Identifying Variations within the Runoff-Runon System of Self-Organizing Arid Vegetation

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Abstract

As global climatic and anthropogenic changes bring increasing resource scarcity to ecosystems across the globe, the resiliency of natural communities to these changes can be the determinant in whether or not the population, and the ecosystem as a whole, survives. This is particularly the case in the self-organization of arid vegetation into distinct, periodic patterns in response to resource scarcity, where theoretical models suggest their formations are an "early warning sign" for future catastrophic shifts and sudden ecosystem collapse. These models rely on a "runoff-runon" system of differential infiltration capabilities between vegetated patches and the surrounding bare soil. However, few empirical studies have been conducted to apply this theory to real arid ecosystems, and those that have often reveal unexpected nuances and cast doubt on the applicability of the large, theoretical literature. Accurately predicting catastrophic shifts in real ecosystems is of the utmost importance, but can only be accomplished through site-specific, empirically driven models that consider an assortment of all active mechanisms in pattern formation. Aerial imagery suggests banded pattern formation in an arid ecosystem in Southern Colorado at Chico Basin Ranch over the last 15 years. Infiltration experiments at this site show significantly higher infiltration rates in vegetated areas than in bare soil, suggesting a runoff-runon system may be active. Moreover, statistical analyses of drone imagery at three Areas of Interest (AOIs) reveal non-random, periodic banded vegetation generally in a North-South orientation. However, the orientations of these vegetation bands in relation to slope are not consistent between AOIs, with the expected perpendicular orientation to slope observed in one AOI, an oblique orientation observed in another, and a parallel orientation observed in the third AOI. In this way, this study identifies periodic vegetation bands in Southern Colorado that have orientations that cannot be fully explained by a runoff-runon system, suggesting other mechanisms are also present.

Introduction

Understanding how biological communities organize in response to resource scarcity remains at the forefront of ecological research, particularly in regards to how and why self-organization varies. There have been numerous observations of spatial self-organization of vegetation on the scales of 10s to 100s of meters in many different ecosystems across the globe; from trees and shrubs in Savannahs (Lejeune et al. 2002), to plants in peatlands (Foster et al. 1983; Swanson & Grigal, 1988; Couwenberg & Joosten, 2005) and arid ecosystems (Klausmeier 1999; HilleRisLambers et al. 2001; Lejeune et al. 2002). At the same time, there is a wide variety of distinct spatial patterns observed around the globe, with similar patterns appearing in different ecosystems, and even multiple patterns occurring in the same ecosystem (Rietkerk et al. 2004). These patterns include spots (i.e. equidistant patches), labyrinths (i.e. dendritic patterns), periodic bands (i.e. tiger bush), and open circles in a vegetation matrix (i.e. fairy-rings) (Fig. 1) (Bromley et al. 1997; Klausmeier 1999; Hardenberg et al. 2001; Shnerb et al. 2003; Penny et al. 2013; Gandhi et al. 2018).

The frequent formation of self-organizing patterns in many different ecosystems is due to the underlying principle of resource concentration in resource scarce ecosystems. Endogenous mechanisms for formation of periodic patterns were first identified by Alan Turing (1953). Turing (1953) proposed that periodic patterns could form as a result of an interaction between a slow-diffusing "activator", and fast diffusing "inhibitor", where the "activator" has the ability to activate itself and activate the "inhibitor" whereas the "inhibitor" has the ability to inhibit both the activator and itself. More recent investigation into periodic patterns in vegetation found that the same species can play the role of "activator" and "inhibitor" and that these "Turing patterns," are products of facilitatory feedbacks over a short distance and inhibitory feedbacks at a longer distance (Rietkerk and van de Kopple 2008). Lejeune et al. (2002) details this process in nutrient-poor savannah systems, where isolated patches of trees are observed in a matrix of grassland. The trees draw in scarce nutrients from the surrounding area through their extensive

root network from surface soil in a large radius around the trees. This increases the soil fertility underneath their canopies through nutrient accumulation and recycling, while simultaneously reducing the fertility of the surrounding area. As a result, the plants within the patches facilitate themselves and each other, while also competing with other patches for the scarce nutrients in the areas between them, leading to the formation of the observed equidistant periodic patches. The mechanism of short-distance facilitation and long-distance competition through resource concentration remains in arid ecosystems, with patterns forming through the concentration of water (Rietkerk et al. 2004). In this way, pattern formation in arid ecosystems can be thought of as an effective mechanism for concentrating scarce resources.

Indeed, as arid ecosystems across the globe undergo desertification due to increasing stress from climate change and/or grazing, pattern formation provides multiple benefits for the organizing species, and the ecosystem as a whole, in the face of external pressures that limit resource availability and reduce survivability. More specifically, the facilitatory feedback within the patterns increases the ecosystem's biodiversity and productivity under such pressures (Lejeune et al. 2002; Gilad et al. 2004; van de Koppel & Rietkerk 2004). In other words, self-organization into patterns leads to increased resilience to disturbance and change, such as severe drought and intense grazing pressure (Meron 2016; Dunkerly 2018).

While self-organization of arid vegetation into patterns makes the system more resilient, this resiliency can become insufficient if the pressures continue to increase; which would result in a 'catastrophic regime change' and ecosystem collapse (Rietkerk et al. 2004; Tirabassi et al. 2014; Bathiany et al. 2018). This phenomenon of 'catastrophic shifts' require multiple prerequisites to occur, as detailed by Scheffer et al. (2001): 1) The ecosystem must have two stable states, or "basins of attraction" of conditions that the ecosystem would fluctuate around (e.g. a fully vegetated grassland and a desert with no grasses and limited vegetation), which the system can alternate between (i.e. alternative stable states). 2) Between the two stable states is an "unstable equilibrium", or a "repelling peak" where the system cannot remain and will very quickly "move" to either of the two basins of attraction. This critical point is

generally the threshold that the system must pass to shift from one stable state to the other. 3) There must be a gradual change in the environmental conditions that progressively decreases the basin of one of the stable equilibria by moving the repelling peak closer to the stable equilibrium, this "pushes" the system towards and beyond the threshold where the stable and unstable equilibria fuse into a catastrophic bifurcation point, at which point the system would suddenly and "catastrophically" shift to the other stable state. In arid ecosystems, this "push" is generally considered through decreased precipitation, and manifests in a shift from full vegetation cover (e.g. grasses) to bare soil with sparse vegetation (e.g. cacti); with patterned vegetation in between (Chen et al. 2015) (Fig. 2). In this way, pattern formation and transitions thereafter can be considered "early warning signs" of a catastrophic shift in the ecosystem's stable state, as they signal the ecosystem moving towards the catastrophic bifurcation point where the grassland shifts to a desert (Kefi et al. 2007; Dakos et al. 2011). However, this process is largely theoretical and to date there have been no instances where these 'early warning signals' were used to avoid a catastrophic shift (Kefi et al. 2014). Moreover, while multiple models have linked pattern formation in arid ecosystems to future catastrophic shifts (Rietkerk & van de Koppel, 1997; Scheffer & Carpenter, 2003; Rietkerk et al. 2004), those shifts are not inevitable, and identified patterns simply suggest the possibility for a catastrophic regime change. At this point in time the usefulness of the self-organization as an early-warning sign is tentative, particularly when empirical data reveal the models are underestimating the ecosystem's resiliency through facilitation and topography (Baartman et al. 2018). Regardless, identifying these patterns and the underlying mechanisms creating them stands as a paramount conservation issue and of notable importance for regional stakeholders (e.g. land managers, cattle ranchers, conservationists).

