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Research

Remotely-sensed slowing down in spatially patterned dryland ecosystems

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Regular vegetation patterns have been predicted to indicate a system slowing down and possibly desertification of drylands. However, these predictions have not yet been observed in dryland vegetation due to the inherent logistic difficulty to gather longer-term in situ data. 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 use recently developed methods using remote-sensing EVI time-series in combination with classified regular vegetation patterns along a rainfall gradient in Sudan to test the predicted slowing down. 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.

Overall, three temporal indicators (responsiveness, temporal autocorrelation, variance) show slowing down as vegetation patterns change from gaps to labyrinths to spots towards more arid conditions, confirming predictions. However, this transition exhibits non-linearities, specifically when patterns change configuration. Model simulations reveal that the transition between patterns temporarily slows down the system affecting the temporal indicators. These transient states when vegetation patterns reorganize thus affect the systems resilience indicators in a non-linear way.

Our findings suggest that spatial self-organization of dryland vegetation is associated with critical slowing down, but this transition towards reduced resilience happens in a non-linear way. Future work should aim to better understand transient dynamics in regular vegetation patterns in dryland ecosystems, because long transients make regular vegetation patterns of limited use for management in anticipating critical transitions.

Keywords: aridity, critical slowing down, regular vegetation patterns, resilience, responsiveness, self-organization, Sudan, transient states



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Introduction

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

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

stress in Mediterranean (Kéfi et al. 2007) and Chinese semi-arid regions (Lin et al. 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 and Scheffer 2007, Dakos et al. 2011, 2015, Veraart et al. 2012). 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 the Western Sector of southern Kordofan State Sudan ($27^{\circ}4'$ – $29^{\circ}2'$ E; $10^{\circ}2'$ – $12^{\circ}4'$ N; Supporting information) (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 to 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 410 m resolution) with time series (2001–2020) 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 (<www.r-project.org>). All spatial data was downloaded using Google Earth Engine (Gorelick et al. 2017) and aggregated to 16-day intervals. 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 trends to be able to avoid bias in the comparison of temporal indicators across sites (Dakos et al. 2012a). EVI time series were detrended by subtracting the mean EVI value of each 16-day period. SPEI time series were constructed using the ‘SPEI’ package using a log-logistic distribution function and a time scale of 1 month. A 1-month lag was chosen because of the short response of dryland vegetation to moisture availability (Vicente-Serrano et al. 2013). Precipitation data was extracted from the climate hazards group infraRed precipitation with station data (CHIRPS) at ca 5×5 km 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).

We estimated two established indicators of slowing down: 1) temporal autocorrelation (TAC) of the EVI anomalies at-lag-1 (16 days), 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. 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):

$$Y_t = \alpha Y_{(t-1)} + \beta \text{SPEI}_{(t-1)} + \varepsilon_{(t-1)}$$

where Y_t and $Y_{(t-1)}$ are the standardized EVI anomaly at time t and $t - 1$ respectively, $\text{SPEI}_{(t-1)}$ 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 from the same 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). The model ignores the existence of slopes or characteristics of soil texture and does not consider trees as vegetation types as done elsewhere (Staver et al. 2019). Instead 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 Supporting information. 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 (Supporting information).

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 1.2 mm day⁻¹ to 0.5 mm day⁻¹ at increments of 0.01 mm day⁻¹) to mimic aridity stress gradient in our modelled landscapes. When rainfall decreases, vegetation patterns change from gaps to labyrinths (roughly at 1.1 mm day⁻¹ of rainfall) and from labyrinth to spots (roughly at 0.7 mm day⁻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 $\sigma=0.5$, Supporting information). As our model was intended to provide a reference of the resilience indicator patterns in qualitative but not quantitative terms, we ignored for the sake of simplicity other forms (coloured noise) or noise intensities.

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 (19 600 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 128 × 128 cells lattice representing a 400 × 400 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 (30% smoothing span) were applied to

investigate potential non-linear patterns between explanatory and response variables in more detail. All statistics were performed in R ver. 4.1.0 (<www.r-project.org>).

