RESEARCH ARTICLE

From nonequilibrium initial conditions to steady dryland vegetation patterns: How trajectories matter

Daniel Caviedes-Voullième | Christoph Hinz

Chair for Hydrology, Brandenburg University of Technology Cottbus-Senftenberg, Cottbus, Germany

Correspondence
Daniel Caviedes-Voullième, Chair for Hydrology, Brandenburg University of Technology Cottbus-Senftenberg, Platz der Deutschen Einheit 1, Cottbus 03044, Germany. Email: caviedes@b-tu.de

Abstract
The multiscale nature of ecohydrological processes and feedbacks implies that vegetation patterns arising in water-limited systems are directly linked to water redistribution processes occurring at much shorter timescales than vegetation growth. This in turn suggests that the initially available water in the system can play a role in determining the trajectory of the system, together with the well-known role of the rainfall gradient. This work explores the role of initial hydrological conditions on vegetation dynamics and vegetation patterns. To do so, the HilleRisLambers–Rietkerk model was solved with different rainfall amounts and a large range of initial hydrological conditions spanning from near-equilibrium to far-from-equilibrium conditions. The resulting vegetation patterns and ecohydrological signatures were quantitatively studied. The results show that not only do initial hydrological conditions play a role in the ecohydrological dynamics but also they can play a dominating one even resulting in divergent vegetation patterns that exhibit convergent mean-field properties, including a new set of hybrid patterns. Our results highlight the relevance of assessing both global ecological and hydrological signatures and quantitatively assessing patterns to describe and understand system dynamics and in particular to determine if the systems are transient or steady. Furthermore, our analysis shows that the trajectories the system follows during its transient stages cannot be neglected to understand complex dependencies of the long-term steady state to environmental factors and drivers.

1 | INTRODUCTION

Vegetation self-organization (VSO) in semiarid regions, in particular into distinctive spatial patterns, has been widely studied by means of mathematical models in the past two decades (e.g., Borgogno, D’Odorico, Laio, & Ridolfi, 2009; Zelnik, Kinast, Yizhaq, Bel, & Meron, 2013). With the aid of models, VSO has been theorized to be the result of scale-dependent feedbacks between water, biomass, and soil—the so-called water redistribution hypothesis (Sherratt, 2016). This theory is extensively supported by observations, mathematical analysis, and direct numerical results, which explain its wide acceptance, although it must be acknowledged that alternative and complementary hypotheses have been proposed, such as solely long-range vegetation competition (Martínez-García, Calabrese, Hernández-García, & López, 2013) and interactions with fauna (Getzin et al., 2016; Tarnita et al., 2017), which remain under intense scientific discussion. Moreover, several feedback mechanisms of soil–vegetation–water interactions have been identified (Meron, 2016) and are supported by experimental evidence (Dunkerley, 2002; Ludwig, Wilcox, Breshears, Tongway, & Imeson, 2005; Tongway, Valentin, & Seghieri, 2001; Yizhaq, Stavi, Swet, Zaady, & Katra, 2019). Mathematical and numerical models are a key tool in exploring and understanding the dynamics...
of these systems (Sherratt, 2016) as the spatiotemporal scales make field studies and experiments expensive and with limited capabilities of producing insights into the dynamics (Meron, 2018). Nonetheless, the collective experiences in this topic support a set of well-established, yet not fully addressed, standing issues in ecohydrological VSO modelling, that is, environmental spatial heterogeneity and temporal variability need to be accounted for in the models (Rietkerk, Dekker, de Ruiter, & van de Koppel, 2004; Gilad, von Hardenberg, Provenzale, Shachak, & Meron, 2007; Jenerette, Barron-Gafford, Guswa, McDonnell, & Villegas, 2011) and further understanding of models and their properties is necessary (Ursino, 2007; Zelnik et al., 2013). It has been widely recognised that steady state vegetation patterns in semiarid flatlands are strongly sensitive to the rainfall gradient (Deblauwe, Barbier, Couteron, Lejeune, & Bogaert, 2008; Rietkerk et al., 2002; Meron, 2018; Gilad et al., 2007). These patterns in turn have been identified as key for resilience (Mueller, Wainwright, Parsons, & Turnbull, 2014; Yizhaq, Sela, Svoray, Assouline, & Bel, 2014), and their variations can be early indicators of change and state shifts (Rietkerk et al., 2004; Barbier, Couteron, Lejoly, Deblauwe, & Lejeune, 2006).

There is a growing awareness that the long-term asymptotically steady states of ecological systems are often not representative of the short-term dynamics (Hastings, 2004; 2010; Siteur et al., 2014; Larsen et al., 2016; Arnoldi, Bideault, Loreau, & Haegeman, 2018) and relevant classical concepts (stability and resilience) require a better understanding of transient dynamics (Arnoldi, Loreau, & Haegeman, 2016; Siteur et al., 2014; Siteur, Eppinga, Doelman, Siero, & Rietkerk, 2016), as well as assessing when the system can be considered steady (Hastings, 2004; Hamann, Schmickl, & Crailsheim, 2012). Furthermore, the role of initial conditions on the transient dynamics may not be captured by the asymptotically steady regime (Arnoldi et al., 2018). One example of this is that how near or far the initial conditions of a system are from equilibrium has implications on the rates and timescales of the dynamics and timescales, a topic yet to be thoroughly addressed (Hastings, 2016; Larsen et al., 2016). Additionally, dryland ecosystems frequently experiment far-from-equilibrium conditions thus staying in a quasipermanent transient condition and exhibit nonlinear responses to boundary conditions and forcing (Puigdefábregas, 1998). That is, the systems of interest here are prone to be strongly affected by initial conditions, which may also lead to long, complex transient trajectories.

The stability of these ecohydrosystems to perturbations and their regions of bistability (Zeng, Shen, Zeng, & Dickinson, 2004; Boggiano et al., 2009) has been a focus of research. This has lead to simulating the system evolution from arbitrary initial conditions into steady states (most often tacitly) defined when mean-field signatures—a quantity characterizing a complex behaviour (Addor et al., 2018)—such as biomass, converge to steady conditions (e.g., Baudena, von Hardenberg, & Provenzale, 2013; Kletter, von Hardenberg, Meron, & Provenzale, 2009; Thompson, Katul, & McMahon, 2008). It must be acknowledged that alternative analytical and mathematical approaches, not requiring an ad hoc definition of a steady state or equilibrium, have also been used (Lejeune, Tlidi, & Lefever, 2004; van der Stelt, Doelman, Hek, & Rademacher, 2012; Zelnik et al., 2013). Many studies have focused on patterns at steady state and their response or dependence to environmental conditions or system properties (e.g., Rietkerk et al., 2004; Gilad et al., 2007), and others have been concerned also with monitoring domain-wide integrated quantities such as total biomass and vegetation cover (e.g., Kletter et al., 2009; Pueyo, Kefi, Diaz-Sierra, Alados, & Rietkerk, 2010). The formulation of these models allows to achieve steady states only in the presence of steady rainfall forcing (Kletter et al., 2009). Natural time-varying rainfall is unlikely to force the system into steady states (Guttal & Jayaprakash, 2007; Kletter et al., 2009). Nonetheless, using idealized set-ups with steady rainfall, many authors have analysed the transient dynamics resulting from these inherently transient partial differential equation (PDE) models and drawn insights on different issues, such as the rates of transitions (Yizhaq et al., 2014), transitions of patterns on the basis of rainfall (Roitberg & Shoshany, 2017; Zelnik & Meron, 2018), response to gradual environmental change (Dagbovie & Sherratt, 2014; Siteur et al., 2014), succession dynamics (Pueyo et al., 2010), the pseudosteady migration of vegetation bands (Rietkerk et al., 2002; Sherratt & Lord, 2007), colonization of a slope (Sherratt, 2016), or the relevance of the transient history of patterns (Sherratt, 2013). This has further been studied using the concepts of pattern selection and wavelength selection (Dagbovie & Sherratt, 2014; Siero et al., 2015; Zelnik & Tzuk, 2017) used to describe the process under which a given pattern (with a particular characteristic wavelength) is established. Pattern (wavelength) selection has been shown to be history dependent (Dagbovie & Sherratt, 2014; Zelnik & Tzuk, 2017).

