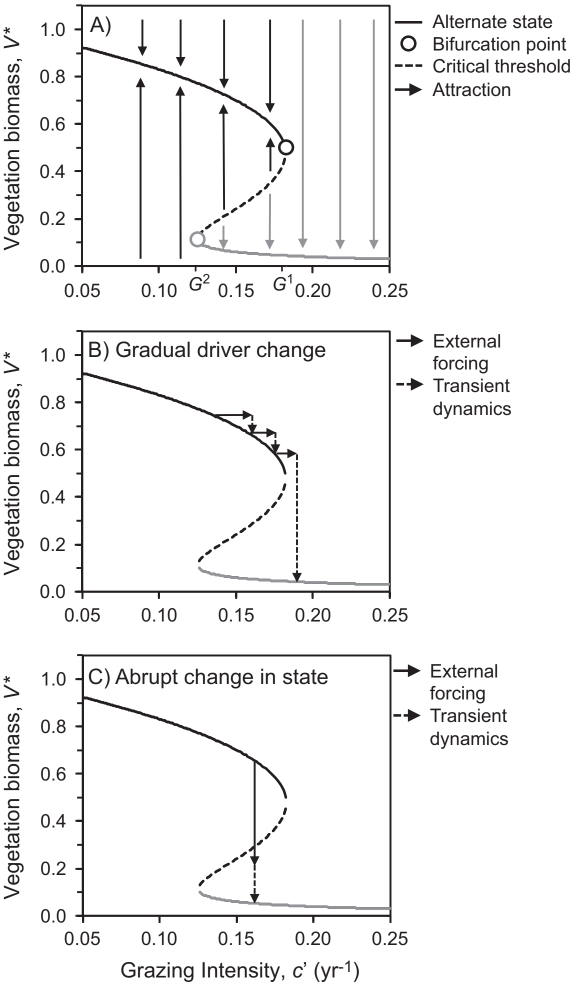

FIG. 2. (A) A fold bifurcation, with two alternative states: a high biomass state (the upper, solid black line) and the a low biomass state (lower, solid gray line). The two alternative states are attractors to which the system tends to converge. Arrows show the trajectory of the ecosystem for different initial conditions. The unstable equilibria (the dotted line), marks the boundaries of the two alternative states. At this boundary, small changes in state can force the system to the upper or lower state. The point G^1 is a bifurcation point, where the system goes from both the lower and upper state being stable, to only the lower state being stable. The system will start to transition to the upper state if the driver variable is reduced to the second bifurcation point, G^2. (B and C) Different types of transitions from one alternative state to another. In both panels, the solid arrows represent changes in driver variables, and dashed arrows show transient dynamics. In panel B, the driver variable increases gradually until exceeding a bifurcation point. In panel C, an event alters the state variable, bringing it below a critical threshold. This specific fold bifurcation is generated using the default parameters of the model (Appendix S1).

Local-scale simulations

For the majority of simulations, we used the grazing model developed by Noy-Meir (1975) and May (1977) and adapted by van Nes and Scheffer (2005). The model is a specific case of the more general "cusp catastrophe" (Ludwig et al. 1978, Petraitis 2013). For example, variations of this model have been used to describe budworm outbreaks (Ludwig et al. 1978), deer browsing in forests (Augustine et al. 1998), grazing impacts in semiarid grasslands (van de Koppel et al. 1997), biomass loss due to fire (D'Odorico et al. 2012) and other systems (van Nes and Scheffer 2005). For simplicity, we focus on a system with two stable states, rather than models with more than two stable states. We also did not consider systems with only a single attractor. Single attractor versions of the model (by relaxing the exponent in Eq. 1) also show displacement during a press or pulse, but they will return to their original state after the press/pulse ends regardless of its intensity or duration, due to the lack of critical thresholds in single-attractor systems (Hughes et al. 2013).

The model describes vegetation (V) dynamics as

$$\frac{\mathrm{d}V}{\mathrm{d}t} = rV\left(1-\frac{V}{K}\right) - c\left(\frac{V^2}{V^2+1}\right) \qquad (1)$$

where r is maximum growth rate of vegetation, K is vegetation carrying capacity, and c is the maximum grazing rate or grazing pressure (an exogenous driving variable in our simulations). The vegetation grows logistically in the absence of grazing pressure. A non-linear relationship between the proportion of vegetation removed per unit grazing pressure and vegetation density, ($c[V^2/V^2 + 1]$), captures an often-observed feedback where vegetation is more resistant to consumption at higher biomass and/or consumer efficiency is lower at higher biomass (Noy-Meir 1975, May 1977). This can reflect changes in tissue palatability and accessibility, among other factors. For instance, in perennial grasslands, new growth patches are poorly protected against herbivores, whereas higher biomass patches have tougher, silicate-rich tissue, which reduces herbivore consumption (McNaughton 1984). Similarly, the meristems of small trees and shrubs are not resistant to the flames of surface fires, resulting in greater mortality until a high biomass is reached (D'Odorico et al. 2012, Hoffman et al. 2012). These dynamics can also arise when the herbivore has a "type III" functional response with respect to vegetation biomass, which exhibits a sigmoidal relationship with increasing vegetation biomass and is common for many vertebrates (Holling 1959, May 1977).

While we recognize that the response to press intensity and duration is likely to depend upon multiple factors, our simulations focus on the intensity of change in grazing pressure (c) and its interactions with vegetation growth rate, r (Dakos et al. 2010). The simulation results are presented in terms of non-dimensional vegetation biomass $V^* = V/K$ (ranging between 0 and 1) as a function of the growth rate r (time^{-1}) and the normalized grazing rate $c' = c/K$ (time^{-1}). While the units for time are not specified, for simplicity we interpret each time-step to be a year. The parameter values used in the simulations cover the same range as other uses of this model (e.g., van Nes and Scheffer 2005, Dakos et al. 2010, Fukami and Nakajima 2011, Hughes et al. 2013; see Appendix S1). All simulations were performed in R (R Core Team 2015).

As a result of the greater proportional loss of vegetation at low vegetation biomass, this model has two alternative states for many levels of grazing: high vegetation biomass that is more resistant to grazing pressure (high biomass state) and low biomass that is less resistant to grazing pressure (low biomass state). At intermediate grazing rates, both high and low biomass states are potentially stable states separated by a critical threshold, with the asymptotic state depending on past events and initial conditions (Fig. 2A). When grazing exceeds a bifurcation point, only the low biomass state is deterministically stable. Once in the low biomass state, the ecosystem can return to the high biomass state if grazing pressure is reduced below a second bifurcation point (Fig. 2B). When we apply presses to the model, we make the assumption that grazing pressure will return to its pre-press value, which falls within the bistable region of the system. If grazing pressure were returned to a lower level, recovery would be guaranteed.

The description of alternative vegetation states in terms of bifurcation points and long-term equilibria, however, does not capture key transient behaviors. The first simulations start with the ecosystem in a high biomass state and grazing rate below the bifurcation point. When we increase grazing pressure beyond the bifurcation point, the system begins a transition towards the low biomass state. If grazing pressure is relaxed before the vegetation biomass falls below a corresponding critical threshold, the vegetation returns to the high biomass state (see the blue lines in Fig. 3D). Otherwise, the vegetation converges on the low biomass state (see the red line in Fig. 3A, D, G) where the vegetation resistance to grazing has declined so greatly that even relatively low grazing pressure precludes a return to the high-biomass state (Noy-Meir 1975, May 1977). The relationship between press duration and regime shifts follows a threshold-like relationship. For instance, with a moderate increase in grazing pressure (changing c' from 0.140 to 0.215 yr^{-1}), the ecosystem returns to the high biomass state if grazing is returned to its initial value after a press of 10 years (orange lines in Fig. 3A, G), but converges to the low biomass state if press duration exceeds 10 years (red lines in Fig. 3A, G).

If the intensity of the grazing press increases, vegetation biomass declines faster (Fig. 3B, H) and therefore, the press duration needed to force a regime shift decreases, eventually approaching a minimum transition time of ~5 years (see the dashed line in Fig. 4A). For instance, the ecosystem returns to a high biomass state after a press with an intensity of $\Delta c' = 0.07$ and duration of 10 years (green lines in Fig. 3B, H), but converges on the low biomass state after a press of slightly higher intensity for 10 years (orange lines in Fig. 3B, H). The press duration needed to force a regime shift decreases steeply and then saturates as press intensity increases (Fig. 4A).

The effects of press intensity and duration might vary between and within ecosystems based on certain endogenous characteristics. Many ecosystems or patches within