While the possibility for catastrophic shifts brings much needed attention to the topic of impending desertification, the predictive abilities of models to accurately determine if, when and how such transitions could occur largely depends on how well they capture the mechanisms occurring in the system (Bel et al. 2012; Zelnik et al. 2013; Meron 2016). However, most of the literature on these patterns rely entirely on remote sensing and modelling, and few incorporate mechanistic and empirical findings on

the ecosystems in question, largely assuming that the underlying mechanisms are slope and a runoff-runon system (Penny et al. 2013; Dunkerly 2018). The theory behind the influence of such mechanisms makes sense: Competition for water is generally understood to be a driving factor in the formation of desert vegetation patterns, and pattern formation can be manifested through a plant's root structure and/or through areas of optimal runoff capture. For the latter, this can be seen in perpendicular orientations to slope gradients (Deblauwe et al. 2011). Specifically, slopes create runoff downslope, providing plants downslope water that would've otherwise fallen beyond their root structure's reach. However, for a plant to receive runoff, that water must not be absorbed by the soil further upslope. Fortunately for the plants, this is often achieved through stark differences in infiltration rates between vegetated patches and bare soil; a phenomenon called a "runoff-runon system" (Pueyo et al. 2013) (Fig. 3). These differences in infiltration rates are created, in large part, by the vegetation. Dry, arid soils are frequently prone to "crusting" along the topmost layer, either by organic or inorganic material, thereby decreasing its porosity and infiltration rates (Pueyo et al. 2013). Vegetation breaks up the underlying soil through its root structure, which increases infiltration in and around the vegetated patches (Bedford and Small, 2008; Rodríguez-Caballero et al. 2018). In turn, this makes it easier for future vegetation to establish at those locations with higher infiltration, creating facilitation over a short distance (Pueyo et al. 2013). At the same time, the depletion of runoff at one location maintains the necessity for the bare directly downslope, creating competition at a further distance between vegetated patches for available runoff. This means that the soil directly downslope from a vegetated patch won't receive any runoff, and therefore is uninhabitable for vegetation establishment. Over some distance, the bare, uninhabitable spots accumulate enough runoff to permit the establishment of a new vegetation patch. In this way, banded vegetation along gentle slopes are a classic example of Turing's Activator-Inhibitor Principle in regular pattern formation (Turing 1953). As mentioned earlier, it is well established that these "Turing patterns" are the theoretical basis for vegetation patterning in arid ecosystems (Rietkerk and Van de Koppel, 2008). Indeed, while the details of the exact mechanisms of facilitation and competition might differ the underlying principle of

Turing pattern formation remains as a dominant pattern-generating mechanism across different ecosystems.

If the runoff-runon system is indeed the mechanism driving vegetation self-organization in arid ecosystems, as most models suggest, then we would see field observations of strictly periodic, banded vegetation in a perpendicular orientation to the slope gradient, with the top of the bands having higher moisture levels than the bottom of the bands, and with gradual upslope migration of the bands over time (Dunkerly 2018). However, there are gaps in results between the model outputs and real-world observations, with deviations from the results we would expect based off of the models frequently reported (Dunkerly & Brown 2002; McGrath et al. 2012; Penny et al. 2013; Dunkerly 2018). In part, this is due to most models using smooth slopes with uniform flow, which fail to account for microtopography (terrain ruggedness) creating convergent and divergent flow across landscapes (but see McGrath et al. 2012; Baartman et al. 2018). In general, as is the case with most real-world systems, the self-organization of arid vegetation are not exclusively or entirely products of runoff-runon systems, or any one variable, and can be influenced by other factors. One can imagine that factors such as wind sheer stress, snow deposition, soil temperature, soil type and grazing all interact with the runon-runoff system. Very few empirical studies even consider alternative mechanisms, and typically modelling studies do not check for new mechanisms. Identifying these additional mechanisms requires empirical data and field experiments at the study site itself, and the models that do incorporate field data typically represent the ecosystem better (e.g. McGrath et al. 2012; Pueyo et al. 2013; Dunkerly 2018). Overall, field data and experiments are a necessary component in identifying the underlying mechanisms creating the patterns at a given location; and by extension, possibly leading the ecosystem towards desertification.

Herein, this study employs a Fourier Transform in R to investigate the periodicity and orientation of three unique instances of banded vegetation with potentially differing relationships to slope and a runon-runoff system, thereby identifying the variability in pattern organization and their potential mechanisms. This, in turn, will open the door for future empirical data collection and fieldwork at the site to quantitatively identify the underlying mechanisms of pattern formation, allowing for accurate

6

predictions of potential catastrophic shifts. Specifically, this study intends to answer three research questions: 1) Is there a pattern that is banded and periodic? 2) How do these patterns correspond to slope, as an indirect test of the runoff-runon mechanism? 3) Are infiltration rates between vegetated patches and bare soil different enough to activate a runoff-runon system?

Study Area and Methodology

Study Site

<u>Chico Basin Ecosystem</u>

This study was conducted at Chico Basin Ranch, a working cattle ranch roughly 50km southeast of Colorado Springs in Southern Colorado (Fig. 4). The ranch encompasses 90,000 acres of shortgrass and sandsage prairie, and is part of the larger Chico Basin Ecosystem, which has been identified as a region of conservation importance by the Nature Conservancy, Colorado Natural Heritage Program, and Bird Conservancy of the Rockies (Rondeau et al. 2016).

However, the Chico Basin Ecosystem has undergone intense grazing pressure in recent decades, and climate change has brought steadily increasing temperatures (roughly 0.06 C per decade) and decreasing precipitation. At the same time, dramatic habitat degradation in shortgrass communities have been observed in other sections of the Chico Basin Ecosystem by at least the start of the 21st century (Rondeau et al. 2016).

While the short-grass steppe in Colorado can be home to a wide variety of grasses, in regions of limited precipitation it is primarily dominated by its two most drought-resistant species: Buffalo Grass (*Buchloë dactyloides*) and Blue Grama Grass (*Bouteloua gracilis*) (Benedict book, page 208). Communications with the property owners further suggest these are the two dominant grass species at the study site (Tess, pers. comm.); however, official identification of both species was not conducted.

Both species are resistant to grazing and droughts. Both species respond to droughts by transferring their sugars and proteins to their root systems, while the above-ground leaves remain

physiologically dormant, and can even appear dead. Both species can recover very quickly after prolonged droughts, with the more drought-resistant Blue Grama grass able to grow with as little as 0.2 inches of rainfall per year (Benedict book, page 208).

Buffalo Grass is a native, warm-season grass distinguishable by it's sod-forming, stoloniferous growth habit, and grows 1-6 inches in length per year (Benedict Book p.211). In comparison, Blue Grama grass is a native bunchgrass that is the taller of the two species (6-24 inches in height) (Benedict Book p.211). Additionally, a recent survey of Blue Grama Grass on the southern edge of the Chico Basin Ecosystem (11 miles south of our study site), showed roughly a 50% decrease in Blue Grama density from 1999-2015 (Rondeau et al. 2016), and similar trends can be expected for Buffalo Grass.

<u>Study site within the Chico Basin Ranch</u>

Our study site was located in the pasture that encompasses the airstrip and the pasture immediately to the east of the airstrip (Fig. 4). There appear to be multiple distinct patterns taking shape at the study site including distinct periodic patterns and dendritic patterns. Visual inspection of historical images show the distinct periodic patterns have begun to appear around early 2010 (within the last decade or so) (Fig. 5).

Fieldwork and Drone Imagery

Data was collected on multiple occasions from September 21st-October 14th 2020. Using the Phantom3Pro drone and a custom-build octocopter, we captured aerial imagery within six Areas of Interest (AOIs) (Fig. 4). Only AOIs 1, 2 and 6 were used for this study, with AOIs 3-5 conducted for a separate study. Within each AOI, the drone recorded images in either RGB (Phantom3Pro) or multispectral 5-band imagery including Blue, Green, Red, Red-edge, NIR (Octocopter) (resampled to a pixel size of 0.5m) of the surface and built a Digital Elevation Model (DEM). Drones flew at an altitude of 35m with image overlap of 85%. These images, together with 13 ground control points, were processed in Pix4D Photogrammetry Program into orthomosaics and Digital Elevation Models (DEMs). The coordinates for the ground control points were logged using a Trimble Geo7X GPS Unit.