From the model perspective, its time evolving nature requires the definition of both the initial vegetation distribution and the initial surface and subsurface water distributions, henceforth initial hydrological conditions (IHCs). Random vegetation distributions have often been selected as initial conditions throughout the literature. Some researchers have reported little qualitative sensitivity to different random distributions (Guttal & Jayaprakash, 2007; Jenerette et al., 2011; Thompson & Katul, 2009). In contrast, Meron, Gilad, von Hardenberg, Shachak, and Zarmi (2004) initialized simulations with random perturbations over unstable uniform vegetated states, showing that different patterns can arise while using the von Hardenberg, Meron, Shachak, and Zarmi (2001) model. Zelnik et al. (2013) showed that different initial vegetation disturbances can lead to different patterns under the same environmental conditions. Similarly, in a-two-species context, Baudena and Rietkerk (2012) showed that different two-species patterns can be obtained from different initial species distributions.

The role of IHC on asymptotic steady-state patterns has received less attention. IHCs have been mostly taken as the so-called plantless-equilibrium conditions (e.g., Rietkerk et al., 2002), that is, setting the IHC as if the domain is homogeneously bare. This has been proven useful when exploring stability properties of such systems (Siteur et al., 2014), although the assumption of near-equilibrium IHC can be viewed as untested and has been increasingly challenged (Vetter, 2005; Mueller et al., 2014). A few notable studies are the exception. Meron et al. (2004) obtained similar patterns from random perturbations over the uniformly vegetated state, or from isolated vegetation spots, while experiencing different transient states including ring-like patterns. Sherratt and Lord (2007) showed that properties of vegetation bands can vary in response to small random variations of initial biomass and initial water. Both studies, relying on randomized small perturbations, concluded that the spatial patterns can depend on initial conditions, including IHC, which is most relevant for this work.
In contrast, Guttal and Jayaprakash (2007) used both well-developed ecohydrological patterns and zero initial water depths and found that the final patterns did not depend on initial conditions. The apparent contradiction between the results of Meron et al. (2004) and Sherratt and Lord (2007) compared with those of Guttal and Jayaprakash (2007) prompts the systematic study of the possible effects of IHC, and the dependency on how specific IHC could generate specific patterns or trajectories remains a gap that motivates this work.

Mathematically, initial conditions are the required, known, and prescribed initial states. In natural systems, initial conditions may be impossible to identify or retrieve (Sherratt, 2015), although systems that have experienced large natural or anthropogenic disturbances—e.g., overgrazing, mining, agriculture, fires, and volcanic eruptions—may allow to identify characteristic initial conditions prior to a (natural or assisted) restoration process. Initial states in such cases may strongly constrain or determine the long-term state of complex natural systems (Perron & Fagherazzi, 2012; Maurer & Gerke, 2016). IHCs can also be viewed as the result of intermittent rainfall or a single (pulsed) event (Schwinning & Sala, 2004). In the context of semiarid vegetation patterns, it has been seldom asked what is the nature of the pulsed events that may be responsible for initializing systems (Eddy, Humphreys, Hart, Mitchell, & Fanning, 1999) or the transients triggered after individual events (Baudena et al., 2013). We argue that IHC deviating from ecohydrological equilibrium can be idealized as singular hydrological disturbances, and studying the transient response to it may lead to insights of the transient dynamics and equilibrium states, without requiring complex and stochastic rainfall signals.

The transient trajectories from the initial conditions to the converged steady state have received less attention due to a wide range of reasons, starting with the inherent difficulties of observing such transient processes in nature and difficulties in model parametrization to allow meaningful comparisons among others (Karssenberg, Bierkens, & Rietkerk, 2017). Modelling efforts to address transient dynamics do exist, and the importance of transients has been highlighted, relating to many issues. Observed patterns have been reported not to coincide with simulated steady-state patterns (Meron, 2016). Ring and spiral patterns have been identified as transient (Bonanomi et al., 2014; Fernandez-Oto, Escaff, & Cisternas, 2019; Sheffer, Yizhaq, Shachak, & Meron, 2011; Tlidi et al., 2018; Yizhaq et al., 2019), likely triggered by excitable behaviour (Fernandez-Oto et al., 2019; Tlidi et al., 2018). Discrete rainfall events have been observed to produce transients (Baudena et al., 2013). The temporal variability of rainfall has been pointed as partially responsible for the rates at which the systems react to environmental change (Zelnik et al., 2013), and the transient behaviour of the systems interact with the rates of variation of external drivers (Siteur et al., 2014). Ecological succession has been explained through modelling ecohydrological interactions (Pueyo et al., 2010). Importantly, patterns have been shown to be history dependent (Sherratt, 2013; 2015; Siteur et al., 2014), and steady patterns can be used to infer the historical origin of the system (Sherratt, 2015). Additionally, the so-called hybrid patterns (Meron, 2012; Zelnik, Meron, & Bel, 2015)—that is, stable patterns characterized by anomalies in pattern periodicity—have been identified arising from different system trajectories and also strongly affect the response trajectory of the system to perturbations. Mueller et al. (2014) include the dependency on previous states as a central element of the complexity of these ecohydrosysytems.

History dependence (alternatively, trajectory dependence) and the transient dynamics of these systems are the result of time-dependent rainfall (Baudena, Boni, Ferraris, von Hardenberg, & Provenzale, 2007; Baudena et al., 2013; D’Olorico, Laio, & Ridolfi, 2005; Guttal & Jayaprakash, 2007; Kletter et al., 2009; Zhao & Wang, 2014) and many complex responses to spatial heterogeneities (McGrath, Paik, & Hinz, 2012; Siero et al., 2015; Siteur et al., 2014; Sun, Li, Yu, & Jin, 2013; Tietjen, 2016; van der Stelt et al., 2012; Yizhaq et al., 2014; Zhao & Wang, 2014). It has been shown that many of these factors can coerce patterns (Bastiaansen et al., 2018) and can strengthen or weaken the ecosystem (Kletter et al., 2009). We argue that IHC may be considered as one more environmental driver to which the system might show distinctive and alternative responses.

In light of this, we hypothesize that initial water availability can have a long-lasting effect and contribute to determine the ecohydrological steady state (typically defined as a steady biomass signal). We propose that the extent to which such initial water availability can play a significant role on the long-term steady state can be explained by the evolusion trajectory of the system. Therefore, the following research questions are proposed:

1. Which role does initial water availability play in determining the trajectory of the system and the long-term ecohydrological steady state?
2. Which observable variables and behaviours of the system, that is, global signatures (biomass, cover, and hydrological balance) and spatial patterns and quantitative indicators of their properties, can be affected by different IHCs?

We address these questions, performing a numerical sensitivity study along a rainfall gradient and an initial surface water gradient.

