Note

Grazing Away the Resilience of Patterned Ecosystems

Eric Siero,[1,][*] Koen Siteur,[2,3] Arjen Doelman,[4] Johan van de Koppel,[2,5] Max Rietkerk,[6] and Maarten B. Eppinga[6,][†]

1. Institute for Mathematics, Carl von Ossietzky University of Oldenburg, 26111 Oldenburg, Germany;   2. Department of Estuarine and Delta Systems, Royal Netherlands Institute for Sea Research and Utrecht University, PO Box 140, 4400 AC Yerseke, The Netherlands; 3. Shanghai Key Laboratory for Urban Ecological Processes and Eco-Restoration and Center for Global Change and Ecological Forecasting, School of Ecological and Environmental Science, East China Normal University, 200241 Shanghai, China;   4. Mathematical Institute, Leiden University, 2300 RA Leiden, The Netherlands;   5. Groningen Institute for Evolutionary Life Sciences, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands;   6. Department of Environmental Sciences, Copernicus Institute, Utrecht University, 3508 TC Utrecht, The Netherlands

ABSTRACT: Ecosystems' responses to changing environmental conditions can be modulated by spatial self-organization. A prominent example of this can be found in drylands, where formation of vegetation patterns attenuates the magnitude of degradation events in response to decreasing rainfall. In model studies, the pattern wavelength responds to changing conditions, which is reflected by a rather gradual decline in biomass in response to decreasing rainfall. Although these models are spatially explicit, they have adopted a mean-field approach to grazing. By taking into account spatial variability when modeling grazing, we find that (over)grazing can lead to a dramatic shift in biomass, so that degradation occurs at rainfall rates that would otherwise still maintain a relatively productive ecosystem. Moreover, grazing increases the resilience of degraded ecosystem states. Consequently, restoration of degraded ecosystems could benefit from the introduction of temporary small-scale exclosures to escape from the basin of attraction of degraded states.

Keywords: self-organization, positive density dependence, regime shift, land degradation, desertification, global coupling.

Introduction

Understanding the mechanisms driving critical transitions between ecosystem states is a key priority for current ecological research (Rietkerk et al. 2004; Scheffer et al. 2009, 2015). The notion that internal system feedbacks may drive

* Corresponding author; email: eric.siero@uni-oldenburg.de.

† Present address: Department of Geography, University of Zurich, 8057 Zurich, Switzerland.

ORCIDs: Siero, http://orcid.org/0000-0002-9643-8802; Eppinga, http://orcid.org/0000-0002-1954-6324.

critical transitions between ecosystem states emerged from theoretical analyses of dryland grazing systems (Noy-Meir 1975; May 1977). In these pioneering studies, a positive feedback between vegetation scarcity and per capita grazing pressure yielded the occurrence of alternate stable states and the possibility of critical transitions between these states at intermediate herbivore densities (Noy-Meir 1975; May 1977; Yodzis 1989; DeAngelis 1992). Subsequent model studies showed that this positive feedback mechanism still induced alternate stable states when the herbivore population responded dynamically to changes in vegetation density, albeit typically within a narrower range of environmental conditions (van de Koppel and Rietkerk 2000). These studies did not consider spatial interactions between the abiotic environment, vegetation, and herbivores. Instead, such mean-field approaches implicitly assume relatively homogeneous vegetation cover and random movement of herbivores through the landscape (e.g., van de Koppel et al. 2002). Nevertheless, mean-field analyses have clearly identified the potentially important role of grazing in determining the response of dryland ecosystems to changes in environmental conditions (Noy-Meir 1975; May 1977; Yodzis 1989; DeAngelis 1992).

More recent research on dryland ecosystems has focused on the spatial interactions between vegetation and the abiotic environment (e.g., Lefever and Lejeune 1997; Klausmeier 1999; HilleRisLambers et al. 2001; von Hardenberg et al. 2001; Rietkerk et al. 2002; Gilad et al. 2007). These models are in line with observations of vegetation functioning as ecosystem engineers (sensu Jones et al. 1994) by modulating flows of water and nutrients (Aguiar and Sala 1999; Rietkerk et al. 2000). Specifically, these studies showed how transport of such resources toward vegetated patches creates a scale-dependent (short-range positive, long-range negative) feedback that creates self-organized vegetation patterns at inter-

mediate levels of resource input (Rietkerk et al. 2004; Rietkerk and van de Koppel 2008). In this case, the alternate ecosystem states are a patterned and a homogeneous state (uniform vegetation cover or bare soil). These insights motivated the hypothesis that spatial vegetation patterns can serve as an indicator of proximity to critical ecosystem thresholds (Rietkerk et al. 2004). For dryland ecosystems, this hypothesis is particularly relevant because self-organized vegetation patterning is commonly observed in these systems (e.g., Macfadyen 1950; Barbier et al. 2006; Deblauwe et al. 2008, 2012).

Subsequent in-depth analyses of these spatial models, however, emphasized that for a given set of environmental conditions there can be multistability of patterned states (e.g., Sherratt and Lord 2007; Bel et al. 2012; Siteur et al. 2014; Siero et al. 2015). As a result, the response of dryland ecosystems to changes in environmental conditions becomes more gradual, because the system can develop into a pattern of different wavelength (i.e., a pattern with a different distance between vegetation patches). For example, a system subject to decreasing rainfall may undergo a series of transitions toward patterns of increasingly longer wavelengths (i.e., with larger distances between patches). Then, the last transition comprises a shift from a long-wavelength pattern toward a uniform bare state. Importantly, this process leads to a rather gradual decrease in total vegetation biomass (as shown in Sherratt 2013; Siteur et al. 2014). Although these transitions still carry the mathematical properties of a critical transition, they are not in line with an ecological interpretation of a large-scale shift from a fully functional to a fully degraded ecosystem (van de Koppel et al. 2002).

