



Short communication

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

Ning Chen<sup>a,b,\*</sup>, Xin-ping Wang<sup>a</sup>

<sup>a</sup> Shapotou Desert Research and Experiment Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, 320, Donggang West Road, Lanzhou, Gansu 730000, China

<sup>b</sup> University of Chinese Academy of Sciences, 19, Yuquan Road, Shijingshan District, Beijing 100049, China

## 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 0 VU, respectively. (2) The interaction could expand the bi-stability 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.

© 2016 Elsevier B.V. All rights reserved.

### 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

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 in-depth 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

\* Corresponding author at: Shapotou Desert Research and Experiment Station, Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, 320 Donggang West Road, Lanzhou, Gansu 730000, China.

E-mail address: [chenning.cn2015@gmail.com](mailto:chenning.cn2015@gmail.com) (N. Chen).

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; Fearnough 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,

$$v' = a_v(v + \eta_v)s - \varepsilon_v D_p v g(v)s - \gamma D_p^{\frac{2}{3}} v - \Phi_v v b \quad (1a)$$

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

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 ( $r$ ):

$$a_i(r) = \begin{cases} a_{i,max} \left( 1 - e^{-\frac{r - r_{i,min}}{c_i}} \right) & r \geq r_{i,min} \\ 0 & r < r_{i,min} \end{cases} \quad (2)$$

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,

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

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 through a 1 m wide cross section per unit time (generally one year), to represent wind erosion,

$$D_p = \langle U^2 (U - U_t) \rangle \quad (4)$$

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:

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

$D_{p0}$  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 0VU–800VU, spreading over low- to high-wind energy environments (Fryberger and Dean, 1979). Other parameter values were shown in Table 1. More details

**Table 1**  
Model parameters, and associated meanings and values.

Symbols	Meaning	Value/unit
$v$	Vegetation cover	%
$b$	Biocrust cover	%
$D_p$	Drift potential	VU
$a_{v,max}$	Maximal growth rate of vegetation	0.15/year
$a_{b,max}$	Maximal growth rate of biocrust	0.015/year
$r_{v,min}$	Minimal rainfall needed for vegetation to grow	50 mm/year
$r_{b,min}$	Minimal rainfall needed for biocrust to grow	20 mm/year
$c_v$	Saturation coefficient of the vegetation growth rate	100 mm/year
$c_b$	Saturation coefficient of the biocrust growth rate	50 mm/year
$\eta_v$	Spontaneous growth rate of vegetation	0.2
$\eta_b$	Spontaneous growth rate of biocrust	0.1
$\varepsilon_v$	Sand transport induced mortality to vegetation	0.001 VU <sup>-1</sup> year <sup>-1</sup>
$\varepsilon_b$	Sand transport induced mortality to biocrust	0.0001 VU <sup>-1</sup> year <sup>-1</sup>
$\varphi_v$	Net effect of interaction between vegetation and biocrust on vegetation	0.01 VU <sup>-1</sup> year <sup>-1</sup>
$\varphi_b$	Net effect of interaction between vegetation and biocrust on biocrust	0.01 VU <sup>-1</sup> year <sup>-1</sup>
$\gamma$	Mortality induced by direct wind influence to vegetation	0.0008 VU <sup>3/2</sup> year <sup>-1</sup>
$d$	Steepness of sand drift shading effect	15
$v_c$	Critical vegetation cover	0.3
$r$	Annual rainfall	150, 300, 500 mm
$D_{p0}^a$	Drift potential of no considering interaction with vegetation and biocrust	0–800 VU
$C_{dp}^a$	Strength coefficient of interaction between drift potential and system state	0, 50, 100, 150, 200 VU

Notes: Most parameter values we used are adopted from (Kinast et al., 2013).

