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# Potential of grass invasions in desert shrublands to create novel ecosystem states under variable climate

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## ABSTRACT

The invasion of exotic grasses into shrublands is a major disturbance to dryland ecosystems. The presence of exotic grasses enhances the occurrence of wildfire in landscapes that had not evolved in the presence of fire, leading to high rates of mortality of the native vegetation. Exotic grasses could be more prone to water stress and mortality than the shrubs they replaced and may not establish during drought, facts that are crucial in ecosystems undergoing increased climatic variability. Here, we develop a process-based modelling framework to investigate the complex dynamics resulting from the introduction of exotic grasses under variable climate. We find that the system converges towards different steady states, depending on the magnitude of climatic variability. While in the absence of climate fluctuations the shrubland state is replaced by an exotic grassland, interannual climate variability may inhibit grass invasion and stabilize the shrubland state. However, climatic variability also gives rise to a novel third, unvegetated state, with grass invasion being followed by drought, grass mortality and intense soil erosion. Most of the research on climate change effects on ecosystems has historically concentrated on the ecological impact of shifts in mean climate conditions. This study shows that changes in the variance are also important when shifts in vegetation composition (e.g. species invasions) result in different susceptibility to climatic variability. In the presence of random climate fluctuations, ecosystems can display steady states that differ from those that would exist under a constant climate or with a climate trend. Copyright © 2016 John Wiley & Sons, Ltd.



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

KEY WORDS invasive species; fire cycle; climate variability; exotic grasses; unvegetated state

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## INTRODUCTION

Biological invasions are recognized as major contributors to global environmental change (Vitousek *et al.*, 1997; Mooney and Cleland, 2001). It has been observed that biological invasions affect ecosystem dynamics not only through their direct impact on resource competition and pool of available species (e.g. Olsson *et al.*, 2012) but also indirectly through their ability to modify the disturbance regime. For example, invasive plants may change fire intensity and frequency or alter the rate of abiotic processes such as soil erosion (D'Antonio and Vitousek, 1992; Ziska *et al.*, 2005; Miller *et al.*, 2010). This disturbance-mediated effect of species invasions on ecosystems is observed when the invader is functionally different from the native species,

i.e. when it exhibits some traits that (i) affect the disturbance regime and (ii) are missing in the native population (D'Antonio, 2000). For example, the invasion of desert shrublands by exotic annual and perennial grasses has been observed to lead to an increase in fire frequency and intensity because of the increase in grass fuel and in connectivity of vegetation cover (Okin *et al.*, 2009a). The introduction of fires in shrubland ecosystems, where burning has not been historically a major selective force, results in an increase in the mortality rates of shrubland species, particularly if they are not adapted to fire (e.g. Bond *et al.*, 2005; Runyan *et al.*, 2012). The loss of shrub biomass further enhances the establishment and spread of invasive grasses (D'Antonio, 2000). Known as 'the fire cycle' (D'Antonio and Vitousek, 1992), this positive feedback leads to the replacement of fire-intolerant native shrubs with exotic grasses (Figure 1). The grass-fire feedback may induce stable grass-dominated vegetated states in arid and semiarid environments (Grigulis *et al.*, 2005; Keeley and Rundel, 2005), even when shrubs have

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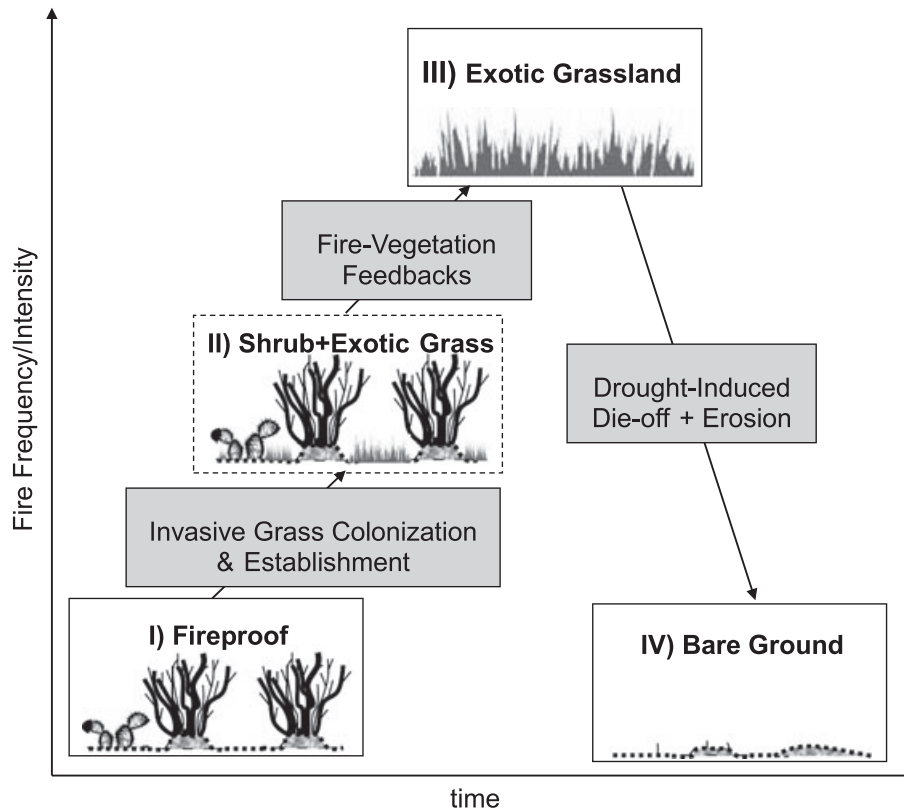


Figure 1. A conceptual representation of the possible four stages of vegetation transition in desert scrublands affected by grass invasions.

competitive advantage with respect to grasses in the access to resources (Okin *et al.*, 2009b).

