INVESTIGATING THE MORPHOLOGICAL DYNAMICS OF VEGETATION PATTERNS IN SEMIARID AREAS: A THEORETICAL AND EMPIRICAL STUDY OF ECOSYSTEM BISTABILITY

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And approved by

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ABSTRACT OF THE THESIS

Investigating the Morphological Dynamics of Vegetation Patterns in Semiarid Areas: A Theoretical and Empirical Study of Ecosystem Bistability

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Dryland ecosystems are vulnerable to desertification, which is a pressing issue in the face of global climate change. In these ecosystems, vegetation often grows in spatially periodic patterns that differ as aridity increases (clumps, labyrinths and gaps), which has been widely studied theoretically to better understand how close the system is to reach the point of desertification. Most theoretical models, however, also predict bistability close to the ecological transition. Bistability adds to the challenges posed by desertification, since environmental fluctuations can make the system switch between two states (here, desert and vegetated states) that are stable for a given environmental condition. Although studies have investigated how to identify whether the system is approaching desertification, none of the existing methods can indicate the presence of bistability. In our study, we combined empirical and theoretical methods to investigate whether there exist early-warning indicators of bistability. Specifically, we found that the morphology of the vegetation pattern, and how it changes with aridity, provide two reliable indicators of bistability and an impending desertification transition. Our approach is simple and accessible with existing data, and therefore can potentially be applied to a diversity of systems to inform future management strategies.
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Introduction

Desertification is an ecological transition that, with the irreversible result of dryland degradation, affects 41% of land cover and about 250 million people globally (Kassas, 1995; Reynolds, 2007; Weissmann and Shnerb, 2014). In dryland ecosystems, vegetation provides vital ecosystem services, including preventing soil erosion, maintaining biodiversity, and water conservation (Vidal-Abarca Gutiérrez et al., 2021). Unfortunately, semi-arid ecosystems are particularly vulnerable to land degradation compared to other types of ecosystems (Montanarella, 2018). Water scarcity is a significant challenge in these regions, and it can exacerbate land degradation due to external pressures such as overgrazing, climate change, and urbanization (Scholes, 2020). Therefore, it is essential to focus on vegetation conservation and management in dryland ecosystems to restore ecosystem function. Protecting native vegetation cover as aridity levels change can help maintain these vital ecosystem services, supporting local production and economic well-being in dryland ecosystems (Guillen-Cruz et al., 2021).

In arid and semi-arid ecosystems, where the average precipitation only meets less than 50% of potential plant water demand, the temporal and spatial variations of vegetation are highly influenced by water availability (Snyder and Tartowski, 2006). In these water-scarce environments, water becomes the main growth-limiting resource which induces plant competition; on the other hand, vegetation patches can also facilitate plant growth as the root systems break soil biocrust thus improving water infiltration, and plant shading contributes to preventing water evaporation (Rietkerk and van de Koppel, 2008). These interacting mechanisms ultimately determine the spatial distribution of
vegetation, which in these ecosystems can arrange spatially in periodic vegetation patterns such as gaps, labyrinths and clumps, all of which have been found globally (Figure 1), from Africa to Australia, South and North America, and Asia (Deblauwe et al., 2008; Borgogno et al., 2009).

**Figure 1**: Vegetation patterns in Africa and Australia. Panel (a) and (b) are stripe and labyrinth patterns in Kordofan, Sudan. Panel (c) shows a spot pattern in Zambia. Panel (d) shows vegetation gaps in Newman (Australia).

A large body of literature has successfully reproduced the three types of vegetation patterns in arid/semi-arid ecosystem by invoking Turing(-like) instabilities and implementing mathematical reaction-diffusion(advection) models (Klausmeier, 1999; HilleRisLambers et al., 2001; von Hardenberg et al., 2001; Lejeune, 2002; Okayasu and
Aizawa, 2001; Rietkerk et al., 2002; Gilad, 2004; Ursino, 2005, 2007). By examining the behavior of two diffusible chemical substances, Alan Turing proposed a reaction-diffusion model in 1952 to explain the mechanism of spatially periodic patterning in nature, whereby substances with different diffusivity (i.e., moving at different speeds in no particular direction) that interact as inhibitors or activators produce periodic patterns. In the absence of diffusion, if the inhibitor diffuses faster than the activator, a long-range negative feedback and short-range positive feedback emerge over time. The initial system becomes unstable to perturbations, and eventually reaches a stationary periodic spatial pattern (phenomena known as “Turing instability” and “Turing patterns”, respectively) (Turing, 1952). This scale-dependent feedback mechanism has provided a theoretical explanation for the self-organized vegetation patterns in dryland ecosystems (Rietkerk and van de Koppel, 2008; Meron, 2012), where water limitation inhibits plant growth in the long range and the plant assemblages facilitate water usage locally (e.g., increased infiltration, shading that reduces water evaporation). These mathematical models successfully simulate the sequence of vegetation patterns as rainfall decreases: gaps, labyrinths, and clumps (Figure 2).
**Figure 2:** Sequence of vegetation patterns with decreasing rainfall level (i.e., increasing aridity). Panels (a), (b) and (c) are gap, labyrinth, and clump patterns respectively, with decreasing rainfall levels indicated by the blue arrow.

Clumped vegetation patterns emerge for the driest condition, which in models ultimately leads to desertification if rainfall keeps decreasing (Deblauwe et al. 2011) (Figure 2(c) and Figure 3(b)). However, whether the predicted desertification transition is continuous or discontinuous depends on the details of the model (Martinez-Garcia et al., 2023; Klausmeier, 1999; Von Hardenberg et al., 2001; Rietkerk et al., 2002; Siteur et al., 2014) (Figure 3). The transition from clumps to desert state suggests that the clump patterns can be used as an early-warning signal for desertification (Scheffer et al., 2009; Dakos et al., 2011). If the transition were continuous as some models suggest, vegetation density by itself could also be used as an early-warning indicator of ecosystem degradation and desertification. However, discontinuous transition from vegetation to desert is a more typical prediction of desertification, which predicts an abrupt and potentially catastrophic transition, and the associated bistability and hysteresis would make the transition even more difficult to predict (Figure 3(b)). Hysteresis loops describe the tendency for the system to follow different paths depending on its history (i.e., its...
previous states). In the context of ecosystem transitions, the rainfall levels needed for the system to be restored after desertification (blue point in Fig. 3(b)) would be different from the rainfall levels for which the system became a desert (red points in the figure). In addition, bistability means the system can potentially reach either one of two stable states (or even switch from one to the other) for the same value of the environmental variables (in this case, rainfall range between the red and blue point in Fig. 3(b)), with the outcome decided by the initial states or environmental fluctuations (Lejeune et al., 2002; Lejeune et al. 2004, Meron et al. 2004, Sherratt and Lord 2007; Kéfi et al., 2010). In other words, this bistability would mean that rainfall levels do not unequivocally predict ecosystem state, as the same rainfall levels can eventually lead to either vegetated or desertic states. Thus, determining whether a system is undergoing bistability is crucial for environmental management and conservation.

**Figure 3:** Schematic diagram illustrating different types of vegetation transition in response to changes in rainfall. Panel (a) shows a continuous transition where vegetation density gradually decreases with decreasing rainfall. Panel (b) depicts discontinuous transitions and features a bistability region with simulated patterns. The red dots are the critical transition point, where the system enters the desert state. In panel (b), the vegetation density experiences an abrupt collapse, unlike in panel (a), where it decreases.
gradually toward zero. Also, in panel (b), the system is bistable, and the transition may occur in the rainfall range between the two dashed lines. The blue dots mark the start of the bistability region, and the grey area is the bistability region.

Existing empirical data and theoretical studies provide a variety of methods to identify and monitor ecological transitions, but none of the existing methods can determine whether the system is in the bistability region. The sequence of patterns as rainfall decreases has been proposed as a way to anticipate the desertification transition (Rietkerk et al., 2004). The transition from clumps to desert state suggests that the clump patterns can be used as an early-warning signal for desertification (Scheffer et al., 2009; Dakos et al., 2011). Moreover, the analysis of pattern morphology using Fourier transforms for system snapshots can help characterize different types of patterns and their corresponding environments (e.g., flag whether there exists a typical wavelength of the pattern and thus whether the pattern is periodic) (Deblauwe et al., 2011). The properties of the self-organized regular patterns such as the wavelength of the pattern has been used in model studies to indicate desertification, as the distance between the clumps has been shown to, in some cases, increase as desertification is approached, which could provide insight into pattern changes before the transition (Siteur et al., 2014). However, neither the type of pattern nor its corresponding wavelength signal bistability, since the same clump patterns can be seen in and outside the bistability region (Figure 3(b)), and wavelength changes (when they occur) are not assured in the totality of the bistability region. In addition, the lack of historical satellite imagery makes it difficult to observe changes in vegetation over time and quantify the risk of ecological transition. In addition to satellite imagery, the remote-sensing EVI time-series has been used to investigate the regular vegetation patterns in Sudan (Veldhuis et al., 2022). With this and other remote-
sensing products, the temporal (responsiveness, temporal autocorrelation and variance) and spatial indicators (correlation, skewness and variance) have been used to understand the upcoming transitions, as they behave in characteristic ways as the transition approaches. However, these indicators are not devised to predict bistability but the transition itself. Thus, since bistability occurs for an ample range of environmental conditions different from those of the transition, relying solely on indicators to predict the critical transition may result in overlooking a range of conditions within the potentially hazardous bistability region. For example, critical slowing down (i.e., system takes longer time to recover from small perturbation if the system is close the transition) seems to be a recurrent phenomenon before a critical transition (Dakos et al., 2011). However, this indicator requires local perturbation experiments to test the recovery time of a particular system, which makes the system management limited by time and location and also ignore the potential risk of having bistability for a larger range of system conditions. Due to the technical and conceptual challenges above, research on testing models with remote sensing data to predict and study bistable ecological systems with spatially regular patterns is still limited. (Martinez-Garcia et al., 2023; Bastiaansen et al., 2018; Weissmann et al., 2017; Veldhuis et al., 2021). Here, we aim to fill this gap by analyzing vegetation patterns and their relationship with bistability, using accessible satellite images and a classic model to that end.