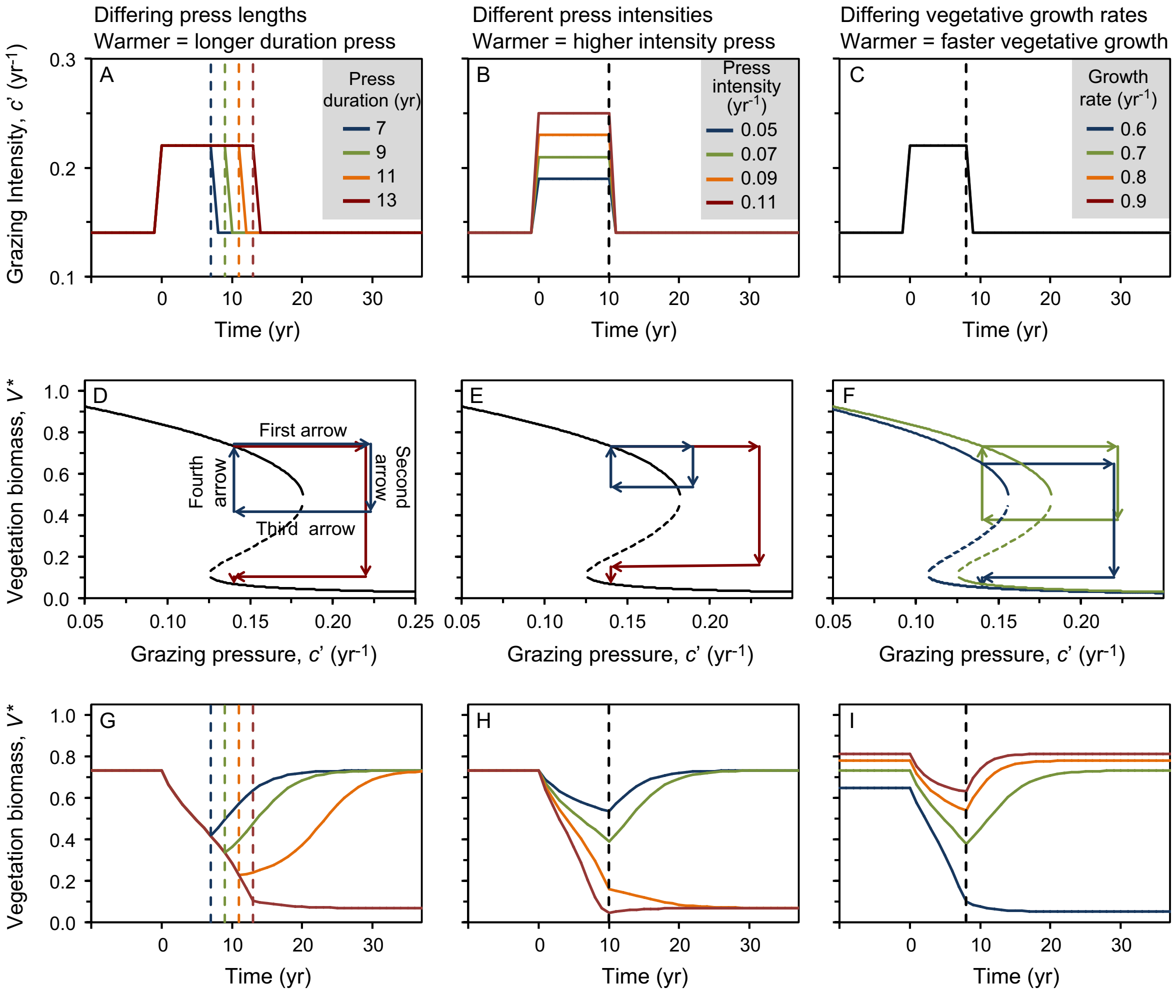

Fig. 3. Application of presses (shown in the first row, A–C) and the ecosystem response over state space (second row, D–F) and time (third row, G–I). The second row (D–F) shows changes in state over time, relative to the fold bifurcation in this system. In this row, the first arrow depicts the onset of the press, the second arrow depicts the change in state that has occurred by the end of the press, the third arrow is the change in grazing associated with the end of the press, and the fourth arrow is how ecosystem state changes after the press ends (see the first row for a labelled example). In the first column, press intensity and vegetation growth remain constant and press duration varies, with "warmer" colored lines corresponding to longer presses and the ecosystem response over state-space and time. In the second column, only press intensity varies, whereas press duration and vegetation growth rate are constant. "Warmer" colors in this column correspond to presses with larger intensities. In the third column, the press duration and intensity are constant, but vegetation growth rate differs. The differences in growth rate result in different underlying fold bifurcations in the system, where "warmer" colors correspond to higher vegetation growth rates (only two of the growth rates are shown in panel F, to avoid clutter). See Appendix S1 for parameter values. Note that some arrows were jittered horizontally in D and F for visual clarity.

ecosystems differ in their growth rate, due to variation in substrate, species composition, and other factors (Levin 1992, Frehlich and Reich 1999, Collins and Xia 2015, Chisholm et al. 2015). To evaluate how differences in growth rate might interact with press duration, we altered growth rate and kept press duration and intensity constant. In the model (Eq. 1), higher vegetation growth rates lead to higher potential equilibrium biomass for a given value of grazing pressure and also increase the grazing pressure needed to exceed a bifurcation point, because greater vegetation growth offsets proportionally more of the biomass removed by grazers (Fig. 3F; May 1977). For an illustration, compare the fold bifurcation depicted by blue lines in Fig. 3F, where $r = 0.6$, to the fold bifurcation depicted by green lines, where $r = 0.7$. Similarly, we found that the press duration needed to precipitate a regime shift decreases as vegetation growth rate decreases. For example, after a moderate-intensity press ($\Delta c' = 0.08$) for 8 yr, the ecosystem recovers to the high biomass state if $r = 0.7$ (green lines in Fig. 3I), but the same press intensity and duration results in a regime shift to a low biomass state if $r = 0.6$ (blue line in Fig. 3I). Considering a range of vegetation growth rates, the press duration needed to force a regime shift varies from 10 to >40 years for a low-intensity grazing press (dashed line in Fig. 4B) and 3–40 years for a high-intensity grazing press (dashed line

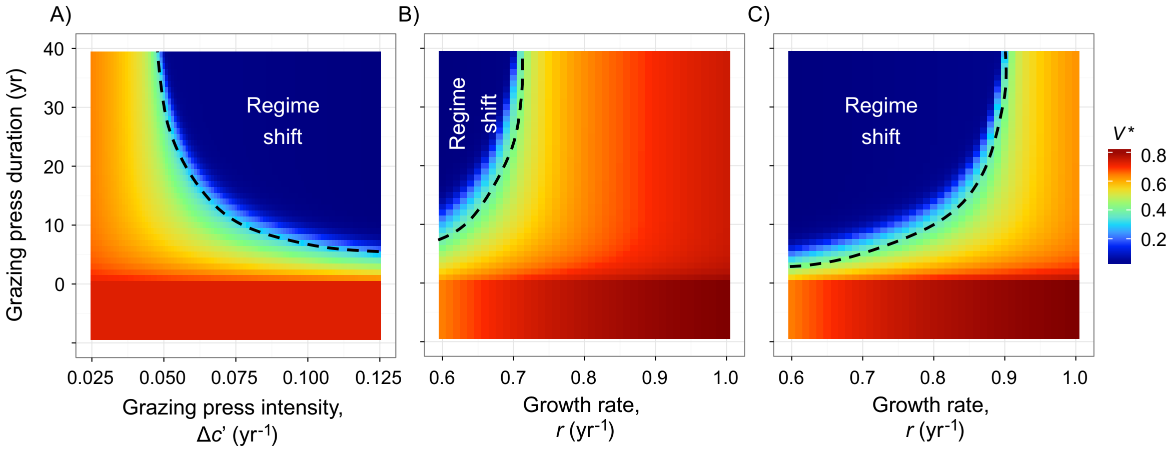

FIG. 4. Factorial simulation experiment altering (A) press duration and intensity, (B) press duration and growth rate for a low intensity increase in grazing, and (C) vegetation growth rate and press duration for a high intensity press. Panel A shows the response of vegetation to sustained presses of different intensity (*x*-axis) over time (*y*-axis), with vegetation growth held constant. Panels B and C shows vegetation response by patches with different vegetation growth rates (*x*-axis) over time (*y*-axis). Panel B is a low intensity press (maximum grazing rate increased by $\Delta c' = 0.05\ \text{yr}^{-1}$) and panel C is a high intensity press (maximum grazing rate increased by $\Delta c' = 0.1\ \text{yr}^{-1}$). In all panels "warmer" colors denote greater biomass and blue, lower biomass. Time 0 is the start of the press. The dashed line demarks a line that, when crossed, results in lasting transitions to the low biomass state. Presses greater than this dashed line on the *y*-axis exceed a duration needed to force a transition to the alternative low biomass state. See Appendix S1 for parameter values.

in Fig. 4C). For both press intensities, the press duration needed to force a regime shift decreases non-linearly as vegetation growth rate decreases (Fig. 4B, C).

Local-scale model with temporal stochasticity

Most ecosystems are affected by stochastic events, such as disease, drought, and emigration/immigration (e.g., Holmgren and Scheffer 2001, Turner 2010, Ridolfi et al. 2011). We accounted for stochasticity by adding a white-noise term ($\sigma\, dW\sigma dW$) to the model

$$\frac{dV}{dt} = rV\left(1-\frac{V}{K}\right) - c\left(\frac{V^2}{V^2+1}\right) + \sigma dW\sigma dW \qquad (2)$$

where notation follows Eq. 1 and σ denotes the strength of normally distributed perturbations. We considered three different noise strengths (0.05, 0.1, and 0.2) over a factorial combination of press intensities and durations, determining the average and standard deviation of the final state 200 time-steps after presses were initiated ($n = 100$ iterations of each combination of noise strength, press intensity, and press duration). Greater standard deviations of the final vegetation biomass (V^*) indicate greater uncertainty, where the vegetation sometimes returns to either the high or transitions to the low biomass state, rather than consistently converging on one of the two states.

When white noise is added to the grazing model, the general relationship between regime shifts and press intensity/duration held; vegetation usually returns to the high biomass state if presses are maintained for less than 3 years and in general, the press duration that will result in a regime shift decreases non-linearly as press intensity increases (Fig. 5). However, the final state of the system becomes more unpredictable as noise strength increases, press intensity decreases, and near the press duration(s) that consistently resulted in regime shifts in the simulations without noise (Fig. 5B–D). For instance, comparing the standard deviation of the final V^* in a system with weak noise strength (Fig. 5F) to a system with strong noise strength (Fig. 5H), the simulations with stronger noise had more combinations of press intensity and duration where the final state varied between iterations (shown by orange to red and fills). These results underscore that estimates of duration thresholds based on past models or experiments should be considered as tentative estimates of duration thresholds that can be altered by stochastic events.

Spatially extended model

To explore the effects of press/pulse duration in both time and in space, we used a spatially extended implementation of the vegetation model (van Nes and Scheffer 2005, Dakos et al. 2010). This spatially extended model gives perhaps the most realistic assessment of how ecosystems will respond to large external presses and pulses, as ecosystems are often spatially heterogeneous and exhibit some degree of patchiness and connectivity between nearby patches (Levin 1992, Turner 2010, Okin et al. 2015). Moreover, many press drivers often have a large spatial footprint (e.g., migrations of herds, nitrogen deposition, climate change). For grazing pressure specifically, press intensity might increase at large scales due to migration patterns, the development of new technologies