The case of exotic grass species invasions into fireproof desert shrublands is the mirror image of shrub encroachment into former desert grasslands, which has been occurring in drylands worldwide over the past two centuries (Van Auken, 2000; Ravi *et al.*, 2009b; D'Odorico *et al.*, 2012). Invasion by exotic – both annual and perennial – grasses coupled with changes to the fire regime has been observed more recently and has been documented for several dryland regions around the world, including Western North America, Australia and Southern Africa (D'Antonio, 2000). For example, native shrublands in the Sonoran Desert have extremely low fire frequency, because of a sparse canopy and the absence of a continuous fuel (grass) layer. The low fire frequency led to the evolution of plants in the region that are not fire-adapted. Thus, in this region, fire sustained by the exotic grasses can kill native vegetation thereby threatening the continued existence of native fire-intolerant desert shrubland (McDonald and McPherson, 2011).

The typical changes in dryland vegetation associated with the invasion of desert shrublands by exotic grasses are shown in Figure 1. We look at this process as a sequence of three major stages plus a potentially novel fourth state characterized by different plant community composition,

fire frequency and ecosystem processes. The initial state (state I) of the system is a fireproof landscape with fire-intolerant native shrubs. After the introduction of invasive grasses, the continuity of the grass layer contributes to fire spread across the landscape. At this stage, invasive grasses and shrubs coexist (state II). The transition from states I to II involves the colonization and establishment of exotic grasses as in most cases of biological invasions (Theoharides and Dukes, 2007). This process has been often associated with anthropogenic introduction (Dukes and Mooney, 1999) and/or increase in atmospheric CO<sub>2</sub> concentrations and changes in climate (i.e. precipitation and/or temperature) (Smith *et al.*, 2000; Davis *et al.*, 2000; Ziska *et al.*, 2005; Sorte *et al.*, 2013). As noted earlier, this mixed grass–shrub community is not stable because its persistence is prevented by fire dynamics. In state II, shrub vegetation is prone to fire-induced mortality because of increase in fire pressure resulting from the introduction of flammable grasses. Thus, the fire cycle, i.e. the positive feedback between fires and vegetation, accelerates the rate of grass invasion at the expenses of the native vegetation (Grigulis *et al.*, 2005; Keeley and Rundel, 2005; Miller *et al.*, 2010). Thus, the system shifts to a state dominated by exotic grasses with no native shrub plants (state III). At this stage, flammable grasses cover the landscape (McDonald and McPherson, 2011).

Climate in arid and semiarid regions is notoriously variable and is expected to become increasingly so, even if there is no long-term aridification trend worldwide; it has been argued that in the arid regions of Western North America, a drying trend will likely occur in the next 50 years (Seager *et al.*, 2007; IPCC, 2013). Moreover, the increase in aridity is often associated with an increase in interannual climate variability (Nicholson, 1980; Easterling *et al.*, 2000a; Easterling *et al.*, 2000b; IPCC, 2013). A considerable number of studies have already addressed the transitions from states I to II and from states II to III (e.g. D'Antonio and Vitousek, 1992; D'Antonio, 2000), while it is less clear whether grass invasions could interact with fire dynamics in the presence of increased rainfall variability to convert these once fireproof shrubland landscapes into highly degraded barren landscapes (state IV).

In this study, we investigate the idea that increase in interannual rainfall variability increases the frequency of extended period of low precipitation (i.e. drought years), and thus, invasive grass cover (annuals or perennials) might be greatly reduced because of plant mortality under drought years to produce a novel unfertile state with little or no vegetation cover, especially when the grasses exhibit a special drought susceptibility or lag in regrowth after drought (state IV) (e.g. Peake *et al.*, 1979; Tilman and Haddi, 1992; Franklin *et al.*, 2006). Although it is possible that the system could transition from states I to IV without going through III, in this study, we focus on the transitions of the vegetation states presented in Figure 1 to investigate whether grass invasions and climate change could act in concert to induce land degradation. We suggest that this novel degraded state may be stable if the landscape is prone to wind and/or water erosion, which deplete soil resources and the seed bank, thereby potentially inhibiting the re-establishment of vegetation, including shrubs, even during wet years (Parsons *et al.*, 2003; Okin *et al.*, 2006; Okin *et al.*, 2009a; Okin *et al.*, 2009b; Ravi *et al.*, 2009a; Alvarez *et al.*, 2012). The emergence of this novel degraded state as a result of grass invasions and interannual rainfall fluctuations would require a long-term drought (i.e. on decadal timescales) following the transition from state I to state III.