<sup>a</sup> Indicates that the parameters are new in this study.

about the usage about MATCONT or CL.MATCONT in Matlab are available in (Dhooge et al., 2003) and <http://www.matcont.ugent.be/>

We described the influences of the interaction on dynamics of regime shifts by measuring the changes in location of tipping points (F1 in the forward path of regime shift – desertification, and F2 in the backward path of regime shift – restoration) and also the width of bi-stability region in the driver space.

If vegetation cover or biocrust cover was larger than 40%, we regarded that the ecosystem was in vegetation or biocrust state, respectively. Otherwise, the ecosystem was in the bare state.

One should differentiate the drift potential-system state interaction and the shielding effect created by vegetation cover (one system variable). The latter denotes that vegetation cover can reduce the influence of drift potential on system state while the former emphasizes that vegetation cover can reduce the strength of drift potential directly.

## 4. Results

### 4.1. The influences of driver-system state interaction on system state

As shown in Fig. 1, the driver-system state interaction could reduce the strength of drift potential, especially when  $D_{p0}$  was low. That is, the interaction improved the environmental conditions suitable for vegetation and/or biocrust to survive. Whereas when  $D_{p0}$  was high (e.g., >600 VU), the effect of the interaction was minor (Fig. 1). The interaction extended the driver space where they could play a role on the strength of drift potential as increasing in annual rainfall (Fig. 1). For example, F1 of on equilibria of regime shifts with  $C_{dp}$  of 200 VU moved from 390 VU under annual rainfall of 150 mm, to 563 VU under annual rainfall of 300 mm and 612 VU under annual rainfall of 500 mm (Fig. 1; Table A.1).

In both kinds of dryland ecosystems we discussed, when  $D_{p0}$  was low, vegetation cover (biocrust) cover was high (low), and vegetation state was the only stable state; at high drift potential, both system variables were low, and the bare state was the only stable state (Figs. 2 and 3). Biocrust cover was relatively high (around 10%–40%) only in bi-stability region outlined by two tipping points (Fig. 3). Moreover, in cases with rainfall of 500 mm and  $C_{dp} < 200$  VU,

a tri-stability region existed within the bi-stability region with mixed vegetation and biocrust state as another alternative stable state (between F3 and F4 in Figs. 2C, 3C).

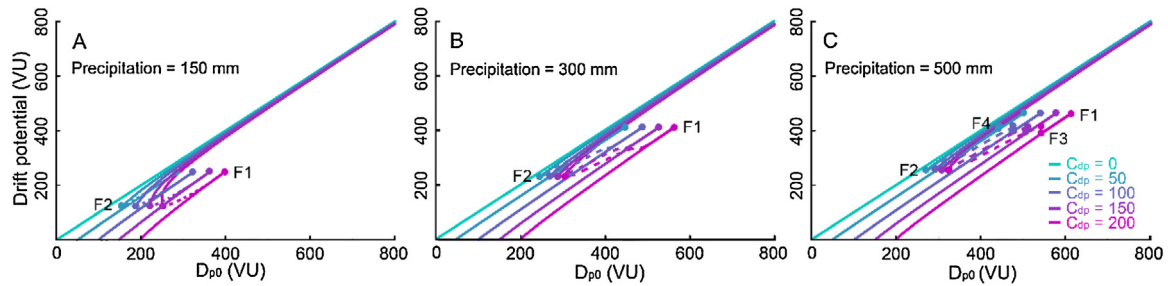
When annual rainfall was 150 mm, as the increasing in the interaction up to 200 VU successively, the locations of F1 changed to 250 VU, 287 VU, 325 VU, 361 VU and 390 VU, these of F2 changed to 125 VU, 158 VU, 190 VU, 221 VU and 245 VU, and thus the ranges of bi-stability region increased from 125 VU, 129 VU, 135 VU, 140 VU to 145 VU, respectively (Figs. 2A, 3A; Table A.1).

