1 **Title:** Remotely-sensed slowing down in spatially patterned dryland ecosystems

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3 **Running title:** Critical slowing down in drylands

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24 **Data availability**

25 Data are located in the zenodo open data repository (zenodo.org).

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31 M.P.V. conceived the project and developed the ideas with V.Da. and R.M.G.. V.Da.
32 constructed and analyzed the model simulations. V.De. quantified the regular
33 vegetation patterns. M.P.V. processed and analyzed the remote sensing time series.
34 M.P.V and V.Da. wrote the first draft of the manuscript and all co-authors contributed
35 substantially to revisions.

36

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38 self-organization; critical slowing down; aridity; Sudan

39

40 **Abstract**

41 Regular vegetation patterns have been predicted to indicate a system slowing down
 42 and possibly desertification of drylands. However, these predictions have not yet
 43 been observed in dryland vegetation due to the inherent logistic difficulty to gather
 44 longer-term in situ data. Here, we use recently developed methods using remote-
 45 sensing EVI time-series in combination with classified regular vegetation patterns
 46 along a rainfall gradient in Sudan to test these predictions. Overall, three temporal
 47 indicators (responsiveness, temporal autocorrelation, variance) show slowing down
 48 as vegetation patterns change from gaps to labyrinths to spots towards more arid
 49 conditions, confirming predictions. However, this transition exhibits non-linearities,
 50 specifically when patterns change configuration. Model simulations reveal that the
 51 transition between patterns temporarily slows down the system affecting the
 52 temporal indicators. These transient states when vegetation patterns reorganize thus
 53 affect the systems resilience indicators in a non-linear way. Our findings suggest that
 54 spatial self-organization of dryland vegetation is associated with critical slowing
 55 down, but this transition towards reduced resilience happens in a non-linear way.
 56 Future work should aim to better understand transient dynamics in regular vegetation
 57 patterns in dryland ecosystems, because long transients make regular vegetation
 58 patterns of limited use for management in anticipating critical transitions.

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62 Introduction

63 Anticipating changes in the resilience (or robustness) of natural systems is of
 64 paramount importance given the increasing climate variability and anthropogenic
 65 disturbance (Levin & Lubchenco, 2008; Scheffer *et al.*, 2012; Lenton *et al.*, 2019).
 66 Various approaches have been developed for defining and measuring resilience
 67 (Hodgson *et al.*, 2015; Angeler & Allen, 2016; Ingrisch & Bahn, 2018), but particular
 68 attention has been given to measuring resilience in ecological systems that run a risk
 69 of abrupt and irreversible responses to external stress (Scheffer *et al.*, 2015). Such
 70 responses mathematically correspond to catastrophic shifts where at the crossing of
 71 a threshold an ecological system abruptly shifts from its current state to an
 72 alternative usually contrasting state (Beisner *et al.*, 2003; Suding *et al.*, 2004).
 73 Examples include the shift to eutrophication in shallow lakes (Scheffer *et al.*, 1993),
 74 the transition to overgrazed kelp forests (Simenstad *et al.*, 1978), the collapse of fish
 75 stocks due to overfishing in the North Atlantic (Hilborn & Litzinger, 2009), or abrupt
 76 desertification in drylands (Garcia & Spitz, 1961). Detecting these shifts in advance
 77 requires a deep mechanistic understanding of the ecological system in question
 78 based either on experiments or sufficiently long and detailed monitored data
 79 (Scheffer & Carpenter, 2003). Yet, as for most ecological systems we still lack the
 80 necessary understanding, measuring changes in the spatial and temporal patterns of
 81 ecological dynamics has been qualified as an alternative approach for anticipating
 82 changes in their resilience and for detecting in time their probability to catastrophic
 83 shifts.