Studies on ecosystem dynamics in response to interannual rainfall variability are crucial but largely restricted by the short record of available data and technical capability to measure all relevant variables (e.g. Fatichi and Ivanov, 2014; Ng *et al.*, 2015). To overcome these limitations, we develop a minimalist process-based model of coupled soil resource-vegetation dynamics to investigate the interactions between native shrubs and exotic invasive grasses. By clarifying the role of increased climate fluctuations in determining land degradation induced by grass invasions, this study contributes to a better understanding of

ecosystem susceptibility to biological invasions and climate change.

## METHODS

### *Modelling framework*

The effect of biotic–abiotic interactions on ecosystem dynamics has been often investigated with simple deterministic models accounting both for interspecific competition and for feedbacks with environmental conditions and disturbance regime. Some of these models have been developed to study changes in plant community composition in a variety of dryland ecosystems and to show the emergence of alternative stable states in their deterministic dynamics (e.g. Noy-Meir, 1975; May, 1977; Walker *et al.*, 1981; Anderies *et al.*, 2002; Van Langevelde *et al.*, 2003; Okin *et al.*, 2009b). Here, we use a similar approach to investigate a different process: the effect of grass invasions on the temporal dynamics of desert shrublands in a randomly fluctuating environment. To this end, we develop a stochastic process-based model of vegetation-resource dynamics accounting for the interactions between shrubs and grasses and for their coupling with the dynamics of soil resources. This model assumes that (i) shrubs and grasses compete for the same soil resources (e.g. Smit and Rethman, 2000; Hipondoka *et al.*, 2003; Beckage *et al.*, 2009), although we acknowledge that in some dryland ecosystems, shrubs could have deeper roots than grasses (i.e. Walter's two-layer hypothesis) (Walter, 1971; Eagleson and Segarra, 1985). (ii) Even though in some ecosystems grasses might be stronger competitors than shrubs (especially at the seedling and sapling stages) (e.g. Scholes and Archer, 1997), here we consider the case of ecosystems where – in the absence of fires and climate fluctuations – shrubs have preferential access to soil resources and therefore are in competitive advantage with respect to exotic grasses (Van Auken, 2000; Sankaran *et al.*, 2004; Beckage *et al.*, 2009; Yu and D'Odorico, 2014); (iii) fires act as a source of disturbance for the native shrub population, i.e. the rate of fire-induced shrub mortality is proportional to the grass biomass (i.e. to the fuel load) (Van Wilgen *et al.*, 2000; Beckage *et al.*, 2009); (iv) the carrying capacities for native shrubs ( $S_{\max}$ ) and exotic grasses ( $G_{\max}$ ) depend on the available soil resources,  $R$ , mainly soil nutrients as well as on soil moisture, which varies from year to year as a result of interannual climate fluctuations. Thus, the carrying capacities of shrubs and grasses are here accounted for by treating  $S_{\max}$  and  $G_{\max}$  as random variables with mean dependent on  $R$ . The sensitivity to these fluctuations is stronger in the invasive grasses than in the native shrubs, which are better adapted to droughts (e.g. Tilman and Haddi, 1992). Thus, the same climate fluctuations cause

stronger variability in the carrying capacity of grasses than in that of shrubs (refer to the section on Stochastic dynamics for details).

#### Soil resource dynamics

The state variables, native shrub biomass ( $S$ ), invasive grass biomass ( $G$ ) and soil resources ( $R$ ) have the dimensions of mass per unit area ( $\text{ML}^{-2}$ ). The temporal variability of  $R$  is the result of an imbalance between the rates of soil resource accumulation,  $R_A$ , and loss,  $R_E$

$$\frac{dR}{dt} = R_A - R_E \quad (1)$$

Overall, the accumulation of soil resources is favoured by the presence of plant canopies because of their ability to reduce erosion and favour deposition (e.g. Okin *et al.*, 2009b). In fact, vegetation tends to provide a more favourable depositional environment for sediments transported by wind and water (Schlesinger *et al.*, 1990). Thus, the accumulation rate,  $R_A$  [with the dimensions ( $\text{ML}^{-2}\text{T}^{-1}$ )], is an increasing function of the total plant biomass,  $G+S$  (Figure 1).

$$R_A = c_1 \left[ 1 - e^{-c_2(S+G)} \right] \quad (2)$$

with  $c_1$  ( $\text{ML}^{-2}\text{T}^{-1}$ ) and  $c_2$  ( $\text{L}^2\text{M}^{-1}$ ) being two parameters determining the magnitude of the accumulation rate and its sensitivity to  $S+G$ , respectively. The rate,  $R_E$  ( $\text{ML}^{-2}\text{T}^{-1}$ ), of resource loss associated with soil erosion is proportional to the amount of existing resources,  $R$ , and decreases with increasing vegetation biomass

$$R_E = \left[ c_3 + c_4 e^{-c_5(S+G)} \right] \quad (3)$$

where the first of the two terms between brackets expresses the biomass-independent erosion rate, while the second term accounts for the dependence of  $R_E$  on total plant biomass. The constants  $c_3$  and  $c_4$  have dimensions of ( $\text{ML}^{-2}\text{T}^{-1}$ ) and  $c_5$  has dimensions of ( $\text{L}^2\text{M}^{-1}$ ).