2 | MATERIALS AND METHODS

2.1 | Mathematical ecohydrological model

The spatially distributed ecohydrological model is based on two hydraulic submodels (surface and subsurface flow) and a biomass submodel, as proposed by HilleRisLambers, Rietkerk, van den Bosch, Prins, and de Kroon (2001) and Rietkerk et al. (2002). The system is comprised by three reaction–diffusion PDEs and has been widely used in literature for similar studies (e.g., Roitberg & Shoshany, 2017; Sherratt, 2016; Thompson et al., 2008; Yizhaq et al., 2014).

\[
\frac{\partial b(x, t)}{\partial t} = D_b \nabla^2 b + c_b \nabla b \cdot (W, b) - d_b \cdot b. \tag{1}
\]

\[
\frac{\partial h(x, t)}{\partial t} = D_h \nabla^2 h + r - i(b). \tag{2}
\]

\[
\frac{\partial W(x, t)}{\partial t} = D_w \nabla^2 W + i(b) - W \cdot (b, W) - pW. \tag{3}
\]

where \( b \) is biomass density (g m\(^{-2}\)), \( h \) is surface water depth (mm), \( W \) is subsurface water depth (mm), \( x \) are the two-dimensional spatial coordinates (m), \( t \) is time (day), \( r \) is rainfall intensity (mm day\(^{-1}\)). The infiltration rate \( i \) (mm day\(^{-1}\)) is a function of biomass in order to model infiltration enhancement due to vegetation.

\[
i(b, h) = a_h \frac{b + kW_0}{b + k}. \tag{4}
\]
The rate at which vegetation uptakes water from the subsurface $V'$ is

$$V'(b, W) = g_w b \frac{W}{W + k_b}. \quad (5)$$

All model parameters are defined in Table 1, along with their selected values for this study. It is noteworthy that Systems (1)–(3) are a set of three diffusion–reaction equations: all water and biomass propagate horizontally by linear diffusion processes. Biomass growth is modelled as linearly dependent on uptake, and biomass death is a first-order decay term. Infiltration couples both water systems directly, and indirectly to the biomass field, whereas uptake directly couples the subsurface water field to biomass.

Systems (1)–(3) are integrated in space using a first-order finite volume approach and in time with a first-order, explicit, and forward Euler method. Because all three PDEs in Systems (1)–(3) are linear diffusion equations, this numerical approximation is conditionally stable and must satisfy the time-step size restriction:

$$\Delta t \leq \frac{\delta x^2}{2 \max(D_h, D_w, D_b)} = \frac{\delta x^2}{2D_b} \quad (6)$$

The solver was implemented in C, with OpenMP-based parallelization, and run in parallel on 20 central processing units i7-6950X at 3.00 GHz.

### 2.2 Study set-up

The computational domain is $300 \times 300 \text{ m}$ representing a flat area, with a spatial discretization of $\delta x = \delta y = 2 \text{ m}$. Both extension and resolution are similar to previous studies (Rietkerk et al., 2002; Pueyo et al., 2010; Roitberg & Shoshany, 2017). Model parameters (Table 1) follow Rietkerk et al. (2002) as many others have (Baudena & Rietkerk, 2012; Dagbovie & Sherratt, 2014; Guttal & Jayaprakash, 2007; Pueyo, Kefi, Alados, & Rietkerk, 2008; Pueyo et al., 2010; Sherratt, 2016; Rietkerk & Shoshany, 2017). Simulation duration is set to 200 years (73,000 days) and exceptionally up to 1,000 years for three IHCs. Simulation duration varies largely among published studies: those based on the Rietkerk model report duration from 8 to 22 years (Rietkerk et al., 2002; Baudena & Rietkerk, 2012; Pueyo et al., 2010; Realpe-Gomez, Baudena, Galla, McKane, & Rietkerk, 2013; Thompson et al., 2008; Thompson & Katul, 2009). Studies on the basis of other similar models report duration in the range of 37 to 166 years (Gilad et al., 2007; Gilad, Shachak, & Meron, 2007; Kletter et al., 2009; Sheffer, Yizhaq, Gilad, Shachak, & Meron, 2007; Yizhaq et al., 2019; Zelnik et al., 2015) and exceptionally up to 500 years (Baudena et al., 2013). In some studies, the duration is not reported (e.g., Guttal & Jayaprakash, 2007; Pueyo et al., 2008; Roitberg & Shoshany, 2017). Here, the simulation duration is set significantly larger than most of the reported simulations to ensure that the final states are steady or nearly steady.

A semiarid rainfall gradient was selected (Table 2). All previous studies using this model have set IHC to the so-called “plantless equilibrium” (e.g., Rietkerk et al., 2002; Roitberg & Shoshany, 2017). Such IHC is in fact the steady bare soil solution of the system, that is, the water depth $h$ and subsurface water depth $W$ fields are set equal to their steady states solutions when biomass is 0. This can be shown to be a uniform state $h(x, t = 0) = r(\alpha W_0)^{-1}$ and $W(x, t = 0) = r/p$. Therefore, IHCs are a function of rain and satisfy that the infiltration–rain ratio $I/R = (rA)^{-1}\int_{x}^{y} h(x, y) \text{d}A$ is equal to 1. The reader should note that, despite that this condition is termed plantless, it does not mean that the initial vegetation condition is set to $b(x, t = 0) = 0$. In fact, initial biomass conditions are set in a similar fashion as previous studies (e.g., Pueyo et al., 2010) as randomly located biomass peaks of biomass density $b_0$ and 0 biomass elsewhere, that is,

$$b(x, t = 0) = \begin{cases} b_0 & \forall x \in S \\ 0 & \forall x \not\in S. \end{cases} \quad (7)$$

where $S$ is a set of randomly determined areas (computational cells), such that initial vegetation cover fraction is $V_s = A_s/A$, where $A_s$ is the vegetated area and $A$ is the total domain area. Initial biomass density was set to $b_0 = 90 \text{ g m}^{-2}$, and initial vegetation cover was set to $V = 0.01$. All simulations use the same initial biomass distribution. Note that, although plantless equilibrium conditions are a relevant solution of the system, their use as an IHC is rather arbitrary. In this study, plantless equilibrium IHC and both wetter and drier surface water IHC are used. Only surface water IHCs are varied herein by increasing or decreasing IHC by factors of 2. Subsurface IHCs are always set to plantless equilibrium so that only a single IHC is varied. The reasoning for favouring varying surface IHC over subsurface IHC is that the system’s evolution is expected to be less sensitive to the latter. There are two reasons for this: the infiltration feedback has a higher interaction with surface flow, and the first-order decay percolation/evaporation sink term allows for a net loss of water directly from the subsurface, which strongly pushes the system back into equilibrium (refer to the supporting information for some illustrative results on this). For every rainfall scenario, twelve different surface IHC are tested (Table 2). Boldface values in the table correspond to plantless equilibrium IHC. Column colours in Table 2 describe the initial surface water depths, and row colours describe precipitation. These colours are systematically used throughout the paper. Nonzero surface IHCs must be interpreted within the context of a closed system (periodic boundaries), from which water cannot escape. It is therefore possible to conceptually interpret the initial water depths as the accumulated rainfall of events occurring before the (arbitrary) initial time. Although this study is mainly concerned with surface IHC, illustrative examples of the effects of different initial subsurface water and initial biomass $b_0$ are included as a supporting information, showing that the sensitivities to either subsurface and biomass initial conditions are much lower than for surface initial conditions. In consequence, henceforth, only surface IHC variations are explored.

### 2.3 Postprocessing and indicators

The results are assessed in of terms mean-field (i.e., integrated in the whole domain) ecological signatures (total biomass $B$, and vegetation cover, and mean density) and mean-field hydrological signatures—for example, infiltration/rain ratio $I/R$ and surface water fraction—together with the spatial patterns themselves and quantitatively statistical descriptors of the spatial patterns (number of patches, patch area, area–perimeter ratio, patch circularity, and patch separation). These metrics do not require any base assumption on the shapes or periodicity of patterns. We purposely avoid using metrics that assume periodicity (e.g., wavelength and frequency), which are often used to describe periodic patterns (e.g., Deblauwe, Couteron, Lejeune,
### Table 1: Model parameters

| Description                              | Parameters | Value | Units       |
|------------------------------------------|------------|-------|-------------|
| Water-biomass conversion rate            | $c_b$      | 10    | g m⁻² /mm   |
| Maximum uptake per unit biomass          | $g_b$      | 0.05  | mm / (g day m²) |
| Half-saturation water-uptake constant    | $k_b$      | 5     | mm          |
| Death rate coefficient                   | $d_b$      | 0.25  | day⁻¹       |
| Biomass diffusion rate                    | $D_b$      | 0.1   | m² day⁻¹    |
| Fully vegetated infiltration coefficient | $a$        | 0.2   | day⁻¹       |
| Half-saturation infiltration constant    | $k$        | 5     | g m⁻²       |
| Bare soil infiltration factor             | $W_0$      | 0.2   | –           |
| Subsurface water diffusion coefficient    | $D_w$      | 0.1   | m² day⁻¹    |
| Surface water diffusion coefficient       | $D_h$      | 100   | m² day⁻¹    |
| Soil losses coefficient                  | $p$        | 0.2   | day⁻¹       |