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 85 In dryland ecosystems, changes in regular vegetation patterns resulting from spatial
 86 self-organization represent a consistent indicator for a catastrophic shift from a
 87 vegetated to a non-vegetated desertified state (Klausmeier, 1999; Rietkerk *et al.*,
 88 2004). Models describing vegetation dynamics accounting for different interactions
 89 between plants and water availability in drylands (Klausmeier, 1999; von Hardenberg
 90 *et al.*, 2001; Lejeune *et al.*, 2002; Rietkerk *et al.*, 2002; Meron *et al.*, 2004) predict a
 91 robust sequential change (Gowda *et al.*, 2016) from gapped to labyrinthine to spotted
 92 regular vegetation patterns along a spatial or temporal gradient of decreasing water
 93 availability (usually rainfall) before vegetation collapses to a desert state. These
 94 predictions have been matched with empirical observations in semi-arid regions
 95 where regular pattern formation appears to be ubiquitous (Deblauwe *et al.*, 2008).
 96 More specifically, changing regular patterns have been identified along both spatial
 97 and temporal aridity gradient in Sudan (Deblauwe *et al.*, 2011), and shifts of
 98 homogenous vegetation to regular gaps responding to climatic and anthropogenic
 99 stress have been found in the Sub-saharan Sahel (Barbier *et al.*, 2006).
 100 Mathematical studies quantified changes in the size and regularity (rather than the
 101 sequence) of vegetation patches driven by environmental disturbances to assess
 102 their resilience (Bastiaansen *et al.*, 2018), while - more generally - changes in
 103 vegetation patch size distributions have been linked to increasing aridity and grazing
 104 stress in Mediterranean (Kéfi *et al.*, 2007) and Chinese semi-arid regions (Lin *et al.*,
 105 2010).

These mathematical predictions have prompted the interpretation of changes in spatial vegetation patterns as a particular set of early-warning signals for approaching catastrophic shifts (Rietkerk *et al.*, 2004; Scheffer *et al.*, 2009). Another set of warning signals for the proximity to catastrophic shifts are related to the observable level of responsiveness of a system to external disturbances. Such signals are based on the generic phenomenon of critical slowing down that implies that, close to a threshold, the system decreases in responsiveness and shows increasingly slower recovery rates following a disturbance. Increasing temporal variance and autocorrelation of system state variable have been theoretically and empirically shown to be indirect measures of critical slowing down in systems approaching catastrophic shifts (Wissel, 1984; van Nes & Scheffer, 2007; Dakos *et al.*, 2011; Veraart *et al.*, 2012; Dakos *et al.*, 2015). The collection of long-term remotely sensed data (e.g. satellite or aerial imaging data) have enabled the estimation of indicators of ecosystem resilience. Using satellite data, rising temporal autocorrelation of vegetation greenness (NDVI, normalised difference vegetation index) has been used as an indicator of decreasing tropical forest resilience along rainfall gradients (De Keersmaecker *et al.*, 2015; Verbesselt *et al.*, 2016), as well as an indicator of loss of resilience of forest mortality to drought in Californian forest (Liu *et al.*, 2019). Rising temporal variance in salt-marsh cover responding to an increasing inundation stress was measured from NDVI derived from aerial images (van Belzen *et al.*, 2017). At a global scale, remote-sensed data have been used to evaluate the responsiveness (or sensitivity) of terrestrial vegetation to climate by quantifying the response of NDVI to climate anomalies (De Keersmaecker *et al.*, 2015; Seddon *et al.*, 2016).

For drylands we thus have two potential sets of early warning signals: 1) spatial indicators (changes in regular vegetation patterns) and 2) temporal indicators (temporal autocorrelation, variation and responsiveness of vegetation). Yet, empirical evidence for the occurrence of critical slowing down in the particular case of dryland ecosystems indicators is, as far as we know, lacking. Spatial indicators could be overlaid with such temporal indicators to test if predicted changes in spatial vegetation patterns are associated with critical slowing down in drylands under stress. If true, it will mean that spatial patterns would indicate slow ecosystem responsiveness due to critical slowing down and thus allow to assess changes in dryland resilience by using highly resolved remotely-sensed data, which is otherwise notoriously difficult to measure.

Here, we evaluate the theoretical prediction that regular vegetation patterns are associated with empirically derived temporal indicators (autocorrelation, variance, responsiveness) of critical slowing down in a dryland ecosystem in Sudan using different remote sensing products. We then compare these empirical findings with results from model simulations to acquire a better fundamental understanding of the empirical results.