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: $F_{1,1105}=281.0$; $p < 0.0001$; Fig. 1) and second order term ($F_{1,1105}=24.7$, $p < 0.0001$). 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: $F_{1,1106}=25.6$; $p < 0.0001$; Fig. 2A). 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: $F_{1,1106}=13.2$, $p < 0.0001$; Fig. 2B).

Temporal autocorrelation first increased and then decreased with rainfall (linear regression: 1st order term: $F_{1,1105}=3.8$, $p=0.004$; 2nd order term: $F_{1,1105}=7.6$, $p=0.006$; Fig. 2C), but showed some important nonlinearities. Temporal autocorrelation increased steadily for gapped vegetation but then suddenly dropped when labyrinthine patterns were formed before increasing again further with increasing aridity. Temporal autocorrelation showed a hump-shaped but insignificant relationship with spatial skewness (linear regression: 1st order term: $F_{1,1105}=3.2$, $p < 0.08$; 2nd order term: $F_{1,1105}=0.009$, $p=0.92$; Fig. 2D) with non-linearities peaking at transitions between patterns.

Temporal variance increased linearly with mean annual rainfall (linear regression: $F_{1,1106}=196.5$, $p < 0.0001$; Fig. 2E). In contrast, temporal variance did not change with spatial skewness until vegetation patterns were labyrinthine after which variance increased sharply (linear regression: 1st order term: $F_{1,1105}=56.3$, $p < 0.0001$; 2nd order term: $F_{1,1105}=28.3$, $p < 0.0001$; 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

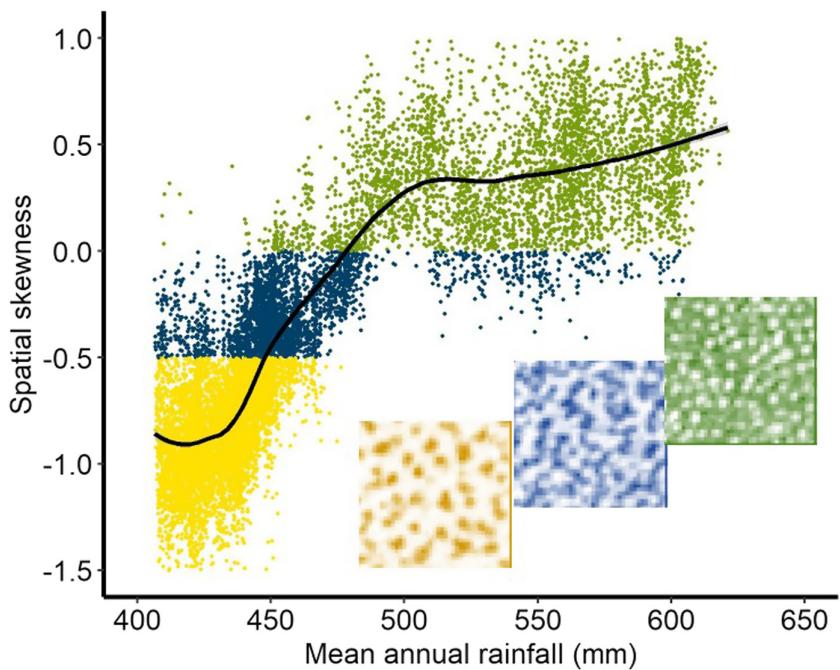


Figure 1. Changing configuration of regular vegetation patterns from gaps (green) to labyrinths (blue) to spots (yellow) with increasing aridity in Sudan. Data points represent observed value on a 410 by 410 m window on the ground. Spatial skewness is a measure of the pixel (10×10 m) distribution between vegetated and bare state across a larger area (410×410 m) and used to assign each a regular vegetation pattern (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). Insets represent examples of real world patterns with spotted (yellow), labyrinthine (blue) and gapped (green) vegetation patterns.

(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 (Supporting information). In contrast, the humps became less pronounced (albeit still present) in later periods (green lines, 15–30 years) that were not affected by transients (Supporting information).