In conjunction with the acquisition of drone imagery, we ran infiltration experiments to the north of AOI2. We poured 500mL of water into sections of plastic pipes (25cm in diameter, 15cm height) that were driven 3-5cm into the ground to eliminate leaking while still minimizing compaction at 12 locations of Bare Soil and 12 locations of Vegetated Patches, and recorded the amount of time until no standing water remained above ground.

Processing Geospatial Data

The relationship between band orientation and slope was visualized using ArcGIS Pro (V2.5.2), where elevation contours of 10cm were extracted from the DEM and overlaid with the orthomosaic images. The visualization of vegetation was made easier by identifying the ranges of… Sampling of cell values between vegetated and non-vegetated areas in orthomosaic images provided insight into the range of cell values representing each, which can then be used to visually highlight vegetated areas, allowing for easier visual comparison between vegetated orientation and slope. The agreement –or lack thereof– of vegetation orientation with slope can be determined primarily through visual inspection, in conjunction with angular analyses described above.

Areas within the AOIs where patterns appeared the most pronounced and representative of the surrounding area were extracted for further analysis into R, so as to remove noise from the analyses.

Data Analysis

Using one clipped area from each AOI, we used a Fast Fourier Transform (FFT) code in RStudio (v1.3.1093) to create a 2D-periodogram. from which we extracted angular (bin size = 5) and radial (bin size = 1) analyses of the strength of signal at given directions and wavelengths, respectively. FFTs take images potentially showing patterns that are products of multiple coexisting waves going in different directions at different wavelengths (i.e. a "complex wave") (e.g. Fig. 7a), it then decomposes the complex

waves into a sum of constituent sine and cosine waves each at explicit spatial wavelengths and orientations, ultimately producing a 2D-periodogram (e.g. Fig. 7b), which is a matrix of gridded cells visualized as an image, where the matrix is centered on x and y axes representing wave numbers (i.e. the frequency of the wave within the image). Each cell value in the matrix represents the amplitude (i.e. signal) of a single wave at a specific wave number in a given orientation within the original image. Angular Spectrum divides the periodogram into bins (e.g. "slices" of a pie) of a circle and aggregates the signal within each "slice", which can determine the directional components of the waves (e.g. Fig. 7c). Similarly, radial spectrum divides the periodogram into bins of equal frequencies (e.g. concentric circular bands) and aggregates the signal within each circular bin, which removes the directional information but provides aggregate information on dominant frequencies and wavelengths (e.g. Fig. 7d). For a wave to be considered periodic, it must repeat itself a minimum of three times (wave number $\geq$ 3). To differentiate the observed results from complete spatial randomness, we compared our results to the outputs of 100 randomly scrambled matrixes.

To identify the location of vegetated bands within the microtopography of AOI6, we ran a lagged correlation in RStudio (v1.3.1093) between orthographic values (a proxy for vegetation presence) and the relief of the slope (taken from DEM) along three transects perpendicular to the series of ridges and valleys in AOI6. Specifically, higher orthographic values represent vegetation, while lower relief values represent valleys, and vice versa. If vegetation organizes predominantly along ridges, we would see positive correlation values, and negative correlation values if it organizes within valleys. Moreover, lagged correlation values, where correlation coefficients are measured every 0.5m, can show the extent of vegetation organization between slopes and ridges, along with potential skewness therein (e.g. vegetation organizing predominantly on north-facing slopes). Potential skewness is further revealed through a hillshade via ArcGIS Pro (V2.5.2), which emphasizes micro-topography and visualizes vegetation presence within it.

Results

Infiltration experiments

Infiltration experiments at 12 separate locations of grassy and bare patches show the grassy patches infiltrated 500mL of water in 2 minutes 34 seconds, on average. In comparison, the average amount of time needed for a patch of bare soil (n=12) to infiltrate 500mL of water is 18 minutes 18 seconds. So, grassy patches can, on average, infiltrate water roughly 7x faster than the bare soil. The difference in infiltration rates between grassy and bare patches was statistically significant (t=3.17, df=11, p=0.009).

Analysis of periodicity in vegetation structure

Fourier Analysis reaffirms what fields observations and aerial imagery suggested: that there are periodic, banded patterns of self-organizing vegetation at Chico Basin Ranch (Fig. 7). At each AOI, the observed periodicities (Fig. 7d-f) orientations (Fig. 7g-i) and wavelengths (Fig. 7j-l) are non-random, in that they clearly diverge from the outputs of 100 randomized scrambles.

Comparing the AOIs reveal consistencies and variabilities between them. For instance, patterns consistently have a dominant wavelength between 0-10 radial bins (Fig. 7j-l). However, since the sizes of the areas measured were different between each AOI (AOI1 = 114m; AOI2 = 90m; AOI6 = 104m on each side), the size of their radial bins will also vary, capturing slightly different wavelengths within them. For specific wavelength values, the periodograms were used by finding the specific locations of cells with strong signal (warmer colors), with their specific location in relation to the center calculated via Pythagorean theorem, and then divided by the length of the AOI.

$$wavelength = \frac{(\sqrt{x^2 + y^2}\,)}{l}$$

For AOI1, the dominant wavelengths are ones directly North-South at a wavelength of 22.35m, and the second most dominant wavelength, which is slightly diagonal from North-South (NW-SE direction), is a wavelength of 15.8m. In AOI1 here is also significant wavelength at exactly wave number of 1, which would indicate a wavelength equal the entirety of the length of the study site. For AOI2, the dominant wavelengths are also ones directly and/or nearly North-South at wavelengths of 17.65 and 10m,

respectively. In this way, the orientations and wavelengths of AOI1 and 2 are very similar, with a predominantly North-South orientation with periodicity in the 10s of meters. This is despite their slope gradients being very different, with AOI1 having gentler slopes and weak concavity; which the vegetation aligns to (Fig. 7a), while AOI2 has slightly steeper slopes and N-S periodic pattern in the vegetation consistently going diagonally to the slope which in the NE-SW direction (Fig. 7b). This consistent North-South orientation in the vegetation on top of a consistent NE-SW slope gradient creates an "oblique" banding pattern in AOI2. This obliqueness is unexpected based on a simple runon-runoff system.

The wavelengths and orientations of AOI6 are notably different from those of AOI1 and 2. AOI6 has very strong periodicity in the Northwest-Southeast direction (roughly 145° (Fig. 7i)) at a wavelength of roughly 36.8m. Within these large bands, there is smaller cross-banding (Fig. 7c), and these can be seen in the East-West signal (roughly 0° and 45°; Fig. 7i). The orientation of the large bands have a striking correspondence with the microtopography of the site, where there is a series of small "ridges" and "valleys" oriented parallel to the large periodic bands (Fig. 7c). The "ridges" and "valleys" have elevation difference approximately 10 cm across the 30+m spacing.

The vegetation appears to be organized on the bottoms of the "valleys" and extending on the south facing slopes of the "ridges". This can be seen by visual inspection of a vegetation overlay over a hillshade of the microtopography (the hillshade was created with the sun is directly south and __15?_ degrees above the horizon): it is revealed that the vegetation is organized almost exclusively on south-facing slopes within the microtopography (Fig. 8). Furthermore, the vegetated bands appear to align closer to the valley bottoms than the ridge peaks (Fig. 8). This suggests the vegetation bands are organized within the bottom of the valleys, but are also skewed towards the south-facing slopes.