In summary, previous studies have explained semiarid ecosystem transitions either through mean-field approaches identifying grazing as a driver of large-scale shifts between uniform states (Noy-Meir 1975; May 1977) or through spatially explicit approaches identifying ecosystem engineering as a driver of more gradual shifts between patterned states (Sherratt and Lord 2007; Bel et al. 2012; Siteur et al. 2014; Siero et al. 2015). Until now, despite the early emphasis on the role of grazing in dryland ecosystems, spatially explicit model frameworks have mostly considered grazing with a constant (per capita) rate (e.g., Klausmeier 1999; Rietkerk et al. 2002), referred to as local grazing, which reflects the implicit assumptions made in mean-field approaches. In semiarid ecosystems, empirical observations show that grazing typically depends on the distribution of vegetation in space (Focardi et al. 1996; Fryxell et al. 2004), thereby altering spatial vegetation structure (Bailey et al. 1996; Hiernaux 1998; Schwinning and Parsons 1999). In turn, these changes in vegetation structure may affect ecosystem functioning (Adler et al. 2001) as well as the nature of ecosystem transitions (Schneider and Kéfi 2016). However, model studies that incorporate grazing pressure in a spatially explicit way are still relatively rare (but see Swain et al. 2007; Schneider and Kéfi 2016; Siero 2018).

In this study, the grazing pressure at any location is dependent on vegetation elsewhere (Siero 2018). This is an important extension, since during foraging herbivores move through the landscape to optimize intake (Arditi and Dacorogna 1988; Focardi et al. 1996), which may lead to aggregation on locations with relatively high vegetation (Bailey et al. 1996). We compare three types of grazing within the classical Klausmeier model for vegetation pattern formation (Klausmeier 1999) to study how grazing by mobile herbivores affects desertification. In the first type, the grazing pressure does not depend on vegetation elsewhere, which corresponds to the original Klausmeier model and serves as a benchmark. The second type is a form of sustained grazing, in which the herbivore population is maintained at a constant size through the provisioning of additional fodder if necessary for survival. The third type is a form of natural grazing, in which herbivores rely on consumption for survival and the herbivore population size depends on the total amount of vegetation in the landscape (e.g., Bayliss and Choquenot 2002).

In the Klausmeier model (Klausmeier 1999) and similar models (Rietkerk et al. 2002; Gilad et al. 2004), vegetation can exhibit both positive density dependence by facilitating the availability and uptake of water resources and negative density dependence by competing for these resources. Grazing by mobile herbivores can also generate positive density dependence or negative density dependence within vegetation. The interplay between these two phenomena creates novel dynamics. Specifically, we found that mobile grazing activity can initiate abrupt, large-scale shifts in ecosystem states in response to changing environmental conditions. Interestingly, ecosystem degradation did not necessarily imply a transition toward a state without any vegetation but could also entail a shift toward a state with a much smaller amount of biomass. These results show that mobile grazers may fundamentally alter the behavior of patterned ecosystems, particularly their response to changing environmental conditions.

Methods

We use an approach similar to Siero (2018), where the grazing terms are derived from initially adding a separate equation for the herbivore density. There, assuming that herbivores move toward locations where the forage per herbivore is largest, an ideal free distribution (Fretwell and Lucas 1969) is derived. In the present article, we assume that herbivores distribute proportionally to the amount of vegetation, so that the amount of vegetation per herbivore is constant in space. Such a distribution has been observed for Serengeti grazers (Fryxell et al. 2004).

Modeling Grazing

As spatial domain we choose the one-dimensional interval $[0, \mathcal{L}]$, with x indicating the location. Let $n(x)$ and $h(x)$ de-

note the density of vegetation and herbivores, respectively. Because herbivores move around the domain, grazing is influenced by the mean vegetation density $\langle n \rangle = (\int_0^{\mathcal{L}} n(x)dx)/\mathcal{L}$.

Grazing at location x is determined by the product of the number of herbivores $h(x)$ and the per capita consumption $F_R(\langle n \rangle)$ (functional response; Solomon 1949; Holling 1959). By grazing pressure g we denote the ratio between vegetation intake at a location (grazing) and total amount of vegetation present at this location. The grazing pressure is thus described as

$$g(\langle n \rangle, x) = \frac{F_R(\langle n \rangle)h(x)}{n(x)}, \qquad (1)$$

and it is a relative rate with the dimension per time. We refer to the mean number of herbivores $\langle h \rangle$ that can be sustained by the vegetation as the demographic response $D_R(\langle n \rangle)$. The assumption that herbivore distribution is proportional to vegetation density, together with $\langle h \rangle = D_R(\langle n \rangle)$, implies that the distribution of herbivores is given by

$$h(x) = D_R(\langle n \rangle)\frac{n(x)}{\langle n \rangle}, \qquad (2)$$

and substitution in equation (1) yields

$$g(\langle n \rangle) = \frac{F_R(\langle n \rangle)D_R(\langle n \rangle)}{\langle n \rangle}. \qquad (3)$$

We distinguish three types of grazing, with differing assumptions on F_R and D_R:

Type I: Local Grazing. Here the grazing pressure $g_{\text{loc}} \equiv m_{\text{loc}}$ is constant. This is a choice that has been made in many earlier analyses, including the original article by Klausmeier (see, e.g., Klausmeier 1999; HilleRisLambers et al. 2001; Okayasu and Aizawa 2001; von Hardenberg et al. 2001; Rietkerk et al. 2002; Shnerb et al. 2003; Gilad et al. 2004, 2007; Meron et al. 2004; Saco et al. 2007). It must hold that $F_R D_R = m_{\text{loc}}\langle n \rangle$ (by comparison with eq. [3]), which seems to be a nongeneric relationship between F_R and D_R, as we are not aware of any literature that would support this assumption. Contrasting this type to the other two types elucidates the effects of grazing by mobile herbivores.