### Table 2: Initial conditions and rainfall

| Rain (mm/day) | 0.25 | 0.50 | 0.60 | 0.75 | 0.85 | 1.00 |
|---------------|------|------|------|------|------|------|
| Multiplier    |      |      |      |      |      |      |
| 0.0           | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  | 0.0  |
| 1/64          | -    | 0.1953 | 0.2343 | 0.2929 | 0.3320 | 0.3906 |
| 1/32          | 0.1953 | 0.3906 | 0.4687 | 0.5859 | 0.6640 | 0.7812 |
| 1/16          | 0.3906 | 0.7812 | 0.9375 | 1.1718 | 1.328 | 1.5625 |
| 1/8           | 0.7812 | 1.562 | 1.875 | 2.343 | 2.656 | 3.125 |
| 1/4           | 1.5625 | 3.125 | 3.75 | 4.6875 | 5.312 | 6.250 |
| 1/2           | 3.125 | 6.25 | 7.5 | 9.375 | 10.625 | 12.5 |
| 1             | 6.25 | 12.5 | 15 | 18.75 | 21.25 | 25.0 |
| 2             | 12.5 | 25.0 | 30.0 | 37.5 | 42.5 | 50.0 |
| 4             | 25 | 50 | 60 | 75 | 85 | 100 |
| 8             | 50 | 100 | 120 | 150 | 170 | 200 |
| 16            | 100 | 200 | 240 | 300 | 340 | 400 |
| 32            | 200 | - | - | - | - | - |

Boldface values correspond to plantless equilibrium initial hydrological conditions. Column colours describe the initial surface water depths, and row colours describe precipitation.

Bogaert, & Barbier, 2011; Dagbovie & Sherratt, 2014; Yizhaq et al., 2019; Zelnik & Tzuk, 2017) because the transient states have nonperiodic patterns, which makes their interpretation unclear. Automatic classification of the patterns as bare, spots, labyrinths, and elongated spots or rings was based on circularity and patch perimeter (see supporting information for details). The sensitivity of the final states to rainfall and initial water availability is studied, as well as the temporal evolution of selected representative cases.

### 3 RESULTS AND DISCUSSION

#### 3.1 Transient results: The 0.75-mm day⁻¹ case

Figure 1 shows, for the 0.75-mm d⁻¹ rainfall (as an example), the evolution of the key domain-wise integrated (mean-field) ecohydrological signatures. Colours in Figure 1 follow Table 2 and represent each IHC.

Biomass evolution (Figure 1a) for all IHCs asymptotically converge to the same final biomass, except for the cases that result in zero biomass (bare states). Total biomass is nearly steady from the first year onward and is clearly steady by the end of simulations with vegetated final states. Biomass evolution is clearly different early on ($t \lesssim 3$ years), with trajectories describing overshooting and undershooting relative to the final biomass, after which the trajectories quickly converge. Biomass dynamics can be argued to be (too) fast and comparable with the rates of water dynamics—that is, large changes in the first year. It also seems implausible that natural systems might achieve a steady state in such short timescales. This is nonetheless ubiquitous in the VSO modelling literature and has been recognized as a modelling limitation (Guttal & Jayaprakash, 2007; Thompson et al., 2008), arguably related to the simplicity of both the model and the selected parametrization (following common parameters in the literature).

The steady forcing and periodic boundaries, all cases necessarily converge to the same $I/R = 1$ global equilibrium steady state, despite being highly variable at the beginning. The reference case of $h_0 = 18.75$ mm (in black) is the least variable one, showing that the system is initially—and remains always—close to global hydrological equilibrium. Complementarily, more water is accumulated on the surface in bare cases (Figure 1c), which shows that there is more surface water (5%) in the bare steady cases than in vegetated cases (0.02%). Figure 1 also shows that the infiltration ratio, and the surface water ratio vary at significantly different rates across IHC, and that the initial period of IHC dominated water availability (in which the systems is not forced exclusively by rain) lasts roughly one tenth of the time that it is required for the system to restabilise.

This suggests that IHC can have a long period of sustained influence, until eventually the global signatures of the system become independent of it. Importantly, it must be noted that the time at which steady conditions can be said to exist, depends on the observed signature. Figure 1 shows that signatures describe steady behaviour at the end
FIGURE 1  Evolution of global ecohydrological indicators for the 0.75 mm d⁻¹ rainfall case – colours by initial condition [−]: 0.0, 1/64, 1/32, 1/16, 1/8, 1/4, 1/2, 1, 4, 8, 16.
Note the logarithmic timescale

FIGURE 2  Transient vegetation patterns for all initial conditions and 0.75 mm rain – The plots are binary: white shows bare soil, colour represents vegetated (b > 0.2), coded by IHC [−]: 0.0, 1/64, 1/32, 1/16, 1/8, 1/4, 1/2, 1, 2, 4, 8, 16

for all cases, but if biomass or infiltration-rain ratio are taken as the meaningful signatures, the steady states are obtained earlier than if steadiness is evaluated from the surface water ratio. It is important to place this in the context of previous literature, in which total biomass has been used to assess steadiness (e.g. Baudena et al., 2013; Kletter et al., 2009; Thompson et al., 2008) but other signatures might behave differently (we note, however these authors report simulations for simulation times far beyond a few years).
Figure 2 shows the transient patterns for \( r = 0.75 \text{ mm d}^{-1} \) (other rainfall cases can be found as Supporting Information). This case is selected as it shows the widest range of patterns and is strongly sensitive to the IHC. For three IHCs, simulations were performed until \( t = 3,000 \) y. The patterns evolve along different trajectories and at different rates for each IHC, and the evolution supports that the patterns are history dependent as suggested by Sherratt (2013). The driest IHCs \( h_0 \leq 0.58 \text{ mm} \) decay into bare states before three years have elapsed. Slightly wetter IHC \( (1.17 \leq h_0 \leq 2.38 \text{ mm}) \) evolve into transient ring patterns—supporting other modelling evidence (Bonanomi et al., 2014; Fernandez-Oto et al., 2019; Sheffer et al., 2011; Tlidi et al., 2018; Yizhaq et al., 2019)—which slowly break down into spotted, hybrid-spotted and spiral patterns. In the central cases \( (4.68 \leq h_0 \leq 37.5 \text{ mm}) \) the biomass peaks smoothly develop into vegetation spots. The wettest cases \( (75 \leq h_0 \leq 300 \text{ mm}) \) develop into an initially high cover, then break into ring spots or gaps, later developing into labyrinth-like arc structures that either break into spots with anomalies \( (75 \leq h_0 \leq 150 \text{ mm}) \) or into a hybrid pattern \( (h_0 = 300 \text{ mm}) \). It is noteworthy that transient rings always result in hybrid patterns in Figure 2, suggesting that the excitable behaviour leads to a hybrid pattern that is stable under \( r = 0.75 \text{ mm d}^{-1} \) (as bands/spots are stable for such rainfall). However, for a lower rainfall \( r = 0.60 \text{ mm d}^{-1} \) (Figure S3), rings only appear for \( h_0 = 60 \text{ mm} \), and the final pattern is one of strongly periodic circular spots. This suggests that, under a lower rainfall, the ring-generating excitable behaviour then leads into an unstable hybrid pattern that breaks back to a stable classical spotted pattern. That is, excitable behaviour will only have an impact on the long-term asymptotically steady state if the hybrid states are stable.