This observation is further corroborated by lagged spatial correlations between the pixel value of the vegetation raster and the relief of the slope along transects that cross several bands of vegetation and associated ridges (Fig. 9). In this analysis the vegetation pixel value was correlated with elevation along the transect, the correlation coefficient was recorded and then the two spatial series were lagged by 50 cm and the process was repeated for 100 successive lag steps. The analysis allows us to answer two important

questions (1) do the two patterns oscillate together, and (2) how are the oscillating patterns oriented with respect to each other (Turchin, 2003 Complex Population Dynamics, Princeton University Press). (1) If the patterns oscillate together then the lagged correlogram should result in a sinusoidal function oscilating between positive and negative correlation, which it clearly does (Figure 7). (2) If the two oscillatory patterns are arranged so that the peaks in vegetation value correspond to the peaks in elevation the correlogram starts with a positive correlation at lag=0 and the correlation decreases towards negative values at an increasing lag. If the peaks in vegetation value correspond to troughs in the elevation profile, then the correlation at lag=0 is negative and increases towards positive values at an increasing lag. If the two patterns are offset with respect to each other, then the location of the peaks and throughs of the correlogram correspond to the spatial lag between the two patterns. At three separate transects (Fig. 9), the troughs of one variable (e.g. plant absence, valley bottoms) are largely lined up with the peaks of the other variable (e.g. plant presence, ridge tops), as the two variables are initially negatively correlated (Fig. 10). In other words, plant presence is associated with valley bottoms, and plant absence is associated with the tops of ridges. In some instances, the troughs of one variable already directly align with the peaks of the other variable (Fig. 9b), but can be realigned if lagged roughly 60-70 cells, or 30-35m, which is around the dominant wavelength of the vegetation bands in AOI6 (Fig. 7f). In other instances, the troughs and ridges directly align if the vegetation is shifted (i.e lagged) slightly (Transect 1 = 7.5m (Fig. 10a); Transect 3 = 3.5m (Fig. 10c)). This suggests the vegetation is skewed from the valley bottoms. Since each transect starts in the North and moves South, the following lagged correlations suggest the vegetation is skewed towards the south-facing slopes.

Additional spatial patterns present at our study site

The aerial imagery from Google Earth also revealed the presence of an additional spatial pattern at Chico Basin Ranch: a "dendritic" pattern of grasses branching out in multiple directions seemingly irrespective of slope. Field observations of tall grasses exhibiting a similar pattern suggest these patterns are formed through the self-organization of Buffalo Grass; as opposed to the distinct, banded patterning of short Gramma Grass. However, official species identifications have not yet been conducted for either

pattern. Furthermore, aerial imagery revealed that the distributions of each pattern do not overlap; but rather, form alternating bands of each pattern in the East-West direction on the scale of 10s to 100s of meters (Fig. 4). Indeed, there appears to be a distinct spatial segregation of the two patterns, where they alternate in a clear and consistent orientation (Fig.). Further exploration of these dendritic patterns is beyond the scope of the present study.

Discussion

Overview

When faced with resource scarcity, arid vegetation can self-organize around resources it concentrates into distinct, "Turing Patterns". Theoretical models suggest the formation of these patterns are early warning signs of a future catastrophic shift in the ecosystem's state (i.e. desertification). However, at this point in time the connection between the presence of periodic spatial pattern and a catastrophic bifurcation is tentative because of the relative scarcity of empirical studies documenting the exact mechanisms responsible for the pattern formation . In some instances of empirical studies cast doubt on significant aspects of model predictions, largely due to their sole reliance on and assumptions of a runoff-runon system acting as the driving mechanism, while ignoring the possibility of additional mechanisms that might drastically alter model outputs (Dunkerly 2018). Truly, a site-specific, empirically-informed model is necessary to make accurate risk-assessments of potential catastrophic shifts . The present study uses preliminary field data and drone imagery on self-organizing arid grasses in Southern Colorado to test whether periodic, banding patterns are present, and to what degree their formations can be explained by a runoff-runon system; specifically identifying deviations from this relationship and outlining potential mechanisms and empirical tests to further understand the ecosystem as a whole.

Periodic Vegetation and The Presence of a Runoff-Runon System

Aerial imagery of grasses at Chico Basin suggested the vegetation was organizing in a banded pattern (Fig. _). Radial spectrum analysis of three separate instances of these patterns confirm that the vegetation was forming in highly periodic bands (Fig. 7), providing yet another example of Turing patterns in arid ecosystems found throughout the globe (Bromley et al. 1997; Klausmeier 1999; Hardenberg et al. 2001; Shnerb et al. 2003; Penny et al. 2013; Gandhi et al. 2018).

Analyses of the wavelengths and orientations of the banded vegetation patterns in AOIs 1 and 2 reveal the predominant directions are North-South with some minor variability. The periodograms also include some wavelengths in diagonal and East-West directions. .In all cases, the data are mostly in low frequencies, corresponding to wavelengths in 10s of meters (Fig. 7). In comparing the three AOIs, AOI1 & 2 are very similar, despite differing slope gradients. Vegetation patterns in AOI6 are in NW-SE direction and appear to be corelated with microtopography.

Currently, most models of banded vegetation on gentle slopes assume they are formed entirely by a runoff-runon system (Dunkerly 2018). To activate a runoff-runon system, there must be stark differences in the infiltration rates between vegetated patches and the surrounding bare soil (Pueyo et al. 2013). A number of empirical studies have identified this phenomenon in arid ecosystems and their corresponding vegetation patterns (Berg & Dunkerly, 2004; Getzin et al. 2020), and this study now does the same, with infiltration rates at Chico roughly 7x faster in grassy patches than in the bare soil (t=3.17). It is important to note that the details of the infiltration methodology vary between studies, including this one, making direct comparisons between specific infiltration results difficult. Regardless, there is a consistent, empirical trend of significantly higher infiltration rates in vegetated areas than in the surrounding bare soil. The presence of the stark contrast in the infiltration rates indicates the potential for the runoff-runon system to operate. Of course, a runoff-runon system is only activated when there is adequate precipitation necessary to generate runoff over the bare patches; which might only occur seasonally in arid ecosystems (Dunkerly 2018). However, the models largely assume homogeneous space and homogeneous conditions (i.e. assumption of constant rainfall across the entire system). In reality, the timing and stochasticity of rainfall can interact with the natural history of the local vegetation, and

understanding this interaction is important to accurately capturing the runoff-runon system in models. Regardless, considering the presence of banded patterns along gentle slopes, coupled with the stark differences in infiltration rates between vegetated patches and bare soil; it is reasonable to assume a runoff-runon system is a mechanism forming the banded patterns at Chico.

Deviations in Band Orientation From Runoff-Runon System

Oblique Orientation in Banded Patterns

However, a runoff-runon mechanism cannot singlehandedly explain the variations observed in the orientation of banded vegetation with respect to slope. If a runoff-runon system was the only mechanism driving pattern formation, then we would expect to see vegetated bands oriented perpendicular to the slope gradient (i.e. contour-parallelism). This pattern is clearly present in AOI1, where the bands orient across slope and the curvature of the vegetation bands follows the curvature of the contour lines (Fig. 7). This is the relationship that traditional models would create (Dunkerly 2018), and it is what one would expect if a runoff-runon system is determining the self-organization of the vegetation. However, significant deviations from this relationship can be observed at AOI2, where one of the components of the angualr spectrum might be consistent with slope, but the dominant orientation is oblique to the slope gradient (Fig. 7). Oblique vegetation has been previously documented at only a few locations (Dunkerly & Brown, 2002; Berg & Dunkerly, 2004). Previous observations of oblique banding having different wavelengths than local instances of contour-aligned banding, despite forming under the same climate conditions, suggest the presence of additional mechanisms in pattern formation and orientation (Dunkerly & Brown, 2002). However, such mechanisms have not yet been identified; and to date, there have not been any empirical studies on the formation of this oblique patterning. Be that as it may, there have been some preliminary hypotheses in the literature explaining their formation. For instance, Dunkerly & Brown (2002) and Dunkerly (2018) suggest the oblique vegetation patterns might have been formed by a different, no longer present mechanism, and is now maintained by pedogenic processes of soil and sediment transportation in the runoff-runon system. This sediment transport decreases the soil porosity by

depositing clay particles into the interstitial space in the soil, potentially preventing root penetration into intergrove soils, thereby freezing the pattern early on and potentially allowing the runoff-runon system to continue to operate, but this time along an oblique orientation. However, they are also careful to mention that this is merely a hypothesis, and they also note that it still doesn't definitively identify the *initial source* of the patterning, but rather can explain how it is maintained. McGrath et al. (2012) produced a model that replicated oblique orientations through a non-periodic, "oblique" orientation of the upper catchment boundary (e.g. a "ridge" from which the water started flowing). In other words, the geometry of the catchment itself could produce such patterns, as it can influence the initial direction of water flow into an oblique direction. This, in turn, could create a feedback loop of water, nutrient and sediment transportation downslope that retains the oblique orientation across the slope. In general, deviations from contour-parallelism might be products of the surrounding microtopography. Penny et al. (2013) also observed some deviations in banded orientation from the slope direction; and found that these deviations predominantly occurred along ridges, streambeds, and roads; however, the oblique orientation did not remain constant as it moved further downslope, like was observed at AOI2. Furthermore, the authors did not connect obliqueness to microtopography, and such features of microtopography have not yet been identified at AOI2.

