Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Short communication

Driver-system state interaction in regime shifts: A model study of desertification in drylands

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ARTICLE INFO

Article history: Received 26 May 2016 Received in revised form 11 August 2016 Accepted 12 August 2016

Keywords: Desertification Dryland ecosystems Drift potential Regime shift Tipping point Bi-stability region

ABSTRACT

An ecosystem may abruptly switch into a contrasting stable state at a critical threshold under the effect of external drivers, a phenomenon called regime shifts. However, drivers are generally assumed to be independent of system states, and thus associated driver-system state interaction is largely ignored when studying regime shifts. With dryland ecosystems as study objective, this study used a mean field model with drift potential as driver to investigate the influences of driver-system state interaction on dynamics of regime shifts. Our results showed following three aspects of influences of the interaction. (1) The interaction pushed the equilibria of regime shifts as a whole into higher drift potential, especially for the forward path. Under annual rainfall of 150 mm, 300 mm and 500 mm, tipping points of the upper branches moved forward 140 VU, 151 VU and 152 VU with strength of the interaction of 200 VU relative to these with strength of the interaction of 0VU, respectively. (2) The interaction could expand the bistability region of regime shifts in driver space, e.g., from 125 VU (annual rainfall of 150 mm), 181 VU (annual rainfall of 300 mm) and 209 VU (annual rainfall of 500 mm) under the interaction of 0 VU up to 145 VU, 257 VU and 290 VU under the interaction of 200 VU, respectively. (3) The interaction might repel ecosystems away from the middle range of system states. These results suggest that the driver-system state interaction should be considered in the studies of regime shifts, and thus to better understand, predict and combat desertification in practice.

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1. Introduction

Drylands cover about 41% of earth's land surface, and are home to around 38% of the global populations (Assessment, 2005). About 10%–20% of drylands have been degraded because of global climate change and more intensified anthropogenic influences (Assessment, 2005; Reynolds et al., 2007). The fact that dryland ecosystems may exhibit threshold behaviors with hysteresis in response to even linear changes in external drivers (e.g., rainfall and wind erosion), a phenomenon called regime shift, exacerbates the influences of degradation in drylands further (Kinzig et al., 2006; Scheffer et al., 2001; Suding and Hobbs, 2009). Meanwhile, regime shifts are generally of great influences, and are difficult to predict and reverse (D'Odorico et al., 2013; Scheffer et al., 2001; Suding and

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http://dx.doi.org/10.1016/j.ecolmodel.2016.08.006 0304-3800/© 2016 Elsevier B.V. All rights reserved. Hobbs, 2009). Therefore, desertification as a possible kind of regime shifts in the forward path in drylands affects the functions and services of dryland ecosystems, which deserves continual and indepth researches (Bestelmeyer et al., 2015; D'Odorico et al., 2013; Kinzig et al., 2006).

Although regime shifts of ecosystems had been studied for several decades (Carpenter et al., 1999; Folke et al., 2004; May, 1977; Wissel, 1984), external driver generally is assumed to be independent of system states, or the change rate of external driver should be much slower than that of system states (Bestelmeyer et al., 2011; Scheffer and Carpenter, 2003). For instance, nutrient input as a driver is 'purely' external for shallow lakes (Carpenter et al., 1999). However, some researches in the Sahel region in West Africa and tropical forests in a past decade suggested that drivers (rainfall) might be coupled with system states (Janssen et al., 2008; Li et al., 2015; Scheffer et al., 2005; van Nes et al., 2014; Wang and Eltahir, 2000; Webb et al., 2005; Zeng et al., 1999). That is, drivers may interact with system states. The feedback between drivers and system states can influence the dynamics of regime shifts greatly, such as moving the location of tipping point (where the ecosystems







switch into the alternative stable state) into more harsh conditions and causing greater hysteresis (Dekker et al., 2007; Janssen et al., 2008; van Nes et al., 2014).

However, there is still a large knowledge gap in the effect of feedback of drivers and system states on regime shifts in other ecosystems (e.g., dryland ecosystems). For drylands, limited knowledge come from studies on the interaction between fire frequency a driver and system state. For example, D'Odorico et al. (2006) reported that the interaction between fire frequency and system state greatly influenced the tree-grass coexistence and thus the dynamics of regime shifts in semi-arid lands.

As one of the most important external drivers in drylands, wind erosion leads to about 42% of total desertification (Belnap et al., 2011; Ravi et al., 2011). Although wind erosion has been studied for a long time in physics and geography (Bagnold, 2012; Dupont et al., 2014; Lockeretz, 1978; Okin, 2008; Wiggs et al., 1995), relevant researches in ecology, especially about regime shift theory in ecosystem level, are relatively scarce (Bhattachan et al., 2014; Fearnehough et al., 1998; Kinast et al., 2013). Therefore, it is still greatly lacking of the knowledge about the effects of the interaction between wind erosion and system states on dynamics of regime shifts in drylands. Previous studies suggested that the existence of vegetation could reduce the strength of wind erosion and further influence ecosystem stability, which indicated the importance of the interaction between wind erosion and system state (Breshears et al., 2009; Dupont et al., 2014; Mao et al., 2014; Wiggs et al., 1995). To combat desertification, studying the interaction between wind erosion and system states in regime shifts are of great implications and significances, especially under background of global climate change, which may increase the frequency and intensity of desertification in future (D'Odorico et al., 2013; Kinast et al., 2013; Scheffer et al., 2001; Thomas and Leason, 2005; Young et al., 2011).