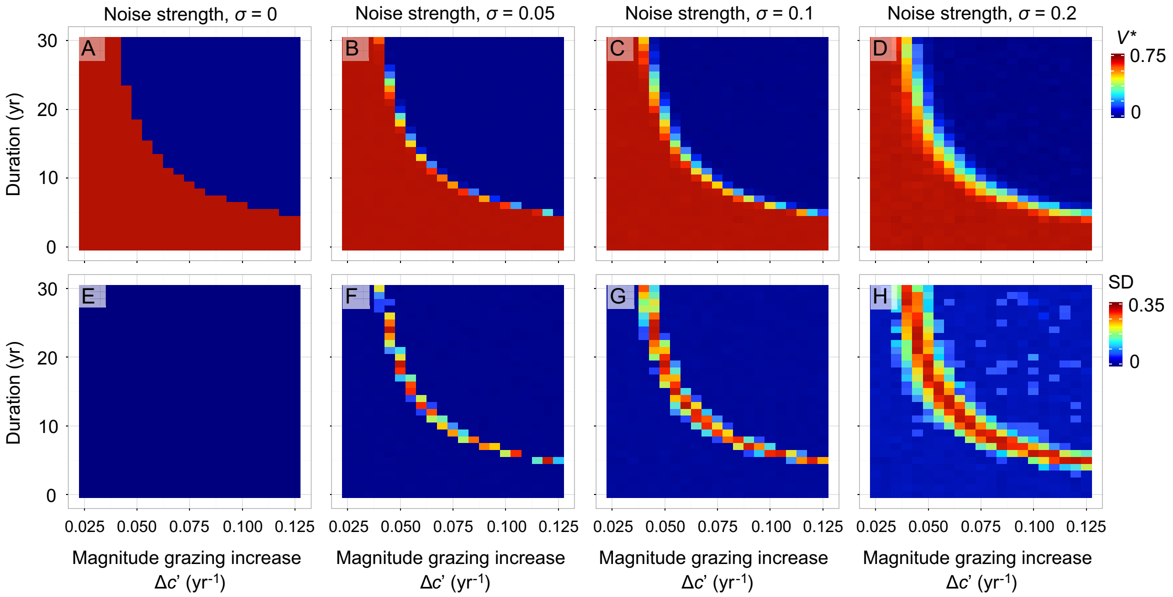

FIG. 5. Implementation of the grazing–vegetation model with white noise (Eq. 2) as a source of temporal stochasticity. Noise strength increases from left to right, ranging from a noise strength of $\sigma = 0$ (A and E) to $\sigma = 0.2$ (D and H). Panels A–D show the average final states 200 time steps after presses were initiated, for presses with different intensities (*x*-axis) and durations (*y*-axis). "Warmer" fills denote that on average, the ecosystem recovered to a high biomass state more often. Panels E–H show the standard deviation of the final state for each combination of press intensity and duration, with "warmer" fills indicating a greater standard deviation in the final state for the 100 iterations for each combination of press intensity and duration.

or norms that allow grazer concentration (i.e., barbed wire) or when multiple managers respond to the same market forces (i.e., a large increase in the price of beef).

In the spatially extended model, the system is composed of a mosaic of 2500 patches arrayed across two dimensions (*i* and *j*) with each patch ($V_{i,j}$) following the dynamics of Eq. 1, but with spatial interactions between direct neighbors (vertical and horizontal) expressed by a diffusion term

$$\begin{aligned} dV_{i,j}/dt = {} & r_{i,j}V_{i,j}(1 - V_{i,j}/K) - c(V_{i,j}^2/V_{i,j}^2 + 1) \\ & - D(V_{i+1,j} + V_{i-1,j} + V_{i,j+1} + V_{i,j-1} - 4V_{i,j}) \end{aligned} \qquad (3)$$

Biomass diffuses from high to low biomass patches, with a rate that depends on the differences in biomass between adjacent patches and a diffusion coefficient (*D*). This is not a perfect represention of spatial dynamics in real-word grazing systems, but has the benefit of approximating many different common spatial processes (Levin 1992), such as mass-flow of water and the spread of tillers towards areas of low vegetation density. Underlying spatial variability was included by drawing the vegetation growth rate for each patch, $r_{i,j}$, from a normal distribution. Relative to other spatially extended implementations of this model (e.g., van Nes and Scheffer 2005, Dakos et al. 2010), we use a low to intermediate degree of spatial connectivity (the diffusion coefficient, $D = 0.01$, between directly adjacent patches) and an intermediate to high degree of spatial heterogeneity (captured by the standard deviation of the normal distribution used to generate values of $r_{i,j}$; Appendix S1). Our implementation has edges that constrain biomass diffusion, rather than using a torus. This is a more realistic implementation, as many ecosystems have edges due to human-made or natural barriers.

Applying presses of uniform intensity to all patches of the spatially extended system, similar relationships between press duration, press intensity, vegetation growth rate, and the potential for regime shifts are evident. After a 5-year press of moderate intensity is relaxed, almost all patches return to the high biomass state (blue lines in Fig. 6A, B), whereas after a press of the same intensity but a duration of >12 years, nearly all patches converge on the low biomass state (red lines in Fig. 6A, B). For presses with the same intensity but falling between these two durations (>5 and <12 years long), an increasing number of patches converge on the low biomass state as press duration increases (see green, yellow, and orange lines in Fig. 6B for responses over time and Fig. 6C for how the long-term average state is related to press duration). When these presses end, patches with lower vegetation growth rate have usually lost more biomass and are less likely to return to the high biomass state (third column Fig. 7, second column Fig. 8). However, some patches with lower vegetation growth rates are able to remain in the high biomass state because of the buffering effect of spatial interactions, as biomass diffuses from patches with high vegetation growth rates ($r_{i,j}$) to patches with lower growth rates (Figs. 7 and 8). These results suggest that if a press of uniform intensity is applied to heterogeneous landscapes, it may produce patchy regime shifts over a range of different press durations (Figs. 6–8).

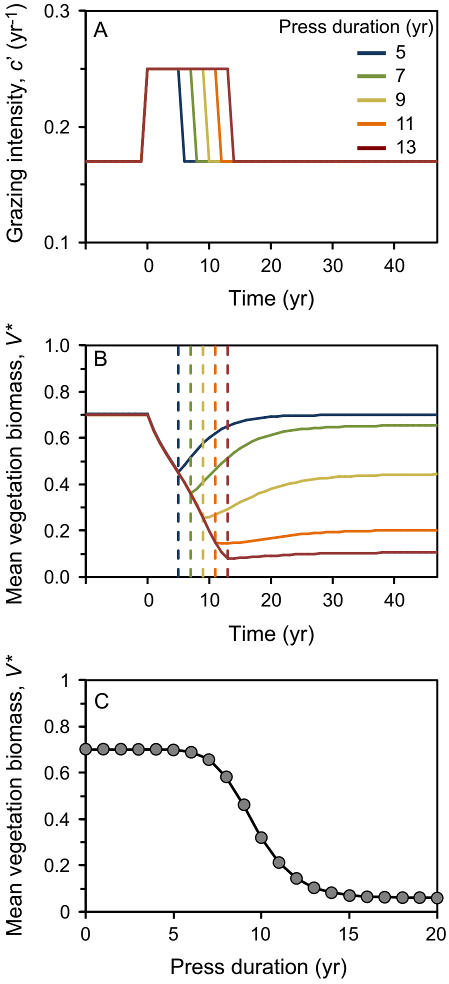

FIG. 6. (A, B) Results from the spatially extended implementation of the grazing model, subject to uniform press intensity ($\Delta c' = 0.08$) and (A) press durations ranging from 5 to 13 yr. In both panels A and B, warmer line colors denote longer press durations and their ecological responses, respectively. (B) The vegetation response (the average V^* across all of the patches) for each press duration in panel A. Note that the mean V^* is strongly correlated with the number of patches that remain in a high biomass state. In other words, a mean V^* of ~0.4 indicates that approximately half of patches transitioned to the low biomass state. (C) The relationship between press duration and mean vegetation biomass (V^*) 100 years after presses end. Each line in panel B and point in panel C is the median of 100 iterations. Variability between runs in panels B and C is not shown because it was barely visible graphically.

In line with the base model (Eq. 1), the press duration needed to force a transition in all patches decreases as press intensity increases (Fig. 9). For instance, at the highest press intensity we considered, a press of 8 yr results in regime shifts to the low biomass state in nearly all the patches, whereas for the lower press intensity, a press duration >13 years is needed to force a regime shift across most patches. The press duration needed to result in regime shifts across most patches is a saturating function of press intensity, where at a certain point (~$\Delta c' = 0.11$) further increases in grazing pressure only lead to slightly faster transitions to the low biomass state (Fig. 9). As press intensity increases, the range of press durations that results in spatially patchy regime shifts also shrinks, such that most press durations result in either all patches returning to a high biomass state or almost all patches transitioning to the low biomass state. This relationship is shown by the sharper vertical transition from “warm” to “cold” colored cells as press intensity increases in Fig. 9. Results from the base model can explain these increasingly binary outcomes at high press intensities. Fig. 4B depicts responses to a low-intensity press as a function of the vegetation growth parameter r, and shows that decreasing r from 0.7 to 0.6 results in a 600% faster transition to the low biomass state (Fig. 4B). In contrast, the same change in r only slows the transition by about 50% for a high intensity press (Fig. 4C).

Larger ecosystems are often characterized by more than just their average state. For instance, landscapes can exhibit different degrees of spatial variability between patches, varying degrees of spatial patchiness, and pattern formation (Levin 1992). To capture other landscape characteristics of the vegetation-grazing model responses to driver presses, we assessed spatial variance, spatial skewness, and spatial auto-correlation of vegetation biomass before, during, and after four presses of varying intensity. These three metrics are thought to increase as an ecosystem approaches a bifurcation point (Scheffer et al. 2012, Kefi et al. 2014). Therefore, an increase in any of these three spatial properties might serve as an “early warning sign” or “resilience indicator” that a driver variable is approaching a bifurcation point (Scheffer et al. 2012, Kefi et al. 2014). Spatial variation was measured as the statistical variance of all patches, skewness was calculated as the third statistical moment (using the “moments” package in R), and spatial autocorrelation was measured using Moran’s I, at a lag of +1 (from the earlywarnings package in R; Dakos et al. 2012, Kefi et al. 2014). Moran’s I (lag+1) ranges from −1 to 1, with positive values indicating that the state of adjacent patches tend to be more similar than would be expected by chance and negative values indicating that the state of adjacent patches tend be more dissimilar than would be expected by chance. All three metrics were calculated at the end of each time step, using all 2500 patches.