#### Vegetation dynamics

Following other studies (e.g. Anderies *et al.*, 2002; Van Langevelde *et al.*, 2003; Beckage *et al.*, 2009; Yu and D'Odorico, 2014), the rate of change of shrub biomass is proportional to the existing shrub biomass,  $S$ , and to the resources available for new shrub growth,  $S_{\max}-S$ , while fire-induced disturbance kills shrubs at a rate that is proportional to the existing shrub biomass and to fire frequency,  $f(G)$ ,

$$\frac{dS}{dt} = \alpha S(S_{\max} - S) - \beta f(G)S \quad (4)$$

with  $\alpha$  and  $\beta$  ( $\text{L}^2\text{M}^{-1}\text{T}^{-1}$ ) being two parameters determining the rates of shrub growth and of fire-induced mortality, respectively. As assumed in the preceding texts, in the

absence of fires and climate fluctuation, shrubs are in competitive advantage with respect to exotic grasses in the access to soil resources (Van Auken, 2000; Beckage *et al.*, 2009; Yu and D'Odorico, 2014); thus, the resources available to shrubs are expressed as  $S_{\max}$ , while the resources available to grasses are expressed as  $G_{\max}-S$ . Experimental evidence suggests that fire frequency is an increasing function of grass biomass (Van Wilgen *et al.*, 2000). Even though in this study we do not model fire as a sequence of intermittent events occurring at a given frequency (D'Odorico *et al.*, 2006a), we account for the effect of grasses on fires by expressing the fire pressure as a deterministic function of grass biomass. Following Van Wilgen *et al.* (2000), we express fire frequency,  $f(G)$ , as

$$f(G) = \frac{\exp(q)}{1 + \exp(q)}$$

where  $q = -2.47 + 2.35G$ .

Consistent with other studies (e.g. Anderies *et al.*, 2002; Van Langevelde *et al.*, 2003; Beckage *et al.*, 2009; Yu and D'Odorico, 2014), this model does not account for resprouting of shrubs after fires, a trait that is species-specific and is expected to favour state II (e.g. Chidumayo, 2004; Vesk *et al.*, 2004; Moreira *et al.*, 2012). Thus, grasses may limit shrub growth only through fire dynamics but not through a preferential access to the available resources.

Similarly, the rate of change of grass biomass is modelled as proportional to grass biomass and to the resources left available to new grass growth [i.e. to  $G_{\max}-(S+G)$ ], while a grass invasion term accounts for the effects of grass invasion,

$$\frac{dG}{dt} = \gamma G(G_{\max} - S - G + F_a S) + I \delta(t - t_I) \quad (5)$$

with  $\gamma$  ( $\text{ML}^{-2}\text{T}^{-1}$ ) being a parameter determining the rates of grass growth,  $F_a S$  a facilitation term expressing the facilitation effects of shrubs on grasses through shade ( $F_a$ , a facilitation coefficient) (e.g. Holzapfel and Mahall, 1999; Yu and D'Odorico, 2015 a, b) and  $I$  ( $\text{ML}^{-2}\text{T}^{-1}$ ) being a one-time event of invasive species introduction occurring at time  $t=t_I$ . Thus, if  $F_a$  is positive, shrubs have a facilitative effect on grasses, while if  $F_a$  is negative, shrubs only exert a competitive effect on grasses. During this event, a relatively small amount of exotic grass biomass is successfully introduced and established. The function  $\delta(t-t_I)$  in Equation 5 is equal to 1 at time  $t=t_I$  and 0, otherwise. Note that invasion of grasses into bare soil state during periods of sufficient water availability may lead to a small increase in soil resources, and multiple invasions may convert the bare soil state to grassland state if no drought conditions are experienced before significant establishment. To account for the faster dispersal and growth of invasive grasses with respect to the native shrubs, the constant of proportionality in Equation 5,  $\gamma$ , must be greater than  $\alpha$ .

### Stochastic dynamics

If the carrying capacities are constant and have the same value for shrubs and grasses, the vegetation dynamics expressed by (4) and (5) have only one stable state, which is either ( $G=G_{\max}$ ,  $S=0$ ) or ( $G=0$ ,  $S=S_{\max}$ ), depending on the relative importance of the parameters controlling shrub growth and fire-induced mortality. To investigate how these dynamics are modified by interannual climate variability that influences water availability and by feedbacks between vegetation and available resources,  $R$ , we express both  $G_{\max}$  and  $S_{\max}$  as random variables with synchronous fluctuations with mean,  $\langle G_{\max} \rangle = \langle S_{\max} \rangle = R$ , and lognormal distribution (Okin *et al.*, 2009b). To account for the higher sensitivity of invasive grasses to drought occurrences, we assume that the same climate fluctuations induce a stronger variability in the response of invasive grasses than in native shrubs by using two different values for the standard deviation of the lognormal distribution of the carrying capacities for grasses ( $\sigma_G$ ) and shrubs ( $\sigma_S = k \sigma_G$ ), with  $\sigma_G > \sigma_S$  (i.e.  $k < 1$ ). More specifically, the simulation of both  $G_{\max}$  and  $S_{\max}$  is conducted by sampling at each time step a random number from a normal distribution of random numbers with mean 0 and standard deviation 1 [i.e.,  $N(1,0)$ ]. The same number is then converted into a value,  $G_{\max}$ , with lognormal distribution, mean  $R$  and standard deviation  $\sigma_G$  and a value  $S_{\max}$  with the same mean (i.e.  $\langle G_{\max} \rangle = \langle S_{\max} \rangle = R$ ) and standard deviation  $\sigma_S = k \sigma_G$ . In this way, the carrying capacities of grasses and shrubs are random variables with the same mean  $R$  and synchronous fluctuations of different amplitude (i.e. different standard deviation).