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 and 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

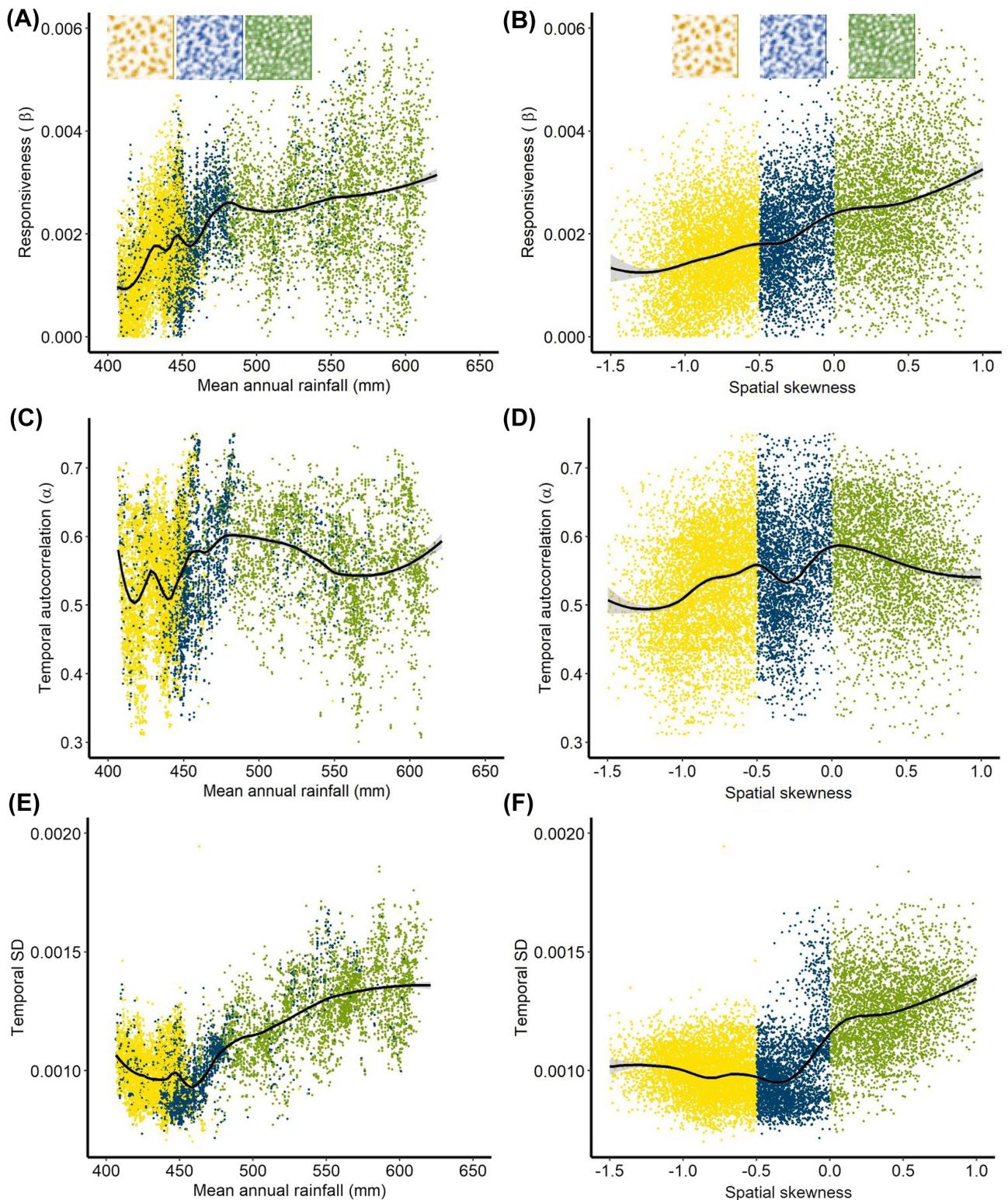


Figure 2. Critical slowing down with decreasing rainfall and vegetation cover in Sudan. Data points represent observed value on a 410 by 410 m window on the ground. Change of the responsiveness (A, B), temporal autocorrelation (C, D) and temporal variance (E, F) of vegetation greenness in relation to 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 hiccups when pattern configuration changes. Lines represent a loess regression with 50% smoothing span and 95% confidence interval (grey shading). Insets represent examples of real world patterns with spotted (yellow), labyrinthine (blue) and gapped (green) vegetation patterns.