After presses initiated a regime shift, spatial variance increased over time, peaked about halfway through the transition to a low biomass state, and then decreased to approximately pre-press values (Fig. 10B). Spatial autocorrelation and skewness followed similar patterns, except that increases in spatial autocorrelation were fairly small (Fig. 10C) and spatial skewness peaked long after both spatial variance and autocorrelation (Fig. 10D). Peaks in all three of these measurements came sooner for higher-intensity presses, but reached lower maximum values. If presses are ended shortly before spatial variance peaks, regime shifts occurred in less than one-half of the patches (see dashed arrows in Fig. 10B–D), suggesting that increases

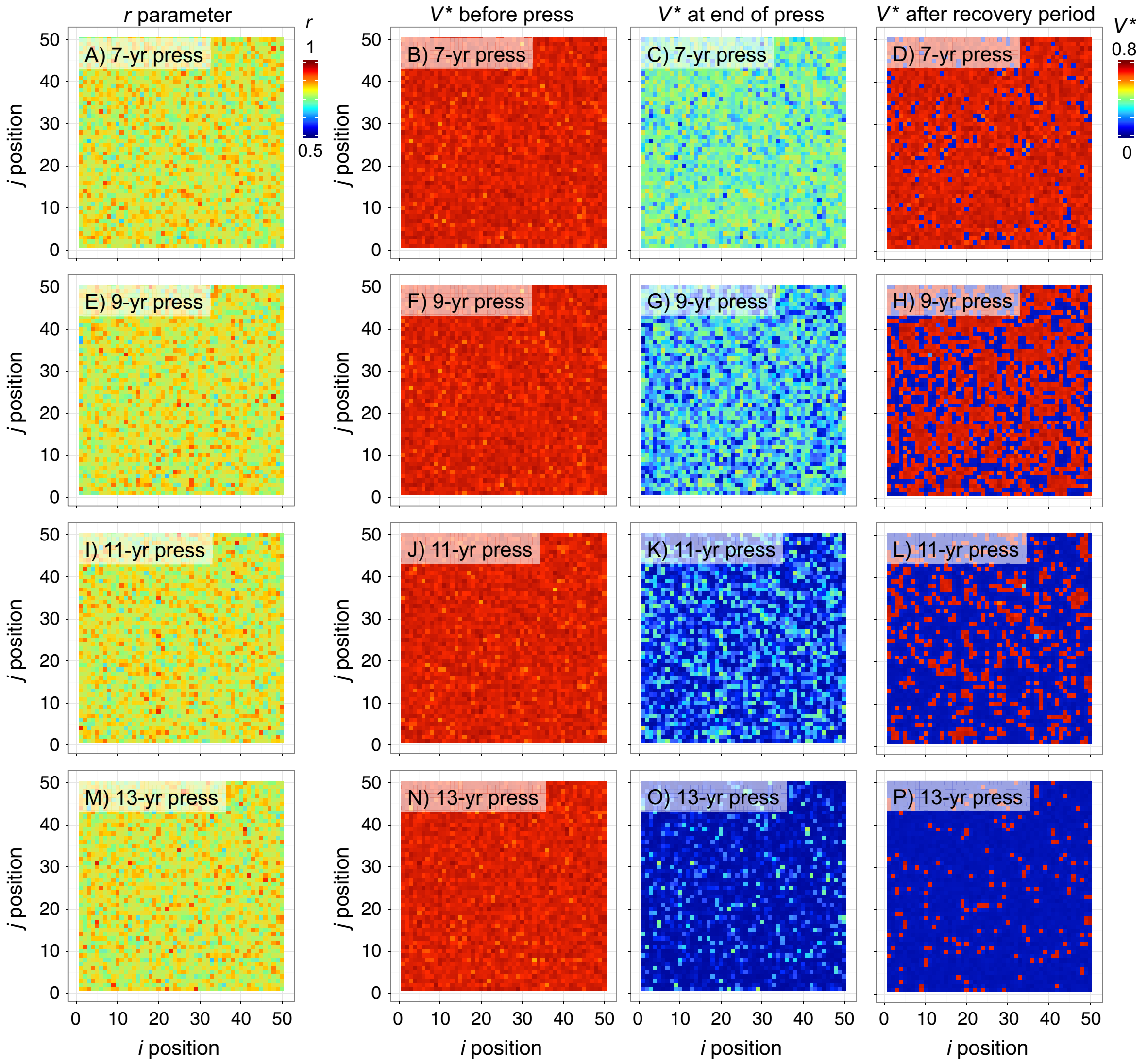

FIG. 7. Overhead views of single runs of the spatially extended model responding to a driver press with the same moderate intensity as in Fig. 6 and for varying durations of (A–D) 7, (E–H) 9, (I–L) 11, or (M–P) 13 years. The first column of panels depicts variation in the vegetation growth rate, r, with warmer colors corresponding to greater values of r (see scale to the right of panel A). The second, third, and fourth columns are overhead views of vegetation biomass, V^*, with warmer colors corresponding to greater values of V^* (see scale next to panel D). The second column depicts V^* before the press is applied, the third column is V^* at the end of the press, and the fourth column is 100 years after the press ends. In all panels, each box or "pixel" represents one patch of the system, the x-axis is dimension i and the y-axis is dimension j.

in spatial variance might be useful as an indicator that the duration of a press is reaching a threshold, beyond which large-scale regime shifts occur. In comparison, a press with an intensity too weak to initiate regime shifts (the lightest gray lines in Fig. 10) resulted in a slight increase in spatial variance and autocorrelation, and a slight decrease in skewness over the time frame we considered (Fig. 10; similar to Guttal and Jayaprakash 2009, Dakos et al. 2010).

Spatial variance and skewness increased during the transient phase of regime shifts, because small patch-scale differences in vegetation growth rate lead to large differences in how fast a patch transitions to a low biomass state. For instance, before a press is applied to the system, vegetation growth rate ($r_{i,j}$) is positively correlated with vegetation biomass (V^*), but the slope of this relationship is shallow (see the first column of Fig. 8). In contrast, partway through the transition to a low biomass state, the slope between vegetation growth rate and vegetation biomass is still positive, but steep, indicating that patches with low values of r_{ij} transition to a low biomass state much faster (second column of Fig. 8). This behavior is effectively an inverse of "critical slowing down," which refers to the tendency of ecosystems to return to equilibrium slowly as they near a bifurcation point (Wissel 1984, van Nes and Scheffer 2007). In the case of a press driver, patches with higher vegetation growth rates are

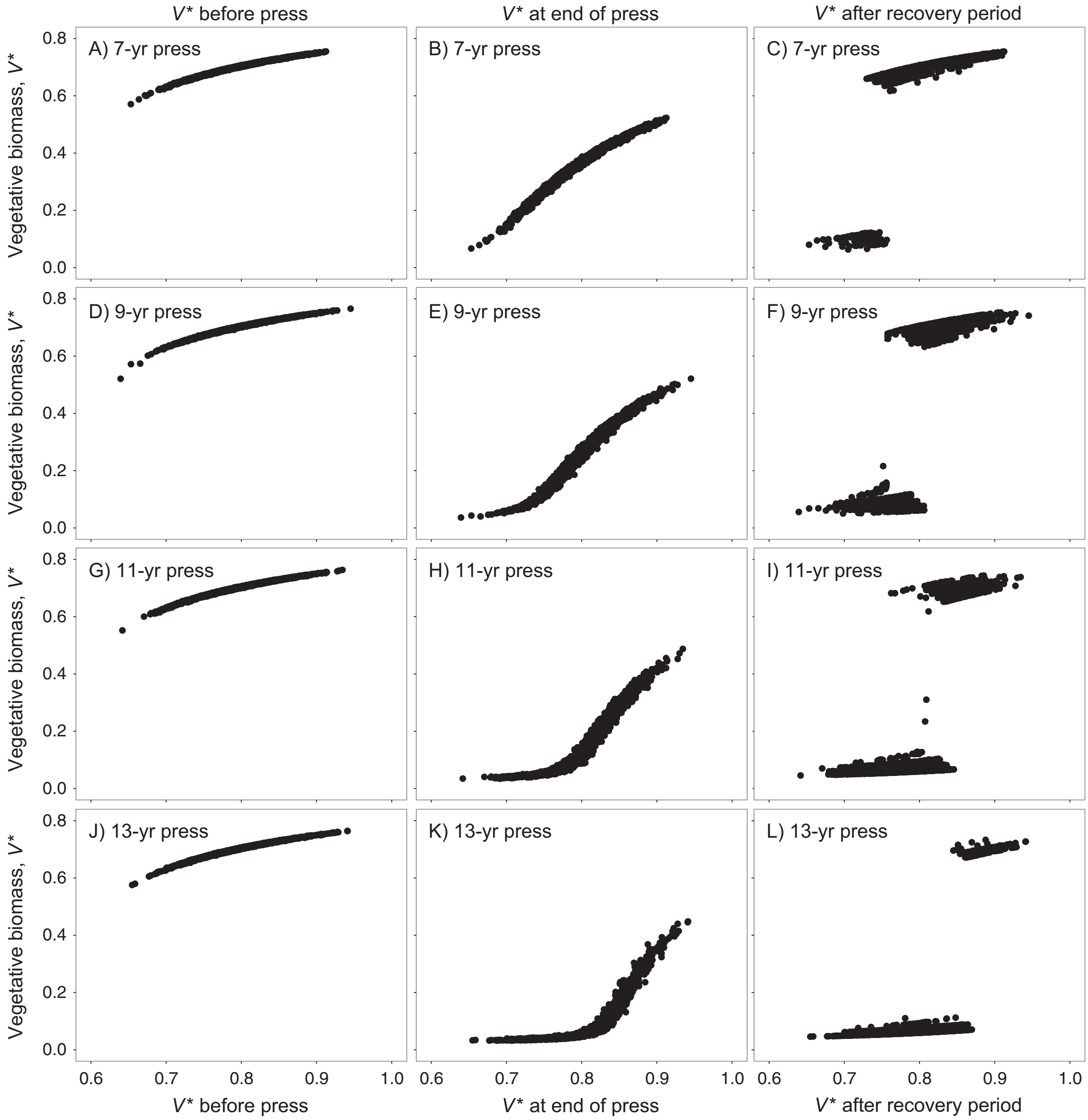

FIG. 8. Relationships between patch-scale vegetation growth rate, r (yr^{-1}), and vegetation biomass, V^*, in the spatially extended model. Each row is a single iteration of the spatially extended model, subjected to a press of the same moderate intensity as in Fig. 6 and varying durations of (A–C) 7, (D–F) 9, (G–I) 11, or (J–L) 13 years. The first column depicts V^* before the press is applied, the second column is V^* at the end of the press, and the third column is 100 years after the press ends. Each point is one of the 2500 patches.

pushed just beyond a bifurcation point, and as a result, approach their new equilibrium biomass slowly. For instance, compare how much farther a patch is beyond its bifurcation point under a low vegetation growth rate (blue lines in Fig. 3F), to a patch with a slightly higher vegetation growth rate (green lines in Fig. 3F), even though the driver press itself is the same. A key difference between this behavior and critical slowing down is that the distance to a bifurcation point is affecting how fast a patch or ecosystem moves towards a new attractor, rather than how fast the ecosystem returns to an antecedent equilibrium (see van Geest et al. 2007 for similar behaviors in shallow lakes).