We use the model to investigate the interplay among vegetation dynamics, climate fluctuations and changes in available resources. To this end, we consider the case of a system in which, in the absence of fluctuations (i.e.  $\sigma_G = \sigma_S = 0$ ), exotic grasses are able to successfully establish and to completely displace the native shrubs (i.e. in this case, the stable state of the deterministic system is  $G=G_{\max}$ ,  $S=0$ ). We then investigate the stochastic dynamics (i.e.  $\sigma_G > 0$ ,  $\sigma_S > 0$ ). For different values of  $\sigma_G$  and  $\sigma_S$ , we run 1000 iterations of the process and calculate the probability that the system reaches a steady state with shrub biomass ('shrub state'), grass biomass ('grass state') or bare soil ('crash state') in which shrub and grass biomass are zero and soil resources fall to zero. Each simulation is run for 3000 time steps using as initial conditions the native shrub state (i.e.  $G=0$ ;  $S=R=1$ ) and allowing for one-time invasive species introduction at time  $t_I=250$ .

### Sensitivity analysis

Model sensitivity was investigated with respect to the parameter  $k$ , the facilitation effects of shrubs on grasses ( $F_a$ ), the magnitude of one-time grass invasion ( $I$ ) and the

rate of fire-induced shrub mortality ( $\beta$ ) (refer to supporting information for details).

## RESULTS

In the model developed in this study, we characterize the state of the system using three state variables: native shrub biomass ( $S$ ), invasive grass biomass ( $G$ ) and soil resources ( $R$ ). The dynamics of  $S$  and  $G$  are limited both by the resources,  $R$ , which varies in time as a result of random interannual rainfall fluctuations that affect  $G_{\max}$  and  $S_{\max}$ . These fluctuations impose random variability on the carrying capacities of  $S$  and  $G$ , with standard deviations,  $\sigma_S$  and  $\sigma_G$ , respectively. Because of the higher drought sensitivity of grasses,  $\sigma_G$  is bigger than  $\sigma_S$ . We look at the asymptotic state of the system (i.e. at the end of the simulation period) and classify it as shrub state, grass state or crash state, depending on whether it exhibits nonzero shrub biomass (while  $G=0$ ), nonzero grass biomass (while  $S=0$ ) or zero grass and shrub biomass, respectively (Figure 3). All simulations resulted in one of these three final states after 3000 iterations.

The results of this analysis for different levels of climate fluctuations (i.e. different values of  $\sigma_G$  and  $\sigma_S = k \sigma_G$ ) show that, in the deterministic case ( $\sigma_G = \sigma_S = 0$ ), the fire cycle leads to the successful dispersal of invasive grasses (Figure 2). In this case, the system reaches a stable state dominated by exotic grasses, and no other mechanism further disturbs this state. As the amplitude of climate fluctuations is increased, the probability for the system to reach a stable grassland state decreases, while the

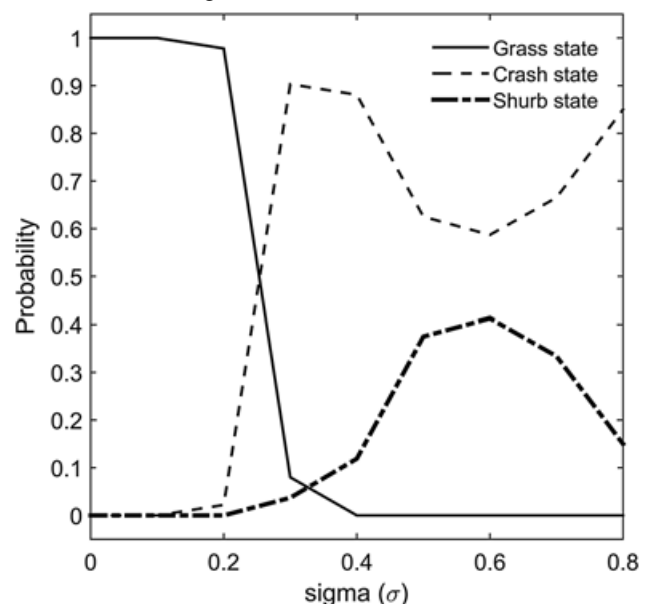


Figure 2. Probability of being in one of three possible states at the final state ( $t=3000$ ) as a function of  $\sigma_G$  (shown for the case of one-time grass invasion with  $\alpha=0.5$ ;  $\beta=1.3$ ;  $\gamma=0.85$ ;  $c_1=0.08$ ;  $c_2=2$ ;  $c_3=0.06$ ;  $c_4=0.06$ ;  $c_5=10$ ;  $F_a=0$ ;  $\sigma_S=0.7 \sigma_G$ ).

probability of converging to a stable shrubland state increases along with the probability of ‘crashing’ to a resource-depleted bare soil state. Thus, climate fluctuations can completely reverse the behaviour of the system and allow for the stable existence of the shrub state, while in the deterministic counterpart of this process, the stable state of the system is a grassland. For intermediate amplitude of climate fluctuations, the probability of reaching the grassland or the shrubland states can be comparable, while there is an even higher probability of crashing to the unvegetated state (Figure 2).