Methods

Resilience indicators estimated from remote sensing data

We used published classifications of regular vegetation patterns in Sudan (Deblauwe *et al.*, 2011) that stretch an area of 22,255 km² and cover a gradient of mean annual rainfall ranging from 370 mm in the Northwest to 600 mm in the Southeast (Deblauwe *et al.*, 2011). Along this gradient, the vegetation forms regular patterns that change from gaps to labyrinths to spots with increasing aridity. Banded vegetation patterns are found on the more hilly parts of the area but were discarded in this study. Vegetation patterns were classified using Fourier-based texture analyses of SPOT (Système Probatoire d'Observation de la Terre) imagery with a 10-m ground resolution. Spatial skewness is a continuous variable that describes the pixel gray level distribution characterizing the relative dominance of vegetation over bare soil and is strongly related to spatial pattern configuration with increasing skewness from spots (< -0.5) to labyrinths (-0.5 – 0) to gaps (> 0) (Deblauwe *et al.*, 2011). See Deblauwe *et al.* (2011) for more detailed information about classifying vegetation patterns.

We overlaid these classified vegetation patterns (ca. 410m resolution) with monthly time series (2001-2016) of Enhanced Vegetation Index (EVI)(Didan, 2015) and Standardized Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano *et al.*, 2010) using the ‘raster’ package (Hijmans, 2018) in R (R Core Team, 2018). SPEI is a commonly used index that takes into account both rainfall and evapotranspiration as a measure of water availability to plants. The EVI and SPEI data were detrended at the pixel level to remove seasonal and long-term trends to be able to avoid bias in the comparison of temporal indicators across sites (Dakos *et al.*, 2012a). EVI time series were detrended using season-trend decomposition by LOESS smoothing (STL) (Cleveland *et al.*, 1990) to remove long-term trends and seasonal periodic patterns using the ‘stl’ function from the “stats” package in R. SPEI time series were constructed using the ‘SPEI’ package using a log-Logistic distribution function and a time scale of 1 month (lag-1). Precipitation data was extracted from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) at ca. 5x5km ground resolution (Funk *et al.*, 2015). Potential evapotranspiration (PET) was obtained from the MODIS Global Evapotranspiration product which estimates PET through the Penman-Monteith equation (Running *et al.*, 2017). All spatial data was downloaded at monthly intervals, resampled to the resolution of the MODIS data (ca. 1km) with nearest-neighbor interpolation and projected to WGS84 UTM 35N coordinate system.

We estimated two established indicators of slowing down: 1) temporal autocorrelation (TAC) of the EVI anomalies at-lag-1 (one month), and 2) temporal variance across the entire time-series. An increasing TAC and temporal variance is suggested to reflect declining recovery potential from perturbations (Scheffer *et al.*, 2009). Previous work found weak increasing temporal autocorrelation and no change in temporal variance in a vegetation model with regular patterns (Dakos *et al.*, 2011). We also estimated the pixel-wise regression slope of EVI anomaly as a function of

SPEI with a one-month timelag. The regression slope is used as a measure of responsiveness of vegetation to climate anomalies and has been referred to as sensitivity (Seddon *et al.*, 2016) or (the inverse of) resistance (De Keersmaecker *et al.*, 2015). Although the regression slope is not per se an indicator of slowing down, it does capture recovery potential but to a specific stressor (SPEI), and here we treat it as an alternative critical slowing related indicator. We then compare these three remotely-sensed temporal indicators of ecosystem resilience to the spatial indicators based on the changing regular vegetation patterns.

The vegetation responsiveness and TAC were modelled for the time-series corresponding to each pixel by considering the EVI anomaly as a linear combination of the history of both SPEI and EVI (at lag 1) (De Keersmaecker *et al.*, 2015; Seddon *et al.*, 2016):

$$Y_t = \alpha Y_{(t-1)} + \beta SPEI_{(t-1)} + \varepsilon_{(t-1)},$$

where Y_t and $Y_{(t-1)}$ are the standardized EVI anomaly at time t and $t-1$ respectively, $SPEI_{(t-1)}$ is the SPEI index at time $t-1$. α and β are the model's coefficients for **TAC** and **responsiveness** (regression slope). The **variance** (standard deviation) was calculated separately using the non-detrended EVI time series as a third indicator of critical slowing down (Scheffer *et al.*, 2009; Dakos *et al.*, 2011).