Synthesis of simulations

Together, the simulation experiments presented here suggest that this often-used model of vegetation with alternative states (Noy-Meir 1975, May 1977, van Nes and Scheffer 2005) can exhibit threshold-like relationships

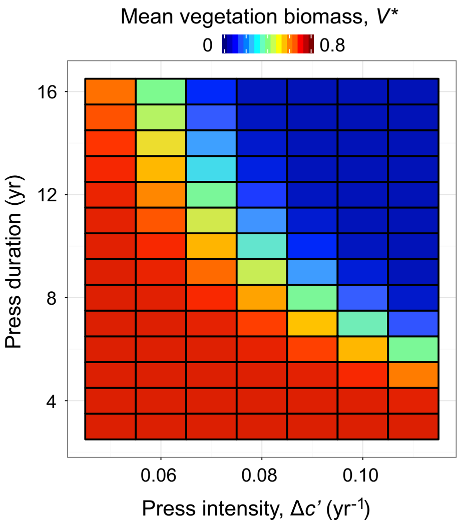

FIG. 9. Average final vegetation biomass in the spatially extended model 100 years after presses end, for presses of different intensity (*x*-axis) and duration (*y*-axis). Warmer colors correspond to greater final average biomass, V^*. Note that the mean V^* is strongly correlated with the number of patches that remain in a high biomass state. In other words, a mean V^* of ~0.4 (green) indicates that approximately half of patches transitioned to the low biomass state. Each cell is the mean of 100 model iterations.

between press duration and the eventual ecosystem state (sensu Briske et al. 2006, Groffman et al. 2006). These results are slightly affected by adding white noise (Fig. 5) and robust to using incremental driver presses, rather than discrete presses (Box 1 and Fig. 11). Moreover, these results were not specific to the model we chose, based on simulations of four other dynamical system models (see Box 2 and Fig. 12). Spatial heterogeneity smoothed out some of the threshold behavior of the local-scale vegetation-grazing model (Figs. 6C and 7), but even the spatially extended version of this model exhibited cut-off values of press duration where the system exhibited almost complete recovery or regime shifts across all patches (Figs. 6C and 9). In the local-scale model, presses of greater intensity have a lower threshold press duration needed to force a regime shift, whereas in the spatially extended model, increasing the intensity and/or duration of presses resulted in an increasing number of patches undergoing transitions. The spatially extended simulations suggest that increases in spatial variance over time can potentially indicate a driver press is reaching the duration where a large proportion of the landscape will undergo a regime shift, unless a press ends immediately (Fig. 10B).

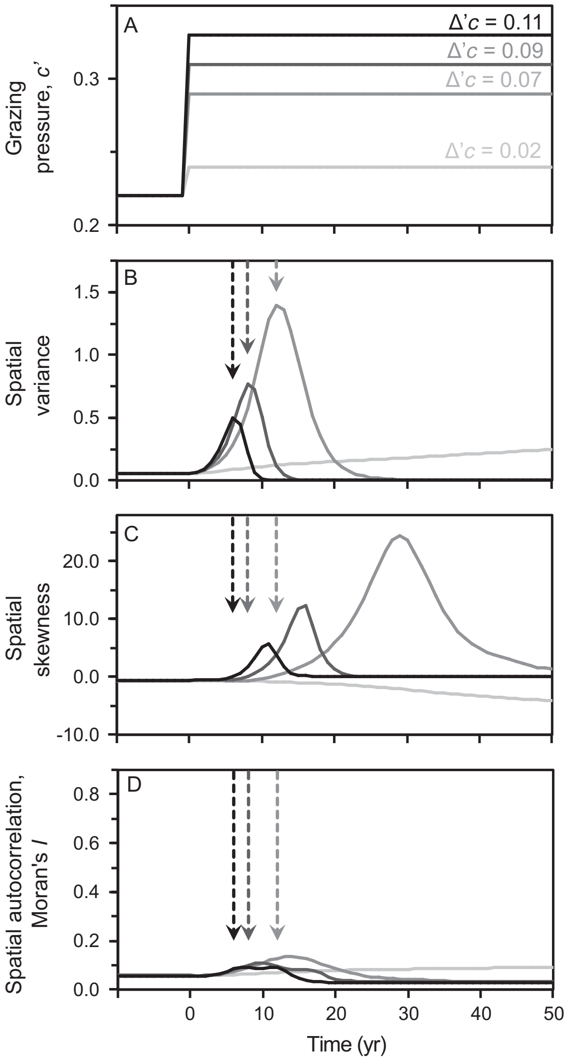

FIG. 10. Changes in (B) spatial variance, (C) skewness, and (D) auto-correlation (lag + 1) over time in response to grazing press intensities (A) of $\Delta c' = 0.02$ (light gray), $\Delta c' = 0.07$ (gray), $\Delta c' = 0.09$ (dark gray), or $\Delta c' = 0.11$ (black). The press of $\Delta c' = 0.02$ leads to a slight decrease in vegetation biomass, but few if any regime shifts at the patch scale. The other press intensities are high enough to result in a transition of all patches to low a biomass state, if the presses are maintained over a long enough period of time. The vertical arrows in panels B–D denote the press duration where approximately one-half of patches will transition to a low biomass state if a press is ended at that time.

EMPIRICAL EVIDENCE

To assess empirically how press duration might affect regime shifts, we provide insights from three experimental case studies. Varying press duration is not a common experimental treatment (but see Schmitz 2004, Augustine et al. 2014), forcing us to rely on indirect inferences for preliminary evidence of whether duration influences regime shifts. In all three cases, this entailed applying driver presses of a finite duration (4, 10, or 20+ years), at press intensities that could eventually result in regime shifts. The exact thresholds underlying the dynamics of these systems are unknown, but there is strong evidence that all three systems exhibit hysteretic state changes in response to grazing (first case study), nitrogen addition (second case study), and fire suppression (third case study), suggesting the existence of

Box 1. Incremental Change in Driver Variable.

Certain driver variables—such as atmospheric CO_2, average temperature, and increases in consumer pressure by organisms with slow regeneration times (i.e., whales, elephants)—tend to change incrementally, not in the discrete steps as we modeled throughout this manuscript. We performed simulations where grazing pressure exceeded bifurcation points smoothly but rapidly, rather than in discrete presses (Fig. 11A–D). Similar patterns emerged as the simulation of discrete presses, with regime shifts being more likely when a bifurcation point is exceeded for longer (Fig. 11A, D), when temporary increases in grazing pressure have a higher intensity (Fig. 11B, E), and if vegetation growth rate is lower (Fig. 11C, F) (see also Hughes et al. 2013).

alternative states (Schlesinger et al. 1990, Gibbens et al. 2005, Yao et al. 2006, Bestelmeyer et al. 2011, Isbell et al. 2013, Twidwell et al. 2013, Ratajczak et al. 2014*a*). In systems known to have alternative stable states we can assess empirically the effect of press intensity and duration on regime shifts, unlike single attractor systems where eventual recovery is guaranteed (Hughes et al. 2013).

Grazing and shrub encroachment

The first case study takes place in upland grassland in the northern Chihuahuan Desert, New Mexico, USA (see Bestelmeyer et al. 2013 for more details). At this site, there is overwhelming evidence that large areas have transitioned to an alternative shrubland state featuring very low grass cover, which has been attributed to high grazing pressure during periods of low precipitation (Yao et al. 2006, Bestelmeyer et al. 2011). Shrubland states have persisted to the present day (over 50 years), even with significant declines in grazing pressure (Gibbens et al. 2005, Yao et al. 2006), suggesting this ecosystem exhibits alternative grassland and shrubland stable states. The persistence of a shrubland state is attributed to a positive feedback with soil loss and decreases in water infiltration and retention when grass and litter biomass decline (Schlesinger et al. 1990, Bestelmeyer et al. 2011, Okin et al. 2015). The experiment in this system imposed a press that increased grazing pressure to over twice the recommended values for the region ($n = 6$, 0.5-ha grass-dominated paddocks). The grazing resulted in 65–80% grass defoliation per year, near the maximum possible amounts that can be harvested (compared to ~30% prior to the experiment). This grazing treatment was designed to exceed the intensity of grazing thought to have caused

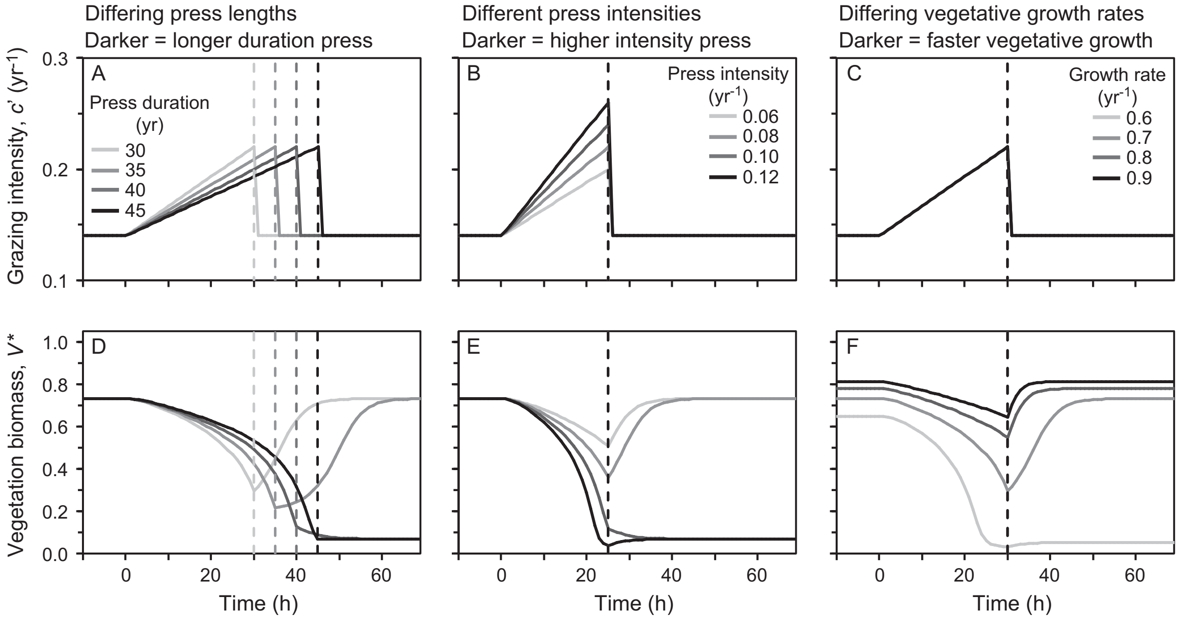

FIG. 11. (A) Vegetation responses to incremental pulses of different durations with the maximum intensity of grazing and vegetation growth rate (D) held constant (maximum $c' = 0.22$; $r = 0.7$). (B) Vegetation responses to incremental increases in grazing pressure, where grazing pressure reaches different maximum values, but duration and vegetation growth rate (E) held constant (duration = 25 yr; $r = 0.7$/yr). (C) The responses of patches with different vegetation growth rates, responding to an increase in grazing rate with (F) a uniform duration and intensity (duration = 30; maximum $c' = 0.22$). Figure interpretation follows Fig. 3, but in grayscale. See Box 1 for further information.

Box 2. Model Generality.