The modelling results also show that in the deterministic case ( $\sigma_G = \sigma_S = 0$ ), the grass biomass and available soil resources are high (Figure 3). The grass biomass in the grass states abruptly goes to zero as interannual climate variability increases, while shrub biomass in the shrub state gradually increase as  $\sigma_G$  increases up to intermediate levels of interannual climate variability (Figure 3). Thus, as interannual climate variability increases, the probability of reaching a final state dominated by shrubs increases up to intermediate levels of interannual climate variability, while the probability of attainment of a grass state rapidly decreases (Figure 2). The decrease in vegetation biomass in the grass states is associated with an increase in erosion rates and with the consequent decrease in available soil resources as shown in Figure 3. Thus, when the final state is a grassland, vegetation biomass decreases with increasing levels of environmental variability. Conversely, whenever the final state of the system is dominated by shrubs, vegetation biomass remains relatively high and no major erosional losses of soil

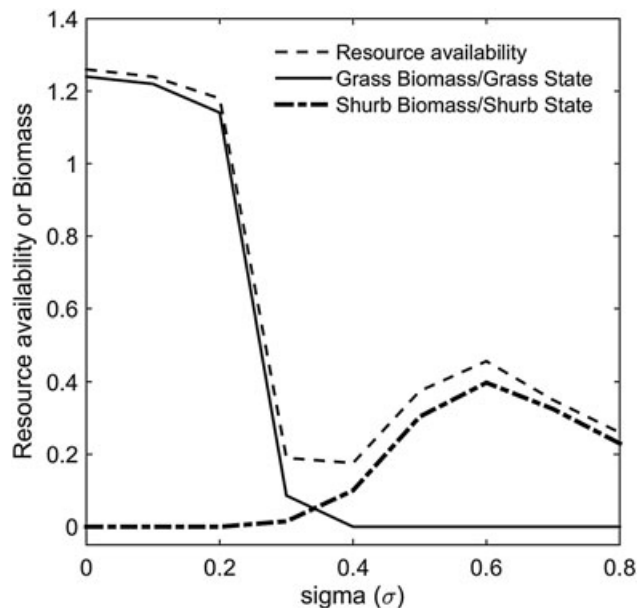


Figure 3. Resource concentration, shrub and grass biomass at the final state ( $t = 3000$ ) as a function of  $\sigma_G$  (shown for the case of one-time grass invasion). Same parameters as in Figure 2. Resource availability is calculated by Equation 1; shrub and grass biomass are calculated as the mean shrub and grass biomass at the final state ( $t = 3000$ ) over 1000 realizations of the (stochastic) process.

resources occur. Overall, the decrease in biomass is paralleled by a decrease in soil resources and vice versa (Figure 3).

## DISCUSSION

This study develops a minimalist process-based model of coupled soil resource-vegetation dynamics to investigate changes in dryland vegetation associated with the invasion of desert shrublands by exotic grasses. Figure 1 describes the typical four stages of vegetation change characterized by different plant community composition, fire frequency and ecosystem processes. Past studies have focused on the transitions from the state of shrubland to shrub/grass associations (states I to II) and from shrub/grass associations to the state of exotic grassland (states II to III) (e.g. D’Antonio and Vitousek, 1992; D’Antonio, 2000). Climate change studies predict an increase in the variability of precipitation across different scales in space and time (Nicholson, 1980; Easterling *et al.*, 2000a; Easterling *et al.*, 2000b; IPCC, 2013). This study investigates the transition from state III to the bare ground state (state IV) under the effect of interannual rainfall variability. While the impact of climate drivers on ecosystems is often investigated by examining only the effect of changes in mean climate conditions (e.g. Walther *et al.*, 2002; Kljun *et al.*, 2006), our modelling results show that grass invasions and interannual rainfall fluctuations could act in concert to induce the transition from states III to IV. Overall, this study highlights the importance of understanding the effect of rainfall variability on the potential ecosystem states.

This modelling study shows that, in the absence of climate fluctuations, invasive grasses (state III) replace the native shrubs (state I) (Figure 2). The factors favouring the replacement of shrubs by grasses include anthropogenic introduction (Dukes and Mooney, 1999), increase in atmospheric  $\text{CO}_2$  concentrations and temperature and/or increase in soil resource availability (i.e. nitrogen) (Smith *et al.*, 2000; Ziska *et al.*, 2005; Sorte *et al.*, 2013). Fluctuations in resource/rainfall availability could provide windows of opportunity in resource enrichment, and thus, species (i.e. grasses) with a high growth rate may quickly take up resources, change the disturbance regime (i.e. fires) and then invade or dominate the landscape (e.g. Davis *et al.*, 2000; Davis and Pelsor, 2001; Corbin and D’Antonio, 2004). However, opposite interactions may occur in arid environments where grasses exhibit slow growth rates (e.g. Teuling *et al.*, 2010; Collins *et al.*, 2012). Indeed, recent field studies at the Jornada Basin (New Mexico) show that increasing interannual rainfall fluctuations could favour shrubs over grasses (e.g. Gherardi and Sala, 2015 a b).