The equilibria diagram of regime shifts under annual rainfall of 300 mm as a whole expanded to higher drift potential (especially the upper branches of equilibria) than that under annual rainfall of 150 mm (Fig. 2A,B). Specifically, the range of bi-stability region increased to 181 VU (F2: 231 VU–F1: 412 VU), 200 VU (F2: 251 VU–F1: 451 VU), 219 VU (F2: 269 VU–F1: 488 VU), 239 VU (F2: 286 VU–F1: 525 VU) and 257 VU (F2: 306 VU–F1: 563 VU) under the intensified interaction strength between drift potential and system states, respectively (Figs. 2B, 3B; Table A.1).

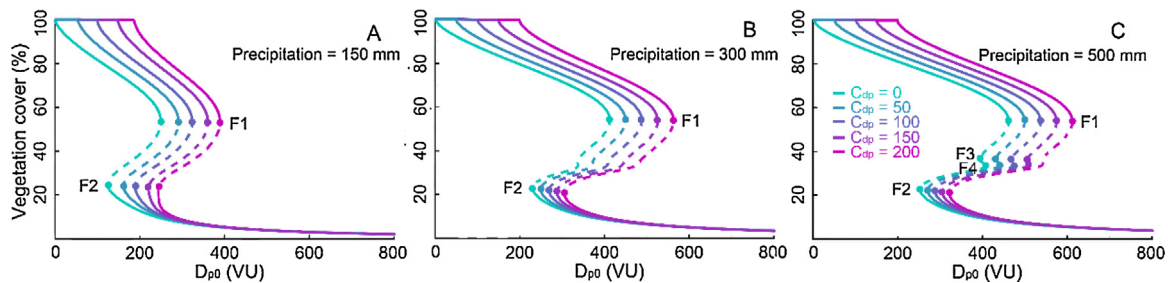
When annual rainfall was 500 mm, the equilibria was pushed into higher drift potential than these in annual rainfall of 300 mm (Figs. 2 and 3). The width of bi-stability region increased from 209 VU, 229 VU, 248 VU, 269 VU to 290 VU (F1 shifting to 460 VU, 500 VU, 536 VU, 574 VU and 612 VU; F2 shifting to 251 VU, 271 VU, 288 VU, 305 VU and 322 VU), as the increasing in the interaction strength from 0 VU up to 200 VU, respectively (Figs. 2C, 3C; Table A.1). Moreover, the third alternative stable state spread in 14 VU, 10 VU, 6 VU and 2 VU when  $C_{dp} = 0$  VU, 50 VU, 100 VU and 150 VU, respectively (Figs. 2C, 3C; Table A.1).

### 4.2. Subtypes of drylands

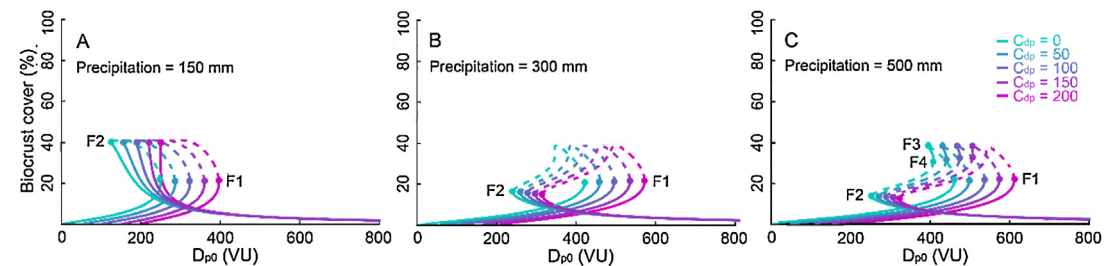
The interaction between drift potential and system states influenced the locations of tipping points (F1 and F2) in similar ways but varied in extents for three levels of annual rainfall in drylands. The shifting of tipping points in forward regime shifts – F1 – was stronger under higher rainfall, from 140 VU, 151 VU to 152 VU under rainfall of 150 mm, 300 mm and 500 mm, respectively; while that in backward regime shifts – F2 – tended to slow down, from 120 VU, 75 VU to 71 VU under rainfall of 150 mm, 300 mm and 500 mm, respectively (Figs. 1–3; Table A.1).