To assess the generality of vegetation-grazing simulations, we ran complementary simulations of three commonly used dynamical systems models and a recently proposed model for savanna–forest transitions in the tropics (see Appendix S2 for equations, parameters, and other details). Model 1 is a simple description of a population with an Allee-effect threshold, below which the population cannot replace itself (Courchamp et al. 1999, van de Leemput et al. 2015). This model can transition to a locally extinct population if harvesting exceeds a threshold. Model 2 describes phosphorus cycling in lakes, which transition from a low-phosphorus state to a self-reinforcing state of high phosphorus concentrations (a eutrophified state) if exogenous phosphorus inputs exceed a threshold (Carpenter et al. 1999). Model 3 describes the relationship between aquatic vegetation and turbidity (Scheffer 1998). If background turbidity exceeds a threshold, this system can transition from a state of high macrophyte cover and low turbidity (i.e., clear water) to a state of low vegetation cover and high vertical light attenuation. Model 4 is by far the most complex and describes transitions between highly flammable savannas and closed canopy tropical forests, with low flammability (van Nes et al. 2014, Staal et al. 2015). Transitions from savanna to forest can occur if precipitation increases above a threshold, because the flammability of the vegetation decreases and tree growth rate increases.

All four models yielded qualitatively similar results as the vegetation-grazing model. Once press intensity crossed a bifurcation point each ecosystem began to converge on an alternative state, but if presses were sustained for only a short duration (0.5 to ~30 time steps, depending on the model and press intensity) the ecosystems consistently returned to their original state (areas with lighter shading in Fig. 12). When presses of the same intensities were maintained for longer durations, all of the ecosystems failed to return to their original state after presses ended (areas with darker shading in Fig. 12). In all the models, the threshold duration that resulted in a regime shift decreased as press intensity increased, and much like the vegetation-grazing model, this was a saturating non-linear relationship (Fig. 12).

regime shifts to a shrubland state at this site in the early to mid 20th century (Bestelmeyer et al. 2011, 2013). After four years, the grazing treatments ended and large grazers were completely removed. Precipitation was variable over the experiment, but below average for all but one year of the grazing press (Bestelmeyer et al. 2013). Over the same time period, three additional paddocks were measured and received no grazing.

The experiment revealed surprising potential for recovery in a semiarid grassland that has experienced widespread regime shifts in the past (Bestelmeyer et al. 2013). Over the first 4 years of the experiment, cover of the dominant grass doubled to ~25% in the control paddocks without grazers. Grazed paddocks followed the opposite trajectory, decreasing to between 1.5% and 10% grass cover. Although these paddocks appeared to be on a trajectory towards or already in a shrubland state, once grazers were removed half of the paddocks exceeded their pre-grazing grass cover after 8 years of recovery time (Fig. 13). However, the other paddocks had yet to reach pre-treatment grass cover and the paddock with lowest grass cover showed exceptionally slow recovery, despite two years with above average precipitation during the recovery period (Fig. 13; Bestelmeyer et al. 2013). This slow recovery time suggests that these patches may have come very close to a critical threshold of grass cover

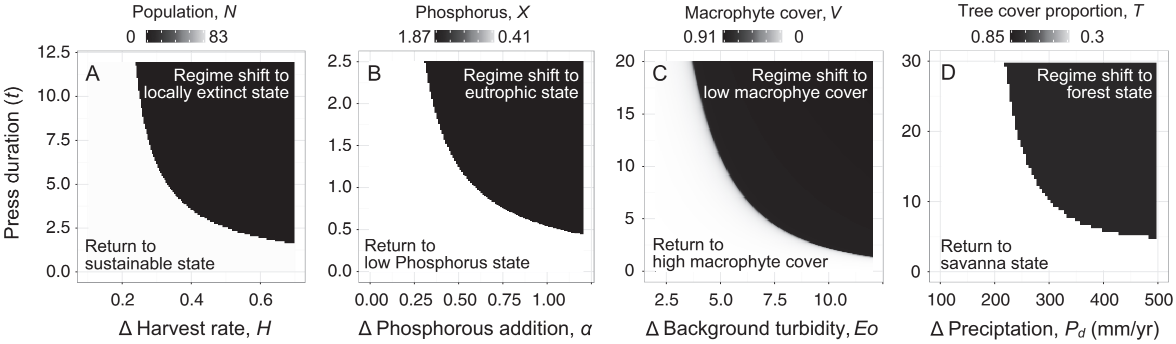

FIG. 12. (A–D) Results from models 1 through 4 (in order). The x-axes report press intensities and y-axes are press durations. Light gray areas denote combinations of press intensity and duration where the ecosystem returns to its original state. Dark gray areas denote combinations of press intensity and duration where the ecosystem converged on an alternative state (see scale bars above panels). Figure interpretation follows Fig. 9, but in grayscale. See Box 2 for further information.

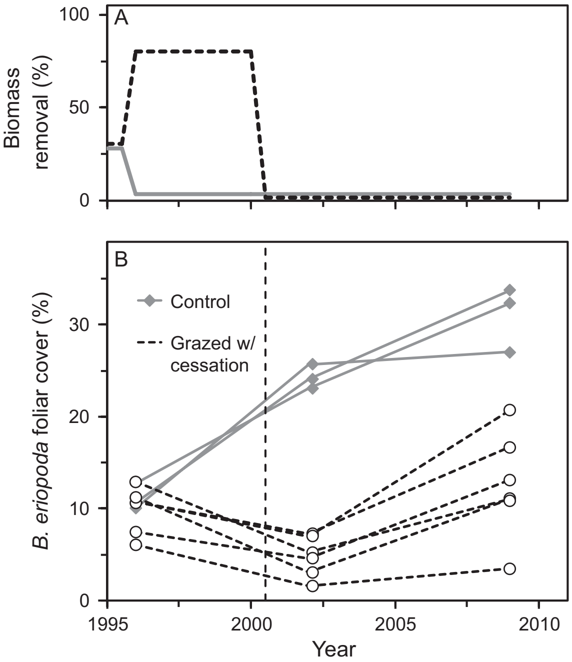

FIG. 13. Response of semiarid grassland to experimental grazing. (A) The timing and intensity of grazing pressure over time and (B) the corresponding change in foliar cover of the dominant grass *Bouteloua eriopoda* in the ungrazed control (gray) and grazed treatment (black, dashed line). Each replicate is the average of a 0.5-ha paddock. Note that these are plots with no shrub removal in Bestelmeyer et al. 2013 (see Havstad 2015, for data).

(Wissel 1984). The lack of regime shifts is unlikely to be due to the lack of alternative stable states in the underlying dynamics, given the substantial evidence for bistability in this system (Gibbens et al. 2005, Yao et al. 2006, Bestelmeyer et al. 2011). Instead, we propose that while the intensity of grazing in this experiment was probably equal to or greater than grazing pressure associated with regime shifts in the past (Gibbens et al. 2005, Yao et al. 2006, Bestelmeyer et al. 2011), a potential explanation for the observed recovery is that the 4-year duration of high grazing pressure was insufficient to trigger a regime shift. The heterogeneous responses across paddocks also illustrates how responses can vary across spatially distinct patches (Fig. 13), much like we observed in our modeling exercises that varied vegetation growth rate (Fig. 4).

Eutrophication and invasion

The second case study takes place in tallgrass prairie in Minnesota, USA. Starting in 1982, a fertilization experiment was established to explore the effects of eutrophication on biodiversity in tallgrass prairie. The design included ambient plots along with experimental treatments where either intermediate (20, 34, 54 kg N·ha^{-1}·yr^{-1}) or high (95, 170, 270 kg N·ha^{-1}·yr^{-1}) concentrations of nitrogen were added annually. Fertilized plots also received micronutrients (see Tilman 1987, Clark and Tilman 2008, Isbell et al. 2013 for more details). Ten years into the experiment, N-addition was ceased in one-half of the replicate plots at each level of nutrient addition, referred to as "cessation" plots, while N-addition continued in the remaining plots, referred to as "continuous" addition plots.

After three decades, the control plots had an average of 11 species/0.3 m^2 and <30% invasive biomass through 2004 (Fig. 14). After 2004, species richness in the control

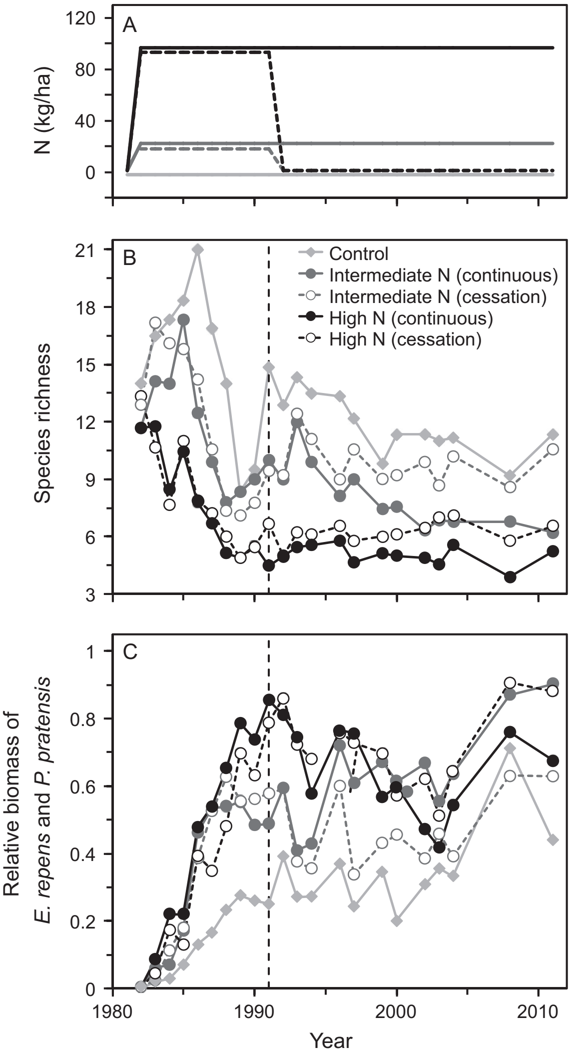

FIG. 14. Response of tallgrass prairie to nitrogen addition. (A) The timing and intensity of N addition over time, (B) the corresponding species richness, and (C) relative biomass of the exotic invasive species *Elymus repens* and *Poa pratensis* (calculated as the proportion of biomass for these two species divided by total biomass). Light gray diamonds denote control, dark gray circles denote intermediate N addition, and black circles denote high N addition. Solid lines are means of continuous treatment replicates and dashed lines are cessation treatments where N addition stopped in 1991 (a point in time marked by the vertical dashed line). Note: the jump in invasive biomass across all treatments starting in ~2008 is attributed to spread of invasive species from adjacent high N-addition plots (Isbell et al. 2013). See Tilman (2015) for data.

plots changed little, but invasive biomass started to increase because exotic species expanded from nearby experimental plots (see Isbell et al. 2013). In contrast to the controls, the high N-addition treatment quickly decreased to an average species richness of <6 species/ 0.3 m^2 and increased to an exotic biomass of >75% after about 8 years of N-addition (Fig. 14; Isbell et al. 2013). Cessation of N-addition in the high-N plots did not result in recovery of plant diversity or declines in invasive dominance, even two decades after N-cessation and despite the fact that soil nitrate concentrations returned to control levels a few years after N-addition ceased (Fig. 14; Isbell et al. 2013). This lack of community recovery, and the hysteretic response of plant species richness to increases and then subsequent decreases in soil nitrate concentrations, suggest that the ecosystem had reached an alternative state (Schroder et al. 2005, Isbell et al. 2013). The persistence of this state is attributed to the accumulation of litter from the dominant exotic species, which decreases light availability (Tilman and Isbell 2015). Some exotic invasive species can invade and persist under this elevated litter cover, whereas native species do not persist or recruit in these low-light conditions, creating a positive feedback between litter biomass and exotic dominance (Isbell et al. 2013; Chisholm et al. 2015). Higher nitrogen availability increased the growth of N-demanding invasive species, allowing this litter-exotic species feedback to become established and explaining why the system has remained in the invaded, low diversity state after N-addition ceased (Isbell et al. 2013; Chisholm et al. 2015).