Resilience indicators estimated from model simulated vegetation dynamics

We tested our empirical findings against theoretical predictions from a stochastic version of a spatial explicit model that has been used to describe vegetation dynamics in drylands under aridity stress (HilleRisLambers *et al.*, 2001; Rietkerk *et al.*, 2002). In the model, vegetation grows depending on soil water that becomes available from surface water infiltrating the soil after rain events. Vegetation, soil water, and surface water are all assumed to diffuse in space. Details on the model description, equations and parameters values used can be found in the Supplementary Information (SI 1, Table S1). The model considers that soil water infiltration is higher in areas with vegetation than in bare soil, which results in the accumulation of water under patches of vegetation and in its depletion further away. Due to this scale-dependent feedback, regular vegetation patterns may emerge for a certain range of rainfall (HilleRisLambers *et al.*, 2001; von Hardenberg *et al.*, 2001; Rietkerk *et al.*, 2002; Meron *et al.*, 2004). These so-called 'Turing patterns' (Turing, 1952) resemble the empirical patterns of vegetation in drylands (Rietkerk *et al.*, 2004) as, among other things, they follow a distinct sequence of shapes from gaps to labyrinths to spots with decreasing rainfall before vegetation collapses into desert (SI Fig S1).

We simulated the model assuming homogeneous conditions across the landscape, i.e. parameter values were the same everywhere in space. We performed simulations for different levels of rainfall (decreasing the mean annual

rainfall from 1.2mm d⁻¹ to 0.5mm d⁻¹ at increments of 0.01 mm d⁻¹) to mimic aridity stress gradient in our modelled landscapes. When rainfall decreases, vegetation patterns change from gaps to labyrinths (roughly at 1.1mm d⁻¹ of rainfall) and from labyrinth to spots (roughly at 0.7mm d⁻¹ of rainfall) with our chosen model parameters. To mimic variation in rainfall we assumed stochasticity on a daily basis both spatially and temporally (we used a multiplicative noise term for rainfall with strength $\sigma = 0.5$ Table S1).

Under these conditions, we simulated vegetation dynamics starting from a fully vegetated landscape (99% cover) for a period of 30 years. We recorded daily vegetation density both spatially as well as temporally as the total vegetation density in the landscape. For each level of rainfall, we repeated 100 simulation runs, each with an independent realization for the stochastic rainfall. For each run and each rainfall level (19600 cases in total), we subsampled vegetation density at monthly intervals to mimic the monthly observations derived from the empirical satellite data. We estimated temporal autocorrelation at-lag-1, variance and skewness of total vegetation density for each level of rainfall as well as spatial skewness of vegetation density. We estimated these statistics following (Rietkerk *et al.*, 2004; Dakos *et al.*, 2011) where trends in these statistics have been suggested to serve as leading indicators of ecosystems approaching shifts to desertification. We reported trends for all indicators from all runs as 5, 50 and 95 percentiles.

We solved the model using a semi-implicit method in a 128x128 cells lattice representing a 400x400 m landscape (Janssen *et al.*, 2008). Environmental stochasticity was added using an Euler-Murayama integration method with Ito calculus. We assumed periodic boundaries. Model simulations and statistical analyses were performed in MATLAB R2017b (MathWorks, 2017).

Statistical analyses

We constructed linear regression models to investigate general relationships between explanatory (mean annual rainfall, spatial skewness) and response variables (responsiveness, temporal autocorrelation, temporal standard deviation) including a Gaussian spatial correlation structure using the x and y coordinates of the center of each pixel to account for spatial autocorrelation. A second order term was included to test for non-linear relationships but removed from the final model when not significant ($p > 0.05$). Subsequently, loess regressions (50% smoothing span) were applied to investigate potential non-linear patterns between explanatory and response variables in more detail. All statistics were performed in R 3.5.2 (R Core Team, 2018).