**Fig. 1.** Equilibria diagram of drift potential with varied interaction strength under annual rainfall of 150 mm (A), 300 mm (B) and 500 mm (C). The upper (lower) points – F1 (F2) on each equilibria indicate the tipping points of forward (backward) regime shifts. The tipping points of F1 and F2 outline the bi-stability region of regime shifts; F3 and F4 on equilibria of  $C_{dp} < 200$  VU mark the region of another stable state – mixed vegetation and biocrust state in driver space. The solid (dashed) lines denote stable (unstable) equilibria.



**Fig. 2.** Equilibria diagram of vegetation cover with varied interaction strength under annual rainfall of 150 mm (A), 300 mm (B) and 500 mm (C). The upper (lower) points – F1 (F2) on each equilibria indicate the tipping points of forward (backward) regime shifts. The tipping points of F1 and F2 outline the bi-stability region of regime shifts; F3 and F4 on equilibria of  $C_{dp} < 200$  VU mark the region of another stable state – mixed vegetation and biocrust state in driver space. The solid (dashed) lines denote stable (unstable) equilibria.



**Fig. 3.** Equilibria diagram of biocrust cover with varied interaction strength under annual rainfall of 150 mm (A), 300 mm (B) and 500 mm (C). The upper (lower) points – F1 (F2) on each equilibria indicate the tipping points of forward (backward) regime shifts. The tipping points of F1 and F2 outline the bi-stability region of regime shifts; F3 and F4 on equilibria of  $C_{dp} < 200$  VU mark the region of another stable state – mixed vegetation and biocrust state in driver space. The solid (dashed) lines denote stable (unstable) equilibria.

## 5. Discussion

In this study, using a mean field model with drift potential as the external driver, we investigated the effects of driver–system state interaction on the dynamics of regime shifts in dryland ecosystems. This work supports our hypotheses: the interaction strongly impacted the dynamics of regime shifts – pushing equilibria of regime shifts as a whole into higher drift potential (i.e., more harsh environment), and extending the bi-stability regions primarily by moving tipping points of the forward regime shifts – F1. Furthermore, we also find that the interaction repels dryland ecosystems away from middle range of system states. Our results suggest that it is greatly necessary to consider the driver–system states interaction in regime shifts when studying desertification in drylands, especially under the background of global change and more intensified anthropogenic influences (Bestelmeyer et al., 2015; Thomas and Leason, 2005; Tsoar et al., 2009; Young et al., 2011). This study contributes in two aspects: (1) verifying previous studies on the

role of driver–system state interaction on dynamics of regime shifts in other ecosystems and/or other drivers; and (2) extending previous studies and highlighting the role of the driver–system state interaction in dryland ecosystems with drift potential as the driver (Janssen et al., 2008; Scheffer et al., 2005; van Nes et al., 2014; Webb et al., 2005).

### 5.1. The effects of the driver–system state interaction on dynamics of regime shifts in drylands

Although the assumption about the independence of drivers and system state has been challenged by studies in Sahel region and tropical forests with annual rainfall as the driver in a last decade (Scheffer et al., 2005; van Nes et al., 2014; Wang and Eltahir, 2000; Webb et al., 2005; Zeng et al., 1999), studies of the effect of the interaction in dryland ecosystems and/or other drivers are still largely lacking (but see D’Odorico et al., 2006).