In order to better assess the pattern trajectories, Figure 3 shows the evolution of several spatial distribution indicators: vegetation cover, number of vegetation patches, and mean patch area for the 0.75-mm-day\(^{-1} \) rainfall (complementary indicators are shown in the supporting information and not here for brevity). Similar to the mean-field indicators (Figure 1), vegetation cover is also highly variable during the early stages and also converges to a common value for all IHC, at a different time than the global ecohydrological signatures in Figure 1. The evolution of the number of patches also shows great variability in the first years and later shows a gradual convergence to a constant number of patches. For some cases, the number of patches is nearly steady early on, but for others, it varies slowly with a decreasing rate for longer times (decades), suggesting that this indicator is asymptotically becoming steady towards the end of the simulations.

The mean patch area shows the complementary behaviour. Comparing Figures 1a and 3a shows that cases with low early biomass yield also have early-on higher vegetation cover. Furthermore, those cases that show higher biomass overshooting exhibit a more intense undershooting of vegetation cover. The reference case \( (h_0 = 18.75 \text{ mm}) \) shows a smooth behaviour on both biomass and cover evolution, with a mild oscillation prior to the asymptotic convergence. Interestingly, the evolution of the \( h_0 = 1.17 \) and 300 mm cases—both of which result in hybrid patterns after experience excitable behaviour—is very similar after the first few months. This symmetry is weaker for the \( h_0 = 2.38 \text{ mm} \) and \( h_0 = 150 \text{ mm} \) cases.

Altogether, from the evolution of the system under different IHC as described by Figures 1, 2, and 3 lead to some insights.

1. A new set of patterns emerges in response to the IHC gradient. There is a clear and symmetric transition from periodic patterns of spots \( (h_0 = 18.75 \text{ mm}) \) into hybrid patterns (Meron, 2012; Zelnik et al., 2015) in which the periodicity is broken. As the IHC go further away from equilibrium, the periodic spots grow larger \( (h_0 = \{4.68, 9.38, 37.5 \text{ mm}\}) \) and eventually exhibit a hybrid pattern of spots with anomalies \( (h_0 = 75 \text{ mm}) \) and transition into hybrid patterns consisting of spots, arcs, spirals, and rings \( (h_0 = \{1.17, 300 \text{ mm}\}) \). Patterns resulting in rather classical periodic patterns \( (e.g., 4.68 \leq h_0 \leq 150 \text{ mm}) \) are the consequence of the well-establish Turing instability mechanism of pattern generation (Meron, 2015). The new hybrid patterns \( (e.g., h_0 = \{1.17, 2.38, 300 \text{ mm}\}) \) for \( r = 0.75 \text{ mm day}^{-1} \), and \( h_0 = 60 \text{ mm} \) for \( r = 0.60 \text{ mm day}^{-1} \) are likely the result not of Turing instability but of excitable behaviour (Fernandez-Oto et al., 2019; Meron, 1992; Tlidi et al., 2018). Excitable behaviour means that a small perturbation or stimulus—that is, the IHC—can generate a strong and propagating response throughout the system and is a phenomenon typical of systems far from equilibrium (Lindner, García-Ojalvo, Neiman, & Schimansky-Geier, 2004).

2. The patterns remain transient after \( t \approx 100 \) years and even by \( t = 3,000 \) years for all IHCs including plantless equilibrium. The rate of change of these patterns significantly slows down after the first 50 years, and the convergence rate depends on the IHC. The small differences may go unnoticed when comparing patterns 5 years apart (see supporting information). These long transients show that global signatures can be steady much faster than the patterns themselves, meaning that spatial reorganization is long lasting despite that the overall productivity of the system.
is established earlier. This must be understood in the context of 2-D domains without environmental heterogeneity. Under 1-D models, these transients have been reported to be shorter, and the presence of underlying heterogeneity capable of breaking symmetry may lock the patterns faster (Zelnik & Meron, 2018).

3. The hybrid patterns are stable, despite remaining transient. The rates of change inferred from the hybrid patterns and their spatial indicators are as low as the periodic patterns obtained from equilibrium IHC. Quantitative pattern indicators, such as number of patches and mean patch area, are quite constant for all cases after 150 years, suggesting that the pattern properties are locked in. This implies that there is no indication that the hybrid patterns may be converging to periodic patterns generated by the near-equilibrium IHC. There is no clear theoretical reasoning indicating that the pattern evolution should shift trajectory to converge the hybrid patterns into the periodic patterns obtained from equilibrium IHC, as the trajectories in the phase space have fallen into an attractor (see supporting information). Although, without explicitly computing for longer times, it cannot be empirically ruled out that an extremely long evolution of the pattern will lead to spotted patterns; the point holds in that long term, stable hybrid patterns are a consequence of certain IHCs. The stable hybrid patterns are likely to be related to homoclinic snaking that results in hybrid patterns (Zelnik et al., 2013), contrary to ring patterns that are inherently transient and not a form of homoclinic snaking (Sheffer et al., 2011).

4. Ring patterns can emerge as part of far-from-equilibrium trajectories triggered by nonequilibrium IHC, extending upon previously identified possible causes such as parametrization (Gilad et al., 2007) and rainfall (Sheffer et al., 2011). Furthermore, we show transient ring patterns emerging in the Rietkerk model, without a root-augmentation feedback present in previously reported ring structures (e.g., Sheffer et al., 2011; Meron, 2016) or other non-hydraulic nonlocal effects (Sheffer et al., 2011; Tlidi et al., 2018; Yizhaq et al., 2019). Nonequilibrium IHC may be viewed as a single pulsed event and therefore these results support that rainfall variability favours ring formation, through a surface water redistribution mechanism (Sheffer et al., 2011; Yizhaq et al., 2019). These observations support and extend the current modelling-based understanding of ring patterns, as (to the authors’ knowledge) the transient nature of rings has still not been clearly shown empirically in field observations.
3.2 Final state indicators and signatures for all cases

In this section, the final state results for all rainfalls are summarized and assessed. Figure 4 shows vegetation patterns at time \( t = 200 \) years for all simulations. The IHC gradient results in different patterns for the same rainfall. Bistability (fully bare/vegetated) can be observed along the IHC gradient for some cases, whereas others are always either bare or vegetated regardless of IHC. For higher rainfalls, symmetry can be observed in the final patterns’ response to IHC. The IHC gradient spawns a gradient of patterns from bare (very low IHC) into hybrid patterns (low IHC), followed by periodic large spots, which become smaller towards equilibrium IHC. Wetter IHCs result in larger spots and hybrid patterns in a symmetric fashion. The IHC-induced transition is strongest for the 0.75-mm day\(^{-1}\) rainfall. The 0.60-mm day\(^{-1}\) case allows only for a transition in spot size and exhibits no hybrid patterns. For the 0.85-mm day\(^{-1}\) case, it exhibits hybrid patterns of spirals and spots towards the extremes of the IHC gradient. For 1.0 mm day\(^{-1}\), the patterns also differ, but the pattern structure remains much more similar. The symmetry along the IHC gradient also manifests in that bare steady states can be obtained for both very dry low and very wet IHC, that is, the relation between IHC and long-term productivity is nonmonotone. This is a novel observation in VSO, which is the result of the different system trajectories spawning from far-from-equilibrium IHC. The patterns vary along the rainfall gradient consistently with the literature along the equilibrium cases (spots to labyrinths with increasing rainfall). Nonetheless, for nonequilibrium cases (e.g., 1/16), because of the hybrid patterns, the well-established variation following rainfall does not hold. Additionally, note that ring structures are not present in the final patterns in Figure 4, although they are present in the transient states (e.g., Figures 2, S3, and S4).

Figure 5 shows mean-field indicators as a function of IHC. Figure 5a confirms and extends the convergence of final biomass shown in Figure 1a, that is, for a given rainfall, the final total biomass is either 0 or practically a constant biomass insensitive to IHC. This signals that total productivity of the system is strongly dependent on rainfall but not on the transient deriving from the IHC. The same is true for vegetation cover and mean vegetated density. High rainfall cases are strongly insensitive to the IHC, and the low rainfall cases show a very small sensitivity. The bistability behaviour along the IHC axis can be very clearly appreciated in Figure 5 in terms of bare versus vegetated states. Mean biomass density in vegetated areas (Figure 5c) is the only mean-field indicator showing clear sensitivity to the IHC and is consistent with the sensitivity of the spatial indicators, though much smaller in magnitude (note the narrow density range). Total biomass and vegetation cover strongly respond to rainfall, as is well known.