Results

Regular vegetation patterns

Spatial skewness increased linearly up to about 500 mm mean annual rainfall after which the slope decreased sharply resulting in a significant first (Linear regression: $R^2 = 0.76$; $F_{1,968} = 129.8$; $P < 0.0001$; Fig. 1) and second order term ($F_{1,968} = 46.8$, $P < 0.0001$). Overall, the spatial patterns changed from gaps to labyrinths to spots with

increasing aridity as expected based on the spatial skewness, although there were some patches classified as labyrinths at higher rainfall.

Remotely sensed time-series indicators

The responsiveness of the vegetation increased with rainfall (linear regression: $R^2=0.76$; $F_{1,968}=129.8$; $P<0.0001$; Fig. 2A) and levelled off when gapped patterns were established (2nd order term; $F_{1,968}=46.8$; $P<0.0001$). This increase was not smooth though, with small interruptions from the general pattern when vegetation patterns changed from spots to labyrinths. Similar trends were found along the skewness gradient (linear regression: $R^2=0.81$; 1st order term: $F_{1,983}=17.6$, $P<0.0001$; 2nd order term: $F_{1,983}=1.8$, $P=0.17$; Fig. 2B).

Temporal autocorrelation decreased with rainfall in general (linear regression: $R^2=0.58$; 1st order term: $F_{1,968}=32.2$, $P<0.0001$; 2nd order term: $F_{1,968}=2.3$, $P=0.12$; Fig. 2C), but showed some important nonlinearities. Temporal autocorrelation increased steadily from gapped to labyrinthine vegetation but then suddenly dropped when spotted patterns were formed before increasing again further with increasing aridity. Temporal autocorrelation showed a hump-shaped relationship with spatial skewness (linear regression: $R^2=0.10$; 1st order term: $F_{1,983}=312.3$, $P<0.0001$; 2nd order term: $F_{1,983}=65.0$, $P<0.0001$; Fig. 2D) peaking at labyrinth patterns.

Temporal variance increased linearly with mean annual rainfall (linear regression: $R^2=0.83$; 1st order term: $F_{1,968}=865.1$, $P<0.0001$; 2nd order term: $F_{1,968}=3.0$, $P=0.07$; Fig. 2E). In contrast, temporal variance did not change with spatial skewness until vegetation patterns were labyrinthine after which variance increased sharply (linear regression: $R^2=0.67$; 1st order term: $F_{1,983}=6741.9.3$, $P<0.0001$; 2nd order term: $F_{1,983}=192.0$, $P<0.0001$; Fig. 2F).

Indicator trends from model simulated vegetation dynamics

To better understand the trends in the empirical data, we investigated the same relationships for simulated vegetation dynamics. In general we found similar trends in the indicators of slowing down between the empirical patterns (Fig 2C-F) and the patterns from the simulated vegetation model (Fig 3). Temporal autocorrelation of mean vegetation density increased with aridity (Fig 3A), while temporal variance (measured as standard deviation) decreased (Fig 3C). Spatial skewness of vegetation was positively correlated to temporal variance (Fig 3D) similar to the empirical data (Fig 2F). Note, however, that the range in spatial skewness was much smaller for the empirical data than the simulated vegetation dynamics. Temporal autocorrelation showed a negative correlation with spatial skewness (Fig 3B), although the relationship in the empirical record was weakly negative but hump shaped (Fig 2D).

Similar to the empirical observations, the relationships were not linear but exhibited changes in trends, especially around the levels of rainfall in which vegetation patterns started to change from gaps to labyrinths and from labyrinths to spots (hatched regions, Fig 3). The local humps in the trends were dependent on the period the indicators were measured. In the first 16-year periods of the simulated

records (blue lines, 5-20 years), local humps were stronger due to the influence of transient dynamics (Fig S2A-C). In contrast, the humps became less pronounced (albeit still present) in later periods (green lines, 15-30 years) that were not affected by transients (Fig S2G-I).