In this study, we analyzed pattern morphology from satellite images from a study region in Sudan, and from models tailored to that region, at different rainfall levels to better understand the diversity of resulting vegetation patterns and how that diversity relates to bistability. We parametrized the model using available data for the study area,
and developed a novel approach to calculate key parameters such as plant and water diffusivity, typically qualitatively estimated in the literature. We used Fourier transforms to monitor pattern regularity, and found a previously overlooked feature (a secondary fundamental peak) that can capture the changes in main properties of the vegetation spatial distribution as well as the transition itself. The changes in this peak as rainfall decreased emerged from changes in clump size and number that were unique to the bistability region, which pointed to simple metrics that can be used to characterize an impending transition, identify the bistability region (if it exists), and thus assess the risk of an ecological transition. We tested our predictions by monitoring the change of clump size and number for our study area in Sudan, and observed similar pattern behavior to those observed in the bistability region of the model. Thus, according to our results the focal area is within the bistability region, and depicts behavior indicative of an impending desertification transition. Our methodology can help assess the risk of transition by flagging when a system enters the bistability region and thus is susceptible to collapsing. Therefore, our approach can be a valuable tool to assess ecosystem health and design and test management policies accordingly.
Methods

Study area

Our study area is located in the western part of South Kordofan in Sudan (Figure 4(a); 11° 42’ 0"-11° 0’ 0" N, 27° 54’ 0"-28° 0’ 0"E). Soil water holding capacity and soil texture data at a 1 km spatial resolution were derived from the Africa SoilGrids online resources (Leenaars and Hengl, 2015; Leenaars and Hengl, 2017). The slope map was derived from ArcGIS Online at a 25 m spatial resolution (Esri, 2013). Topographically, the area shows an overall slope is 0° (Figure 4(b)); at the effective plant root zone depth, the soil texture of this area is loam and the root zone plant-available water holding capacity ranges between 55 and 83 mm, and the overall slope is 0° (Figures 4(c) and 4(d)). The map data shows that there is no significant difference across the study area in terms of slope and soil properties.

The mean annual precipitation in our study area ranged between 220 and 590 mm over the last three decades (CHIRPS Precipitation Data: 1990-2020). The rainy season, from May to October, brings major precipitation, with a monthly rainfall level that decreases from south to north. As rainfall decreases, vegetation patterns change from gaps to labyrinths to clumps (Figure 5). We picked 14 rainfall pixels on the same longitude (27° 54’ 0"-28° 0’ 0"E), which ranged these different types of patterns. This information justified focusing on rainfall as the main environmental feature driving the observed changes in patterns.
Figure 4: Study area and properties. The study area is shown in panel (a). Panel (b) shows that the study site is flat (0°). Panels (c) and (d) show that soil water-holding capacity and soil texture are similar at the effective plant-root zone depth across the region.
**Figure 5**: Optical satellite image of study area and different patterns across rainfall levels. The blue squares are the rainfall pixels from CHIRPS Precipitation Data (1990-2020). The 1km×1km vegetation patterns on the right are clumps, labyrinths, and gaps (from top to bottom).

**Vegetation species**

We focused on *Acacia mellifera* (Figure 6), a native shrub in semi-arid regions in Africa and western Asia including Sudan (CABI, 2022). *A. mellifera* tend to release their seeds in a small radius around the parent shrub and this aggregated dispersal can result in clump-like aggregated growth consisting of different age groups (Hagos, 2001), and various *A. mellifera* patterns have been reported in Kordofan, Sudan (Wickens and Collier, 1971).
Figure 6: *Acacia mellifera* (Photo by JMK, May 2015)

**Description of the modified Klausmeier model**

The periodic vegetation patterns observed in semiarid ecosystems have been reproduced using models that show short-range positive and long-range negative feedbacks which facilitate and inhibit plant growth, respectively. Here, to represent our system, we chose the generalized version of one of the simplest and earliest models for self-organized vegetation pattern in semi-arid ecosystems, the Klausmeier model (Klausmeier, 1999). The original Klausmeier model depicted water movement using an advection term, which represents water flow downhill. In our case, we replaced the water advection term with a water diffusion term to describe the water movement in a flat region:

\[
\frac{\partial w}{\partial t} = r - lw - vw^2 + D_w \nabla^2 w \quad (1)
\]

\[
\frac{\partial p}{\partial t} = vywp^2 - mp + D_p \nabla^2 p \quad (2)
\]
The model describes the dynamics of water density \((w; \text{kg}_H_2_0 \text{m}^{-2})\) and plant density \((p; \text{kg}_\text{drymass} \text{m}^{-2})\). The first term in Eq. (1) represents precipitation (only water input in this model), which occurs at rate \(r (\text{kg}_H_2_0 \text{m}^{-2} \text{year}^{-1})\). The second and third terms represent, respectively, water loss due to evaporation \(lw\) and plant growth water uptake \(vwp^2\), where \(l \ (\text{year}^{-1})\) is the water loss rate and \(v \ ((\text{kg}_\text{drymass} \text{m}^{-2})^{-2} \text{year}^{-1})\) is the water uptake rate. The last term represents water spatial movement, here encoded as diffusion at a rate \(D_w\) is the diffusion coefficient for water in units of \(\text{m}^2 \text{year}^{-1}\). The first term in Eq. (2) represents plant growth, and considers that plant biomass growth is not only due to the water input, but also benefits from the presence of other plants around (local facilitation), where \(y\) represents the yield of plant biomass per unit water consumed \((\text{kg}_\text{drymass} (\text{kg}_H_2_0)^{-1})\). The second term represents plant natural mortality (at a rate \(m; \ \text{year}^{-1}\)), and is the only cause of plant biomass loss considered here. The last term in the equation represents plant dispersal, which happens at a rate \(D_p \ (\text{m}^2 \text{year}^{-1})\).

**Model parametrization**

Values for the parameters of the model were obtained directly from or calculated using the data available literature in an ecologically meaningful way.

**Vegetation-related parametrization**

Some parameters had clear interpretation. For example, for the yield of plant biomass per unit water consumed \((y)\) we used the assumptions made in the literature for encroacher species \((\text{Terminalia sericea} \text{ and } A. \text{ mellifera})\) of 1500 liter of water consumed to produce 1 kg dry mass (NAU, 2010). In addition, two studies have mentioned the mortality rate of \(A. \text{ mellifera}: \text{Joubert et al. (2013)}\) reported that around 1\% of labeled
seedlings survived after 6 years, which means the probability for A. mellifera seedlings to survive for 6 years is 0.01. Assuming that the survival probability does not change over years, A. mellifera has a 0.46 probability to survive for one year. Thus, the annual mortality probability is 0.54. A later study showed that the mortality rate of mature shrubs over a 35-year period is around 61.3% (Joubert et al., 2017), which means the probability for mature A. mellifera to survive for one year is 0.97, and thus the annual mortality probability equals 0.03. These data provided a range of values for A. mellifera mortality probability ($m$) with 0.03 and 0.54 per year as extremes. The parameter accompanying the water uptake term ($v$), however, had units that are not typical for an uptake rate ($\left( \text{kg}_{\text{dry mass}} \text{m}^{-2} \right)^{-2} \text{year}^{-1}$), and therefore we could not find a value following ecological arguments as above. Instead, we calibrated this parameter to obtain patterns of size similar to that of the focal real-world patterns. Once the rest of parameters were fixed to realistic values, a value of $v = 60$ resulted in patterns with a size comparable to those observed in the study area.

On the other hand, we interpreted diffusivity parameters for plants ($D_p$) as the successful dispersal event for the focal species while considering germination rate and first-year seedling survival rate. There is no literature indicating the specific seed dispersal strategy of A. mellifera, but it has been pointed out that the seeds of A. mellifera disperse over a relatively small distance near their parent plant (Donaldson, 1969). This means that the primary seed dispersal strategy can be barochory, and thus the seed dispersal of A. mellifera would primarily rely on gravity and assisted by wind. The average monthly wind speed in the last two decades for our area of interest was under 5 m/s (FNMOC 10 m Surface Winds, erdlasFnWind10). Moreover, according to the
Beaufort Wind Scale, the sample area has light to gentle breeze, which is unlikely to make a long-distance seed dispersal. Thus, we assumed that the seed dispersal distance outside the canopy equals the radius of the canopy (Figure 7), and calculated the circle of diffusion area based on the schematic diagram for the study of the effect of wind direction on seed dispersal (Hagos, 2002).