Figure 6 summarizes quantitative indicators describing the final state patterns \( (t = 200 \) years). Additional spatial indicators are included in the supporting information. Contrary to the mean field indicators in Figure 5, these spatial pattern indicators in Figure 6 are strongly sensitive to the IHC, especially for low and intermediate rainfalls. For a given rainfall, the number of patches dependency on IHC describes a nonmonotone behaviour, that is, a maximum number of patches are obtained for some intermediate IHC—remarkably, coinciding with plantless equilibrium or very close to it. Complementarily, a similar number of patches are obtained for significantly different IHC; for example, for \( r = 0.75 \) mm day\(^{-1}\), the number of patches for the 1.17 mm (1/16) and the 300 mm (16) cases is similar. These two hybrid patterns also behave similarly in terms of area and ratio.

Figure 6 also shows that the final number of patches depends both on total rainfall and IHC, in contrast to the mean field variables (Figure 5) that only depend on rainfall. This interesting behaviour has some theoretical underpinnings as discussed by Meron (2015) who found, using a model equation for pattern formation analysis, that while keeping the same domain-wise average value of a state variable, different patterns may arise depending on initial conditions. In the results here, the cases resulting in a higher number of patches result in smaller patches (smaller area) that are clustered closer to each other (smaller separation), both along the rainfall and the IHC gradients. Labyrinth patterns \( (r = 1.00 \) mm day\(^{-1}\)) are characterized by a few large patches with a high area–perimeter ratio and high perimeter. Spot patterns are comprised of a variable number of small patches with high circularity and low area–perimeter ratios. The new hybrid patterns are characterized by a mix of spots, spirals, and labyrinth-like patches, with fewer and larger patches with a high area–perimeter ratio and lower circularity than spots. For spot-pattern rainfalls, the plantless-equilibrium IHC results in patterns with the highest number of patches of smallest area and area–perimeter ratio and highest circularity.

The quantitative indicators of Figure 6 contain information on the sensitivity of the patterns to the IHC, which appears to depend on rainfall. The 0.5-mm day\(^{-1}\) rainfall only results in a vegetated state for 12.5-mm initial water depth; thus, it can be argued that the pattern sensitivity to the IHC cannot be established beyond the bare-vegetated extremes. The next two higher rainfalls (0.6 and 0.75 mm day\(^{-1}\)) show a growing sensitivity, that is, a wider range of number of patches in response to different IHC are obtained for vegetated states. Higher
rainsfalls (0.85 and 1.0 mm day\(^{-1}\)) are progressively less sensitive to the IHC. This suggests that there is an intermediate range of total rainfall over which the IHC may have a long-term impact on VSO. This may explain why Guttal and Jayaprakash (2007) did not observe a dependency on the IHC.

4 | SUMMARY AND CONCLUSIONS

The results of the study allow the formulation of the following conclusions regarding the posed research questions, as well as additional insights and implications:

1. Initial water availability can have an important impact in VSO phenomena and can contribute to determine the long-term stable patterns. This is supported by an extended set of stable, yet still transient (with extremely low rates of change) patterns generated by different initial surface water, for the same rainfall (commonly accepted as the most relevant environmental driver). Very dry and very wet initial conditions can result in uniform unvegetated states, whereas the intermediate initial surface water conditions result in vegetated patterns, which range from periodic spots to hybrid patterns containing bands, spots, and spirals. The sensitivity of the VSO to the initial conditions is nonmonotonic with respect to the rainfall gradient: rainy systems are less sensitive, arid systems are essentially bare, but intermediate rainfalls result in VSO that can be strongly sensitive to IHC. Moreover, simulations show that VSO is history dependent (trajectory dependent), that is, different IHC spawn different trajectories and thus resulting patterns. This suggests that transient states and trajectories cannot be neglected to explain why such pattern is established, further supporting recent modelling insights (Sherratt, 2013, 2016). Some of the simulated trajectories are the result of excitable behaviour, signalling that rainfall “disturbances” could have a similar effect. This also implies that the temporal variability of water availability—that is, rainfall variability—cannot be neglected when attempting to understand VSO in semiarid regions. Furthermore, history dependency and the diversity of transient states and trajectories of different duration are highly relevant to the issue of unclear timescales for ecohydrological transitions (Hastings, 2010; Konings, Dekker, Rietkerk, & Katul, 2011; Zelnik et al., 2013; Karsenberg et al., 2017). If state transitions are to be properly understood, and their rates and characteristic times well represented, this study suggests that both a better assessment and treatment of IHC is necessary and that the transient dynamics still require significant study. Theoretical reasoning and observations in broader ecohydrological settings, which also highlight the need for better transient understanding and assessing nonequilibrium dynamics (Larsen et al., 2016; Ratajczak et al., 2017), are concurrent with this conclusion.

2. Spatial features of the patterns can be dependent on initial hydrological conditions. However mean-field signatures such as total biomass yield, vegetation cover, and hydrological partitioning still converge either to bare states or to the same vegetated steady state for different IHCs for a given rainfall. This implies that mean-field estimations of biomass and cover on the basis of total rainfall are history independent and that they are robust relative to the IHC. However, total rainfall alone is not a robust predictor of the spatial distribution of such biomass.

3. The study also raises interesting questions on how to define or assess if an ecohydrological system (in the semiarid VSO context) has reached a steady state. Mean-field (global) signatures can achieve steady states quickly in contrast to spatial patterns and their indicators, which can exhibit transient behaviour long after the mean-field indicators suggest a steady state. This implies that mean-field signatures are insufficient to assess steadiness, and spatial patterns and indicators are a necessary complement, complementing recent insights arising in broader studies (Bastiaansen et al., 2018). How relevant this is for particular natural ecohydrological systems is difficult to assess given that—as eloquently stated by Puigdefábregas (1998)—the variable forcing keeps the systems in a quasipermanent transient condition. Although this is of course a modelling study, practical implications for field observations exist, as systems that may seem steady in terms of vegetation cover, normalized difference vegetation index, or evaporation estimations might still be experiencing transient spatial reorganization. In part, due to this ambiguous definition for steadiness, but also due to the clear transient nature of VSO and its dependency on initial conditions, this study strongly shows that transient dynamics require much more attention than they have been given.

4. The ubiquitous assumption of IHC near equilibrium—in particular, satisfying plantless equilibrium, a condition for which total rainfall and total infiltration are instantaneously equal (\(I/R = 1\))—results in an incomplete understanding of the systems dynamics, as such set-up always results in the smoothest, most stable, and fastest converging trajectory, which always results on global hydrological equilibrium \(I/R = 1\). Nonetheless, this global hydrological equilibrium \(I/R = 1\) occurs one or more times prior to the steady state (see Figure S8 for additional evidence), showing that such conditions can be satisfied under multiple states of the system. This in turn suggests that widely used “plantless equilibrium” initial conditions, on the basis of the \(I/R = 1\) construct, are simply one of many possible global hydrological equilibrium states (which may lead to different trajectories). Setting IHC as “plantless equilibrium,” a vegetation-disturbed global hydrological equilibrium may be convenient (because the system converges faster to an asymptotic steady state) but seems to be a rather arbitrary choice, as it is not a unique state. Moreover, far-from-equilibrium IHCs result in a new set of hybrid patterns and characteristically different rates of change and temporal scales of the response of the system, implying that generalizing modelling results based exclusively on near-equilibrium conditions may not be straightforward.