The transition from state I to state III occurs through an intermediate state (state II) in which the introduction of a relatively continuous cover of exotic grasses favours the

occurrence and spread of fires in the native shrubland (Figure 2) (D'Antonio, 2000). This intermediate state is not stable because grass establishment triggers the fire-vegetation feedback resulting in a stable grass cover (Grigulis *et al.*, 2005; Keeley and Rundel, 2005). Such a transition from state I to state III could also occur in ecosystems where shrubs have deeper roots than grasses (Smit and Rethman, 2000; Hipondoka *et al.*, 2003; Beckage *et al.*, 2009) because in these dynamics, shrub displacement by grass is not because of competition but to the ability of grasses to enhance fire-induced shrub mortality.

This study also shows that increases in climate fluctuations could reduce the probability for the system to reach a stable grassland state but increase the probability of converting to a stable shrubland state along with the probability of crashing to a bare soil state (Figure 2). This pattern corresponds with change in grass/shrub biomass and resource concentration as observed in Figure 3. The key in this modelled pattern is that the increasing frequency of drought under increased climate fluctuations may extend periods in which patches invaded by exotic grasses have no or low cover, especially when the grasses are susceptible to drought or lag in regrowth after drought (state IV) (e.g. Peake *et al.*, 1979; Tilman and Haddi, 1992; Franklin *et al.*, 2006). Plant mortality induced by moisture stress (a key determinant of the crash state) is expected to become

more frequent in the future because of the combined effect of drought and temperature extremes (Volder *et al.*, 2010). Thus, depending on their intensity (i.e.  $\sigma_G$ ), climate fluctuations could limit the establishment of exotic grasses before they are able to displace the native shrubs through the fire cycle, which leads to a stable shrubland (Figure 2). Alternatively, grass mortality could occur at a later stage after the fire cycle has killed all native shrubs. In this case, low or no vegetation cover (grasses and/or shrubs) leads to soil erosion and depletion of the seedbank and other soil resources [Equation 1] (e.g. Peake *et al.*, 1979; Tilman and Haddi, 1992; Franklin *et al.*, 2006; Alvarez *et al.*, 2012; Bhattachan *et al.*, 2014). Erosive losses will then likely lead to lower vegetation productivity, thereby completing a positive feedback loop that slows down or prevents the regrowth of vegetation, including shrubs, even during wet years (e.g. Okin *et al.*, 2009b). We also note that the regrowth of grass seeds during wet years can be limited by the short seed lifetime (e.g. Ellis, 1991; Bakker *et al.*, 1996), which depends on seed size, shape, vertical distribution in the soil profile and environmental conditions (e.g. temperature and soil moisture availability) (e.g. Ellis, 1991; Bakker *et al.*, 1996; Bekker *et al.*, 1998).

Experimental evidence (Table I) has been extensive in documenting a high sensitivity of perennial grasses in response to drought (e.g. Herbel, 1972; McClaran and

Table I. A summary of evidence of a high sensitivity of perennial grass to drought.

Region	Perennial grass investigated	Main findings	References
Southern New Mexico, USA	<i>Bouteloua eriopoda</i>	Drought can rapidly reduce grass cover across space; drought leads to the loss of perennial grasses during woody plant expansion	Buffington and Herbel (1965); Herbel (1972); Yao <i>et al.</i> (2006)
Southern Arizona, USA	<i>Eragrostis lehmanniana</i> , <i>Bouteloua rothrockii</i> , <i>Digitaria californica</i> , <i>Muhlenbergia porteri</i>	Mean annual rainfall below the threshold of 350 mm greatly limits grass cover	McClaran and Angell (2006)
Southern Arizona, USA	<i>Eragrostis lehmanniana</i> , <i>Bouteloua rothrockii</i> , <i>Digitaria californica</i> , <i>Aristida</i> spp.	Low rainfall is an more important factor limiting perennial grass cover than grazing	Mashiri <i>et al.</i> (2008)
College Station, Texas, USA	<i>Schizachyrium scoparium</i>	Drought leads to the greatest reduction in leaf-level net photosynthesis of <i>S. scoparium</i> compared with shrubs (i.e. <i>Quercus stellata</i> , <i>Juniperus virginiana</i> )	Volder <i>et al.</i> (2010)
Southwestern USA <sup>a</sup>	Several perennial grass	Reduction in summer rainfall greatly reduce cover of perennial grasses as compared with woody species	Munson <i>et al.</i> (2012a, 2012b, 2013)
Southern New Mexico, USA	<i>Bouteloua eriopoda</i>	Perennial grasses are more vulnerable to drought than shrubs, which explain the shrub encroachment into desert grasslands	Baez <i>et al.</i> (2013)

<sup>a</sup> Long-term vegetation data are from four sites in the Sonoran Desert of Southern Arizona: Organ Pipe Cactus National Monument, the Rincon District of Saguaro National Park, the Desert Laboratory and the Santa Rita Experimental Range.