![Diagram of canopy and seed dispersal area](image)

**Figure 7:** Schematic diagram showing the *A. mellifera* seed dispersal event.

In this case, we considered the seeds that disperse outside the canopy as a potential successful dispersal event, success that we weighted by the survival probability after a year (and thus establishment probability). On one hand, 14% of *A. mellifera* seeds disperse outside the canopy (Hagos, 2002); on the other hand, the germination rate of *A. mellifera* seeds is around 50-80% (Bein et al. 1996), and the calculated first-year survival rate of seedlings outside the canopy is around 42% (Joubert et al., 2013). Altogether, the maximum plant diffusivity calculated from the data above was 2.4 m² per year (Eq. 3).

\[
D_p = \text{Seed dispersal rate} \times \text{Outside canopy ratio} \times \text{Germination rate} \times \text{Seedling survival rate}
\]  

(3)
**Water-related parametrization**

The water loss rate \((l)\) was obtained by dividing the theoretical water evapotranspiration amount for one year by the yearly water availability (precipitation). We used the Thornthwaite Potential Evapotranspiration equation (Eq. 4) to calculate the theoretical water evapotranspiration for Al Nahud and Muglad, two cities with data collection that overlapped with the study area (Thornthwaite, 1948; Alam et al. 2012).

\[
PET = 16\left(\frac{L}{12}\right)\left(\frac{N}{30}\right)\left(\frac{10T_d}{l}\right)^a
\]  

(4)

\(PET\) is the estimated potential evapotranspiration (mm/month),

\(T_d\) is the average daily temperature (degrees Celsius) of the month,

\(N\) is the number of days in the month,

\(L\) is the average day length (hours) of the month, \(I\) is a heat index which depends on the mean temperature,

and the exponent \(a\) is given by the formula:

\[
a = (6.75 \times 10^{-7})I^3 - (7.71 \times 10^{-5})I^2 + (1.792 \times 10^{-2})I + 0.49239
\]

To calculate PET, we set the averaged day length of the month \((L)\) to 12 hours and the number of days in the month \((N)\) to 30 days. The average daily temperature \((T_d; \) Al Nahud: 27.8 °C; Muglad: 28.5 °C) and precipitation data (1960-1990) for these two cities (Al Nahud: 315 mm; Muglad: 471 mm) were derived from Alam et al. 2012. Based on the average daily temperature and the heat index table (Seed and Malik, 1968), the heat index \(I\) for Al Nahud was 13.49 and for Muglad was 13.94. Therefore, we could calculate the
PET for each city and get the estimated water loss rate by dividing the annual PET to the mean annual precipitation. The estimated water loss rate range was from 3.7 to 5.4 \( \text{year}^{-1} \).

Similar to the plant diffusivity parameter, models for vegetation in arid/semi-arid ecosystems rarely determine water diffusivity \((D_w)\) in an ecologically meaningful way (Sherratt, 2016). To keep the same thoroughness as with the rest of parameters, here we estimated the diffusion of water by assuming that the water is surface water with perfect infiltration, meaning that all of the water is available for the root systems. The estimated range of water diffusivity is calculated by using the classic Manning equation for the velocity of a liquid (Manning, 1891).

\[
V = \frac{1}{n} R^{\frac{2}{3}} S^{\frac{1}{2}}
\]

where \(V\) is the cross-sectional average velocity (m/s),

\(n\) is Manning's Roughness Coefficient for different surface material,

\(R\) is the hydraulic radius (m, see Table 1), and

\(S\) is the slope (elevation difference/section length)

| Section | Area \(A\) | Wetted perimeter \(P_w\) | Hydraulic radius 
\(R = \frac{A}{P_w}\) |
<table>
<thead>
<tr>
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</tr>
</thead>
<tbody>
<tr>
<td><img src="image" alt="Rectangle" /></td>
<td>(B \times h)</td>
<td>(B + 2h)</td>
<td>(\frac{Bh}{B + 2h})</td>
</tr>
</tbody>
</table>

**Table 1**: Chanel section geometry and associated parameters.
To use Eq. (5), we assumed that the intense rainfall during the rainy season creates a very shallow sheet flow with width $B = 1 \text{ m}$ and depth $h = 0.0001 \text{ m}$ in a horizontal area with small local slope (0-0.2%). These two values allowed us to calculate the hydraulic radius for a channel with a given rectangle cross-section (Table 1). For Manning's roughness coefficient, we assumed that the surface material for the shallow sheet flow was similar to a clean and straight natural stream with no rifts or deep pools, which led to a value of 0.03 (Arcement and Schneider, 1989). With this information and a local slope of 0.2%, Eq. (5) resulted in a flow velocity is 0.00321 m/s. Water diffusivity is the result of considering the flow velocity in all directions, which leads to a maximum theoretical water diffusivity when we consider the flow velocity in a circle and convert the units from per second to per year (maximum $D_w$: 1021 $m^2\text{year}^{-1}$).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Biological description</th>
<th>Units</th>
<th>Calculated range</th>
<th>Simulation value</th>
<th>Reference</th>
</tr>
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<tbody>
<tr>
<td>$w$</td>
<td>Water density</td>
<td>$kg_{H_2O} m^{-2}$</td>
<td>variable</td>
<td>variable</td>
<td>-</td>
</tr>
<tr>
<td>$p$</td>
<td>Plant density</td>
<td>$kg m^{-2}$</td>
<td>variable</td>
<td>variable</td>
<td>-</td>
</tr>
<tr>
<td>$r$</td>
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<td>$kg_{H_2O} m^{-2} \text{year}^{-1}$</td>
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<td>431-507</td>
<td>-</td>
</tr>
<tr>
<td>$l$</td>
<td>Water loss rate</td>
<td>$\text{year}^{-1}$</td>
<td>3.7-5.4</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>$v$</td>
<td>Water uptake rate</td>
<td>$(kg_{drymass} m^{-2})^{-2} \text{year}^{-1}$</td>
<td>-</td>
<td>60</td>
<td>-</td>
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<tr>
<td>$y$</td>
<td>Yield of plant biomass per unit water consumed</td>
<td>$kg_{drymass}(kg_{H_2O})^{-1}$</td>
<td>0.00067</td>
<td>0.00067</td>
<td>NAU, 2010</td>
</tr>
<tr>
<td>$m$</td>
<td>Plant mortality rate</td>
<td>$\text{year}^{-1}$</td>
<td>0.03-0.54</td>
<td>0.5</td>
<td>Joubert et al., 2013; Joubert et al., 2017</td>
</tr>
<tr>
<td>$D_w$</td>
<td>Diffusion coefficient for water</td>
<td>$m^2\text{year}^{-1}$</td>
<td>0-1021</td>
<td>170</td>
<td>-</td>
</tr>
<tr>
<td>$D_p$</td>
<td>Diffusion coefficient for plant</td>
<td>$m^2\text{year}^{-1}$</td>
<td>0-2.4</td>
<td>1</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 2: Model Parameters

<table>
<thead>
<tr>
<th>$t$</th>
<th>Time</th>
<th>$year$</th>
<th>variable</th>
<th>variable</th>
<th>-</th>
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</thead>
<tbody>
<tr>
<td>$dN$</td>
<td>Perturbation</td>
<td>$kg m^{-2}$</td>
<td>-</td>
<td>0.7/0.1</td>
<td>-</td>
</tr>
</tbody>
</table>

Analytical calculations

We assumed that the observed patterns correspond to stationary patterns, i.e., patterns that are stable. From a theoretical standpoint, such patterns emerge from stationary states of the model that are stable when considering spatial homogeneity but develop periodic heterogeneities when considering the diffusion of water and vegetation (Turing patterns). Thus, following standard methods, we first calculated the homogeneous stationary states, i.e., the stationary states obtained by setting equations (1) and (2) to zero in the absence of diffusion, and assessed the stability of each stationary state by applying the Routh-Hurwitz criterion. We then checked for which region of the parameter space the stable stationary states became unstable to periodic perturbation (and therefore vegetation patterns emerge).

Model simulation

Our simulations took place in a 250×250 spatial mesh with periodic boundary conditions, to minimize the finite-size and border effects. The model parameters were chosen based on the calculated range and adjust to mimic the size of the patterns observed in Sudan (Table 2). The spatial resolution ($dx$) was 4 meters, and the time resolution ($dt$) is 0.001 year. The value of $dx$ is small enough to resolve motifs with several pixels and large enough to cover a big area, thus allowing for many iterations of the pattern. The value of $dt$ is large enough to capture the dynamics of the system and small enough to avoid the overflow of the simulation calculations. We used the Jacobi
method to discretize the two-dimensional Laplacian because it provides a simple and efficient approach to numerically solving partial differential equations (Jacobi, 1845). For solving the system of differential equations, we used the Euler method due to its simplicity and ease of implementation (Euler, 1768). We used two methods to explore the rainfall ranges observed in the focal area:

1. “Turing method”. This method is reflective of the analytical steps developed after Alan Turing’s seminal work (Turing, 1952). We started simulations at the homogeneous stable state for the specific rainfall value and perturbed randomly chosen locations representing one percent of the system by adding a certain amount of plant biomass (Table 2). We then let the system run 50,000 years for stable patterns to emerge. We also implement this method by replacing the constant rainfall parameter with a stochastic rainfall function generated from the monthly rainfall data, which allows us to resolve seasonality within the focal semi-arid climate. We characterized the rainfall of each pixel: First, we estimated over a 30-year period the medians and interquartile ranges of monthly precipitation, which provided us with a seasonal resolution of rainfall that we fitted to a skewed-Gaussian function. Second, we estimated annual rainfall \( r \) as the sum of the monthly medians from January to December over the 30-year period. The stochastic rainfall data could be described using the skewed-Gaussian function below:

\[
R(M) = r \left( \frac{1}{\sqrt{2\pi\omega^2}} \right) e^{-\frac{(M - \psi)^2}{2\omega^2}} \left( 1 + \text{erf} \left( \frac{\lambda(M - \psi)}{\sqrt{2\omega^2}} \right) \right) \quad (6)
\]

Where \( r \) is annual precipitation rate (mm/year).