In this study, we used a mean field model, which did not consider the spatial circumstance, with drift potential (one index of wind erosion) as driver to explore how driver-system state interaction affected the dynamics of regime shift in dryland ecosystems. We hypothesized that the interaction influenced the regime shifts in drylands in two ways: 1) shifting the region in driver space where vegetation could survive into more harsh conditions; 2) expanding the bi-stability region in equilibria of regime shifts.

2. Model

The model describes the dynamics of vegetation cover (v) and biological soil crust (biocrust hereafter) cover (b). The primary environmental factors influencing the growth of vegetation and biocrust include annual rainfall and wind. We used the following model, consisting of two coupled ordinary differential equations,

$$\nu' = a_{\nu}(\nu + \eta_{\nu})s - \varepsilon_{\nu}D_{p}\nu g(\nu)s - \gamma D_{p}^{\frac{2}{3}}\nu - \Phi_{\nu}\nu b$$
(1a)

$$b' = a_b (b + \eta_b) s - \varepsilon_b D_p bg(v) s - \Phi_b v b$$
^(1b)

where s = 1 - v - b indicates the remaining cover of bare sand. The right side of Eq. (1a) represents the growth of vegetation (the first term), indirect influence of wind erosion on vegetation (the second term), direct influence of wind erosion on vegetation (the third term) and the effect of competition between vegetation and biocrust on vegetation (the fourth term), respectively. For Eq. (1b), there is no the third term – direct influence of wind erosion on biocrust.

The growth rates of vegetation and biocrust depend on annual rainfall (r):

$$a_{i}(r) = \begin{cases} a_{i,max} \begin{pmatrix} -\frac{r-r_{i,min}}{c_{i}} \end{pmatrix} r \ge r_{i,min} \\ 0 \qquad r < r_{i,min} \end{cases}$$
(2)

where i denotes v or b.

Vegetation can decrease the indirect influence of wind by inducing a *skimming flow* effect, which is described by a continuous step-like function as following,

$$g(v) = 0.5(\tan h[d(v_c - v)] + 1)$$
(3)

where *d* indicates the stepness of sand shading effect, v_c denotes the critical vegetation cover to induce the *skimming flow* effect.

We use drift potential D_p , the potential sand volume that can be transported by the wind trough a 1 m wide cross section per unit time (generally one year), to represent wind erosion,

$$D_p = \langle U^2 \left(U - U_t \right) \rangle \tag{4}$$

where *U* is the wind speed at 10 m above the ground measured in knots (1 knot \approx 0.5 m/s), and *U*_t is the threshold velocity that is necessary for sand transport, the units of *D*_p are defined as *vector unit* (VU).

To take the interaction between drift potential and system states into account, we treat drift potential as a system state variable instead of a parameter (van Nes et al., 2014) and build another equation, which is given by:

$$D_p = D_{p0} - C_{dp} (v + b)$$
(5)

 D_{p0} indicates drift potential of no considering the interaction with vegetation and/or biocrust, C_{dp} denotes the strength of drift potential-system state interaction. We assume that both vegetation cover and biocrust cover could impact D_p by increasing the roughness of ground surface, which is consistent with previous studies (Dupont et al., 2014; Li et al., 2007; Mao et al., 2014).

More detailed introduction to the model, parameters and associated values is available in Table 1. This model is developed based on that of Kinast et al. (2013). Interested readers about the model can also refer to (Bel and Ashkenazy, 2014; Janssen et al., 2008; Kinast et al., 2013; van Nes et al., 2014; Yizhaq and Ashkenazy, 2016; Yizhaq et al., 2007).

3. Parameterizations and simulations

To explore the influences of the interaction between drift potential and system states on the dynamics of regime shifts in drylands, we investigated the equilibria of system variables (vegetation cover, biocrust cover and drift potential) in Eq. (1) with considering different strength of the interaction – C_{dp} as shown in Table 1. To further consider the respective situations in arid (annual rainfall of 100 mm–250 mm) and semi-arid (annual rainfall of 250 mm–600 mm) lands, two major subtypes of drylands (Assessment, 2005; D'Odorico et al., 2013), we set up three levels of annual rainfall (we partition drylands according to annual rainfall) of 150 mm, 300 mm and 500 mm.

We implemented graphical, numerical continuation packages MATCONT 6.2 in Matlab 2015a to do the bifurcation analyses of the ordinary differential equations interactively (equally, another toolbox could be used either as a general-purpose non-interactive continuation in Matlab: CL_MATCONT). The solver we used in this study was *ode45*. We detected the equilibria using codimension 0 bifurcation 'EP'. The range of D_{p0} is 0 VU–800 VU, spreading over low- to high-wind energy environments (Fryberger and Dean, 1979). Other parameter values were shown in Table 1. More details

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