Type II: Sustained Grazing. The herbivores are kept at a constant demographic response in a human-controlled grazing system (Noy-Meir 1975; van de Koppel et al. 2002) by supplying additional fodder as necessary. This means that $D_R \equiv h_{\text{imp}}$ at an imposed level. The herbivores exhibit a type II (saturating) functional response (Holling 1959): $F_R(\langle n \rangle) = c_{\text{max}}\langle n \rangle/(K + \langle n \rangle)$ depends on mean vegetation density $\langle n \rangle$, with c_{max} the maximum consumption per herbivore and K the level of vegetation where the functional response is only half c_{max}. Based on these assumptions, the sustained grazing pressure is given by $g_{\text{sus}} = m/(K + \langle n \rangle)$, with $m = h_{\text{imp}}c_{\text{max}}$ the maximal grazing rate.

Type III: Natural Grazing. The functional response is constant at a sufficient level $F_R \equiv c_{\text{suf}}$ for self-maintenance. The total number of herbivores that can be sustained in a landscape now depends on the amount of available forage. Following general theory on energy transfer across trophic levels (Oksanen et al. 1981), we assume that there is a threshold in available forage above which a sizable herbivore population can be sustained. Such a threshold response can be approximated by a type III (Holling 1959) demographic response. So $D_R(\langle n \rangle) = h_{\text{max}}\langle n \rangle^2/(K^2 + \langle n \rangle^2)$ depends on the mean vegetation density $\langle n \rangle$, with h_{max} the maximal number of herbivores and K the level of vegetation where the number of herbivores is only half h_{max}. With these assumptions, the natural grazing pressure becomes $g_{\text{nat}} = m\langle n \rangle/(K^2 + \langle n \rangle^2)$, with $m = h_{\text{max}}c_{\text{suf}}$ the maximal grazing rate.

The distinction of these three types of grazing is by no means exhaustive but already allows us to study how different grazing responses affect the ecosystem. The only difference with the usual Holling response functions (Holling 1959) is that the grazing pressure is a function of mean vegetation density $\langle n \rangle$ instead of some local quantity.

The dependence of grazing pressure (type II and III) on mean vegetation density creates conditions under which the vegetation exhibits positive density dependence with respect to grazing. The range of this effect is the whole range of $\langle n \rangle$ for sustained (type II) grazing and $\langle n \rangle > K$ for natural (type III) grazing (see fig. 1). The strength of the positive density dependence relates to the slope of $g(\langle n \rangle)$ so that it is maximal at $\langle n \rangle = 0$ for sustained (type II) grazing and at $\langle n \rangle = \sqrt{3}K$ for natural (type III) grazing.

Including Grazing in the Klausmeier Model

To understand how grazing alters the desertification process, we include the different grazing terms in an existing dryland vegetation model. Here we choose the extended Klausmeier model (Klausmeier 1999; Siteur et al. 2014). The nondimensional form of this two-component (surface water w, vegetation n) model on flat ground with grazing pressure g is given by

$$\begin{cases} w_t = ew_{xx} + a(t) - w - wn^2, \\ n_t = n_{xx} - (m_0 + g)n + wn^2, \end{cases} \qquad (4)$$

with the dimensional model and scaling process described in the appendix.

The terms ew_{xx} and n_{xx} model water diffusion and plant dispersal, where we choose $e = 500$ as in Siteur et al. (2014). The term $-w$ models evaporation; $\pm wn^2$ models water uptake by the vegetation. The parameter a models rainfall
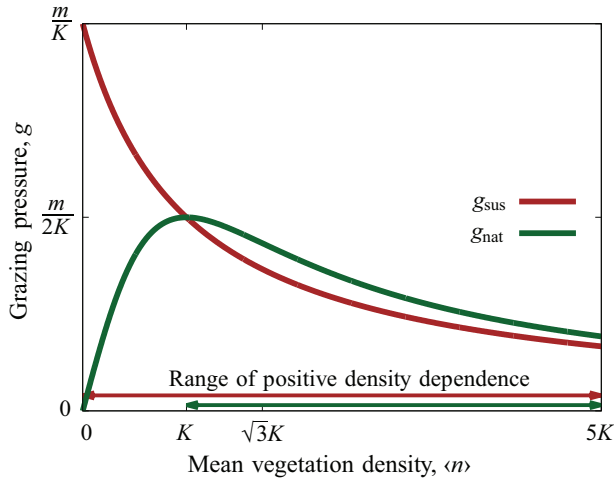
Figure 1: Sustained (g_{sus}) and natural (g_{nat}) grazing pressure as a function of spatial mean vegetation density $\langle n \rangle$. For both types, the grazing pressure is approximately inversely proportional to $\langle n \rangle$ when vegetation is abundant. The function g_{sus} monotonically increases to m/K as all vegetation disappears, resulting in positive density dependence over the whole range, whose strength (related to minus the slope) also monotonically increases as all vegetation disappears. In contrast, g_{nat} initially increases to a maximum at $\langle n \rangle = K$ (with positive density dependence up to that point) but then converges to zero for ever smaller amounts of vegetation. For this type, the strength of the positive density dependence is maximal at $\langle n \rangle = \sqrt{3}K$.

and changes as a function of time (climate change). The initial level of rainfall $a = 3$ ($\sim$800 mm year^{-1}) is chosen high enough to sustain a homogeneously vegetated state.

The mortality of vegetation has been split into a nongrazing part ($-m_0 n$) and a grazing part ($-gn$); in this study, we choose $m_0 = 0.225$ ($\sim$0.9 year^{-1}). For local (type I) grazing, we equally choose $m_{loc} = 0.225$, so that $m_0 + m_{loc} = 0.45$ ($\sim$1.8 year^{-1}), in accordance with Klausmeier (1999). For the types of nonlocal grazing (type II and III), we choose maximal grazing rate $m = 1.5$ ($\sim$1.2 kg m^{-2} year^{-1}) and half-persistence $K = 0.3$ ($\sim$0.06 kg m^{-2}).