\( M \) is the specific month of the year, and \( \omega = 1.8, \psi = 8.8 \) and \( \lambda = -1.5 \). To represent the stochasticity inherent to rainfall, we used a stochastic version of Eq. (6).
Thus, we added to $R(M)$ a random number generated from a normal distribution with mean 0 and standard deviation $0.3R(M)$. This generated a random rainfall value with mean $R(M)$ and standard deviation 30% of the given rainfall. We used these simulations with stochastic rainfall to check whether vegetation patterns changed seasonally or remained stable across seasons.

2. “Natural initial condition method (NIC method)”. This method resembles more closely how rainfall changes may occur in the focal area. We started simulations with the stationary pattern from the previous (fixed) rainfall level, with a simulation time for each rainfall value set to ensure stable patterns. We explored the patterns emerging from sweeping the rainfall axis both from low to high values and from high to low values.

For both methods above, the parameter values remained as in Table 1. For Turing and NIC methods, we ran 20 and 10 replicates, respectively, and stored snapshots of the plant density matrix for further analysis every $5 \times 10^6$ (Turing method) or $1 \times 10^6$ (NIC method) time steps.

**Pattern analysis**

**Stability landscape**

In the past, bistability and the landscape of potential stable states of an ecological system have been studied by constructing stability landscapes, a depiction of the most probable values e.g., vegetation density or a probability distribution for vegetation abundance constructed measuring local vegetation (Scheffer et al. 2001). Modes in an abundance probability distribution correspond to wells in a stability landscape, which helps identify the stable states of the system. However, if spatial patterns occur, the
stability landscape can be misleading because organisms are heterogeneously distributed. For example, regular vegetation patterns result in stability landscapes that flag vegetation clusters and the bare soil in between as two stable states, regardless of whether bistability occurs.

To compare the stability landscape of simulation results inside and outside the bistability region, we first measured the probability distribution \( P \) for the vegetation density matrix using the histplot function in Python Seaborn library, and then calculate the associated effective potential \( V \):

\[
V = -\ln (P),
\]

which shows the minima wells for the most probable values of vegetation density.

*Image preparation*

The sample optical satellite images with 1.2 \( m \) spatial resolution for the real-world patterns were extracted from Google Earth Pro. Because we lacked information about biomass density for the focal area, and in order to ensure a meaningful comparison with the model, before further analyses, we converted all the images to black-and-white scale, and thus analyzed images only indicated the presence of vegetation at a given pixel. This approach also prevented the influence of color differences caused by variability in satellite image quality and environmental conditions. We determined the threshold value for the black and white conversion by transforming the sample images to gray scale and using the skewed normal mixture model to find two clusters of pixels (one representing “black” and one representing “white” pixels); the black-and-white threshold was the intersection of two skewed normal functions from the mixture model results. Thus, we
converted the pixel points in the gray image that were less than the threshold to 0 (white) and those that are greater than the threshold to 1 (black). Because the simulation results showed the vegetation density directly, the black-and-white threshold for simulations was determined by the skewed normal mixture model of the vegetation density distribution.

**Power spectrum analysis**

To analyze the patterns, we calculated the radially averaged one-dimensional power spectrum associated with each snapshot collected at each rainfall level to better observe the changes in spatial periodicity. We first obtained the two-dimensional discrete Fourier Transform (2D FFT) to decompose the patterns and measure them as combinations of sines and cosine waves, then calculated the 2D power spectrum as the squared value of the shifted 2D FFT. The computation of the 2D FFT was performed using the well-established algorithm in NumPy package in Python (Harris, et al. 2020). Finally, we computed the radially averaged power spectrum by averaging across all radii from the center of the 2D power spectrum in all directions. The radii ranges were the wavenumbers of the patterns to monitor the change of pattern regularity. To improve the visualization and interpretation of the results, we applied the semi-logarithmic transformation to the 1-D power spectrum.

**Clump size and count distribution**

As justified below, measuring clump size, and number of clumps can be informative when the rainfall levels are close to catastrophic levels. In order to measure the size and number of clumps from snapshots, we used the Opencv-python package and the function inside to find the contour line for each clump and collected the size and count of clumps. For both simulation and satellite images, we calculated the mean counts of clumps over
replicates for each rainfall level. For the clump size, we fitted a kernel density estimation plot (Kdeplot) using the function from Python Seaborn library, finding the clump size with the highest probability density (i.e., the mode) for each replicate. For locations that showed different rainfall level, the final clump size was calculated as the average mode across replicates.
Results

Analytical calculations and ecological implications

Stationary states and feasibility

Since we were looking for patterns that emerged from homogenous stationary states of the model, we first calculated those stationary states. By setting both Eq. (1) and (2) to zero and solving for the value of the variables (see steps in Appendix A), we obtained one trivial stationary state (trivial stationary state: \( p_1^* = 0, w_1^* = r/l \)) that represents the desert state (i.e., no plant survives), and two non-trivial stationary states (1st non-trivial stationary state: \( p_2^* = \frac{ry}{2m} + \sqrt{(\frac{ry}{2m})^2 - \frac{l}{v}}, w_2^* = \frac{m}{vy\frac{ry}{2m} + \sqrt{(\frac{ry}{2m})^2 - \frac{l}{v}}} \); 2nd non-trivial stationary state: \( p_3^* = \frac{ry}{2m} - \sqrt{(\frac{ry}{2m})^2 - \frac{l}{v}}, w_3^* = \frac{m}{vy\frac{ry}{2m} - \sqrt{(\frac{ry}{2m})^2 - \frac{l}{v}}} \), both representing a vegetated state (see steps in Appendix A). In order to ensure that the stationary states are ecologically feasible, both the plant and water densities should be real, positive numbers. Accordingly, the condition \((\frac{ry}{2m})^2 > \frac{l}{v}\) ensures the feasibility of the two vegetated stationary states.

Conditions for diffusion-driven instability (DDIs)

As explained in the Introduction, diffusion-driven (also called Turing) instabilities can lead to pattern formation. These instabilities emerge when a large difference in the diffusion of the facilitatory and inhibitory agents that interact makes a stable homogenous stationary state of the system unstable to non-uniform perturbations; these perturbations thus grow to ultimately produce the different stationary patterns. Thus, for diffusion-driven instability to occur, the stationary state must be first stable under homogeneous
perturbation (which imposes mathematical conditions DDI1 and DDI2 in Appendix B) and unstable under heterogeneous perturbation (conditions DDI3 and DDI4 in Appendix B). These conditions can be obtained by applying the Routh-Hurwitz stability criterion to the non-diffusive homogenous system (DDI1 and DDI2) and the complete system (DDI3 and DDI4). Thus, the (homogenous) desert stationary state is stable as long as the water loss rate \( l \) and the plant mortality rate \( m \) are positive (see Appendix B), which is the case due to their ecological meaning. Therefore, the desert stationary state is always stable to homogeneous perturbations. Moreover, based on DDI3 (see Appendix B), for this state to develop diffusion-driven instabilities, it would need to satisfy \( D_w m + D_p l < 0 \), which is impossible given that all those parameters are ecologically meaningful only when they have positive values. Therefore, this condition cannot be fulfilled, and Turing patterns cannot emerge for the desert stationary state. For both vegetated stationary states, DDI1 requires \( p^2 > (m - l)/v \) and DDI2 requires \( p^2 > l/v \) (see steps in Appendix B). If \( m < 2l \) then DDI1 is automatically fulfilled and only DDI2 needs to be checked to understand the stability of the (homogeneous) state, and \( m > 2l \) then DDI2 is fulfilled and only DDI1 needs to be checked. Thus, when \( m < 2l \) the second stationary state can fulfill DDI2 as long as this state is feasible \( \left( \frac{rv}{2m} \right)^2 > \frac{l}{v} \); when \( m > 2l \), DDI1 is fulfilled for the first vegetated state when \( \frac{rv}{2m} + \sqrt{\left( \frac{rv}{2m} \right)^2 - \frac{l}{v}} > \sqrt{\frac{m-l}{v}} \). Based on these two conditions, the first vegetated state can fulfill DDI3 if \( \frac{D_w}{D_p} > \frac{2l}{m} (m < 2l) \) or \( \frac{D_w}{D_p} > 1 (m < 2l) \) (see steps in Appendix B). These conditions indicate that \( D_p \) needs to be smaller than \( D_w \) for DDI3 to be fulfilled, which is ecologically meaningful as the expectation is for water diffusion to occur faster than plant dispersal. Finally, DDI4 will be also satisfied (and therefore
patterns will emerge) if $p^2 < \frac{D_{w m} - D_{p} (1 - v p^2)}{8 D_{w} D_{p} m v p^2}$ (see steps in Appendix B). The second vegetated state cannot meet the criteria for DDI1 and DDI2, which means that this state is always unstable and therefore will never be reached by the dynamics of the system.

In summary, the analytical results above show that one of the vegetated states is susceptible to developing Turing patterns. Moreover, the parameter values that fulfill the conditions for patterns to emerge were ecologically meaningful for our study system (see Methods and Table 2).

**Simulation results**

**Vegetation patterns**

![Figure 8](image)

**Figure 8**: Simulated vegetation patterns and real patterns from our study area. Panels (a), (b) and (c) are satellite images derived from Google Earth pro after a binarization (i.e.,
black-and-white) transformation (see Methods), with annual precipitation 430.8, 478.0 and 508.9 mm/year, respectively. Panels (d), (e) and (f) correspond to the stochastic rainfall simulations with annual precipitation $A$ (see Eq. (6)) $A = 435, 475$ and 500 mm/year, respectively. Panels (g), (h) and (i) correspond to the fixed rainfall simulation with fixed annual precipitation $r = 435, 475$ and 500 mm/year, respectively. For all snapshots, black indicates the presence of vegetation and white means bare soil.