Oblique orientation might also be caused by internal heterogeneity of overland flow, leading to skewed upslope migration of the bands where sections receiving less water would migrate at a slower rate than other sections (McGrath et al. 2012). Small variations in microtopography can lead to variations in overland flow which are further amplified by the vegetation structure itself. It is worth pointing out that the bunchgrass vegetation stands on micro-elevated platforms approximately 1-2cm above the elevation of the soil crust. The positioning of the vegetation micro-platforms can thus direct overland flow of water.

In addition to the perpendicular banding orientation, mathematical models also consistently predict slow and consistent upslope migration of the vegetation bands (Dunkerly 2018). As of yet, our study has not found any evidence of the band's migrating upslope, although we recognize that all analyses

17

of historical imagery necessary to identify such migrations has been largely preliminary, but visual inspection of Google Earth images does not support migration of the bands in the past 10 years.

Clearly, the patterned vegetation at Chico Basin Ranch is not behaving 100% in line with the predictions of simple mathematical models based on the runoff-runon system. Our current understanding does not fully capture the dynamics of the system; and as Dunkerly (2018) states, the vulnerability of an ecosystem to catastrophic regime change cannot be accurately determined until the mechanisms creating their patterns are properly identified. With this in mind, future research at Chico should directly investigate these specific locations of oblique patterning. At the same time, future work should consider the historical legacies of the pattern's formation; recognizing that patterns might've formed through mechanisms that are no longer operating, but are currently maintained through strong enough feedbacks in a runoff-runon system.

Banded Patterns and Dunes

Even greater deviations can be observed at AOI6, where the big bands of vegetation are oriented parallel to the slope gradient. Figure 6 shows that the banded vegetation patterns align with the microtopography of ridges and valleys that are also parallel to the slope gradient. This microtopography is a series of ridges and valleys roughly 25-35m apart that resemble linear dunes (Tsoar et al. 1986). The microtopography is imperceptible in the field, with the height differences between the crests of the ridges and the troughs in the valleys only roughly 10-20cm over a distance of 10-20 meters. Lagged correlations between the periodic microtopography and the periodic vegetation patterns show that the vegetation organizes on the south-facing micro-slopes and micro-valley bottoms; whereas north-facing micro-slopes are mostly bare of vegetation (Fig. 9). Gandhi et al. (2018) identifies that systems where vegetation only occurs within the valleys and not the ridges are indicative of very low water availability, as they can only effectively concentrate water in areas of topographic water convergence, rather than divergence. Interestingly, the vegetation is not only located at the bottom of the valleys, which is where optimal runoff capture would be expected, but rather they are skewed to the south-facing slopes of the valleys,

with no vegetation found along the north-facing slopes (Fig. 9). Considering the aridity of the region, a higher plant biomass is typically observed along north-facing slopes (for example in forests on ridge-valley systems along the Front Range, personal observation), which receive less solar radiation than south-facing slopes. With this in mind, the south-facing skewness of the vegetation bands suggests water availability is not the only driver of pattern formation in AOI6. Possibly, an interaction between vegetation-induced soil stability and wind erosion could be a factor in forming the observed patterns.

In the context of dunes, this interaction has been well documented (Tsoar et al. 1986; Duran & Moore, 2013). Linear dunes are formed through differential wind shear on the windward and leeward slopes, with greater wind erosion on the former (Tsoar 1989). In this way, reduced wind erosion on the leeward slopes allows for finer particles of silt and clay, which are important for vegetation to retain organic matter, to settle (Tsoar et al. 1986; Duran & Moore, 2013). In general, linear dune formations provide vegetation refuge from wind erosion on its leeward slopes, while the vegetation also stabilizes the surrounding soil through its root structure, further reducing wind erosion around it on the leeward slopes of dunes (Duran & Moore, 2013). This feedback culminates in vegetation organizing almost exclusively along the leeward slopes of dunes (Duran & Moore, 2013). In fact, an unpublished study of dune formations further north in the Chico Basin identified vegetation forming primarily along the leeward slopes of dunes, with there being smaller grain sizes on the leeward side than the windward sides of dunes (Kelso et al. unpub.). Aerial Imagery of these dunes reveals the north-facing slopes are scoured, while the south-facing slopes are vegetated, which is similar to the orientation of vegetated and bare sites of the "dunes" in AOI6; despite different dune structures, where the dune field had "scalloped" dunes several meters high, while AOI6 had linear "ripples" 10-20cm high resembling linear dunes. Not only does this show that dunes can form within the study ecosystem, it also strongly suggests the effect of wind erosion as a mechanism in vegetation formation within AOI6. Interestingly, the orientation of the dune fields at Chico Basin and of the "dunes" in AOI6 suggests the wind erosion is coming from Northwesterly winds (Fig.), which largely occur in the winter (Kummel pers. Comm.; Kelso et al. unpub.).

Overland flow in a runoff-runon system still appears to influence the pattern morphology in AOI6, as there is consistent cross-banding within the large bands, where the crossbanding is perpendicular to the slope gradient (Fig. 8). This cross-banding is largely thin bands of bare soil interrupting the vegetation from being fully uniform. In general, the presence of banding within valleys is indicative of higher aridity and lower water availability (Gandhi et al. 2018), conditions which are consistent with the conditions at Chico Basin Ranch. Moreover, this cross-banding might have a convex-upslope orientation, which has been previously documented in 80% of bands in valleys in Western Australia (Gandhi et al. 2018).

This crossbanding pattern contains additional significant and interesting details. The crossbanding pattern changes along the upslope margins of the large bands, where there are smaller, secondary bands that are perpendicular or go at an angle to the slope in a "branching" pattern off of the bigger bands (Fig. 7). These patterns are interesting for multiple reasons: 1) These "branches" only occur to the North of the larger bands, along the southward-facing slopes of the valleys, potentially as a result of wind erosion as explained earlier. 2) These smaller bands also seem to go at an oblique angle to the slope, rather than directly convex-upslope (Fig. 7). In this way, there appear to be greater deviations from contour-parallelism in the cross-banding as they move further upslope. Penny et al. (2013) noted that deviations in pattern orientation to slope gradient in their study in AAABBBCCC were observed 50% more frequently by ridges and streambeds, with more pronounced deviations closer to the ridges and further upslope. Overall, there are distinct and observable patterns at multiple wavelengths and orientations in AOI6; and these can each be formed by a confluence of exogenous and endogenous processes that would not be predicted by simple runoff-runon models, requiring extensive empirical tests in future research.

In summary, divergent infiltration rates and the general cross-slope orientation of vegetation banding in multiple instances at different wavelengths suggest a runoff-runon system is operating at Chico, and that it has some degree of influence on pattern formation and morphology. However, deviations from the expected perpendicular orientation to slope in AOI2 and 6, which exhibit oblique and

parallel orientations to slope, suggests the presence of additional mechanisms that are not included in

models and need to be explicitly identified in future research.

Other Potential Mechanisms in Banded Pattern Formation

Overall, the runoff-runon system seems to have some effect on the system, but it remains

uncertain how important it is in pattern formation, and it does not seem to be the only mechanism in

place. Potentially, an additional mechanism is wind erosion. Field observations of dust devils at the site,

along with larger grains of sediment present on top of the clay crust in the bare soil than in the vegetated

patches (2-3mm across, which suggests wind removal of finer sediment), observations of the vegetated

soil standing slightly higher than the bare soil, coupled with the south-facing skewness of valley bands in

AOI6, suggest that wind erosion can play an important role in pattern formation and/or pattern

maintenance.