5. Methodologically, our analysis shows the relevance of studying both ecological and hydrological signatures and quantitative spatial indicators because together they allow for a much better understanding of the underlying dynamics. It further highlights that vegetation patterns coexist with hidden hydro-soil patterns as the feedback theory implies. Moreover, quantifying pattern properties and their temporal evolution allows to objectively assess the degree of transientness of the system. A detailed quantitative assessment of the patterns can reveal persisting, very low rate transient evolution that is not observable in the mean-field signa-
tures, also suggesting significantly longer transients than shown by mean-field signatures. In light of this, how researchers assess (and have assessed) the steadiness of systems, especially those for which dynamics and states are far from equilibrium, is evermore significant. Our selection of spatial indicators could be enriched by the use of other indicators classically used for periodic patterns, such as wavelength (Dagbovie & Sherratt, 2014; Zelnik et al., 2013), amplitudes and frequencies of Fourier decompositions (Deblauwe et al., 2011; Yizhaq & Bel, 2016), and the ring index (Sheffer et al., 2011). A complete study of how these metrics behave is out of the scope of this work but may provide further insights.

The main limitation of our study is that the conclusions are model based and cannot be blindly extrapolated into natural reality. The main reason is that the resulting temporal scales and rates are too short and too fast compared with natural systems for several reasons. First, the interpretation of what the IHC mean in natural systems is difficult and which IHC actually can be expected is not well defined. Second, some sources of complexity have not been considered (e.g., rainfall variability and heterogeneity). Third, the accepted parametrization has only accounted for steady state, qualitative, pattern-matching validation (Bastiaansen et al., 2018; Bokulich, 2014), therefore not guaranteeing correctly reproducing rates. It may be that alternative parametrizations, accounting for different physiological rates of vegetation, may affect these results (see supporting information for a minimal example). It remains open to explore if the trajectories observed in this work can be generalized to other parametrizations or under which conditions these behaviours are likely to occur or not. Nonetheless, this study sheds some light on these issues. The interpretation of the systems’ response to an arbitrary IHC can be understood as the transient response of the ecohydro system to a discrete hydrometeorological event. Therefore, the magnitude of rainfall events, which may trigger colonization processes in natural systems, may determine the resulting pattern to the same extent—or even more—than annual rainfall. Semiarid regions do not exhibit constant, steady precipitation but rather a highly pulsed and intermittent rainfall regime (Modarres & de Paulo Rodrigues da Silva, 2007; Dunkerley, 2018; Pilgrim, Chapman, & Doran, 1988). This work points out that each of those pulsed events may act as a new initial condition, which triggers a new transient process whose final steady state may be determined by the magnitude of the event together with yearly rainfall, as suggested by Ratajczak et al. (2017) and Schwinning and Sala (2004). In light of this, the challenge of accurately modelling water redistribution in response to such pulsed events, and analysing the resulting transient signals, is all the more relevant. This may prove essential to reproducing rates and timescales of natural responses to hydrometeorological events, which are not as dramatic as the modelling results suggest.

An interesting question relating to the resilience of systems with patterns rising from nonequilibrium and far-from-equilibrium initial conditions is hinted by this study. The new set of hybrid patterns, qualitatively and quantitatively different from those spanning from near-equilibrium trajectories, allows to ask if their stability (in terms of resilience and resistance) to environmental perturbations (e.g., drought and climate change) or disturbances (e.g., grazing and fires) might be different from patterns generated by near-equilibrium initial conditions for which stability and resilience have been extensively studied along rainfall gradients. The literature shows that resilience is sensitive to the spatial structure of vegetation (Rietkerk et al., 2004; von Hardenberg et al., 2001; Baudena et al., 2013; Realpe-Gomez et al., 2013); particular patterns, for example, spots, have also been identified to favour facilitation over other patterns that favour resilience, for example, bands (Gilad et al., 2007), and nonperiodic patterns induced by heterogeneity have been noted to be more resilient (Yizhaq & Bel, 2016). The diversity of patterns reported warrants to explore their stability, as it may behave differently from periodic patterns, and also suggest that not only the spatial structure at any given time may affect resilience but the instantaneous trajectory and the ongoing rate of change at the time of disturbance may also play a role. Alternatively, by not assuming that VSO ecohydro systems are steady, it becomes natural to ask if particular trajectories are more or less prone to be affected by environmental changes.

ACKNOWLEDGEMENTS

The first author is very grateful to Dr. Yolanda Pueyo (IPE - CSIC, Spain) for countless, deep, and motivational discussions on these issues. The authors also thank Dr. Yuval Zelnik for his insightful comments and review. The authors also acknowledge the anonymous reviewers who contributed greatly to sharpening and strengthening the paper.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data were used in this study. All parameters required for simulation reproducibility are reported.

ORCID

Daniel Caviedes-Voullième https://orcid.org/0000-0001-7871-7544
Christoph Hinz https://orcid.org/0000-0003-0691-7402

REFERENCES

Addor, N., Nearing, G., Prieto, C., Newman, A. J., Vine, N. L., & Clark, M. P. (2018). A ranking of hydrological signatures based on their predictability in space. Water Resources Research, 54(11), 8792–8812.
Arnold, J.-F., Bideault, A., Loreau, M., & Haegeman, B. (2018). How ecosystems recover from pulse perturbations: A theory of short- to long-term responses. Journal of Theoretical Biology, 436, 79–92.
Arnold, J.-F., Loreau, M., & Haegeman, B. (2016). Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. Journal of Theoretical Biology, 389, 47–59.
Barbier, N., Couteron, P., Lejoly, J., Deblauwe, V., & Lejeune, O. (2006). Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. Journal of Ecology, 94(3), 537–547. https://doi.org/10.1111/j.1365-2745.2006.01126.x
Bastiaansen, R., Jaibi, O., Deblauwe, V., Eppinga, M. B., Siteur, K., Siero, E., ..., & Rietkerk, M. (2018). Multistability of model and real dryland ecosystems through spatial self-organization. Proceedings of the National Academy of Sciences, 115(44), 11,256–11,261.
Baudena, M., Boni, G., Ferraris, L., von Hardenberg, J., & Provenzale, A. (2007). Vegetation response to rainfall intermittency in drylands: Results from a simple ecohydrological box model. Advances in Water Resources, 30(5), 1320–1328. https://doi.org/10.1016/j.advwatres.2006.11.006

Baudena, M., & Rietkerk, M. (2012). Complexity and coexistence in a simple spatial model for arid savanna ecosystems. Theoretical Ecology, 6(2), 131–141. https://doi.org/10.1007/s12080-012-0165-1

Baudena, M., von Hardenberg, J., & Provenzale, A. (2013). Vegetation patterns and soil–atmosphere water fluxes in drylands. Advances in Water Resources, 53, 131–138. https://doi.org/10.1016/j.advwatres.2012.10.013

Bokuilch, A. (2014). How the tiger bush got its stripes: ‘How possibly’ vs. ‘how actually’ model explanations. Monist, 97(3), 321–338.

Bonanomi, G., Incerti, G., Stinca, A., Cartenì, F., Giannino, F., & Mazzoleni, S. (2014). Ring formation in clonal plants. Community Ecology, 15(1), 77–86.

Borgogno, F., D’Odorico, P., Laio, F., & Ridolfi, L. (2009). Mathematical models of vegetation pattern formation in ecohydrology. Reviews of Geophysics, 47(1). https://doi.org/10.1029/2007RG000256

D’Odorico, P., Laio, F., & Ridolfi, L. (2005). Noise-induced stability in dryland plant ecosystems. Proceedings of the National Academy of Sciences, 102(13), 10,819–10,822. https://doi.org/10.1073/pnas.0502884102

Dagbovie, A. S., & Sherratt, J. A. (2014). Pattern selection and hysteresis in the Rietkerk model for banded vegetation in semi-arid environments. Journal of The Royal Society Interface, 11(99), 20140465. https://doi.org/10.1098/rsif.2014.0465

Deblauwe, V., Barbier, N., Coutron, P., Lejeune, O., & Bogaert, J. (2008). The global biogeography of semi-arid periodic vegetation patterns. Global Ecology and Biogeography, 17(6), 715–723. https://doi.org/10.1111/j.1466-8238.2008.00413.x

Deblauwe, V., Coutron, P., Lejeune, O., Bogaert, J., & Barbier, N. (2011). Environmental modulation of self-organized periodic vegetation patterns in sudan. Ecography, 34(6), 990–1001. https://doi.org/10.1111/j.1600-0587.2010.06694.x

Dunkerley, D. (2002jun). Infiltration rates and soil moisture in a groved landscape. Journal of Geophysical Research, 107(D), 4103. https://doi.org/10.1029/2001JD001031

Dunkerley, D. (2002). How the tiger bush got its stripes: ‘How possibly’ vs. ‘how actually’ model explanations. Monist, 97(3), 321–338.