Our simulations of the model equations, for the chosen parametrization, were thus able to generate clump, labyrinth, and gap patterns at similar rainfall levels to those observed in the study system. As shown in Figure 8, both the stochastic rainfall simulation and fixed rainfall simulation exhibited similar patterns at similar rainfall levels, indicating that the vegetation patterns generated by this model are robust under stochastic and seasonal changes from the rainfall function. For simplicity, we used fixed rainfall for our subsequent simulations and analyses.

**Figure 9:** Averaged vegetation density and average water density across locations in the system change with time. The three rainfall levels selected here were associated with three types of patterns: 435 mm/year resulted in clumps, 475 mm/year in labyrinths, and 500 mm/year in gaps. Both panels show that the densities stopped changing after approximately 1000 years.
Figure 10: Pattern formation in the model. The snapshots show the forming of clump, labyrinth, and gap patterns for rainfall level 435, 475 and 500 \text{mm/year}, respectively. After 10,000 years, the patterns stopped changing and became effectively stable, with some minor variations.

The changes of mean vegetation and water density over time suggested that the system reached stationarity after 100 years (Figure 9), which a priori could be an indication of patterns also reaching stationarity. However, by looking at the sequence of patterns (Figure 10) revealed that the system required over 10,000 years to become spatially stationary, after which patterns showed only minor changes.
Phase diagram and bistability

\[\text{Figure 11:} \text{ Phase diagram, obtained representing the values of the mean vegetation density as a function of rainfall levels, for the Turing (a) and NIC (b) methods. The bistability region was filled with pink color.}\]

To facilitate better observation of the system's phase changes (i.e., desertification transition), we constructed phase diagrams for both the Turing and NIC methods. Figure 11(a) displays the relationship between mean vegetation density (spatial average of the density across pixels for a given snapshot, averaged across replicates) and rainfall levels obtained with our simulations using the Turing method. Given the sensitivity to initial
conditions expected for systems with bistability, we used two different initial perturbation values (0.7 \text{ kg m}^{-2} and 0.1 \text{ kg m}^{-2}). Both perturbations resulted in similar patterns for rainfall levels under 380 and over 430 \text{ mm/year}. The desert state was observed if rainfall was under 380 \text{ mm/year}; clumps emerged when rainfall ranged from 431 to 445 \text{ mm/year}; labyrinths were observed when rainfall ranged from 450 to 498 \text{ mm/year}; and gaps were found when rainfall ranged from 498 to 510 \text{ mm/year}. However, the two perturbations led to very different results, from 380 to 430 \text{ mm/year}, which thus defined the bistability region: the simulation with an initial perturbation value of 0.7 \text{ kg m}^{-2} generated clump patterns, while the simulation with an initial perturbation value of 0.1 \text{ kg m}^{-2} resulted in extinction. Figure 11(b), on the other hand, shows the results of using the NIC method, in which the initial condition for a simulation was obtained from the stationary pattern obtained with the previous rainfall level. In order to generate two different paths of historical conditions, we ran two simulations, one from high to low rainfall levels and another one from low to high rainfall levels. Notably, the bistability region observed with this method was larger than that of the Turing method. As we observed for the high-to-low rainfall simulations, vegetation patterns that persisted for a lower rainfall range than with the Turing method. In the bistability region, the high-to-low iterations led to clump patterns from 280 to 430 \text{ mm/year}, whereas the low-to-high path remained within the desert state. Comparing to the Turing method, the NIC method obtains clump patterns at a lower rainfall level (280 \text{ mm/year}) than the Turing method (380 \text{ mm/year}). Outside the bistability region, both high-to-low and low-to-high simulations showed the same patterns: clump patterns within a rainfall range of 430 to 440 \text{ mm/year}, labyrinth patterns
within a rainfall range of 450 to 490 mm/year, and gap patterns within a rainfall range of 500 to 510 mm/year.

Both the Turing and NIC methods displayed clump patterns inside and outside the bistability region. However, this poses a challenge in identifying the bistability region using potential wells. For a system with no spatial heterogeneity, two wells in the potential at different population densities reveal the presence of bistability. However, in our case, we obtained two similar sets of wells for the clump patterns inside and outside the bistability region (Figure 12). As the figure shows, the analysis of the probability distribution of vegetation density and associated potential cannot differentiate between these two clump patterns, and therefore cannot be used to identify whether the system had entered the bistability region.

**Figure 12**: Probability distribution of vegetation density and the associated potential. Panels (a) and (b) show the probability distribution and potential for a snapshot inside the...
bistability region with rainfall level 430 mm/year, which resulted in clumps. Panels (c) and (d) show the probability distribution and potential for a snapshot outside the bistability region with rainfall level 435 mm/year, which also showed clumps.

**1-D radial averaged power spectrum can reveal bistability**

To understand if the properties of the pattern (e.g., periodicity) changed across the rainfall gradient, we calculated the power spectrum for each snapshot and observed the changes occurring across different rainfall levels. Figure 13 depicts a heatmap of the power spectrum obtained across rainfall levels after averaging over replicates of the simulations using the Turing method. The semi-log version of the power spectrum revealed a first fundamental peak for all types of patterns with spatial frequencies ranging from 10 to 20 cycles/km, with a mode around 16 cycles/km. The first fundamental peak represents the wavelength of the most prominent feature in the pattern. As the pattern changed from clumps to gaps, the spatial frequencies of the first fundamental peak decreased. As expected, the power spectrum exhibited secondary harmonic peaks twice (mode ~32 cycles/km) and thrice (mode ~48 cycles/km) the spatial frequency of the first fundamental peaks for all simulated rainfall levels.

Interestingly, the clump patterns outside the bistability region and the gap pattern displayed a constant second fundamental peak, located at a spatial frequency between the first fundamental peak and its secondary harmonic peak (26 cycles/km, with a harmonic around 52 cycles/km). However, inside the bistability region, this second fundamental peak changed with rainfall. Specifically, the height of the peak diminished when the rainfall level exceeded 405 mm/year (see colors in the heatmap) and disappeared: as the rainfall level decreased further, this second fundamental peak reappeared with a lower
spatial frequency. This change of the second fundamental peak resulted from changes in clump size in our system (see Appendix C for details).

**Figure 13:** Heatmap of semi-log transformed power spectra of simulated patterns. Rows are the spatial frequency of the pattern and columns are rainfall levels ranging from 380 to 510 mm/year. The color represents the power of the spatial frequency, with yellow means the highest power and dark blue means the lowest. The light blue dashed lines were used to separate different types of patterns (clump: 380-445 mm/year; labyrinth: 450-498 mm/year; gap: 498-510 mm/year). To the left of the red dashed line is the bistability region (380-431 mm/year).

Guided by the prediction above, we calculated the power spectrum to images from our study area, to explore whether they would allow us to identify a changing secondary peak and therefore the bistability region. Unfortunately, due to the irregularity and stochasticity associated with real patterns and environmental conditions, the second fundamental peak was not discernable. Figure 14 shows the radial-averaged power spectrum of clump patterns with rainfall levels ranging from 430.8 to 463.6 mm/year. This analysis, nonetheless, revealed that patterns with rainfall levels of 463.1 and 463.6 mm/year showed a clump-labyrinth transition, i.e., the merging of clumps and the formation of labyrinths. The power spectrum was able to identify this transition as the
spatial frequency for the first peak was distinctly smaller than the peaks of curves obtained for the other rainfall levels.

Figure 14: Radial-averaged power spectrum of real-world clump patterns ranging from 430.8 to 463.6 mm/year. For rainfall 463.1 and 463.3 mm/year, the pattern entered the clump-labyrinth transition stage, as evidenced by the appearance of merging clumps.

Clump size and number drive the changes in the secondary peak

Given the failure to measure such a peak with real images, but the link identified between the secondary peak of the power spectrum and the size and count of clumps within the pattern (see Appendix C), we measured and compared the corresponding features (size and count) of the clump patterns across rainfall levels. Figures 15(a) and 15(b) show the clump size and count obtained with the Turing method. In the bistability range, clump size remained constant for rainfall levels between 380 and 400 mm/year. Beyond this range, a positive correlation emerged between clump size and rainfall level. The number of clumps increased until the rainfall level reached 430 mm/year, after which
a decline was observed as the patterns transitioned into the clump-labyrinth phase.

Figures 15(c) and 15(d) display the clump size and count outcomes from simulations using the NIC method (high-to-low rainfall branch). Unlike the Turing method, the NIC method exhibited a constant number of clumps before 320 mm/year, followed by a sudden collapse in clump number. While the clump number remained constant, the size of the clumps decreased until 320 mm/year and remained constant between 280 and 320 mm/year. No clear distinction was found between clump patterns within and outside the bistability region. For satellite images, on the other hand, clump size remained constant as rainfall increased after clumps transitioned into labyrinth (Figures 15(e) and 15(f)). For lower rainfall levels, a positive correlation emerged between the number of clumps and rainfall levels, which then decreased as the patterns entered the range of rainfall that results in labyrinths.
Figure 15: Size and number of clump changes with rainfall level. Panels (a) and (b) are simulation results with Turing method. Panels (c) and (d) are simulated with NIC method. Panels (e) and (f) are derived from black-and-white transformed satellite images.
Discussion

In this study, we combined model prediction and satellite images at different rainfall levels to analyze the variability of vegetation patterns and their relation to bistability. By parametrizing the model to the specific study areas where we obtained satellite images, we found that the change in clump sizes and clump numbers as aridity increases can be used to characterize an impending desertification transition and identify the associated bistability region.