Moisture can be delivered to arid ecosystems through both rain and snow; yet to date, no studies

have investigated the role of snow as a potential mechanism in arid vegetation's self organization. As

established earlier, the movement of liquid water is determined by overland flow in a runoff-runon system

(McGrath et al. 2012). If precipitation comes in the form of rainfall, then the initial dispersal of liquid

water can be considered uniform across small spatial scales (i.e. little variation in precipitation levels over

10s or 100s of meters, or the scale of observed vegetation patterns). However, the same might not be true

for the dispersal of snowmelt, as wind can alter the distribution of snow after it reaches the ground.

Moreover, the susceptibility of snow redistribution might not be analogous between vegetated areas and

non-vegetated areas. Indeed, previous studies on alpine treelines reveal the vegetation there could trap

snow and act as "snow fences," while the snow in the surrounding area would scour, thereby influencing

the accumulation of snow over space (Hiemstra et al. 2002). It is reasonable to expect a similar

relationship between vegetation and snow distribution at Chico, which would be seen in the banded

vegetation capturing snow while the wind would be scouring the snow over the bare soil. When the snow

melts, differences in snow accumulation can further contribute to moisture differences between the vegetated patches and the bare soil. Preliminary drone images suggest the snow at Chico is organizing into "puddles" over the bare soil, with the vegetated patches acting as "islands" (Kummel, pers. comm.). However, detailed analysis of these images, and the addition of multiple other drone images in the future, combined with empirical experiments, is necessary before the influence of and dynamics within this mechanism can be ascertained.

Additionally, temperature differences between vegetated areas and bare soil might also influence pattern formation and morphology. Getzin et al. (2020) found that the shading from vegetation organized in Fairy Circles made the underlying soil up to 25 C cooler than the surrounding bare soil during the hottest part of the day; however, they did not elaborate much on the implications of this finding. Regardless, such a marked difference at Chico, or any site, would likely have drastic effects on the evapotranspiration rates and the overall survival and resilience of vegetated patches to climate change.

Finally, it is important to recognize the influence of each grasses' natural history and phenology in pattern formation. This includes, but is not limited to, their seed dispersal processes (Thompson et al. 2008; Thompson & Katul 2009) and root structure (Barbier et al. 2008; Lefever et al. 2009).

Potential Species Coexistence Through Large-Scale Alternating Bands

This paper focuses mainly on the self-organization of Buffalo Grass into banded patterns at Chico Basin. However, aerial imagery reveals that these patterns are only half the story, as these patterns alternate with dendritic self-organization of Buffalo Grama grass, creating large, alternating bands of distinct patterns in the North-South direction on the scales of hundreds of meters (Fig. 6). Such distinct segregation of two self-organizing species has not been extensively documented in arid ecosystems, but it might have connections to species coexistence. This patterning could be due to spatial front pinning, which allows for coexistence of multiple patterns across stable mosaics, even though they exclude each other locally (Uecker & Wetzel, 2014; Meron 2016).

At the same time, it could also be a product of competition and the system being "frozen" in place by the runoff-runon system. In other words, the organization of each species is a product of optimal resource capture, which is now determined by their respective root structures. As a result, neither grass species can establish in the bare areas, and differences in root structure means each grass would be outcompeted by the other if they established in the other's patches. In short, the runoff-runon system makes each grass the best competitor where it is currently distributed, allowing for coexistence of multiple stable states across space.

This still begs the question of why are the two grass species organized into such distinct bands in the first place. Perhaps, this can be due to banding in the underlying soil types, which can vary over 100s of meters and have significant effects on the overlying vegetation patterns (Penny et al. 2013). While both grasses have similar root structures, the Blue Grama grass is more resilient than the Buffalo Grass; so it might establish in soils with poorer conditions than Buffalo Grass (Benedict Book). In fact, a recent soil survey in Chico Basin taken 11 miles south of our study site revealed a highly variable soil substrate to the scale of hundreds of meters (Rondeau et al. 2016). More importantly, this soil primarily varied in the same direction as the larger bands of dendritic and banded vegetation patterns.

It is also possible that this banding of alternating patches of grass of the two competing species already existed before they each began self-organizing in the early 2000s. On the other hand, it is possible that their coexistence was spatially homogenous and non-periodic, and that worsening environmental conditions and self-organization ultimately created these alternating bands of competing species.

Overall, it is important to recognize that the natural history and phenology of the two grasses are different, and can interact with the same environmental conditions and mechanisms in different ways; thereby producing different patterns. This paper focuses mainly on the banded patterning of the Grama Grass, and equivalent research is needed for the Buffalo grass in the future. Indeed, both species can have different resilience to environmental change, so if one population crashes, it could be possible that the other won't, and might benefit from such a shift and establish in the other's previous range. On the other hand, the climate feedbacks that each grass provides to the ecosystem might result in an entangling of

their crashes. Regardless, modelling the risk of ecosystem crash requires adequate research on both species.

Implications for Future Work

The theoretical literature suggests the emergence of periodic vegetation patterns in arid ecosystems is an "early warning sign" for future catastrophic shifts in the ecosystem state; resulting in a more barren landscape (Kefi et al. 2007). Similarly, model predictions rely on a runoff-runon system as the mechanism for pattern formation. While the theoretical literature and models provide interesting results that bring attention to the importance of studying pattern formation in arid ecosystems; in real ecosystems, pattern formation is often more complex and cannot be fully explained by one mechanism, resulting in inaccurate models that overpredict an ecosystem's potential for catastrophic shifts (Dunkerly 2018). To date, identifying pattern formation has never prevented a catastrophic shift in arid ecosystems (Kefi et al. 2014), but empirically-driven, site-specific models might be able to accomplish this feat in the future. The present study identifies periodic, banded vegetation at Chico Basin Ranch in Southern Colorado, along with evidence for a runoff-runon system; but also identifies deviations in pattern formation that suggest other mechanisms --either active or inactive-- are at play. Most of the mechanisms hypothesized in this paper have rarely been considered within the context of pattern formation in arid ecosystems, if at all. In order to accurately predict the potential for a catastrophic shift at Chico Basin Ranch, extensive field experiments should be conducted at the site to identify all mechanisms involved in pattern formation.

Within this framework, future studies should involve tests of overland flow at each of the identified locations (e.g. through a sprinkler system to simulate rain showers). Definitive pedologic studies should be conducted to identify soil depth, type and characteristics throughout the study site, and especially between the banded and the dendritic patterns and their respective root architectures. Future studies should also replicate the analyses of this paper at the same locations using historical aerial imagery (provided by Google Earth) to test whether patterns are migrating upslope, and specifically

whether the boundaries between the banded and dendritic patterns move over time, in order to ascertain competition and coexistence. If possible, a weather station should be placed at the site year-round to collect precipitation levels, along with wind speed and direction, providing insight on how each plant's natural history might interact with the climate (e.g. seed dispersal, activation of runoff-runon system, the effect of wind erosion and the creation of dunes, etc.). Infiltration experiments should also be conducted at each of the locations where the band's orientation deviates from contour-parallelism to see whether the runoff-runon system is homogeneously activated. Wind speed tests should also be conducted on the south-facing and north-facing slopes of the "linear dunes" identified in AOI6 to see whether the microtopography is creating refugia from harmful wind erosion. Aridity levels should also be calculated along the south-facing and north-facing slopes to build a cost-benefit analysis of wind speed and aridity for vegetation presence in dune formations. The role of snowfall in arid ecosystems has not been adequately studied, and future work should include additional drone-imagery and empirical tests of snow distribution following recorded snow events in the region. Tests should also be conducted on the temperature differences between the vegetated patches and the bare soil (following the methodology in Getzin et al. 2020). Additionally, further analyses on the effects of grazing on the ecosystem should be done, particularly asking whether nutrient cycling through cow poop leads to future vegetation, and what the immediate and long-term effects of cow's trampling and consuming grasses are on the ecosystem. Finally, future research must dive into the biology and natural history of the particular grass species, as small details of their biology and life history can make a big difference in how the ecosystem operates.