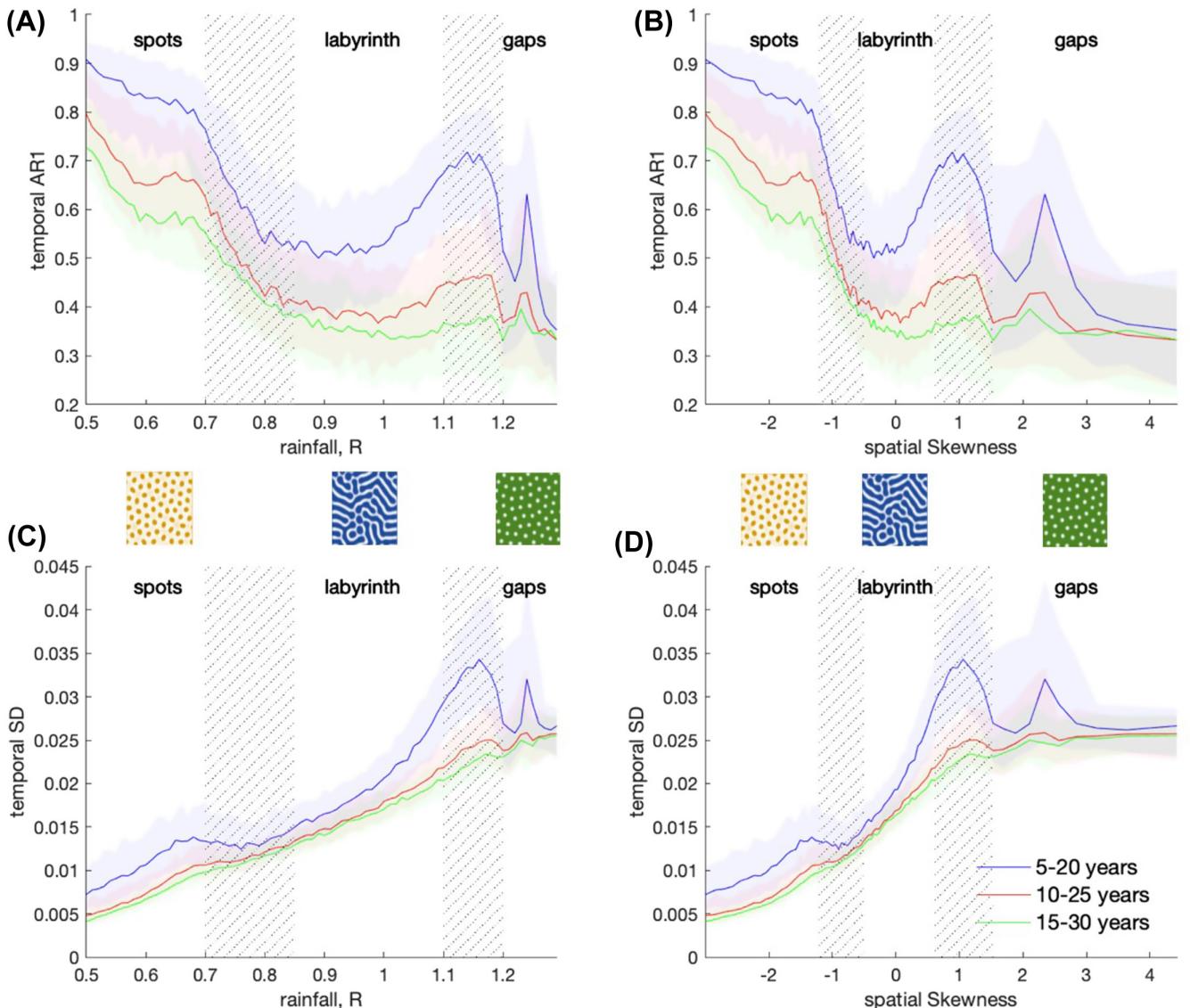


Figure 3. Relationships between temporal indicators (autocorrelation and variance) of average vegetation density with rainfall and with spatial skewness of vegetation density based on model simulations. Different colors represent different temporal intervals (all 15 years long) that the indicators were 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). Insets represent examples of simulated patterns with spotted (yellow), labyrinthine (blue) and gapped (green) vegetation patterns. Note the different limits of skewness between patterns to the limits in Fig. 2 are due to differences in the criteria to identify patterns in modeled and empirical data (Methods).

stochasticity (Supporting information) consistent with the empirical observations of a positive relationship between average annual rainfall and annual rainfall variability (Supporting information). 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 of vegetation density in the short term simulations (Supporting information) confirms this expectation). 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), 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, Staver et al. 2019).

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). Rainfall variation might introduce strong lags and transient dynamics. We can imagine a long period of dry years to inflict very slow dynamics even in the presence of intermittent rainfall if vegetation biomass is already low. On the other hand, a long dry period in the case of intermediate vegetation biomass may induce fast changes followed by fast or slow recovery depending not only on the duration but also on the intensity of rainfall. Furthermore, seasonality or other sources of disturbances including those of human origin (Barbier et al. 2006, Gowda et al. 2016), as well as heterogeneity in the landscape are not part of the model. This could result in additional variation 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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Author contributions

Michiel P. Veldhuis: Conceptualization (lead); Formal analysis (equal); Writing – Original draft (lead); Writing – review and editing (equal). **Ricardo Martinez-Garcia:** Conceptualization (supporting); Writing – review and editing (equal). **Vincent Deblauwe:** Formal analysis (supporting); Writing – review and editing (equal). **Vasilis Dakos:** Conceptualization (supporting); Formal analysis (equal); Writing – Original draft (supporting); Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Zenodo Digital Repository. The vegetation pattern classification in Sudan (<<https://doi.org/10.5281/zenodo.4500000>>).