Angell, 2006; Yao *et al.*, 2006; Munson *et al.*, 2012a, 2012b). Annual grasses have been found to be more sensitive to drought than perennial grass, likely because of their lower biomass per individual, small roots and, consequently, more limited access to soil water resources (e.g. Tilman and Haddi, 1992; Germino *et al.*, 2016). In fact, invasions by exotic grasses, particularly annuals such as *Bromus* species, leads to changes in litter, fire and soil properties that appear to feedback to reinforce *Bromus*' dominance and further portends desertification under increased rainfall fluctuations (Germino *et al.*, 2016). Overall, exotic grasses (perennial or annual) will not establish or grow significantly during a drought and are thus more sensitive to interannual rainfall variability and water deficits (Breman and Cissé, 1977a, 1977b; Mack and Pyke, 1983). The carrying capacity for grasses has therefore been modelled with the same mean but a higher variance than the carrying capacity for shrubs to reflect the higher susceptibility of exotic grasses to changes in biomass induced by interannual rainfall variability. Moreover, we also note that, in the case of annual grasses, there is a higher soil vulnerability to erosion because the soil surface is sheltered only by seasonal grass cover and weak root systems (e.g. Kort *et al.*, 1998; Beyers, 2004). On the other hand, we also note that some invasive annuals and/or perennials may have unique physiological traits that allow them to tolerate rainfall variability and drought (e.g. Vaughn *et al.*, 2011; Marshall *et al.*, 2012).

The model's sensitivity is investigated with respect to changes in some important parameters. If the drought sensitivity of shrubs is further reduced with respect to that of grasses (i.e. smaller  $k$ ), the probability of a stable shrub state increases, while the probability of a 'crash' state decreases, especially for high values of climate fluctuations (Supporting Information, Figure S1). Grass facilitation by shrubs increases grass biomass (e.g. Yu and D'Odorico, 2015a, 2015b) and the chance of fire-induced shrub mortality, thereby reducing the probability of a stable shrub state along with an increase in the probability of crash state (Supporting Information, Figure S2). A similar pattern is observed with an increase in the magnitude of one-time grass invasion (Supporting Information, Figure S3). As expected, a reduction in fire-induced shrub mortality (i.e. in  $\beta$ ) increases the probability of a stable shrub state, while reducing the probability of the crash state (Supporting Information, Figure S4). Overall, these sensitivity analyses indicate that the pattern shown in Figure 2 emerges within a relatively wide range of parameter values.

Overall, this study shows how climate fluctuations may lead to qualitatively different ecosystem states that cannot be maintained in the deterministic counterpart of the process (i.e. with  $\sigma_G = 0$ ). Random climate fluctuations are often associated with an effect of ecosystem disturbance,

whereby environmental variability induces random oscillations of the state of the system around the stable states of the underlying deterministic dynamics. The results presented in this study show that the effect of random environmental variability on ecosystem dynamics may be more profound. Indeed, it can induce the emergence of novel stable states that differ from those of the deterministic system. The ability of noise to induce new bifurcations and new dynamical behaviours has been documented and explained for a number of dynamical systems (Horsthemke and Lefever, 1984; Garcia-Ojalvo and Sancho, 1999). In the case of environmental dynamics, it has been found that random environmental fluctuations may enhance biodiversity (Benedetti-Cecchi *et al.*, 2006; D'Odorico *et al.*, 2008), form spatial patterns (D'Odorico *et al.*, 2006b; D'Odorico *et al.*, 2007) or stabilize the system around an unstable state of the underlying deterministic dynamics (D'Odorico *et al.*, 2005). Known as noise-induced stability, this latter effect seems to occur in the case of Figure 2, where random fluctuations maintain the system in a state that would not be stable without environmental variability (Zeng and Neelin, 2000).

The model captures the main features of these interactions and accounts for the different susceptibility of these two functional groups to fires and drought-induced mortality. We note, however, that the goal of this model is not to provide an accurate simulation of these complex dynamics but to offer a conceptual framework for the analysis of the possible combined effects of grass invasions, fires, erosion and climate fluctuations in arid and semiarid landscapes, particularly in terms of the production of a novel bare ecosystem state. Overall, the process-based framework developed in this study has allowed us to generate new hypotheses on the effect of grass invasions and interannual rainfall fluctuations on changes in dryland vegetation. Future research will need to test these theories with field observations and manipulative experiments.

## CONCLUSION

The modelling framework presented in this study shows how the combined effect of grass invasion, fire dynamics, erosion and droughts may turn shrubland into exotic grasslands and, potentially, into vegetation- and resource-poor scablands. Although the potential for shrublands to be converted to invasive grasslands has been identified in the past, the possible emergence of the novel crash, or scabland, state under the effect of climate fluctuations is a possible hazard to be mitigated by the management of invasion-prone arid ecosystems. In the degradation mechanism described here, biological invasions and climate change could act in concert to induce land degradation.

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