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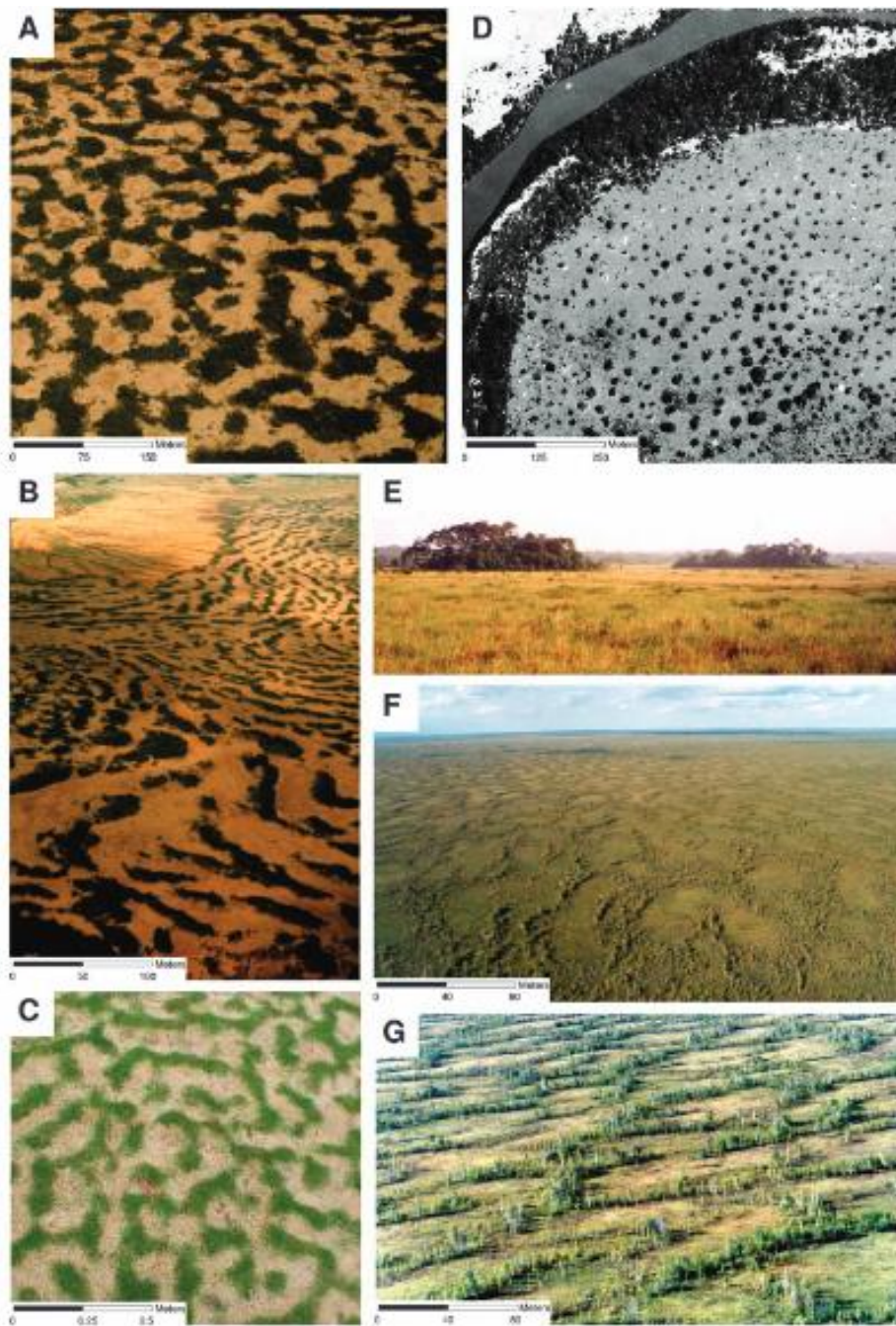
Figures

Fig. 1 Aerial imagery of self-organization of vegetation in real ecosystems. (A to C) Arid ecosystems: a) Labyrinth pattern of bushes in Niger. b) Banded patterns of bushes in Niger c) Labyrinth pattern of perennial grasses in Israel. (D and E) Savannah ecosystems: Aerial and ground photographs of spotted