This way, initially (at $a = 3$) there is no distinction between the different types of grazing. As we will see, for all three types the system starts in the same homogeneously vegetated state $n \approx 6.5$ ($\sim$1.3 kg m^{-2}), with $g_{sus} \approx g_{nat} \approx g_{loc}$ ($=0.225$). Differences later on can thus be accounted for only by the varying dependency of the grazing pressures on vegetation.

As spatial domain we use the one-dimensional interval [0, 500] (corresponding to 250 m) with periodic boundary conditions. In the model runs, we apply white multiplicative noise of small amplitude 0.05% on both the water and the biomass component at every integer t to decrease the delay from destabilization to transition (Siteur et al. 2014). The rainfall is slowly decreased from $a = 3$ to $a = 0$, with $da/dt = -10^{-4}$. The computer code (GNU Octave/MATLAB), along

with all data, is deposited in the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.pb62bk0 (Siero et al. 2019). To study hysteresis and restoration, we also perform a model run with slowly increasing rainfall ($da/dt = 10^{-4}$), with and without exclosures.

Results

Overgrazing and Regime Shift

We compare model runs of the extended Klausmeier model with either local ($m_{loc} = 0.225$), natural, or sustained ($m = 1.5$, $K = 0.3$) grazing. For all three types, initially (at rainfall $a = 3$) the grazing pressure g is the same and the vegetation is spatially uniform. As rainfall is set to slowly decrease, the homogeneous state becomes Turing unstable (Turing 1952): a vegetation pattern forms. The subsequent desertification process, leading up to a uniform bare desert state, shows striking differences depending on the grazing type.

For local grazing (fig. 2, left column), a cascade of transitions to patterns with larger and larger wavelength follows from right to left (Sherratt 2013; Siteur et al. 2014). During the process, the mean vegetation density $\langle n \rangle$ gradually decreases (Siteur et al. 2014).

The local grazing pressure g_{loc} does not depend on $\langle n \rangle$, but the sustained g_{sus} and natural grazing pressure g_{nat} do. For sustained grazing (fig. 2, middle column), the related positive density dependence becomes stronger and stronger as $\langle n \rangle$ decreases (fig. 1), eventually dominating negative density dependence, resulting in a regime shift to the bare desert state.

Likewise, for natural grazing, overgrazing can invoke a regime shift. But contrary to sustained grazing, the related positive density dependence is maximal when $\langle n \rangle = \sqrt{3}K$ and turns into a negative density dependence for $\langle n \rangle < K$ (fig. 1), making a low-vegetation degraded state a viable option (fig. 2, right column). For this type, the grazing-related positive density dependence is dominant only in the vicinity of $\langle n \rangle = \sqrt{3}K \approx 0.52$.

In summary, overgrazing initiates a regime shift for both sustained and natural grazing. However, the difference is that for sustained grazing the regime shift is toward a fully degraded state, whereas for natural grazing it is toward a degraded state that still contains a small amount of vegetation. For both types, the transition to a degraded state occurs at higher rainfall compared to local grazing, making the ecosystem less resilient to drought.

Hysteresis and Restoration

Reaction-diffusion models of dryland vegetation with local (type I) grazing are known to exhibit hysteresis: under con-
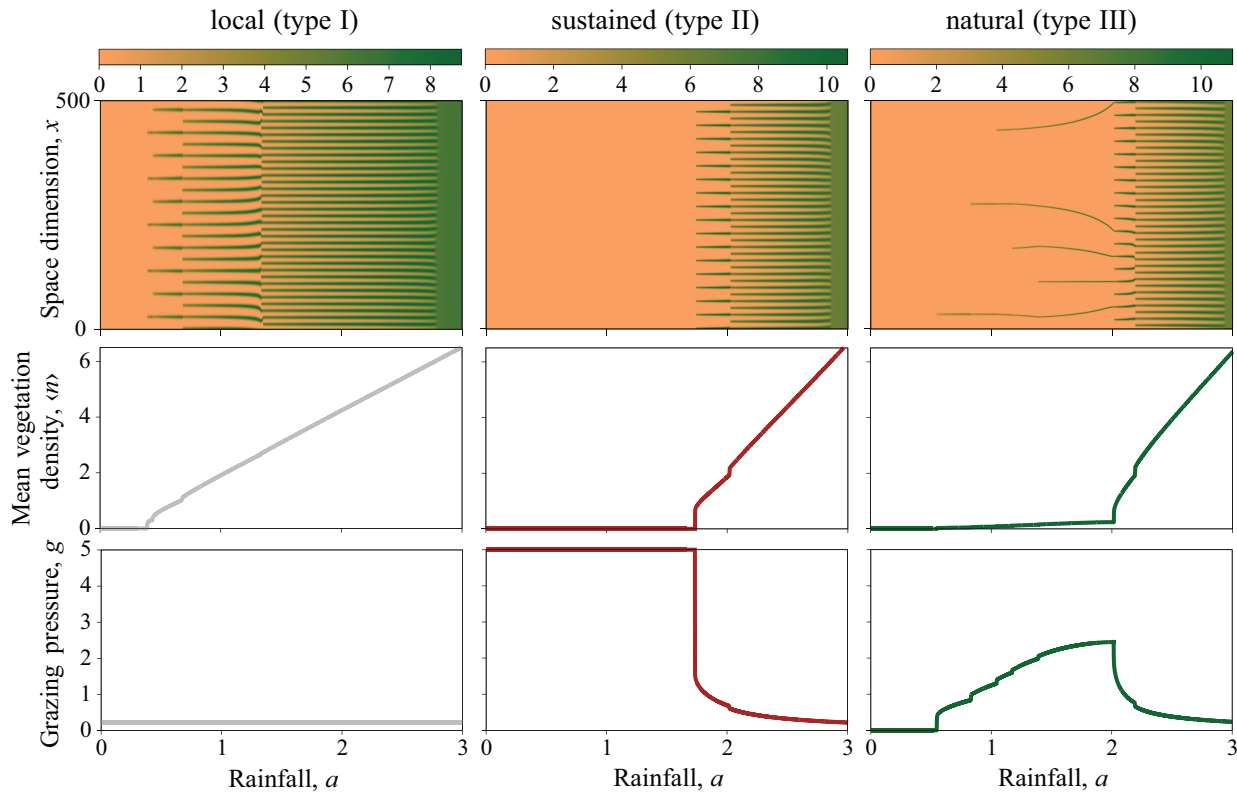
Figure 2: Response of ecosystems under conditions of slowly decreasing rainfall a ($da/dt = -10^{-4}$), starting at $a = 3$ (on the right side) with spatially homogeneous vegetation, showing a comparison of (from left to right) local ($m_{\text{loc}} = 0.225$), sustained, and natural ($m = 1.5$, $K = 0.3$) grazing. From top to bottom, vegetation density distribution $n(x)$ (indicated by the color bar), mean vegetation density $\langle n \rangle$, and grazing pressure g are shown. The left column shows local grazing, with a gradual decline in $\langle n \rangle$ all the way to very small biomass. Local grazing pressure is constant (by definition). The middle column shows sustained grazing, with a gradual decline in biomass up to a critical point ($a \approx 1.7$), at which overgrazing leads to an abrupt shift to a bare desert state. Sustained grazing pressure monotonically increases for decreasing a until reaching the maximum value $m/K = 5$. The right column shows natural grazing, with characteristics similar to sustained grazing except that the abrupt shift ($a \gtrsim 2$) is toward a state with low (but nonzero) biomass. Natural grazing pressure likewise leads to overgrazing but does not grow beyond $m/(2K) = 2.5$ and for small a (and $\langle n \rangle$) returns to smaller values.