[org/10.5281/zenodo.6328576>](https://doi.org/10.5281/zenodo.6328576)), remote-sensing dataset ([https://doi.org/10.5281/zenodo.6393459>](https://doi.org/10.5281/zenodo.6393459)) and simulated dataset of dryland vegetation model ([https://doi.org/10.5281/zenodo.6299903>](https://doi.org/10.5281/zenodo.6299903)).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Angeler, D. G. and Allen, C. R. 2016. Quantifying resilience. – *J. Appl. Ecol.* 53: 617–624.
- Barbier, N. et al. 2006. Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. – *J. Ecol.* 94: 537–547.
- Barbier, N. et al. 2014. Case study of self-organized vegetation patterning in dryland regions of Central Africa. – In: Mueller, E. et al. (eds), *Patterns of land degradation in drylands*. Springer, pp. 347–356.
- Bastiaansen, R. et al. 2018. Multistability of model and real dryland ecosystems through spatial self-organization. – *Proc. Natl Acad. Sci. USA* 115: 11256–11261.
- Beisner, B. E. et al. 2003. Alternative stable states in ecology. – *Front. Ecol. Environ.* 1: 376–382.
- Bestelmeyer, B. T. et al. 2013. A test of critical thresholds and their indicators in a desertification-prone ecosystem: more resilience than we thought. – *Ecol. Lett.* 16: 339–345.
- Brock, W. A. and Carpenter, S. R. 2010. Interacting regime shifts in ecosystems: implication for early warnings. – *Ecol. Monogr.* 80: 353–367.
- Chen, N. et al. 2018. Rising variability, not slowing down, as a leading indicator of a stochastically driven abrupt transition in a dryland ecosystem. – *Am. Nat.* 191: E1–E14.
- Dakos, V. et al. 2011. Slowing down in spatially patterned ecosystems at the brink of collapse. – *Am. Nat.* 177: E153–E166.
- Dakos, V. et al. 2012a. Methods for detecting early warnings of critical transitions in time series illustrated using simulated ecological data. – *PLoS One* 7: e41010.
- Dakos, V. et al. 2012b. Robustness of variance and autocorrelation as indicators of critical slowing down. – *Ecology* 93: 264–271.
- Dakos, V. et al. 2015. Resilience indicators: prospects and limitations for early warnings of regime shifts. – *Phil. Trans. R. Soc. B* 370: 591–596.
- De Keersmaecker, W. et al. 2015. A model quantifying global vegetation resistance and resilience to short-term climate anomalies and their relationship with vegetation cover. – *Global Ecol. Biogeogr.* 24: 539–548.
- Deblauwe, V. et al. 2008. The global biogeography of semi-arid periodic vegetation patterns. – *Global Ecol. Biogeogr.* 17: 715–723.
- Deblauwe, V. et al. 2011. Environmental modulation of self-organized periodic vegetation patterns in Sudan. – *Ecography* 34: 990–1001.
- Didan, K. 2015. MOD13A2 MODIS/Terra vegetation indices 16-day L3 global 1 km SIN grid. – NASA EOSDIS Land Processes DAAC, <<https://doi.org/10.5067/MODIS/MOD13A2>>.
- Funk, C. et al. 2015. The climate hazards infrared precipitation with stations – a new environmental record for monitoring extremes. – *Sci. Data* 2: 150066.
- Garcia, R. V. and Spitz, P. 1961. The roots of catastrophe. – *The roots of catastrophe*. Elsevier, pp. 3–54.