Around year 20 of the experiment (2002), the continuous intermediate N-addition treatment reached and remained at a similar state as the high N-addition plots, characterized by low species diversity (Isbell et al. 2013), low species richness, and dominance by exotic grasses (Fig. 14). Assuming the critical threshold for this ecosystem lies somewhere between the state variable values of the control and high N-addition treatments (Chisholm et al. 2015), then the convergence of the intermediate and high-N treatments to similar ecosystem states is consistent with our press intensity-duration model in which low level intensity perturbations result in similar changes in state as higher intensity press perturbations, but over longer time frames. In the intermediate cessation treatment, species richness returned to control levels shortly after N-addition ended in year 10 and exotic grass dominance initially decreased to control levels, and then increased again due to expansion from adjacent high-N plots (Clark and Tilman 2008, Isbell et al. 2013). Thus, while the intermediate N-addition rate might exceed the rate of N addition needed to force a transition to an alternative state (i.e., exceeds a bifurcation point), this intensity of N-addition needs to be applied for a duration of >10 years before the potential for hysteresis occurs. In this instance the duration of the press appears to play a role in regulating regime shifts and hysteresis, a phenomenon that could be applied to grasslands receiving nitrogen inputs from agricultural or atmospheric deposition (Vitousek et al. 1998, Pardo et al. 2011, Simkin et al. 2016).

Nutrients and pollutants, such as nitrogen, differ somewhat from the previous grazing example in that they can accumulate in ecosystems. Therefore, nutrients and pollutants may have "critical loading thresholds", which is usually the total amount added over time, based on annual assessments (Pardo et al. 2011, Simkin et al. 2016). Critical loading values can be connected to the duration of loading, because total loading is the product of the average (e.g., annual) addition rate and the duration of nutrient/pollutant addition. Extreme rates of N addition, therefore, may be able to force a regime shift in a single addition event (Fig. 15), even though changes in ecosystem structure may not appear for several years (Milchunas and Lauenroth 1995). As before, even very low rates of N addition may still precipitate regime shifts over long periods of time, as long as they exceed the baseline rate of loss of reactive N from the system. Thus, press duration is more likely to be important under low intensities of press perturbations involving nutrients and pollutants, while playing a lesser role for high intensity nutrient/pollutant presses (Fig. 15).

Watershed-scale fire suppression and shrub expansion

Finally, we present a case study to assess patterns of grassland recovery following decades of fire suppression that resulted in woody plant expansion in North American tallgrass prairie. This experiment takes place at the Konza Prairie Biological Station (an LTER site in northeastern Kansas, USA), which burned historically at

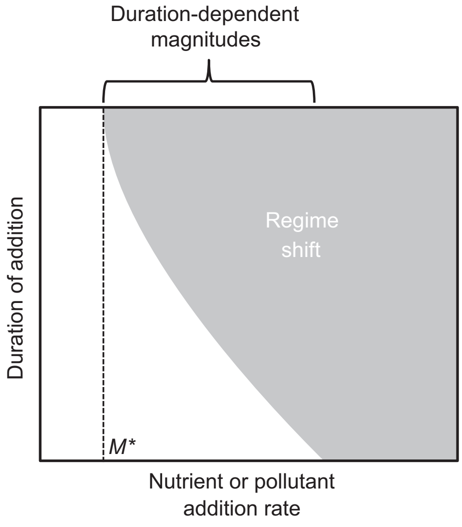

FIG. 15. Expected responses to global change drivers (e.g., N deposition) that have a long residency time in the system after a press ceases. M^* is the intensity change needed to exceed a bifurcation point and the gray shaded area depicts the combinations of press intensity and duration that can result in a regime shift to an alternative state.

a mean inter-fire interval of 2.5 to 4 years (estimated over the last several hundred years; Desantis et al. 2010, Allen and Palmer 2011, Stambaugh et al. 2013). Ignitions in tallgrass prairie are now largely human controlled, making landscape fire frequency effectively an exogenous driver variable. The C_4 grasses that dominate the productivity in tallgrass prairie are capable of quickly producing flammable fuels and are strong interference competitors, allowing the system to remain in a grass-dominated state when the interval between spring fires is <3 years (Briggs et al. 2005, Collins and Calabrese 2012, Ratajczak et al. 2014*a*). If the interval between spring fires exceeds 3 years, lowland and slope landforms become susceptible to shrub and tree establishment (Ratajczak et al. 2014*a*). Once established, shrubs and trees can disrupt the feedbacks that favor grasses, as woody species are superior competitors for light, allowing them to reduce grass cover and productivity (Heisler et al. 2004, Briggs et al. 2005). At this point, increasing spring fire frequency generally fails to restore the system to grass dominance, because fuel loads have declined and shrubs have the ability to resprout when their aboveground tissues are destroyed by fire (Heisler et al. 2004, Twidwell et al. 2013, Ratajczak et al. 2014*a*, Wonkka et al. 2016).

The experimental treatments at this site were initiated in 1977 in areas dominated by warm-season (C_4) grasses after a long-term history of burning approximately every two years. The experimental treatment used is a 40-ha watershed where a 20-year inter-fire interval was maintained from 1977 to 2000, after which it was switched to a 1-year inter-fire interval from 2001 onward (referred to as the "fire suppression press" from here onward; Fig. 16A). This ecosystem transitions to closed canopy woodland after total fire suppression for approximately 30–45 years, (Hoch et al. 2002). Thus, our experimental fire suppression press was approximately half of the duration needed to force a complete transition to a woodland state. The data were recorded annually from 1993 to 2001, and again in 2006, in 40 permanently located 10-m^2 vegetation monitoring plots. We also report shrub/tree cover from nearby watersheds that were burned annually or at 20-year intervals from 1977 to 2006 (Fig. 16A).

Annual burning maintained a grass-dominated state through 2006, with 0% shrub cover in all plots (Fig. 16G, H; Ratajczak et al. 2014*b*). From 1977 to 2001, plots with a 20-year fire interval saw gradual increases in shrub cover over time (Fig. 16B, D, F). When annual fires were introduced to some of these plots in 2001, most plots quickly returned to approximately 0% shrub cover (Fig. 16B, C). However, a small set of plots showed continued increases in shrub cover from 2001 to 2006, with six plots reaching >50% shrub cover and three reaching ≥70% shrub cover. While the recovery period we consider here is somewhat

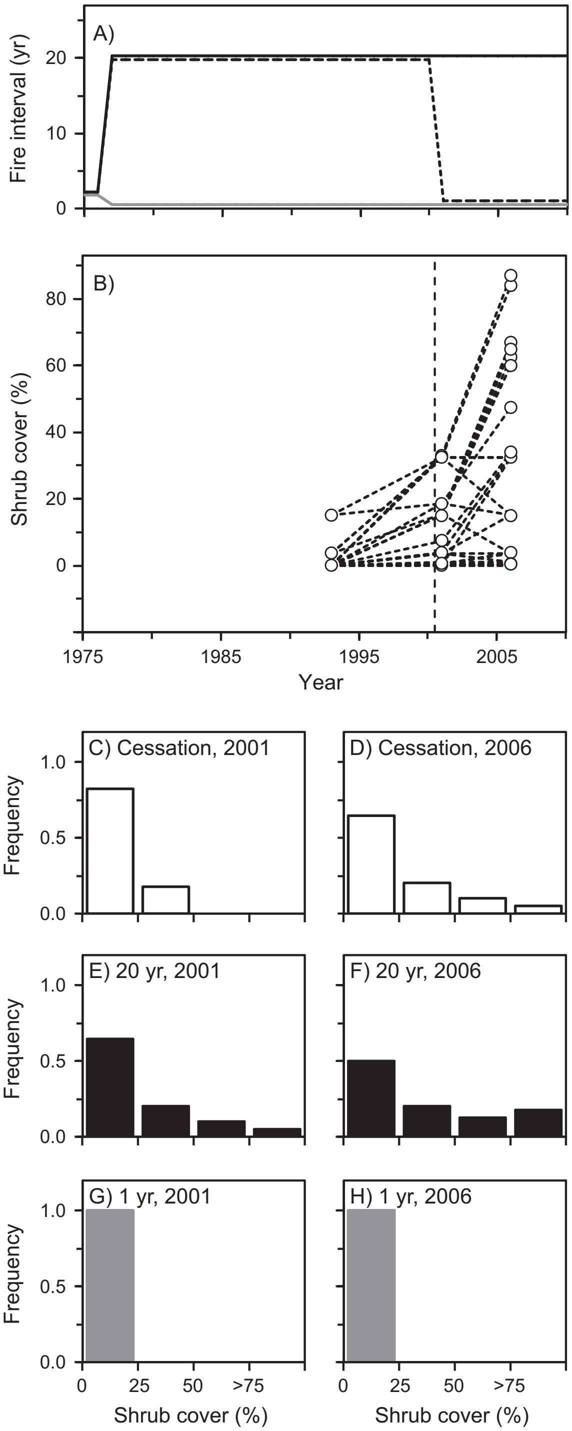

FIG. 16. Response of tallgrass prairie to changes in fire frequency. (A) Changes in ignition frequency over time, with solid black lines demarking the continuous 20-yr fire interval treatment, dashed black lines demarking the temporary fire suppression press treatment, and solid gray lines demarking continuous 1-yr fire interval treatment. (B) Shrub cover over time in each 10-m^2 plot affected by the fire suppression press experiment (n = 40). Note that, in panel B, some points have been vertically jittered. The dashed line in panel B marks when annual burning treatments were returned to the system. (C–H) Histograms of shrub cover in 2001 (C, E, G) and 2006 (D, F, H) for the fire suppression press (C, D), the continuous 20-yr fire interval (E, F), and continuous 1-yr fire interval treatments (G, H). For details on the data, see Appendix S3. Data available in Collins and Hartnett (2016).

short, annual burning is an aggressive fire regime for this region (Desantis et al. 2010, Allen and Palmer 2011, Stambaugh et al. 2013), which should theoretically accelerate the rate at which shrub cover declines and the patches return to a grassland state. Moreover, given that shrubs continued to expand despite annual fires, these plots are unlikely to revert to grass dominance in the near future (Fig. 16B, D). These results are consistent with the idea that after a uniform press is applied to a patchy spatially heterogeneous system, the ability to return to the original community state may vary among patches within a catchment or landscape. In this case, when the press was about one-half the duration needed to force a grassland to woodland state transition, some patches failed to return to their original state of low shrub cover.