ditions of decreasing rainfall, the wavelength is smaller than under increasing rainfall (Sherratt 2013; Siteur et al. 2014). Yet the observed hysteresis in mean vegetation density $\langle n \rangle$ is only modest in these model studies.

Sustained (type II) or natural (type III) grazing, in combination with decreasing rainfall, leads to a regime shift (fig. 2), which in turn is associated with hysteresis (Scheffer et al. 2001). For sustained grazing, the regime shift extends all the way to $\langle n \rangle = 0$, so that the ecosystem ends up in the fully degraded state. In the extended Klausmeier model (4), this state is stable for all values of rainfall for all types of grazing. This means that the transition is irreversible and that the system will not recover in response to increasing rainfall. In other models (e.g., von Hardenberg et al. 2001), recovery to a vegetated state can occur if rainfall increases beyond a threshold. If a sustained grazing term is added to these models, recovery will likely be suspended, however, because of the maximal grazing mortality incurred for $\langle n \rangle = 0$ (fig. 1).

For natural grazing, a small amount of vegetation does initially survive, and we now study how it responds to increasing rainfall. As initial condition we take the result of decreasing rainfall (fig. 2, right column), stopping at $a = 2$, with only five vegetated patches. Starting again but now with increasing rainfall ($da/dt = 10^{-4}$), the grazing pressure remains high and the number of vegetated patches stays at five (fig. 3). Only when $a \approx 3.15$ does the positive density dependence related to grazing dominate negative density dependence. At this point "undergrazing" leads to extra vegetation, which itself results in a smaller grazing pressure. As a result, the system undergoes a regime shift to the homogeneously vegetated state.

We conclude that in the presence of natural grazing, for the same amount of rainfall a (between 2.05 and 3.15), depending on history, two types of states are observable: states with a relatively large amount of vegetation and low grazing pressure and states with a relatively small amount of vegetation and high grazing pressure (fig. 3). Since recovery to ho-
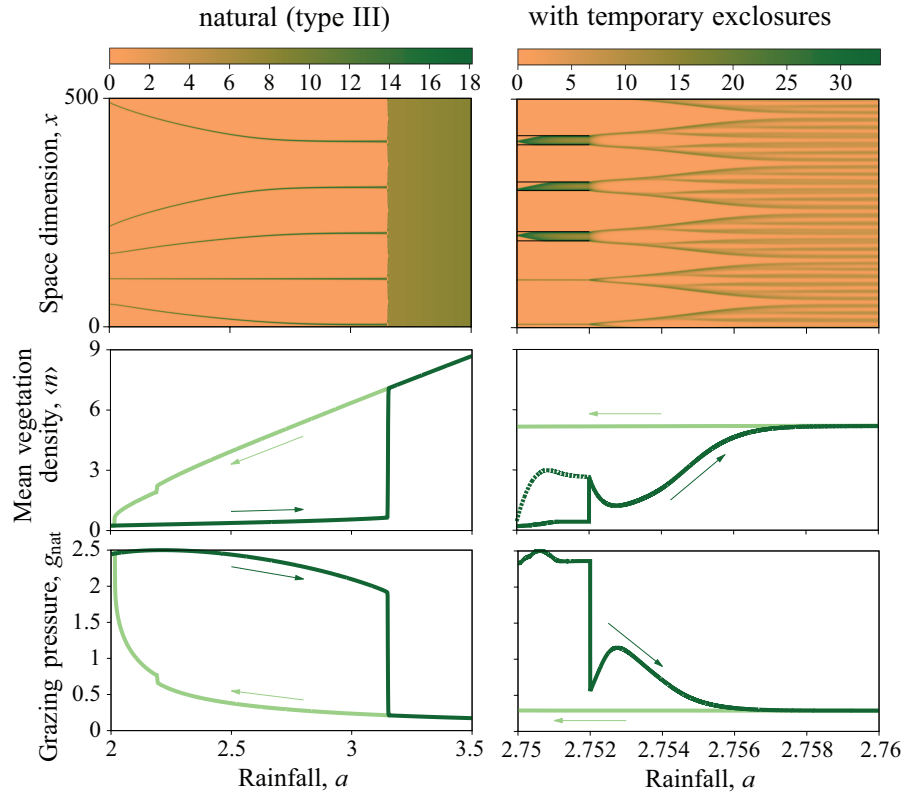
Figure 3: Recovery of ecosystem under conditions of slowly increasing rainfall a ($da/dt = -10^{-4}$), with natural (type III) grazing ($m = 1.5$, $K = 0.3$) without (left column) and with (right column) temporary exclosures. From top to bottom, vegetation density distribution $n(x)$ (indicated by the color bar), mean vegetation density $\langle n \rangle$, and grazing pressure g_{nat} are shown. The data in the left column start at $a = 2$ (on the left), with initial condition taken from the model run of the right column in figure 2. Continued large grazing pressure while rainfall is increasing (dark green curve, bottom panel), relative to the grazing pressure while rainfall was decreasing (light green curve), delays recovery. The system returns to the homogeneously vegetated state at a rainfall value $a \approx 3.15$. The right column shows a model run identical to that in the left column except for the installation of three exclosures (of width 20~10 m) at $a = 2.75$ until $a = 2.752$ (thus, for 20 time units corresponding to 5 years). The solid dark green curve depicts the average biomass outside the exclosures; the total average biomass is given by the dashed dark green curve. The ecosystem already recovers to the more productive state at $a = 2.76$ (instead of $a \approx 3.15$).