Bonanomi, G., Incerti, G., Stinca, A., Cartenì, F., Giannino, F., & Mazzoleni, S. (2014). Ring formation in clonal plants. Community Ecology, 15(1), 77–86.

Borgogno, F., D’Odorico, P., Laio, F., & Ridolfi, L. (2009). Mathematical models of vegetation pattern formation in ecohydrology. Reviews of Geophysics, 47(1). https://doi.org/10.1029/2007RG000256

D’Odorico, P., Laio, F., & Ridolfi, L. (2005). Noise-induced stability in dryland plant ecosystems. Proceedings of the National Academy of Sciences, 102(13), 10,819–10,822. https://doi.org/10.1073/pnas.0502884102

Dagbovie, A. S., & Sherratt, J. A. (2014). Pattern selection and hysteresis in the Rietkerk model for banded vegetation in semi-arid environments. Journal of The Royal Society Interface, 11(99), 20140465. https://doi.org/10.1098/rsif.2014.0465

Deblauwe, V., Barbier, N., Coutron, P., Lejeune, O., & Bogaert, J. (2008). The global biogeography of semi-arid periodic vegetation patterns. Global Ecology and Biogeography, 17(6), 715–723. https://doi.org/10.1111/j.1466-8238.2008.00413.x

Deblauwe, V., Coutron, P., Lejeune, O., Bogaert, J., & Barbier, N. (2011). Environmental modulation of self-organized periodic vegetation patterns in sudan. Ecography, 34(6), 990–1001. https://doi.org/10.1111/j.1600-0587.2010.06694.x

Dunkerley, D. (2002). How the tiger bush got its stripes: ‘How possibly’ vs. ‘how actually’ model explanations. Monist, 97(3), 321–338.

Bonanomi, G., Incerti, G., Stinca, A., Cartenì, F., Giannino, F., & Mazzoleni, S. (2014). Ring formation in clonal plants. Community Ecology, 15(1), 77–86.

Borgogno, F., D’Odorico, P., Laio, F., & Ridolfi, L. (2009). Mathematical models of vegetation pattern formation in ecohydrology. Reviews of Geophysics, 47(1). https://doi.org/10.1029/2007RG000256

D’Odorico, P., Laio, F., & Ridolfi, L. (2005). Noise-induced stability in dryland plant ecosystems. Proceedings of the National Academy of Sciences, 102(13), 10,819–10,822. https://doi.org/10.1073/pnas.0502884102

Dagbovie, A. S., & Sherratt, J. A. (2014). Pattern selection and hysteresis in the Rietkerk model for banded vegetation in semi-arid environments. Journal of The Royal Society Interface, 11(99), 20140465. https://doi.org/10.1098/rsif.2014.0465

Deblauwe, V., Barbier, N., Coutron, P., Lejeune, O., & Bogaert, J. (2008). The global biogeography of semi-arid periodic vegetation patterns. Global Ecology and Biogeography, 17(6), 715–723. https://doi.org/10.1111/j.1466-8238.2008.00413.x

Deblauwe, V., Coutron, P., Lejeune, O., Bogaert, J., & Barbier, N. (2011). Environmental modulation of self-organized periodic vegetation patterns in sudan. Ecography, 34(6), 990–1001. https://doi.org/10.1111/j.1600-0587.2010.06694.x

Dunkerley, D. (2002). How the tiger bush got its stripes: ‘How possibly’ vs. ‘how actually’ model explanations. Monist, 97(3), 321–338.

Bonanomi, G., Incerti, G., Stinca, A., Cartenì, F., Giannino, F., & Mazzoleni, S. (2014). Ring formation in clonal plants. Community Ecology, 15(1), 77–86.

Borgogno, F., D’Odorico, P., Laio, F., & Ridolfi, L. (2009). Mathematical models of vegetation pattern formation in ecohydrology. Reviews of Geophysics, 47(1). https://doi.org/10.1029/2007RG000256

D’Odorico, P., Laio, F., & Ridolfi, L. (2005). Noise-induced stability in dryland plant ecosystems. Proceedings of the National Academy of Sciences, 102(13), 10,819–10,822. https://doi.org/10.1073/pnas.0502884102

Dagbovie, A. S., & Sherratt, J. A. (2014). Pattern selection and hysteresis in the Rietkerk model for banded vegetation in semi-arid environments. Journal of The Royal Society Interface, 11(99), 20140465. https://doi.org/10.1098/rsif.2014.0465
Zelnik, Y. R., & Meron, E. (2018). Regime shifts by front dynamics. Ecological Indicators, 94, 544–552.

Zelnik, Y. R., Meron, E., & Bel, G. (2015). Gradual regime shifts in fairy circles. Proceedings of the National Academy of Sciences, 112(40), 12,327–12,331.

Zelnik, Y. R., & Tzuk, O. (2017). Wavelength selection beyond turing. The European Physical Journal Special Topics, 226(9), 2171–2184.

Zeng, X., Shen, S. S. P., Zeng, X., & Dickinson, R. E. (2004). Multiple equilibrium states and the abrupt transitions in a dynamical system of soil water interacting with vegetation. Geophysical Research Letters, 31(5), L05501. https://doi.org/10.1029/2003GL018910

Zhao, X.-X., & Wang, J.-Z. (2014). Rich spatiotemporal dynamics of a vegetation model with noise and periodic forcing. Discrete Dynamics in Nature and Society, 2014, 218053. https://doi.org/10.1155/2014/218053

How to cite this article: Caviedes-Voulliéme D, Hinz C. From nonequilibrium initial conditions to steady dryland vegetation patterns: How trajectories matter. Ecohydrology. 2020;13:e2199. https://doi.org/10.1002/eco.2199

How to cite this article: Caviedes-Voulliéme D, Hinz C. From nonequilibrium initial conditions to steady dryland vegetation patterns: How trajectories matter. Ecohydrology. 2020;13:e2199. https://doi.org/10.1002/eco.2199

Zelnik, Y. R., & Meron, E. (2018). Regime shifts by front dynamics. Ecological Indicators, 94, 544–552.

Zelnik, Y. R., Meron, E., & Bel, G. (2015). Gradual regime shifts in fairy circles. Proceedings of the National Academy of Sciences, 112(40), 12,327–12,331.

Zelnik, Y. R., & Tzuk, O. (2017). Wavelength selection beyond turing. The European Physical Journal Special Topics, 226(9), 2171–2184.

Zeng, X., Shen, S. S. P., Zeng, X., & Dickinson, R. E. (2004). Multiple equilibrium states and the abrupt transitions in a dynamical system of soil water interacting with vegetation. Geophysical Research Letters, 31(5), L05501. https://doi.org/10.1029/2003GL018910

Zhao, X.-X., & Wang, J.-Z. (2014). Rich spatiotemporal dynamics of a vegetation model with noise and periodic forcing. Discrete Dynamics in Nature and Society, 2014, 218053. https://doi.org/10.1155/2014/218053

How to cite this article: Caviedes-Voulliéme D, Hinz C. From nonequilibrium initial conditions to steady dryland vegetation patterns: How trajectories matter. Ecohydrology. 2020;13:e2199. https://doi.org/10.1002/eco.2199

Zelnik, Y. R., & Meron, E. (2018). Regime shifts by front dynamics. Ecological Indicators, 94, 544–552.