Duration Effects in General

Consistent with earlier theory (Holling 1973, Noy-Meir 1975, Walker et al. 1981), the simulations and N-addition and fire-suppression experiments showed that when driver variables exceed a threshold for a sufficient period of time, persistent regime shifts and hysteresis occur in some locations within these patchy systems. The desertification experiment did not reveal persistent regime shifts under a short duration/high intensity grazing press, yet there is historical evidence that regime shifts have occurred in this region under extended grazing pressure (Gibbens et al. 2005, Yao et al. 2006, Bestelmeyer et al. 2011). The more novel observation here is that press drivers with intensities capable of forcing a regime shift over long time-spans may fail to trigger a regime shift when applied for shorter, yet substantial durations. This is particularly evident in the simulations, and consistent with (although not fully demonstrated by) results from the three long-term experiments. Our simulations also suggest that the duration needed for a press perturbation to force a regime shift decreases non-linearly as press intensity increases (Figs. 4A and 12, Box 2) and when forces counteracting a regime shift weaken (e.g., higher vegetation growth rates in our model) (Figs. 4B, C and 8). These insights might apply to large-scale responses as well (e.g., catchments, watersheds or landscapes). In our simulations of a patchy, spatially heterogeneous system, a smaller proportion of the landscape recovers to a high biomass state after longer presses, and eventually a press duration is surpassed where none of the landscape can return to a high biomass state (Figs. 6C and 9).

A key question related to the role of press/pulse duration is how common are slow transitions between alternative states? Information on non-equilibrium dynamics in ecosystems with alternative states is scant (Hastings 2010, Fukami and Nakajima 2011), but the idea that ecosystems are often not at equilibrium is well established (Noy-Meir 1975, May 1977, Westoby et al. 1989, Hastings 2010). Press/pulse duration has also been suggested to be a potential control of regime shifts beyond the systems assessed here (Frehlich and Reich 1999, Schwinning and Sala 2004, Nowacki and Abrams 2008, Smith et al. 2009, Blackwood et al. 2012, Hoffman et al. 2012, Peters et al. 2012, Augustine et al. 2014, Bozec and Mumby 2015, Chisholm et al. 2015). For instance, reducing herbivore abundance for 2 or 3 years resulted in a shift to an alternative plant community state in forest meadows, but suppression of herbivores for a shorter duration resulted in a return of the plant community to its original state (Schmitz 2004). Moreover, portions of the tropics with a dry season longer than 7 months are more likely to exist in a flammable savanna state, whereas areas that receive the same annual precipitation but have shorter dry season are more likely to be in an alternate forest state (Staver et al. 2011). This suggests that it is not only the intensity, but also the duration of the dry season that moderates savanna–forest regime shifts. Finally, simulations of lakes, coral reefs, and forest fragment dynamics subjected to different intensity presses show that transition rates between alternative states increase with larger changes in driver variables (Hanski and Ovaskainen 2002, van Geest et al. 2007, Mumby 2009, Blackwood et al. 2012), similar to our simulations of different press intensities and the nitrogen addition experiment (Figs. 4, 12 and 14).

In general, press duration should be more likely to regulate regime shifts in systems with ecological characteristics that lead to slower rates of change and greater ecological memory. For example, many species have persistent life stages, which by nature, change slowly (e.g., Rohde and Bhalerao 2003). Examples are dormant belowground buds or spores, seeds that remain viable for several years, and microbial cysts. Exogenous forcing can only affect a small proportion of these populations annually, which should result in an incremental transition toward a critical threshold in response to a change in resources or disturbance. Similarly, larger or adult organisms often have a greater ability to resist disturbance, exert competitive effects, or ameliorate their environment, whereas juveniles often have higher mortality rates (e.g., Higgins et al. 2000, van Wessenbeeck et al. 2008, Fauchald 2010). Therefore, even if a change in external drivers halts recruitment by the species defining the current alternative state, these long-lived adults may persist, again slowing the rate of equilibration to changing conditions (Svenning and Sandel 2013). Scale-dependent processes can also slow transition rates because some feedbacks are weak and exhibit time lags until a threshold in patch connectivity is reached (Petraitis and Latham 1999, Peters et al. 2004).

Caveats and future directions

Spatiotemporal variability and interactions between driver variables are likely to have a major influence on the predictability of durational thresholds. Ecosystems near or beyond bifurcation points can be especially susceptible to stochastic events that “trigger” transitions to an alternative attractor (Holmgren and Scheffer 2001, Mumby et al. 2007, Mumby 2009, Suding and Hobbs 2009). We saw a similar effect of stochasticity, where simulations with strong background noise sometimes underwent regime shifts at shorter press durations than in systems with weaker background noise (Fig. 5). Changes in multiple drivers can also trigger rapid regime shifts in otherwise slow-moving ecosystems (Suding and Hobbs 2009), such as the interactive effects of climate change and fire management in tropical deforestation (Hoffman et al. [2012] compared to Brando et al. [2014]) and Arctic ecosystems (Svenning and Sandel 2013) or interactions between hurricanes and enhanced fishing pressure in coral reefs (Hughes et al. [2013] compared to Mumby et al. [2007]). Spatial heterogeneity and connectivity can have similarly confounding effects, because inherent characteristics such as growth rate can result in heterogeneous responses to presses and their duration (Figs. 4 and 8 also see van Geest et al. 2007). For instance, by including short-range spatial connectivity between patches, the fate of an individual patch becomes even more unpredictable, as the eventual state of a patch depends on its inherent vegetation growth rate, as well as its neighbors (Fig. 8).

A persistent limitation we encountered was identifying direct experimental tests of if/how the duration of presses or pulses regulate regime shifts (but see Schmitz 2004). The experiments we included in this synthesis provide limited glimpses regarding whether press duration exerts control on regime shifts. To fill this gap, we propose several experimental designs using press duration as an experimental treatment that would provide more direct assessments than those reported here (see Appendix S4). The more robust experimental designs require a large number of plots (Appendix S4), and therefore, fast-responding systems, such as lakes, annual plant communities and microbial communities, are a promising avenue for initial hypothesis generation and testing.

The idea of "duration thresholds" and slow regime shifts in general, also presents new, intertwined theoretical and managerial challenges. To start, more theoretical and empirical work is needed to determine whether transient dynamics can indicate if an ecosystem has multiple attractors and thus is capable of regime shifts. Since systems with a single attractor should also exhibit displacement during driver presses or pulses (Hughes et al. 2013), these tools will be instrumental for determining whether a system exhibits recovery because the system lacks driver thresholds or because the ecosystem has multiple attractors, but the duration of a press or intensity of a pulse was insufficient to force a regime shift.

In systems with a high probability of regime shifts, metrics are needed to distinguish when a driver is approaching a bifurcation point versus when a change in driver variables has already initiated a slow regime shift. Most existing concepts on warning signs are based on the notion of critical slowing down in near-equilibrium systems (Wissel 1984, van Nes and Scheffer 2007). Critical slowing down and its spatial manifestations may indicate an approaching bifurcation point as a result of gradually changing driver variables (Wissel 1984, Dakos et al. 2010, Scheffer et al. 2012). The regime shifts we investigated are fundamentally different because drivers were rapidly increased to exceed a bifurcation point. Considering that slow regime shifts are potentially reversible over some time frame (Figs. 3–9; Hughes et al. 2013), it would be useful to identify indicators that signal the onset of slow regime shifts. In our simulations, we found that increases in spatial variance were an effective indicator that a driver press had initiated a transition to an alternative state, whereas increases in spatial skewness came after regime shifts were reversible difficult to reverse and increases in spatial auto-correlation were minimal (Fig. 10). Similar results have been obtained in yeast cultures (Drake and Griffen 2010) and grasslands (Augustine et al. 2014, Ratajczak et al. 2017), but more work is needed to determine the generality of these results and compare them to other proposed forecasting tools.

Conclusions

Resilience theory and the concept of thresholds have made important contributions to applied ecology, theoretical ecology, and the theory behind social-ecological systems (Westoby et al. 1989, Holling 2001, Folke et al. 2004). However, crucial steps are still needed to build more realism into the theoretical understanding of regime shifts, to test these concepts empirically, and to apply this knowledge for management and policy (Groffman et al. 2006, Donohue et al. 2016). While the understanding of regime shifts has often described thresholds in terms of the intensity of change in a driver variable(s) or pulsed perturbations to ecosystem state, our models and experimental results (Figs. 3–10 and 12–16) highlight the importance of spatiotemporal heterogeneity while supporting the idea that the duration of changes in driver variables can be an important control of regime shifts at multiple scales. Our analyses also suggest that the threshold duration needed to elicit regime shifts declines as press/pulse intensity increases, which could be tested by monitoring multi-factor press experiments and ecological responses to naturally occurring pulses.

The concept of ecosystem thresholds accommodates a set of social-ecological interactions, driver presses, pulses, and rapid change, which represent some of the most widespread and transformative types of interactions between humans and the environment (Jentsch et al. 2007, Collins et al. 2011), as well as some of the most common experimental designs in global change biology. Indeed, humans often initiate environmental presses and wait to see their effects, sometimes to our detriment (Horan et al. 2011). Many important ecological drivers also vary cyclically (Ludwig et al. 1978, Stenseth et al. 2003, Knapp et al. 2015), with expected changes in the duration and intensity of driver variables during these cycles. Better accounting for transient dynamics and threshold responses to press duration might aid in forecasting and avoiding unwanted regime shifts or in fostering desired regime shifts. These tools are crucial as many ecosystems could be operating near or beyond their safe operating space now and in the near future (Barnosky et al. 2012, Steffen et al. 2015).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecm.1249/full

DATA AVAILABILITY

Code to perform simulations are available in GitHub: https://doi.org/10.5281/zenodo.204614