The driver-system state interaction ameliorates the environments to support vegetation and biocrust (Figs. 1–3). The primary reason underlying this phenomenon is that vegetation can reduce the strength of drift potential by increasing roughness of ground surface (Dupont et al., 2014; Okin, 2008; Tsoar, 2005), which process is generally ignored in previous models of regime shifts with drift potential as drivers (Kinast et al., 2013; Yizhaq and Ashkenazy, 2016; Yizhaq et al., 2007). For instance, under annual rainfall of 150 mm, the only stable state of the regime shift with no considering the interaction is bare state when  $D_{po}$  is equal to 300 VU (Fig. 2A). However, if the driver-system state interaction is strong ( $C_{dp} = 200$  VU), the stable state can also be the vegetation state besides the bare state (Fig. 2A). Meanwhile, the effects of the interaction on the forward path of regime shifts are stronger than these on the backward path, because vegetation and biocrust cover are higher in the vegetation state and thus can reduce the drift potential more dramatically (Figs. 1–3; Table A.1). Accordingly, the bi-stability region of the equilibria of regime shifts expands, which is consistent with previous studies in other ecosystems (D'Odorico et al., 2006; Dekker et al., 2007; Janssen et al., 2008; van Nes et al., 2014). This phenomenon has implications for desertification and restorations that the interaction makes desertification more difficult and makes restorations somewhat easier. In preventing desertification and restoring degraded ecosystems, one can enhance the strength of the interaction between drift potential and system state by ways such as connecting the elements of the ecosystems (Kinzig et al., 2006; Ravi et al., 2011).

Moreover, there is another alternative stable state in regime shifts under rainfall of 500 mm and  $C_{dp} < 200$  VU (Figs. 1C, 2C, 3C). The emergence of the alternative stable state may likely be induced by the weaker effect of drift potential under high annual rainfall (Belnap et al., 2011; Field et al., 2009; Kinast et al., 2013). The width of the third alternative stable state in driver space shrinks as the increasing in the strength of driver-system state interaction (Figs. 1C, 2C, 3C; Table A.1). The interaction may repel system states from the middle region in states space: when vegetation cover is high, the interaction can push the ecosystem into the vegetation state; when vegetation cover is low, the interaction can push the ecosystem into the bare state (D'Odorico et al., 2006; van Nes et al., 2014). The fact that the interaction enhance the role of drift potential in regime shifts may be responsible for the shrinkage and vanishing of the third alternative stable state (D'Odorico et al., 2006; van Nes et al., 2014). Therefore, stakeholders should be aware of the possible existence of the third alternative stable state, and should not surprise that if an ecosystem stays in a state with mixed vegetation and biocrust for a long time, in the process of desertification or restoration.

### 5.2. The effects of the interaction on dynamics of regime shifts under varied annual rainfall

The results show that the shifting of tipping points in forward regime shifts – F1, induced by the interaction between drift potential and system states, tends to accelerate under higher annual rainfall; while that in backward regime shifts – F2 tends to slow down (Figs. 1–3; Table A.1). For forward regime shifts that ecosystems in vegetation state initially, the vegetation cover and/or biocrust cover will be higher under higher annual rainfall, leading to that the effect of the interaction becomes stronger, and thus the shifting of tipping points tends to accelerate (Fig. 1). The opposite is valid for the backward regime shifts. The distinct dynamics of forward and backward paths of regime shifts suggest that one should on one hand pay attention to the phenomenon that forward and backward path of regime shifts may perform differently (Carpenter et al., 1999; Scheffer et al., 2001), and on the other hand explicitly consider the underlying processes (e.g., vegetation and biocrust

cover reduce the strength of drift potential) to better understand and predict the dynamics of regime shifts and also desertification. Meanwhile, under the background of global climate changes, the dynamics of regime shifts in one ecosystem may be altered greatly because of increasing or decreasing annual rainfall. For example, in an increasing annual rainfall scenario, when  $D_{po}$  of 400 VU the only stable state of a dryland ecosystem under annual rainfall of 150 mm is the bare state; while the stable state also can be the vegetation state under rainfall of 300 mm (Figs. 1A, 2A, 3A). In practice, one can regulate on annual rainfall/water input to the ecosystems under management to promote restorations and to prevent desertification (Kinast et al., 2013; Kinzig et al., 2006; Li et al., 2015).