mogeneous vegetation occurred at a rainfall a that is higher than the critical value for Turing pattern formation (fig. 2), there is a range (a between 2.95 and 3.15) of "tristability" of the fully degraded state, homogeneous vegetation, and patterns (Zelnik et al. 2018).

The late recovery to the more vegetated state indicates that restoration at an earlier moment in time could be worthwhile. In drylands where there is still some vegetation cover, passive restoration techniques, such as herbivore exclosure for a certain period, can be effective (Yirdaw et al. 2017). In a rewilding experiment in the Oostvaardersplassen (Netherlands), small-scale natural grazing exclosures were found to be necessary for sapling establishment (Smit et al. 2015). Such an approach could also be useful in drylands, as we show next.

In the right column of figure 3, we use the exact same model as in the left column, except that we add three ex-

closures when $a = 2.75$ and remove these exclosures again when $a = 2.752$. The additional biomass produced in these exclosures is enough so that, after an initial stage of spatial reconfiguration, the positive density dependence related to grazing becomes dominant and the ecosystem converges to the more productive state autonomously.

Discussion

In this study, we have shown that the dependence of grazing pressure on mean vegetation density influences how patterned ecosystems respond to changing environmental conditions. Specifically, for sustained or natural grazing (type II or III), focusing of herbivores on remaining vegetation leads to positive density dependence. When this effect dominates negative density dependencies, (almost) all vegetation disappears at once. As such, desertification can be less gradual

than suggested in other model studies that considered local (type I) grazing only (Sherratt 2013; Siteur et al. 2014). We conclude that grazing, when dependent on mean vegetation density, hampers the ability to smoothly respond to changing environmental conditions. Consequently, transition to a degraded state occurs at higher rainfall, making the ecosystem less resilient against drought.

Our results provide implications for restoration of dryland ecosystems subject to grazing. For natural (type III) grazing, after degradation due to low rainfall, vegetation is still present (fig. 2). We have shown in our model how temporary, small-scale grazing exclosures could pave the way for autonomous recovery to a more productive ecosystem state at the landscape scale.

The goal of this study was to identify the potential consequences of grazing by mobile herbivores for the resilience and functioning of dryland ecosystems. Therefore, we used a modeling framework that maximized the possibility of inferring cause-effect relationships between grazing and ecosystem dynamics, an approach in line with the exploratory modeling philosophy (Larsen et al. 2014). More specifically, we allowed the grazing pressure to depend on mean vegetation density and included this in the extended Klausmeier model (Klausmeier 1999; Siteur et al. 2014), one of the simplest models of vegetation patterning in dryland ecosystems. Future research could explore to what extent the observed effects are maintained in more realistic models. Given that our results can be understood through relatively general interactions between grazing pressure and vegetation density, we expect that the observed impacts of grazing will be relatively robust.

An assumption we made is that herbivores distribute proportionally to vegetation, so that the grazing pressure becomes independent of the local availability of vegetation (Siero 2018). Alternatively, grazing pressure could be relatively small in areas with large vegetation due to associational resistance (Barbosa et al. 2009). If associational resistance depends on the amount of vegetation in a local neighborhood, then most of the grazing is concentrated on vegetation patch boundaries, which also leads to increased risk of catastrophic shifts (Schneider and Kéfi 2016). The opposite effect, associational susceptibility (Barbosa et al. 2009), would lead to disproportionate aggregation of herbivores at maxima in vegetation. If this effect is sufficiently strong, it leads to the suppression of pattern formation (Siero 2018).

The observation of transitions between vegetation patterns requires satellite images or aerial photography over a decadal time span (Deblauwe et al. 2011). In a study of vegetation bands in Somalia, it was found that either vegetation bands completely disappeared or wave number changes were imperceptible (Gowda et al. 2018). As degradation was observed in areas with increasing human activity (Gowda et al. 2018), this might be related to sustained grazing. To test such

hypotheses, the vegetation pattern and the spatial distribution of grazing both need to be measured (Adler et al. 2001).

Degradation of dryland ecosystems due to overgrazing was a key observation that spawned the development of ecological theory of alternate stable states and ecosystem transitions between these states (Holling 1973; Noy-Meir 1975; May 1977). Previous studies suggested that pattern formation could attenuate the magnitude of degradation events in response to decreasing rainfall (Sherratt and Lord 2007; Bel et al. 2012; Siteur et al. 2014; Siero et al. 2015). Our current study instead shows that mobile grazers in patterned ecosystems may induce relatively large degradation events in response to decreasing rainfall, highlighting the importance of grazing management for sustaining ecosystem functions and services of drylands in variable and changing climates.