Vegetation in our study area self-organizes in periodic patterns

The study area was selected because it featured the paradigmatic three types of patterns across locations with the same soil properties (slope, soil water holding capacity, and soil texture) but with varying rainfall levels (Figure 4), which highlights the latter as the primary factor influencing pattern variation in this region. The area displays clump, labyrinth, and gap patterns, which are also obtained with a range of reaction-diffusion models, across a gradient of low to high rainfall levels (Figure 5). For this reason, many studies have used this region to explore self-organized vegetation patterns (Deblauwe et al., 2008; Deblauwe et al., 2011; Veldhuis et al., 2022), justifying the presence of patterns as a result of scale-dependent feedbacks (long-term negative feedback from competition for water and short-term positive feedback from plant growth and facilitation). The vegetation patterns we found with satellite pictures provided an excellent opportunity to observe how pattern morphology relates to rainfall and a real-world example to compare with our model results. Specifically, we used the modified Klausmeier model as it is one of the simplest ecological models able to generate clump, labyrinth and gap patterns as rainfall increases. The fact that these patterns were found to be correlated with varying
rainfall levels in reality and model simulation suggests that water availability plays a crucial role in determining vegetation patterns in this region. This has important ecological implications as it implies that changes in precipitation patterns due to climate change or other factors could have a significant impact on the vegetation communities in this area.

**Novel, ecologically grounded parameterization for the modified Klausmeier model**

We modified the original Klausmeier model to replace an advection term (that illustrated water movement downhill) with a diffusion term, as the study area we focused on was a flat region with little to no slope, i.e., there would be no directional water movement.

Several studies have utilized this modification to the Klausmeier model, or similar models, to study vegetation patterns. The typical approach to parameterization reutilizes values from classic papers like Klausmeier et al, normally imposing values for the diffusivity parameters that will trigger Turing instabilities (Siteur et al., 2014; Sherratt, 2016; Eigentler and Sherratt, 2020). To ensure the ecological relevance of our parametrization, however, here we explored the literature to find values for the parameters tailored to our particular system, including the diffusivity parameters. We identified a native plant species *A. mellifera* that is highly likely to be composing the observed vegetation patterns, and derived ranges for such parameters that corresponded to this species. For the plant diffusivity, we considered it as a successful plant dispersal event that takes into account seed dispersal rate, outside canopy ratio, germination rate and seedling survival rate. Regarding water diffusion, there is surprisingly very little information in the modeling literature about what that really means. In the case of the
Klausmeier model, for example, there is no clear distinction as to whether water refers to superficial or subterranean water. This distinction is important because, ultimately, only subterranean water can be utilized by the root system. Here, we chose to interpret the water variable as superficial water and assume perfect water infiltration (i.e., all superficial water is available for the root system), which facilitated the calculation of the diffusion coefficient. Despite the importance of this parameter for Turing models, there is no definition or standardized way to calculate this parameter. This knowledge gap regarding the definition and calculation of water diffusion in self-organizing vegetation patterns also means that there are no clear instructions for future fieldwork to measure this important parameter. Thus, we drew inspiration from the Manning equation for liquid velocity and calculated a plausible range of diffusion rates. The Manning equation is a widely used method for calculating stream velocity, which means that by relating it to the calculation of water diffusion, it also provides the possibility of conducting real measurements in the field.

The ranges we obtained for our parameters were ecologically relevant, and provided patterns that were comparable to those of the study area, thus validating the parametrization. Our efforts to obtain a parametrization tailored to our study area differ markedly from those of previous studies and thus may serve as a guide for future studies utilizing both theoretical and empirical methods.

**Changes in the power spectrum reveal bistability**

Our model predicted that desertification would occur in the presence of bistability. The modified Klausmeier model showed bistability for both Turing and NIC methods (Figure 11). In a system with bistability, two stable states can occur under the same
environmental conditions, with the outcome depending on the system’s path (e.g., initial conditions) or changeable external factors (e.g., environmental fluctuations). Even if the system is in one of the stable states, it can switch to the other stable state if the system experiences a perturbation sufficiently large to overcome the potential barrier between the two states. A system in bistability remains at risk of transitioning to another state as long as it remains in the bistability region. Therefore, our research highlighted the importance of not only monitoring desertification but also determining if it occurs through a bistability region. We observed clump patterns inside and outside the bistability region, which ruled out using pattern type as an indication of bistability. Moreover, the potentials from the stability landscape obtained for the clump patterns, both inside and outside the bistability region, exhibited two wells that reflected the spatial heterogeneity of vegetation, and thus were not indicative of the system being in the bistability region (Figure 12). This problem underscores the limitations of using stability landscapes as a diagnostic tool for bistability detection in spatially heterogeneous systems with spatial patterns.

Without the semi-log transform, the power spectrum may lose information about the spatial frequency of patterns. The 1-D radial averaged power spectrum is typically used to differentiate between different types of patterns based on the existence or location of a primary peak in a linear system of coordinates (Deblauwe et al., 2011). However, in this study, the use of the semi-log version of the power spectra revealed a secondary (non-harmonic) peak, which showed a distinctive behavior when the system is bistable (Figure 13). Indeed, a heatmap with this semi-log version of the power spectrum with varying rainfall levels revealed that, inside the bistability region, a decrease in rainfall caused the
second fundamental peak for clump pattern to decrease with rainfall level and disappear when the system entered the bistability region. This change resulted from the overlap of the power well and the power peak (see Appendix C). The change in the power well reflects the change in the clump size, which gave us a hint of the size of the clump matters in identifying the bistability region. In consequence, our analysis predicted that, within the bistability region, a decrease in rainfall leads to a reduction in the spatial frequency of clump patterns, indicating a decrease in the number of clumps. The understanding of the mechanisms underlying the behavior of the second fundamental peak enables bypassing the power spectrum to focus on properties that are easily measurable with satellite images.

**Clump size and count are early-warning signals for bistability and desertification**

As the changes in clump number and size are the primary factors contributing to the changes in power spectrum peaks, and these are general properties that can be easily captured from snapshots of vegetation patterns, we examined these properties for both the Turing and NIC methods as well as satellite images.

The study results indicate that the clump number and size are general properties that can be used to assess the health of vegetation in semi-arid areas. From the simulation results of the Turing method, we found that the curve of the clump number showed a maximum outside the bistability region, when the system became bistable, the number of clumps started to decrease as rainfall decreases (Figure 15(a) and 15(b)). Outside the bistability region, the number of simulated clumps reached the maximum value and started to decrease when the rainfall increased because the clumps merged into larger pieces and the patterns transitioned from clump to labyrinth. Moreover, within the
bistability region, the slope of the clump number curve became slower when rainfall level reached 400 mm/year. In addition, we observed a positive linear correlation between clump size and rainfall level both inside and outside the bistability region, but the slope of the line outside the bistability region was steeper than that inside the bistability region. Also, at 400 mm/year (i.e., within the bistability region), the clump size stopped changing and remained constant as rainfall decreased, and remained so until desertification. Thus, this constant clump size can serve as an early warning signal for system collapse.

Unexpectedly, however, clumps obtained with the NIC method did not show a distinct behavior in and out the bistability region (Figure 15(c) and 15(d)). Clump size was negatively correlated with rainfall with no clear slope changes, and clump number increased with rainfall above 320 mm/year. Nonetheless, below 320 mm/year clump size remained constant while the number of clumps decreased dramatically. Thus, the combination of a constant clump size and a decreasing clump number remains a clear signal that the system is within the bistability region and is approaching desertification.

With only a difference in the initial conditions, the Turing and NIC methods led to two different situations. In the Turing method, the number of clumps inside the bistability region kept decreasing, which means that the vegetation pattern for each rainfall level would not be the same and the pattern itself would be changing. However, unlike the Turing method, which starts with a homogeneous condition, the NIC method allowed the system to obtain the previous vegetation pattern, and the vegetation pattern itself is more robust and can resist changes in rainfall over a longer range. The constant clump number for the NIC method means that the clump location did not change until the rainfall level was low enough. Several studies have found that self-organized vegetation patterns can
persist for a longer range of rainfall, which is not expected to support vegetation survival (Siteur et al., 2014; Rietkerk et al., 2021). This difference in behavior between the two methods could be explained by the more robust nature of the vegetation pattern obtained by the NIC method.

After applying the method above to the satellite images, we observed a behavior very similar to that obtained with the NIC method (Figure 15(e) and 15(f)). Thus, according to our predictions with the NIC method, the study area would be within a bistability region, and the constant clump size would be an early warning signal of desertification. This provides insight into dealing with desertification by only monitoring the clump number and size through satellite images in recent years when the rainfall levels change over time. If the rainfall decreases over the years and the clump number remains constant while the clump size keeps decreasing, the system is in bistability and requires extra attention or management efforts to control large external disturbances like grazing or human activities. If we notice that the clump number is decreasing while the clump size remains constant, then ecosystem management should take immediate action to devote resources to the recovery of the vegetation since the system is close to a critical transition. For other systems with similar self-organized patterns, our work provides a complete workflow to investigate the pattern morphology and its relationship with the bistability region, which combines empirical and theoretical work.