Discussion

The aim of this study was to confront theoretical predictions of regular vegetation patterns indicating loss of resilience in dryland ecosystems with empirically derived critical slowing down indicators using remote-sensing derived EVI time series. Previous theoretical work has suggested that self-organised regular vegetation patterns change in predictable ways from gaps to labyrinths to spots prior to abrupt (catastrophic) transitions in drylands (Kéfi *et al.*, 2010; Dakos *et al.*, 2011), and that at the same time the transitions are preceded by critical slowing down (Dakos *et al.*, 2011). However, this theoretical expectation was never empirically tested. Here, we found that changes in vegetation patterns indeed predicted the expected resilience of vegetation to changes in water availability, indicated by a slower responsiveness of EVI to rainfall, increased temporal autocorrelation of EVI, and, contrary to expectations, decreased variance.

The decreased variance we observed in the empirical and simulated data appears to be counterintuitive to the expected increasing variance due to critical slowing down (Scheffer *et al.*, 2009). Indeed, variance has been shown to be less robust indicator of critical slowing down compared to autocorrelation (Dakos *et al.*, 2012b). Reduction in the magnitude of environmental noise prior to a shift decreases variance (Dakos *et al.*, 2012b); slow responding systems could cause variance to decrease approaching a shift (Dakos *et al.*, 2012b); interacting regime shifts can “muffle” variance (Brock & Carpenter, 2010). In previous work, Dakos *et al.* (2011) found no conclusive variance trend in a similar dryland vegetation model with regular vegetation patterns. The decreasing variance pattern we find in the simulated data follows from the fact that we assumed a decrease in rainfall stochasticity (SI Model eq4) consistent with the empirical observations of a positive relationship between average annual rainfall and annual rainfall variability (Fig. S4). Thus, critical slowing down leads to an increase in autocorrelation but not in variance which instead reflects the decreasing rainfall stochasticity.

More importantly, however, all three temporal indicators showed non-linear relationships with annual rainfall and spatial skewness. The model simulations showed similar non-linearities especially at the transition between patterns suggesting that transient effects, which appear as the vegetation reorganizes into a different pattern, are responsible for the increased temporal autocorrelation and variance (Dakos *et al.*, 2011). Interestingly, these spikes of variance and indicators at the border between changing patterns were the strongest when estimated at the early parts of simulated timeseries (5-15 years) during which vegetation transient dynamics have not yet faded out. The expected equilibrium for a given amount of

rainfall becomes especially sensitive to disturbances at the transitions between vegetation patterns, when transients towards the stationary pattern configuration get longer. In theory, in the absence of any transient there should be only an increasing trend for temporal autocorrelation and decreasing for variance (removing a linear trend confirms this expectation Fig S3). But in reality variation in rainfall or other sources of disturbances would create such transients and lead to reconfiguration to vegetation patches and longer transients (Bastiaansen *et al.*, 2018). Rainfall intermittency (or seasonality) has been theoretically studied in models with patterned vegetation and shown that the long term dynamics remain qualitatively the same (Kletter *et al.*, 2009). Yet, the transient dynamics of vegetation in these systems unfold very slowly. The influences of stochasticity and more realistic complex dynamics increase the likelihood, and possibly the temporal extent, of transient dynamics (Hastings *et al.*, 2018). The non-linear relationships found in the empirical remote-sensing indicators suggest that transient dynamics occur in these ecosystems, but it remains unclear how slowly vegetation responds to rainfall and how slowly regular patterns reorganize in particular. Previous work showed that feedbacks between rainfall and land could lead to slow changes in pattern morphology that could take up to 5 years (Konings *et al.*, 2011)(Konings *et al.* 2011), while estimates in Niger suggest it could take decades (Barbier *et al.*, 2014). This pace of response is critical information as delayed responses might result in unrecognized regime shifts, yet might borrow time to reverse them (Hughes *et al.*, 2013).