It is also found that the acceleration (slowing down) of the shifting of tipping points in forward (backward) regime shifts tends to suspend when annual rainfall reaches 300 mm (Table A.1). The effect of drift potential reaches the maximum and becomes limited relative to that of rainfall when annual rainfall approaches to 300 mm, which once again verifies previous studies about the relative roles of wind erosion and rainfall (Belnap et al., 2011; Field et al., 2009; Ravi et al., 2011).

### 5.3. Limitations and extensions

To include the interaction between drift potential and system states into our model, we suppose that both vegetation cover and biocrust cover linearly decrease the strength of drift potential relative to that in the bare state. In other words, the interaction is uni-direction (i.e., vegetation and biocrust cover decrease the strength of drift potential), which is in accord with previous study in tropical forest (van Nes et al., 2014). Of course, the interaction may be bi-direction or even more complex in behaviors, which needs further studies to explore in future. In this study, the highest strength of the interaction was set to 200 VU because the existence of vegetation (and/or biocrust) might be not able to overturn the general pattern of drift potential in theoretical and empirical (Li et al., 2007; Mao et al., 2014; Wiggs et al., 1995). Whereas it may be reasonable to set the strength up to 600 VU or even 1000 VU in cases such as coastal sand dune ecosystems in Ceará State, NE Brazil (Goudie and Middleton, 2006; Tsoar et al., 2009; Yizhaq et al., 2007).

## 6. Conclusion

This work presents a simple numerical model to extend our knowledge about the effects of the interaction between driver (drift potential) and system states on regime shifts in dryland ecosystems. The results suggest that the interaction strongly impacts the dynamics of regime shifts in various ways: (1) pushing regime shifts as a whole into higher drift potential, i.e., ameliorating more harsh environments to allow vegetation or biocrust to survive; (2) expanding the bi-stability region in driver space; (3) repelling ecosystems away from middle range of system states. Therefore, it may be necessary to take the interaction between drivers and system states into account in regime shift studies. If one do not take driver-system states interaction into consideration when studying the dynamics of desertification in drylands, it may be not able to correctly predict the occurrence and dynamics of desertification, or even yield 'wrong' conclusions. Namely, this model study also has many practical implications for better predicting the dynamics of and thus combating desertification, and for restoring desertified ecosystems. In current study, we only explore the interaction between drift potential and system states in drylands theoretically. Empirical tests are still needed. Meanwhile, the role of driver-system state interaction on dynamics of regime shifts for other drivers and/or other ecosystems could be investigated in future.

## Acknowledgements

This work was supported by the National Natural Science Foundation of China (grant nos. 41530750, 41371101). The authors wish to thank Drs. Ya-feng zhang, Lei Huang and Di-nghai Zhang for helps in model simulations. We are also grateful to the anonymous reviewer for his constructive comments and suggestions.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.08.006>.