Limitations

The limitations of this study can be divided into three parts: 1) study area and parameterization; 2) model; and 3) real-world imagery. The lack of high-resolution historical satellite images made temporal analysis impossible if we want to examine high-
resolution images before the 1990s, and despite efforts to ensure that our sequence of patterns had similar environmental conditions, other factors for which we did not have information such as foraging, and soil nutrition could also influence the pattern. Additionally, since we have not been to the study area, we had to assume that the plant species was *A. mellifera*. As for the model and parameterization, the parameter $v$ does not have ecologically meaningful units and, although to some extent can be interpreted as an uptake rate, we eventually had to adjust its value based on pattern size. Lastly, although we devised a methodology, the black-and-white transformation threshold that we developed for our real-world imagery can to some extent be seen as arbitrary, and may lead to potential under- or overestimation of vegetation especially when the image conditions were not optimal (e.g., clouds, differences in lighting conditions).
Conclusions

This study highlights the potential of using both simulation and satellite imagery to monitor and predict desertification in semi-arid regions. The findings suggest that monitoring clump size and number can be a simple method for assessing the health of vegetation in semi-arid areas, which involves only the analysis of images without temporal and spatial constraints. This approach offers the flexibility to monitor ecosystems remotely and requires less spatial and temporal data, which can be difficult to access in some cases. Governments can use the information to develop policies that encourage sustainable land use practices and protect the livelihoods of local communities from land degradation. Farmers can also use this information to improve their own wellbeing by adapting their agricultural practices to better suit the changing conditions of the land. However, certain limitations of this study suggest further research directions. It is essential to check whether the observed patterns are stationary, and it will be better to obtain additional locations with different rainfall levels to establish a more robust correlation between model predictions and satellite imagery. Also, extending this research to other locations would offer the opportunity to measure model parameters in the field and enhance our understanding of the mechanisms governing vegetation dynamics. However, it remains uncertain whether the constant clumps size will indeed lead to desertification, and confirmation can only be obtained through empirical observations. Therefore, it is imperative to measure model parameters and test our predictions in the field to avoid parametrization assumptions and validate our findings. Future work could focus on other model systems with clumps both inside and outside the bistability region to test whether the size and number of clumps can be used as an
indicator of bistability. More research is required to validate the stability of the observed patterns, enhance the correlation between model predictions and satellite imagery across different locations and rainfall levels, and confirm if constant clump size results in desertification through empirical evidence.
Appendix A. Stationary States

First, we will represent the equations by breaking them down into a reaction
cOMPonent and a diffusion component:

\[
\frac{\partial w}{\partial t} = r - lw - vwp^2 + D_w \nabla^2 w = f(w, p) + D_w \nabla^2 w \quad (1)
\]

\[
\frac{\partial p}{\partial t} = vyp^2 - mp + D_p \nabla^2 p = g(w, p) + D_p \nabla^2 p \quad (2)
\]

For Turing patterns to develop, the stationary state must first be stable to a spatially
homogenous perturbation in the absence of diffusion. Thus, we first study the system
with \(D_w \nabla^2 w\) and \(D_p \nabla^2 p\) equal to zero and we need to find the stationary states for Eq. (1)
and Eq. (2) first.

Setting Eq. (1) and Eq. (2) with \(D_w \nabla^2 w = D_p \nabla^2 p = 0\) to zero:

\[f(w^*, p^*) = 0 \Rightarrow f(w^*, p^*) = 0 = r - lw^* - vw^*p^{*2} = r - w^* (l + vp^{*2}) \quad (a1)\]

\[g(w^*, p^*) = 0 \Rightarrow g(w^*, p^*) = 0 = vlw^*p^{*2} - mp^* = n(vlw^*p^* - m) \quad (a2)\]

a. From Eq. (a2), we can get \(p_1^* = 0\) or \(w_2^*p_2^* = \frac{m}{vy}\)

b. Bringing \(p_1^* = 0\) into (a1), we get \(w_1^* = r/l\) (desert stationary state)

c. For the second stationary state, we apply the second condition from (a) to Eq.

(a1): \(w_2^*p_2^* = \frac{m}{vy} \Rightarrow w_2^* = \frac{m}{p_2^{vy}} \Rightarrow \) bring \(w_2^* = \frac{m}{p_2^{vy}}\) into Eq. (a1) →

\[r - \frac{m}{p_2^{vy}} (l + vp_2^{*2}) \Rightarrow rp_2^* - \frac{ml}{vy} - \frac{m}{y} p_2^{*2} = 0 \quad (a3)\]
Applying the quadratic formula to solve Eq. (a3) provides two solutions, and therefore the vegetation density for two vegetated stationary states (see results in the Table S1).

Feasibility: to make sure the two vegetated stationary states are ecological meaningful, $w^*$ and $p^*$ should be positive, which imposes the following condition: 
\[
\left( \frac{ry}{2m} \right)^2 > \frac{l}{v}
\]

**Table S1**: Summary table: Three (homogeneous) stationary states:

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<tbody>
<tr>
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<td>$p_1^* = 0$</td>
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<tr>
<td>Desert stationary state:</td>
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<td>$w_1^* = r/l$</td>
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|               | $p_2^* = \frac{ry}{2m} + \sqrt{\left( \frac{ry}{2m} \right)^2 - \frac{l}{v}}$ |               |
| 1st vegetated stationary states: |               |               |
|               | $w_2^* = \frac{m}{vy \frac{ry}{2m} + \sqrt{\left( \frac{ry}{2m} \right)^2 - \frac{l}{v}}}$ |               |

|               | $p_3^* = \frac{ry}{2m} - \sqrt{\left( \frac{ry}{2m} \right)^2 - \frac{l}{v}}$ |               |
| 2nd vegetated stationary states: |               |               |
|               | $w_3^* = \frac{m}{vy \frac{ry}{2m} - \sqrt{\left( \frac{ry}{2m} \right)^2 - \frac{l}{v}}}$ |               |
Appendix B. Stability and Diffusion-Driven Instability (DDIs)

As stated above, the development of a diffusion-driven instability requires the stability of the homogeneous state first. In the absence of diffusion, the stationary state is stable to spatially homogenous perturbation, which means $k = 0$. For the stationary state to be stable under homogenous perturbation, the Routh-Hurwitz criterion must be fulfilled, which in this case:

$$\text{Trace}(J(0)) < 0 \text{ and } \text{Det}(J(0)) > 0$$

Thus, we get:

$$DDI_1: f_w + g_p < 0$$
$$DDI_2: f_w g_p - f_p g_w > 0$$

Where $f_w, f_p, g_w, \text{ and } g_p$ represent the partial derivatives of the reaction functions with respect to the variables of the system. Details of why the conditions above are needed for the stability of the stationary state can be found in the steps below for the diffusive system after imposing $k = 0$ in the calculations.

To find the conditions for the stability of the stationary states once diffusion is present, we need to linearize the complete system:

$$\frac{\partial w}{\partial t} = f_w w + f_p p + D_w \nabla^2 w \quad (b1)$$
$$\frac{\partial p}{\partial t} = g_w w + g_p p + D_p \nabla^2 p \quad (b2)$$

To understand how the system responds to small periodic perturbations, we assume a spatially dependent perturbation with wavenumber given by $k$:
\[ w(x, t) = w_k(t)e^{ikx}, \quad w(x, t) = p_k(t)e^{ikx} \rightarrow \]

And therefore:

\[ \frac{\partial w}{\partial t} = \frac{\partial w_k}{\partial t} e^{ikx} \quad (b3) \]

\[ \frac{\partial p}{\partial t} = \frac{\partial p_k}{\partial t} e^{ikx} \quad (b4) \]

Substituting equations (b3) and (b4) into equations (b1) and (b2) leads to a system of equation that provides the Jacobian of the system:

\[
\frac{d}{dt} \begin{pmatrix} w_k \\ p_k \end{pmatrix} = \begin{pmatrix} f_w - D_w k^2 & f_p \\ g_w & g_p - D_p k^2 \end{pmatrix} \begin{pmatrix} w_k \\ p_k \end{pmatrix}
\]

And we can thus calculate its trace and determinants:

\[
Trace(J(k)) = (f_w + g_p) - (D_w + D_p)k^2
\]

\[
Det(J(k)) = D_w D_p k^4 - (D_w g_p + D_p f_w)k^2 + f_w g_p - f_p g_w
\]

For DDI to develop, the stationary state needs to be unstable to spatially heterogeneous perturbations in the presence of diffusion. Therefore, there must be a value \( k > 0 \) such that the Routh-Hurwitz criterion above is broken:

\[
\text{either } Trace(J(k)) > 0 \text{ or } Det(J(k)) < 0
\]

Since \( Trace(J(k)) = (f_w + g_p) - (D_w + D_p)k^2 < Trace(J(0)) < 0 \), DDI can only emerge if \( Det(J(k)) < 0 \) for at least one \( k > 0 \).
To check under which conditions $\text{Det}(J(k)) < 0$, we can define: $Q(k^2) = ak^4 + bk^2 + c$,

with

$$a = D_w D_p, \quad b = -D_w g_p - D_p f_w, \quad c = \text{Det}(J(0)) > 0;$$

$$b < 0 \text{ and } b^2 > 4ac$$

And, for at least one $k$ value to make the determinant negative:

**DDI3:** $-D_w g_p - D_p f_w < 0$

**DDI4:** $( -D_w g_p - D_p f_w )^2 > 4D_w D_p ( f_w g_p - f_p g_w )$

**Actual calculation with model parameters**

Calculating the partial derivatives for $f(w,p)$ and $g(w,p)$:

$$f_w = -l - v p^2 \quad f_p = -2vwp$$
$$g_w = v y p^2 \quad g_p = 2v yp - m$$

The conditions for the homogenous stationary state to be stable are:

Routh-Hurwitz criterion (DDI1&2): $f_w + g_p < 0 \& f_w g_p - f_p g_w > 0$

**DDI1:** $-l - v p^2 + 2v ywp - m < 0$

**DDI2:** $(-l - v p^2)(2v ywp - m) - (-2vwp)(v y p^2) > 0$

And the conditions for the stationary state to be unstable to inhomogeneous perturbations are:

**DDI3:** $-D_w g_p - D_p f_w < 0 \Rightarrow -D_w (2v y wp - m) - D_p (-l - v p^2) < 0$
DDI4: \((D_w g_p - D_p f_w)^2 > 4D_w D_p (f_w g_p - f_p g_w)\) →

\((-D_w (2vywp - m) - D_p (-l - vp^2))^2 \\
> 4D_w D_p ((-l - vp^2)(2vywp - m) - (-2vwp)(vyp^2))\)

In particular, for our three stationary states:

1. **Desert Stationary State**:

   DDI1: \(-l - m < 0\)
   
   DDI2: \(lm > 0\)
   
   Because \(l\) and \(m\) are positive, the desert stationary state is always stable.