Although the overall patterns in empirical data and simulations are qualitatively similar, the humps in the empirical data do not fully match those of the model simulations, which could have several explanations. First, the model lacks realism in the variation of rainfall (lack of extreme events and the alteration of wet and dry periods). Furthermore, seasonality or other sources of disturbances, as well as heterogeneity in the landscape are not part of the model. This could result in additional noise in the empirical data. Second, if transient dynamics are indeed responsible for the humps in the data, as suggested by the model simulation, the quantified spatial skewness and corresponding vegetation patterns would represent historical conditions and cause additional noise across the rainfall and skewness gradients. Using the same vegetation pattern classifications, Deblauwe *et al.* (2011) observed that spotted patterns did not disappear even during prolonged drought spells, suggesting serious time-lagged vegetation responses to climate variations or transients. Still, deviations from theoretically expected patterns in empirically measured resilience indicators have been reported elsewhere. Long-term pulse-perturbation experiments to test threshold dynamics in a Chihuahuan Desert grassland showed that pattern-based early-warning indicators might be of little added value relative to simple cover measurements (Bestelmeyer *et al.*, 2013). More recently, prior to the transition from a bare to a grass cover state in a Chinese dryland ecosystem, weak signatures of critical slowing were found, but a rising variance was reported probably due the stochastic nature of the transition (Chen *et*

al., 2018). More strikingly, theoretical work argues that changes in spatial patterns might not be consistent with critical slowing down indicators in systems with irregular pattern formation (Sankaran *et al.*, 2019). These discrepancies imply that the measurement and interpretation of pattern-based and critical slowing down indicators is context-dependent (Dakos *et al.*, 2015) and needs to be further explored.

Conclusion

This study suggests that spatial vegetation patterns in Sudan indeed indicate the responsiveness of plant biomass to changes in climate, as predicted by theoretical models. However, the possibility that transient dynamics are important in these dryland ecosystems might make regular vegetation patterns of limited use for management in anticipating critical transitions if the transients are sufficiently long. Future work should aim to better understand transient dynamics in regular vegetation patterns in dryland ecosystems, because forecasting critical transitions without considering transients may give misleading conclusions that could hamper appropriate interference.

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Figure legends

Figure 1. Changing configuration of regular vegetation patterns from gaps (green) to labyrinths (blue) to spots (yellow) with increasing aridity. Spatial skewness is a measure of the pixel (10x10m) distribution between vegetated and bare state across a larger area (410x410m) and used to assign each a regular vegetation pattern (see Deblauwe et al 2011). Increasing skewness indicates higher vegetation cover. Line represents a loess regression with 50% smoothing span and 95% confidence interval (grey shading).

Figure 2. Critical slowing down with decreasing rainfall and vegetation cover. Change of the responsiveness (A,B), temporal autocorrelation (C,D) and temporal variance (E,F) of vegetation greenness in relation to annual rainfall (A,C,E) and spatial skewness (B,D,F). Overall, the responsiveness increases, temporal autocorrelation decreases and variance increases with both rainfall and spatial skewness. Responsiveness, temporal autocorrelation and variance do not change linearly and often show hickups when pattern configuration changes. Lines represent a loess regression with 50% smoothing span and 95% confidence interval (grey shading). Colors represent spotted (yellow), labyrinthine (blue) and gapped (green) vegetation patterns based on spatial skewness.

Figure 3 Relationships between temporal indicators (autocorrelation and variance) of average vegetation density with rainfall and with spatial skewness of vegetation density based on model simulations. Different colors represent different temporal intervals (all 15 years long) that the indicators were estimated. Specifically, these intervals correspond to the 15 first years of the 30 year long simulation (5-20 years blue line), to the middle 15 years (10-25 years red line), and to the end 15 years (15-30 years, green line). Lines are the 50th percentiles derived from 100 iterations whereas the shaded area covers the 5th and 95th percentiles. Hatched regions mark the transition between vegetation patterns (gaps->labyrinths->spots).