## References

- Assessment, M.E., 2005. *Ecosystems and Human Well-being*. Island Press, Washington, DC.
- Bagnold, R.A., 2012. *The Physics of Blown Sand and Desert Dunes*. Courier Corporation.
- Bel, G., Ashkenazy, Y., 2014. The effects of psammophilous plants on sand dune dynamics. *J. Geophys. Res.: Earth Surf.* 119, 1636–1650.
- Belnap, J., Munson, S.M., Field, J.P., 2011. Aeolian and fluvial processes in dryland regions: the need for integrated studies. *Ecology* 4, 615–622.
- Bestelmeyer, B.T., Ellison, A.M., Fraser, W.R., Gorman, K.B., Holbrook, S.J., Laney, C.M., Ohman, M.D., Peters, D.P., Pillsbury, F.C., Rassweiler, A., 2011. Analysis of abrupt transitions in ecological systems. *Ecosphere* 2, art129.
- Bestelmeyer, B.T., Okin, G.S., Duniway, M.C., Archer, S.R., Sayre, N.F., Williamson, J.C., Herrick, J.E., 2015. Desertification, land use, and the transformation of global drylands. *Front. Ecol. Environ.* 13, 28–36.
- Bhattachan, A., D'Odorico, P., Dintwe, K., Okin, G.S., Collins, S.L., 2014. Resilience and recovery potential of duneland vegetation in the southern Kalahari. *Ecosphere* 5, 14.
- Breshears, D.D., Whicker, J.J., Zou, C.B., Field, J.P., Allen, C.D., 2009. A conceptual framework for dryland aeolian sediment transport along the grassland-forest continuum: effects of woody plant canopy cover and disturbance. *Geomorphology* 105, 28–38.
- Carpenter, S.R., Ludwig, D., Brock, W.A., 1999. Management of eutrophication for lakes subject to potentially irreversible change. *Ecol. Appl.* 9, 751–771.
- D'Odorico, P., Laio, F., Ridolfi, L., 2006. A probabilistic analysis of fire-induced tree-grass coexistence in savannas. *Am. Nat.* 167, E79–E87.
- D'Odorico, P., Bhattachan, A., Davis, K.F., Ravi, S., Runyan, C.W., 2013. Global desertification: drivers and feedbacks. *Adv. Water Resour.* 51, 326–344.
- Dekker, S.C., Rietkerk, M., Bierkens, M.F., 2007. Coupling microscale vegetation–soil water and macroscale vegetation–precipitation feedbacks in semiarid ecosystems. *Global Change Biol.* 13, 671–678.
- Dhooge, A., Govaerts, W., Kuznetsov, Y.A., 2003. MATCONT: a MATLAB package for numerical bifurcation analysis of ODEs. *ACM Trans. Math. Softw. (TOMS)* 29, 141–164.
- Dupont, S., Bergametti, G., Simoens, S., 2014. Modeling aeolian erosion in presence of vegetation. *J. Geophys. Res.—Earth* 119, 168–187.
- Fearnough, W., Fullen, M.A., Mitchell, D.J., Trueman, I.C., Zhang, J., 1998. Aeolian deposition and its effect on soil and vegetation changes on stabilised desert dunes in northern China. *Geomorphology* 23, 171–182.
- Field, J.P., Breshears, D.D., Whicker, J.J., 2009. Toward a more holistic perspective of soil erosion: why aeolian research needs to explicitly consider fluvial processes and interactions. *Aeolian Res.* 1, 9–17.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* 35, 557–581.
- Fryberger, S.G., Dean, G., 1979. Dune forms and wind regime. A study of global sand seas, 1052, 137–169.
- Goudie, A., Middleton, N.J., 2006. *Desert Dust in the Global System*. Springer Science & Business Media.
- Janssen, R.H.H., Meinders, M.B.J., van Nes, E.H., Scheffer, M., 2008. Microscale vegetation–soil feedback boosts hysteresis in a regional vegetation–climate system. *Global Change Biol.* 14, 1104–1112.
- Kinast, S., Meron, E., Yizhaq, H., Ashkenazy, Y., 2013. Biogenic crust dynamics on sand dunes. *Phys. Rev. E* 87, 020701.
- Kinzig, A.P., Ryan, P., Etienne, M., Allison, H., Elmqvist, T., Walker, B.H., 2006. Resilience and regime shifts: assessing cascading effects. *Ecol. Soc.* 11.
- Li, J., Okin, G.S., Alvarez, L., Epstein, H., 2007. Quantitative effects of vegetation cover on wind erosion and soil nutrient loss in a desert grassland of southern New Mexico. *USA. Biogeochemistry* 85, 317–332.