APPENDIX

Scaling of the Extended Klausmeier Model with Grazing

We present the scaling used to obtain the nondimensional model from the dimensional extended Klausmeier model (Klausmeier 1999; Siteur et al. 2014) with grazing (Siero 2018). The dimensional model (without advection) is given by

$$\begin{cases} W_T = EW_{xx} + A - LW - RWN^2, \\ N_T = DN_{xx} - (M + \tilde{g})N + RJWN^2, \end{cases} \quad \text{(A1)}$$

where the grazing pressure $\tilde{g}$ is given by

$$\tilde{g} = \tilde{m}_{\text{loc}} \qquad \text{for local (type I) grazing} \qquad \text{(A2)}$$

and

$$\tilde{g} = \begin{cases} \dfrac{\tilde{m}}{\tilde{K} + \langle N \rangle} & \text{for sustained (type II) grazing,} \\[3ex] \dfrac{\tilde{m}\langle N \rangle}{\tilde{K}^2 + \langle N \rangle^2} & \text{for natural (type III) grazing.} \end{cases}$$

$$\text{(A3)}$$

The variables and parameters that are not related to grazing are scaled as in Klausmeier (1999) and Siteur et al. (2014):

$$w = WJ\sqrt{\frac{R}{L}}, \quad n = N\sqrt{\frac{R}{L}}, \quad x = X\sqrt{\frac{L}{D}}, \quad t = TL,$$

$$a = \frac{AJ}{L}\sqrt{\frac{R}{L}}, \quad m_0 = \frac{M}{L}, \quad e = \frac{E}{D}.$$

$$(A4)$$

The other parameters are scaled as follows:

$$m_{loc} = \frac{\tilde{m}_{loc}}{L}, \quad m = \frac{\tilde{m}}{L}\sqrt{\frac{R}{L}}, \quad K = \sqrt{\frac{R}{L}}\tilde{K}, \quad (A5)$$

and the nondimensional extended Klausmeier model with grazing is given by

$$\begin{cases} w_t = ew_{xx} + a - w - wn^2, \\ n_t = n_{xx} - (m_0 + g)n + wn^2, \end{cases} \quad (A6)$$

with g equal to $\tilde{g}$ but with $\tilde{m}_{loc}$ replaced by m_{loc} or with $\tilde{m}$ and $\tilde{K}$ replaced by m and K, respectively.

The values of the evaporation rate L and uptake coefficient R are given by $L = 4$ year^{-1} and $R = 100$ kg^{-2} m^4 year^{-1} (for grass; Klausmeier 1999), so that (through eq. [A5]) the dimensional parameters related to grazing correspond to the nondimensional ones as follows:

$$\tilde{m}_{loc} = 4m_{loc} \text{ year}^{-1}, \quad \tilde{m} = \frac{4m}{5}\text{kg m}^{-2}\text{ year}^{-1},$$

$$\tilde{K} = \frac{K}{5}\text{kg m}^{-2}. \quad (A7)$$

Literature Cited

Adler, P., D. Raff, and W. Lauenroth. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479.

Aguiar, M., and O. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14:273–277.

Arditi, R., and B. Dacorogna. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. American Naturalist 131:837–846.

Bailey, D., J. Gross, E. Laca, L. Rittenhouse, M. Coughenour, D. Swift, and P. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386–400.

Barbier, N., P. Couteron, J. Lejoly, V. Deblauwe, and O. Lejeune. 2006. Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. Journal of Ecology 94:537–547.

Barbosa, P., J. Hines, I. Kaplan, H. Martinson, A. Szczepaniec, and Z. Szendrei. 2009. Associational resistance and associational susceptibility: having right or wrong neighbors. Annual Review of Ecology, Evolution, and Systematics 40:1–20.

Bayliss, P., and D. Choquenot. 2002. The numerical response: rate of increase and food limitation in herbivores and predators. Philosophical Transactions of the Royal Society B 357:1233–1248.

Bel, G., A. Hagberg, and E. Meron. 2012. Gradual regime shifts in spatially extended ecosystems. Theoretical Ecology 5:591–604.

DeAngelis, D. 1992. Dynamics of nutrient cycling and food. Chapman & Hall, New York.

Deblauwe, V., N. Barbier, P. Couteron, O. Lejeune, and J. Bogaert. 2008. The global biogeography of semi-arid periodic vegetation patterns. Global Ecology and Biogeography 17:715–723.

Deblauwe, V., P. Couteron, J. Bogaert, and N. Barbier. 2012. Determinants and dynamics of banded vegetation pattern migration in arid climates. Ecological Monographs 82:3–21.

Deblauwe, V., P. Couteron, O. Lejeune, J. Bogaert, and N. Barbier. 2011. Environmental modulation of self-organized periodic vegetation patterns in Sudan. Ecography 34:990–1001.

Focardi, S., P. Marcellini, and P. Montanaro. 1996. Do ungulates exhibit a food density threshold? a fieldstudy of optimal foraging and movement patterns. Journal of Animal Ecology 65:606–620.

Fretwell, S., and H. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Fryxell, J., J. Wilmshurst, and A. Sinclair. 2004. Predictive models of movement by Serengeti grazers. Ecology 85:2429–2435.

Gilad, E., J. von Hardenberg, A. Provenzale, M. Shachak, and E. Meron. 2004. Ecosystem engineers: from pattern formation to habitat creation. Physical Review Letters 93:1–4.

———. 2007. A mathematical model of plants as ecosystem engineers. Journal of Theoretical Biology 244:680–691.

Gowda, K., S. Iams, and M. Silber. 2018. Signatures of human impact on self-organized vegetation in the Horn of Africa. Scientific Reports 8:3622.

Hiernaux, P. 1998. Effects of grazing on plant species composition and spatial distribution in rangelands of the Sahel. Plant Ecology 138:191–202.