- Gorelick, N. et al. 2017. Google Earth Engine: planetary-scale geospatial analysis for everyone. – *Remote Sens. Environ.* 202: 18–27.
- Gowda, K. et al. 2016. Assessing the robustness of spatial pattern sequences in a dryland vegetation model. – *Proc. R. Soc. A* 472: 20150893.
- Hastings, A. et al. 2018. Transient phenomena in ecology. – *Science* 361: eaat6412.
- Hijmans, R. J. 2018. raster: geographic analysis and modeling with raster data. – R package ver. 2.7-15, <<https://cran.r-project.org/web/packages/raster/index.html>>.
- Hilborn, R. and Litzinger, E. 2009. Causes of decline and potential for recovery of Atlantic cod populations. – *Open Fish Sci. J.* 2: 32–38.
- HilleRisLambers, R. et al. 2001. Vegetation pattern formation in semi-arid grazing systems. – *Ecology* 82: 50–61.
- Hodgson, D. et al. 2015. What do you mean, ‘resilient’? – *Trends Ecol. Evol.* 30: 503–506.
- Hughes, T. P. et al. 2013. Living dangerously on borrowed time during slow, unrecognized regime shifts. – *Trends Ecol. Evol.* 28: 149–155.
- Ingrisch, J. and Bahn, M. 2018. Towards a comparable quantification of resilience. – *Trends Ecol. Evol.* 33: 251–259.
- Janssen, R. H. H. et al. 2008. Microscale vegetation–soil feedback boosts hysteresis in a regional vegetation–climate system. – *Global Change Biol.* 14: 1104–1112.
- Kéfi, S. et al. 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. – *Nature* 449: 213–217.
- Kéfi, S. et al. 2010. Bistability and regular spatial patterns in arid ecosystems. – *Theor. Ecol.* 3: 257–269.
- Klausmeier, C. a. 1999. Regular and irregular patterns in semiarid vegetation. – *Science* 284: 1826–1828.
- Kletter, A. Y. et al. 2009. Patterned vegetation and rainfall intermittency. – *J. Theor. Biol.* 256: 574–583.
- Konings, A. G. et al. 2011. Drought sensitivity of patterned vegetation determined by rainfall–land surface feedbacks. – *J. Geophys. Res. Biogeosci.* 116: G04008.
- Lejeune, O. et al. 2002. Localized vegetation patches: a self-organized response to resource scarcity. – *Phys. Rev. E* 66: 010901.
- Lenton, T. M. et al. 2019. Climate tipping points – too risky to bet against. – *Nature* 575: 592–595.
- Levin, S. A. and Lubchenco, J. 2008. Resilience, robustness, and marine ecosystem-based management. – *Bioscience* 58: 27–32.
- Lin, Y. et al. 2010. Spatial vegetation patterns as early signs of desertification: a case study of a desert steppe in Inner Mongolia, China. – *Landsc. Ecol.* 25: 1519–1527.
- Liu, Y. et al. 2019. Reduced resilience as an early warning signal of forest mortality. – *Nat. Clim. Change* 9: 880–885.
- MathWorks, T. 2017. MATLAB (R2017b). – MathWorks Inc., USA.
- Meron, E. et al. 2004. Vegetation patterns along a rainfall gradient. – *Chaos Solit. Fract.* 19: 367–376.
- Rietkerk, M. et al. 2002. Self-organization of vegetation in arid ecosystem. – *Am. Nat.* 160: 524–530.
- Rietkerk, M. et al. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. – *Science* 305: 1926–1929.