- Li, Z., Liu, X., Niu, T., Kejia, D., Zhou, Q., Ma, T., Gao, Y., 2015. Ecological restoration and its effects on a regional climate: the source region of the Yellow river, China. *Environ. Sci. Technol.* 49, 5897–5904.
- Lockeretz, W., 1978. The lessons of the dust bowl: several decades before the current concern with environmental problems, dust storms ravaged the Great Plains, and the threat of more dust storms still hangs over us. *Am. Sci.* 66, 560–569.
- Mao, D.L., Lei, J.Q., Zeng, F.J., Zaynulla, R., Wang, C., Zhou, J., 2014. Characteristics of wind erosion and deposition in oasis-desert ecotone in southern margin of Tarim Basin, China. *Chin. Geogr. Sci.* 24, 658–673.
- May, R.M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471–477.
- Okin, G.S., 2008. A new model of wind erosion in the presence of vegetation. *J. Geophys. Res.—Earth* 113, 11.
- Ravi, S., D'Odorico, P., Breshears, D.D., Field, J.P., Goudie, A.S., Huxman, T.E., Li, J.R., Okin, G.S., Swap, R.J., Thomas, A.D., Van Pelt, S., Whicker, J.J., Zobeck, T.M., 2011. Aeolian processes and the biosphere. *Rev. Geophys.* 49, 45.
- Reynolds, J.F., Smith, D.M.S., Lambin, E.F., Turner, B., Mortimore, M., Batterbury, S.P., Downing, T.E., Dowlatabadi, H., Fernández, R.J., Herrick, J.E., 2007. Global desertification: building a science for dryland development. *Science* 316, 847–851.
- Scheffer, M., Carpenter, S.R., 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* 18, 648–656.
- Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. *Nature* 413, 591–596.
- Scheffer, M., Holmgren, M., Brovkin, V., Claussen, M., 2005. Synergy between small-and large-scale feedbacks of vegetation on the water cycle. *Global Change Biol.* 11, 1003–1012.
- Suding, K.N., Hobbs, R.J., 2009. Threshold models in restoration and conservation: a developing framework. *Trends Ecol. Evol.* 24, 271–279.
- Thomas, D.S.G., Leason, H.C., 2005. Dunefield activity response to climate variability in the southwest Kalahari. *Geomorphology* 64, 117–132.
- Tsoar, H., Levin, N., Porat, N., Maia, L.P., Herrmann, H.J., Tatumi, S.H., Claudino-Sales, V., 2009. The effect of climate change on the mobility and stability of coastal sand dunes in Ceará State (NE Brazil). *Quat. Res.* 71, 217–226.
- Tsoar, H., 2005. Sand dunes mobility and stability in relation to climate. *Phys. A: Stat. Mech. Appl.* 357, 50–56.
- van Nes, E.H., Hirota, M., Holmgren, M., Scheffer, M., 2014. Tipping points in tropical tree cover: linking theory to data. *Global Change Biol.* 20, 1016–1021.
- Wang, G., Eltahir, E.A., 2000. Role of vegetation dynamics in enhancing the low-frequency variability of the Sahel rainfall. *Water Resour. Res.* 36, 1013–1021.
- Webb, T.J., Woodward, F.I., Hannah, L., Gaston, K.J., 2005. Forest cover–rainfall relationships in a biodiversity hotspot: the Atlantic forest of Brazil. *Ecol. Appl.* 15, 1968–1983.
- Wiggs, G.F.S., Thomas, D.S.G., Bullard, J.E., 1995. Dune mobility and vegetation cover in the southwest Kalahari desert. *Earth Surf. Processes Landf.* 20, 515–529.
- Wissel, C., 1984. A universal law of the characteristic return time near thresholds. *Oecologia* 65, 101–107.
- Yizhaq, H., Ashkenazy, Y., 2016. Periodic temporal oscillations in biocrust–vegetation dynamics on sand dunes. *Aeolian Res.* 20, 35–44.
- Yizhaq, H., Ashkenazy, Y., Tsoar, H., 2007. Why do active and stabilized dunes coexist under the same climatic conditions? *Phys. Rev. Lett.* 98, 188001.
- Young, I.R., Zieger, S., Babanin, A.V., 2011. Global trends in wind speed and wave height. *Science* 332, 451–455.
- Zeng, N., Neelin, J.D., Lau, K.-M., Tucker, C.J., 1999. Enhancement of interdecadal climate variability in the Sahel by vegetation interaction. *Science* 286, 1537–1540.