HilleRisLambers, R., M. Rietkerk, F. Bosch, H. Prins, and H. Kroon. 2001. Vegetation pattern formation in semi-arid grazing systems. Ecology 82:50–61.

Holling, C. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. Canadian Entomologist 91:234–261.

———. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Jones, C., J. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373–386.

Klausmeier, C. 1999. Regular and irregular patterns in semi-arid vegetation. Science 284:1826–1828.

Larsen, L., C. Thomas, M. Eppinga, and T. Coulthard. 2014. Exploratory modeling: extracting causality from complexity. Eos 95:285–286.

Lefever, R., and O. Lejeune. 1997. On the origin of tiger bush. Bulletin of Mathematical Biology 59:263–294.

Macfadyen, W. 1950. Vegetation patterns in the semi-desert plains of British Somaliland. Geographical Journal 116:199–211.

May, R. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269:471–477.

Meron, E., E. Gilad, J. von Hardenberg, M. Shachak, and Y. Zarmi. 2004. Vegetation patterns along a rainfall gradient. Chaos, Solitons, and Fractals 19:367–376.

Noy-Meir, I. 1975. Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology 63:459–481.

Okayasu, T., and Y. Aizawa. 2001. Systematic analysis of periodic vegetation patterns. Progress of Theoretical Physics 106:705–720.

Oksanen, L., S. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

Rietkerk, M., M. Boerlijst, F. van Langevelde, R. HilleRisLambers, J. van de Koppel, L. Kumar, H. Prins, and A. de Roos. 2002. Self-organization of vegetation in arid ecosystems. American Naturalist 160:524–530.

Rietkerk, M., S. Dekker, P. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926–1929.

Rietkerk, M., P. Ketner, J. Burger, B. Hoorens, and H. Olff. 2000. Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. Plant Ecology 148:207–224.

Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. Trends in Ecology and Evolution 23:169–175.

Saco, P., G. Willgoose, and G. Hancock. 2007. Eco-geomorphology of banded vegetation patterns in arid and semi-arid regions. Hydrology and Earth System Sciences Discussions 11:1717–1730.

Scheffer, M., J. Bascompte, W. Brock, V. Brovkin, S. Carpenter, V. Dakos, H. Held, E. van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Scheffer, M., S. Carpenter, V. Dakos, and E. van Nes. 2015. Generic indicators of ecological resilience: inferring the chance of a critical transition. Annual Review of Ecology, Evolution, and Systematics 46:145–167.

Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Schneider, F., and S. Kéfi. 2016. Spatially heterogeneous pressure raises risk of catastrophic shifts. Theoretical Ecology 9:207–217.

Schwinning, S., and A. Parsons. 1999. The stability of grazing systems revisited: spatial models and the role of heterogeneity. Functional Ecology 13:737–747.

Sherratt, J. 2013. History-dependent patterns of whole ecosystems. Ecological Complexity 14:8–20.

Sherratt, J., and G. Lord. 2007. Nonlinear dynamics and pattern bifurcations in a model for vegetation stripes in semi-arid environments. Theoretical Population Biology 71:1–11.

Shnerb, N., P. Sarah, H. Lavee, and S. Solomon. 2003. Reactive glass and vegetation patterns. Physical Review Letters 90:038101.

Siero, E. 2018. Nonlocal grazing in patterned ecosystems. Journal of Theoretical Biology 436:64–71.

Siero, E., A. Doelman, M. Eppinga, J. Rademacher, M. Rietkerk, and K. Siteur. 2015. Striped pattern selection by advective reaction-diffusion systems: resilience of banded vegetation on slopes. Chaos 25:036411.

Siero, E., K. Siteur, A. Doelman, J. V. D. Koppel, M. Rietkerk, and M. Eppinga. 2019. Data from: Grazing away the resilience of patterned ecosystems. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.pb62bk0.

Siteur, K., E. Siero, M. Eppinga, J. Rademacher, A. Doelman, and M. Rietkerk. 2014. Beyond Turing: the response of patterned ecosystems to environmental change. Ecological Complexity 20:81–96.

Smit, C., J. Ruifrok, R. van Klink, and H. Olff. 2015. Rewilding with large herbivores: the importance of grazing refuges for sapling establishment and wood-pasture formation. Biological Conservation 182:134–142.

Solomon, M. 1949. The natural control of animal populations. Journal of Animal Ecology 18:1–35.

Swain, D., M. Hutchings, and G. Marion. 2007. Using a spatially explicit model to understand the impact of search rate and search distance on spatial heterogeneity within an herbivore grazing system. Ecological Modelling 203:319–326.

Turing, A. 1952. The chemical basis of morphogenesis. Philosophical Transactions of the Royal Society B 237:37–72.

van de Koppel, J., and M. Rietkerk. 2000. Herbivore regulation and irreversible vegetation change in semi-arid grazing systems. Oikos 90:253–260.

van de Koppel, J., M. Rietkerk, F. van Langevelde, L. Kumar, C. Klausmeier, J. Fryxell, J. Hearne, et al. 2002. Spatial heterogeneity and irreversible vegetation change in semiarid grazing systems. American Naturalist 159:209–218.

von Hardenberg, J., E. Meron, M. Shachak, and Y. Zarmi. 2001. Diversity of vegetation patterns and desertification. Physical Review Letters 87:3–6.

Yirdaw, E., M. Tigabu, and A. Monge. 2017. Rehabilitation of degraded dryland ecosystems—review. Silva Fennica 51:1–32.

Yodzis, P. 1989. Introduction to theoretical ecology. Harper & Row, New York.

Zelnik, Y., P. Gandhi, E. Knobloch, and E. Meron. 2018. Implications of tristability in pattern-forming ecosystems. Chaos 28:033609.

Giraffe in an area covered with tiger bush south of Niamey, Niger, in 1999. Local people suggested that the giraffe were driven into the area, and hence herbivore grazing pressure is possibly determined by human impact. Photo credit: Johan van de Koppel.