- Running, S. et al. 2017. MODIS global terrestrial evapotranspiration (ET) product (NASA MOD16A2) NASA earth observing system MODIS land algorithm. – Numerical Terradynamic Simulation Group.
- Sankaran, S. et al. 2019. Clustering and correlations: inferring resilience from spatial patterns in ecosystems. – *Methods Ecol. Evol.* 10: 2079–2089.
- Scheffer, M. and Carpenter, S. R. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. – *Trends Ecol. Evol.* 18: 648–656.
- Scheffer, M. et al. 1993. Alternative equilibria in shallow lakes. – *Trends Ecol. Evol.* 8: 275–279.
- Scheffer, M. et al. 2009. Early-warning signals for critical transitions. – *Nature* 461: 53–59.
- Scheffer, M. et al. 2012. Anticipating critical transitions. – *Science* 338: 344–348.
- Scheffer, M. et al. 2015. Generic indicators of ecological resilience. – *Annu. Rev. Ecol. Evol. Syst.* 46: 145–167.
- Seddon, A. W. R. et al. 2016. Sensitivity of global terrestrial ecosystems to climate variability. – *Nature* 541: 229–232.
- Simenstad, C. A. et al. 1978. Aleuts, sea otters and alternate stable-state communities. – *Science* 200: 403–411.
- Staver, A. C. et al. 2019. Spatial patterning among savanna trees in high-resolution, spatially extensive data. – *Proc. Natl Acad. Sci. USA* 116: 10681–10685.
- Suding, K. N. et al. 2004. Alternative states and positive feedbacks in restoration ecology. – *Trends Ecol. Evol.* 19: 46–53.
- Turing, A. M. 1952. The chemical basis of morphogenesis. – *Phil. Trans. R. Soc. B* 237: 37–72.
- van Belzen, J. et al. 2017. Vegetation recovery in tidal marshes reveals critical slowing down under increased inundation. – *Nat. Commun.* 8: 15811.
- van Nes and Scheffer 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. – *Am. Nat.* 169: 738–747.
- Veraart, A. et al. 2012. Recovery rates reflect distance to a tipping point in a living system. – *Nature* 481: 357–359.
- Verbesselt, J. et al. 2016. Remotely sensed resilience of tropical forests. – *Nat. Clim. Change* 6: 1028–1031.
- Vicente-Serrano, S. M. et al. 2010. A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. – *J. Clim.* 23: 1696–1718.
- Vicente-Serrano, S. M. et al. 2013. Response of vegetation to drought time-scales across global land biomes. – *Proc. Natl Acad. Sci. USA* 110: 52–57.
- von Hardenberg, J. et al. 2001. Diversity of vegetation patterns and desertification. – *Phys. Rev. Lett.* 87: 198101.
- Wissel, C. 1984. A universal law of the characteristic return time near thresholds. – *Oecologia* 65: 101–107.