632 Figure 1

Figure 2

657 Figure 3

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Supplementary Information

SI 1 Model description

We used a three partial differential equations model proposed by Rietkerk et al (2002) describing the dynamics of vegetation density, soil water, and surface water. Vegetation (V) grows due to soil water availability and is lost due to mortality (eq 1). Soil water (W) is surface water that infiltrates in the soil after rain events and is taken up by plants or lost by runoff (eq 2). Surface water (O) is supplied by rainfall and lost due to infiltration in the soil and runoff (eq 3). Vegetation, soil water and surface water all diffuse in two-dimensional space. Rainfall is modeled using a multiplicative white noise $\varepsilon_{t,x}$ with strength σ around a mean interannual value R_o . Parameter definitions and values are given in Table S1.

$$\frac{\partial V}{\partial t} = cg_{max} \frac{W}{W + k_1} V - dV + D_V \Delta V \quad (eq\ 1)$$

$$\frac{\partial W}{\partial t} = \alpha O \frac{V + k_2 W_o}{V + k_2} - cg_{max} \frac{W}{W + k_1} V - r_w W + D_W \Delta W \quad (eq\ 2)$$

$$\frac{\partial O}{\partial t} = R - \alpha O \frac{V + k_2 W_o}{V + k_2} + D_O \Delta O \quad (eq\ 3)$$

$$R = R_o (1 + \sigma \varepsilon_{t,x}) \quad (eq\ 4)$$

678 **Table S1** Model parameters, definition and their units

Model Parameter	Definition, Value and Unit
V	vegetation density, g m^{-2}
W	soil water, mm
O	surface water, mm
c	conversion of water uptake to plant growth, $10 \text{ g mm}^{-1} \text{ m}^{-2}$
g_{max}	maximum specific water uptake, $0.05 \text{ mm g}^{-1} \text{ m}^{-2} \text{ d}^{-1}$
k_1	half-saturation constant of specific plant growth and water uptake, 5 mm
D_p	plant dispersal, $0.1 \text{ m}^{-2} \text{ d}^{-1}$
α	maximum infiltration rate, 0.2 d^{-1}
k_2	saturation constant of water infiltration, 5 g m^{-2}
W_0	water infiltration rate in the absence of plants, 0.2 (-)
r_w	specific water loss due to evaporation and drainage, 0.2 d^{-1}
D_w	diffusion coefficient of soil water, $0.1 \text{ m}^2 \text{ d}^{-1}$
D_0	diffusion coefficient of surface water, $100 \text{ m}^2 \text{ d}^{-1}$
d	specific loss of vegetation density due to mortality, 0.25 d^{-1}
Δ	Laplacian operator for diffusion
R_0	rainfall, range: 0.45 - 1.25 mm d^{-1}
σ	standard deviation of white noise, 0.5
$\varepsilon_{t,x}$	white noise at each gridcell x and time unit t

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In the model, a scale-dependent positive feedback operates because water diffuses much faster than vegetation and the infiltration rate of water in the soil is stronger in areas with vegetation than in bare soil. This effect leads to the accumulation of water under vegetation and to its depletion further away, reinforcing the growth of vegetation and thus the accumulation resulting in the positive feedback. This scale-dependent positive feedback leads to regular vegetation pattern formation: as the system becomes limited by water availability (a decrease in rainfall R), vegetation shifts from a gap, to labyrinth and lastly to spot patterns before the system collapses into desert (Figure S1).

Video animation S1 Sequence of patterns formation as a function of average rainfall
https://www.dropbox.com/s/gxaecz5ly3896yl/movieS1_R1.29-0.5.mov?dl=0

Figure S1 Panel (a): Mean vegetation density as function of rainfall R . Within this rainfall range vegetation patterns emerge as depicted by the snapshots of gaps (c), labyrinths (d, e), and spots (f, g). Rainfall values for the pattern snapshots are indicated with empty circles. The realized standard deviation (STD) in rainfall during the simulations (orange bars in panel a) mimics the decreased variation in rainfall observed in the empirical observations. Panel (b): The evolution of skewness of vegetation density measured along the gradient of rainfall.

Figure S2 Effect of transient dynamics. Different simulated periods 5-20 years, 10-25 years, 15-30 years.

Figure S3 Indicator patterns after removing linear trends for different simulated periods 5-20 years, 10-25 years, 15-30 years. All other parameters similar to figure 3 in the main text.

Figure S4 Interannual rainfall variability (SD) increases with mean annual rainfall for the study area. Rainfall estimates were extracted from the Climate Hazards Group InfraRed Precipitation with Station data (CHIRPS) at ca. 5x5km resolution.