   DDI3: \(-D_w (0 - m) - D_p (-l - 0) < 0 \Rightarrow D_w m + D_p l < 0\)
   
   Because \(D_w, D_p, m\) and \(l\) are all positive, DDI3 is not fulfilled.

   Therefore, Turing patterns should not emerge for the desert stationary state.

2. **Vegetated Stationary States**:

   From Appendix A. 2c we can get: \(w^* p = \frac{m}{vy}\)

   DDI1: \(-l - vp^2 + 2vywp - m < 0 \Rightarrow -l - vp^2 + m < 0 \Rightarrow p^2 > (m - l)/v\)

   DDI2: \(-ml + mvp^2 > 0 \Rightarrow p^2 > l/v\)

   If \(\frac{m - l}{v} > \frac{l}{v} \Rightarrow m - l > l \Rightarrow m > 2l\), as long as \(p^2 > \frac{m - l}{v}\), \(p^2\) will also larger than \(\frac{l}{v}\). On the contrary, if \(m < 2l\), as long as \(p^2 > \frac{l}{v}\), \(p^2\) will also larger than \(\frac{m - l}{v}\).

   If \(m > 2l\), DDI2 is fulfilled if DDI1 is fulfilled. Therefore, we would only need to check DDI1.
If \( m < 2l \), DDI1 is fulfilled if DDI2 is fulfilled, and therefore we would only need to check DDI2.

a. Check DDI2 first if: \( m < 2l \)

For the 1\textsuperscript{st} vegetated stationary state:

\[
p_2^* = \frac{r_y}{2m} + \sqrt{\left(\frac{r_y}{2m}\right)^2 - \frac{l}{v}} > \frac{l}{v} \Rightarrow \sqrt{\left(\frac{r_y}{2m}\right)^2} - \sqrt{\left(\frac{r_y}{2m}\right)^2 - \frac{l}{v}} > 0
\]

DDI2 is fulfilled when \( p_2^* \) is feasible: \( \left(\frac{r_y}{2m}\right)^2 > \frac{l}{v} \)

For the 2\textsuperscript{nd} vegetated stationary state:

\[
p_3^* = \frac{r_y}{2m} - \sqrt{\left(\frac{r_y}{2m}\right)^2 - \frac{l}{v}} > \frac{l}{v} \Rightarrow \sqrt{\left(\frac{r_y}{2m}\right)^2} - \sqrt{\left(\frac{r_y}{2m}\right)^2 - \frac{l}{v}} = 0
\]

\[
\left(\sqrt{\left(\frac{r_y}{2m}\right)^2 - \frac{l}{v}}\right)^2 > \left(\frac{r_y}{2m}\right)^2 - \frac{l}{v} \Rightarrow 2\sqrt{\left(\frac{r_y}{2m}\right)^2} \left(\frac{l}{v}\right) < \frac{2l}{v} \text{ (only when } \left(\frac{r_y}{2m}\right)^2 < \frac{l}{v} \text{ )}
\]

DDI2 is not fulfilled when \( p_3^* \) is feasible.

b. Check DDI1 first if: \( m > 2l, \frac{m-l}{v} > \frac{l}{v} \)

For the 1\textsuperscript{st} vegetated stationary state:

DDI1 is fulfilled for \( p_2^* \) when \( \frac{r_y}{2m} + \sqrt{\left(\frac{r_y}{2m}\right)^2 - \frac{l}{v}} > \frac{m-l}{v} \)

For the 2\textsuperscript{nd} vegetated stationary state:

From DDI2 we can know \( p_3^* < \frac{l}{\sqrt{v}} \), here \( \frac{m-l}{v} > \frac{l}{\sqrt{v}} \), so DDI1 is not fulfilled for \( p_3^* \)

3. Therefore, the 2\textsuperscript{nd} stationary state will never be able to be stable (nor develop a Turing instability). As for the 1\textsuperscript{st} vegetated stationary state:
DDI3: \(-D_w(2vywp - m) - D_p(-l - vp^2) < 0 \rightarrow -D_w m + D_p l + D_p vp^2 < 0\)

\[ \rightarrow D_w m - D_p l > D_p vp^2 \rightarrow p^2 < \frac{D_w}{D_p} \cdot \frac{m}{v} - \frac{l}{v} \]

When \(m < 2l\), we get \(\frac{D_w}{D_p} > \frac{2l}{m}\)

When \(m < 2l\), we get \(\frac{D_w}{D_p} > 1\)

DDI3 is fulfilled as long as \(\frac{D_w}{D_p} > \frac{2l}{m}\) (\(m < 2l\)) or \(\frac{D_w}{D_p} > 1\) (\(m < 2l\)), which in turn requires \(D_p\) to be smaller than \(D_w\).

Finally, for the last DDI condition:

**DDI4:** \(\left( -D_w(2vywp - m) - D_p(-l - vp^2) \right)^2 > 4D_w D_p ((-l - vp^2)(2vywp - m) - (-2vwp)(vp^2))\)

\[ \rightarrow \left( D_w m + D_p (-l - vp^2) \right)^2 > -4D_w D_p ml + 4D_w D_p mp^2 \]

\[ \rightarrow (D_w m)^2 - 2D_w D_p ml + 2D_w D_p mp^2 + D_p (-l - vp^2) > 8D_w D_p mp^2 \]

\[ \rightarrow p_2^2 < \frac{D_w m - D_p (-l - vp^2)}{8D_w D_p mp^2} \]
Appendix C. Fourier transform and power spectrum.

In a Fourier transform and corresponding power spectrum, we should see one peak for every direction where there is periodicity in the pattern. The location should represent how many times the motif is repeated within the system/picture (spatial frequency). For the clump pattern, for example, this means a peak for each line that can be traced crossing clumps. If we trace horizontal lines that cross clump centers within the same row, we should see a peak at a location that matches the number of lines that can fit in the picture. If we trace similar lines diagonally, because of the symmetry of the pattern, we should get the same number of lines and therefore the same peak. This is the so-called fundamental peak, and its presence and location are typically used to characterize regularity within images/patterns (Deblauwe et al., 2011). Theoretically, this peak (and its harmonic peaks, located at twice, thrice, etc. the distance of the first peak) are typically the focus of research.

We, however, realized that the clumps pattern has an additional feature. Vertically, because of the overlap of one row and the following one, we can fit more lines than in any other direction, which produces a second fundamental peak in the power spectrum that is close to, but different from the second harmonic peak (Figure S1).
Figure S1: 2D Fourier transform and 1D power spectrum of hexagonal distributed spots. Panel (a) is the original image with red and blue line indicating the line of spots, which are corresponding to the spatial frequency in panels (b) and (c). Panel (b) shows the 2D FFT result using a color map range from purple to light blue, with purple indicating lower values and light blue indicating higher magnitude values. The x and y-axes correspond to the spatial frequencies in the horizontal and vertical directions respectively. The blue circles and the red circles are corresponding to the lines in panel (a). Panel (c) is the radially-averaged power spectrum calculated from the 2D FFT result. The first fundamental peak, denoted by a dark blue rectangle, represents the spatial frequency of the blue lines in panel (a), while the second harmonic peak is located in the dotted blue square. The second fundamental peak, indicated by the red rectangle, corresponds to the spatial frequency of the red lines in panel (a).

To investigate the behavior of the second fundamental peak in our simulations, we constructed perfectly hexagonal clump patterns and varied the size of the clumps. Our analyses showed that the height of the second fundamental peak was affected by the size
of the clumps, reaching its lowest point at a certain size. In Figure S2, we have denoted the second fundamental peak with a red rectangle. As the position and number of clumps were kept constant, the only variable in our study was the size of the clumps. We observed that the locations of the peak in the power spectrum remained fixed at the same spatial frequencies but, as the diameter of the clumps decreased from 22 to 20 pixels, the second fundamental peak diminished, and then recovered as the clump size continued to decrease from 20 to 18 pixels.

To better understand the effect of clump number on the second fundamental peak, we reduced the number of clumps and observed changes in the power spectrum as a function of clump size (Figure S3). The power spectrum obtained with just five clumps showed now a well instead of a peak, with the location of the well increasing as clump size decreased. We then removed four of the clumps to leave the central one, which produced a power well at the same spatial frequency as the five clumps (Figure S5). Thus, when multiple clumps were present and the second fundamental peak was formed in the location of the well, the peak and the well overlapped and offset each other, which is shown in Figure S4. This could explain the second fundamental peak behavior and point out the clump size is an important feature to look at when analyzing vegetation patterns.
Figure S2: Relationship between the power of the second fundamental peak and the size of clumps. The second fundamental peaks are denoted by red rectangles. The clump patterns on the right were generated with the same clump positions and numbers, but with varying clump sizes.
Figure S3: Relationship between the power well and the size of clumps (five clumps). The power wells are denoted by green rectangles.
Figure S4: Relationship between the power well and the size of clumps (45 clumps). The power wells are denoted by green rectangles.
Figure S5: Relationship between the power well and the size of clumps (one clump). The power wells are denoted by green rectangles.
References