tree patches in Ivory Coast and French Guiana, respectively. (F and G) Peatland ecosystems: Maze patterns of shrubs and trees in Western Siberia. (original figure provided by Rietkerk et al. 2004).
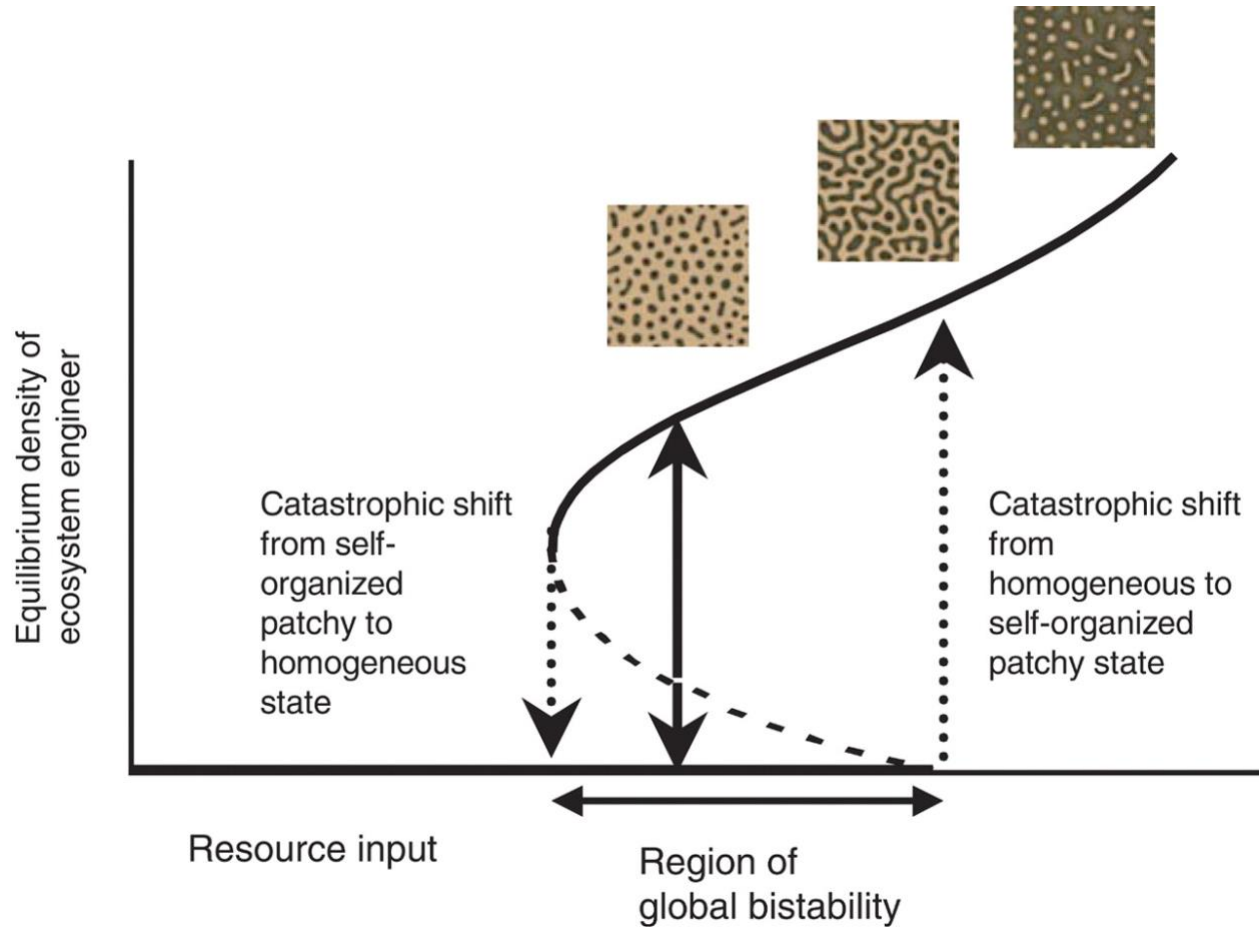
Fig. 2 Graph demonstrating vegetation self-organization and subsequent pattern formation in response to decreased resource availability, along with their potential location within alternative stable states and potential catastrophic bifurcation. (original figure provided by Reitkerk et al. 2004)
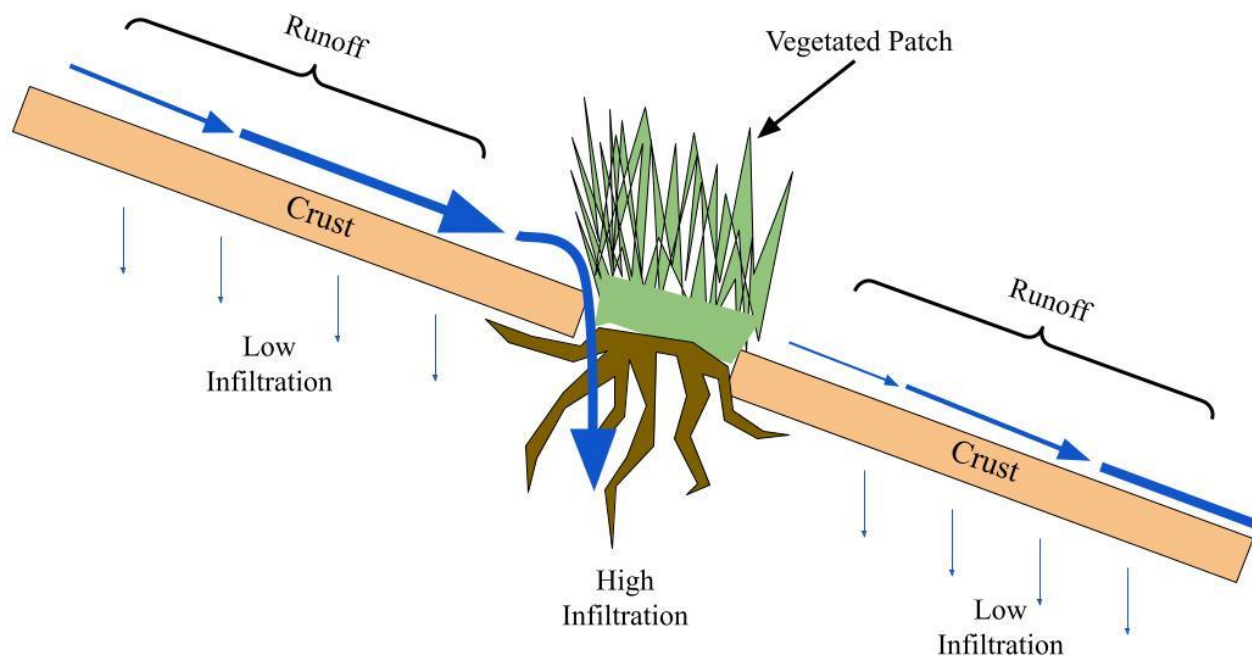
Fig. 3 Illustration of the runoff-runon system along gentle slopes in arid ecosystems. The layer of crust on top of bare soil greatly reduces infiltration, causing the water above it to largely flow downslope. The roots of vegetated areas break up the crust and underlying soil, allowing for the runoff to infiltrate and be absorbed by the vegetation. This process is repeated multiple times along the slope gradient, and can lead to periodic banding of arid vegetation.

Fig. 4 Location of each AOI in the study area of Chico Basin Ranch, located east of the ranch's airport. AOI 1, 2 and 6 were used for this study due to the distinct banded patterns visible there, while AOIs 3-5 were centered around a water tank for cows in a separate study regarding grazing.

Fig. 5 Time series of the same location at Chico Basin around AOI1 between 2006 and 2019 detailing distinct pattern formation through vegetation self-organization between that timeframe.

Fig. 6 Highlighted areas of the two emerging patterns at the study site: banded vegetation (yellow) and dendritic vegetation (white). The areas that each patterns occupy do not overlap, and create alternating bands in a distinct, East-West direction. Their location with respect to the airport is also highlighted, however the highlighted pattern extends through and beyond the entire study area.
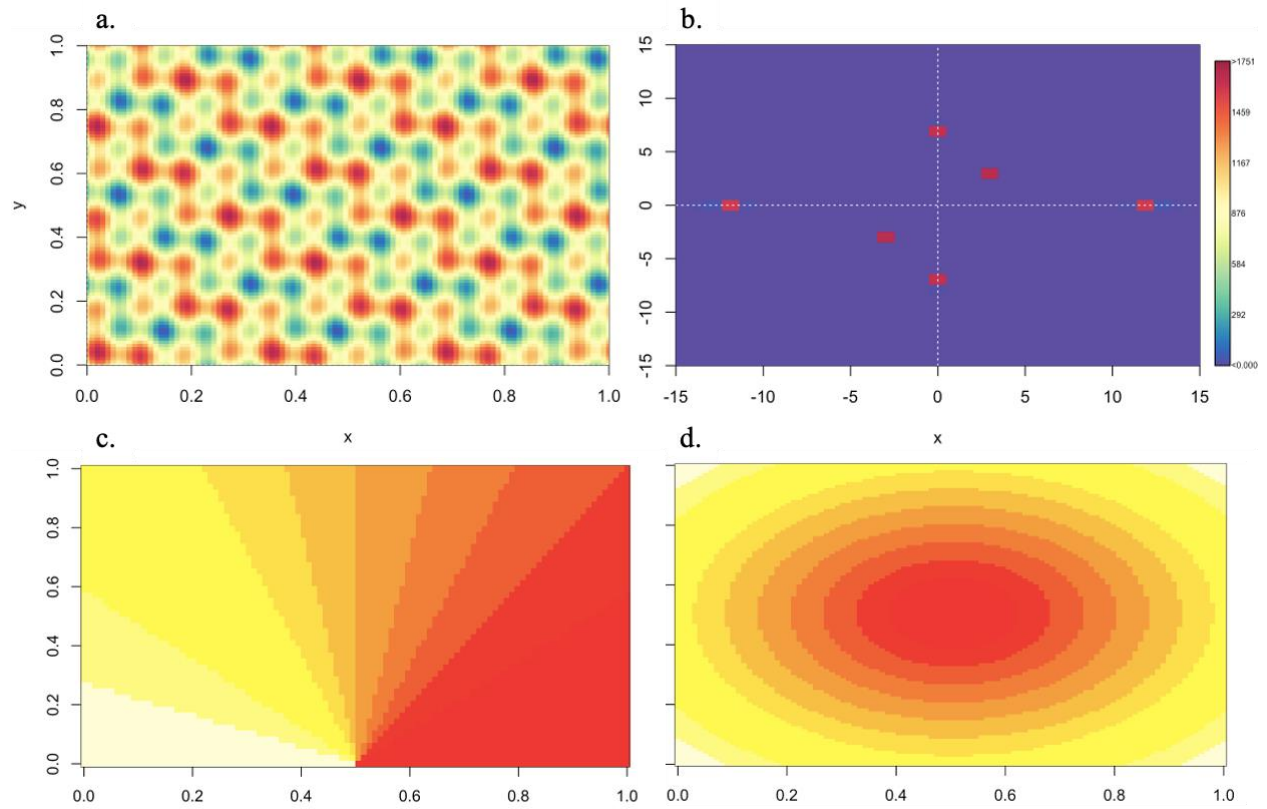
Fig. 7 Examples of simulated data (a), and the resulting periodogram (b), angular spectrum (c) and radial spectrum (d) (Provided by Kummel 2021).
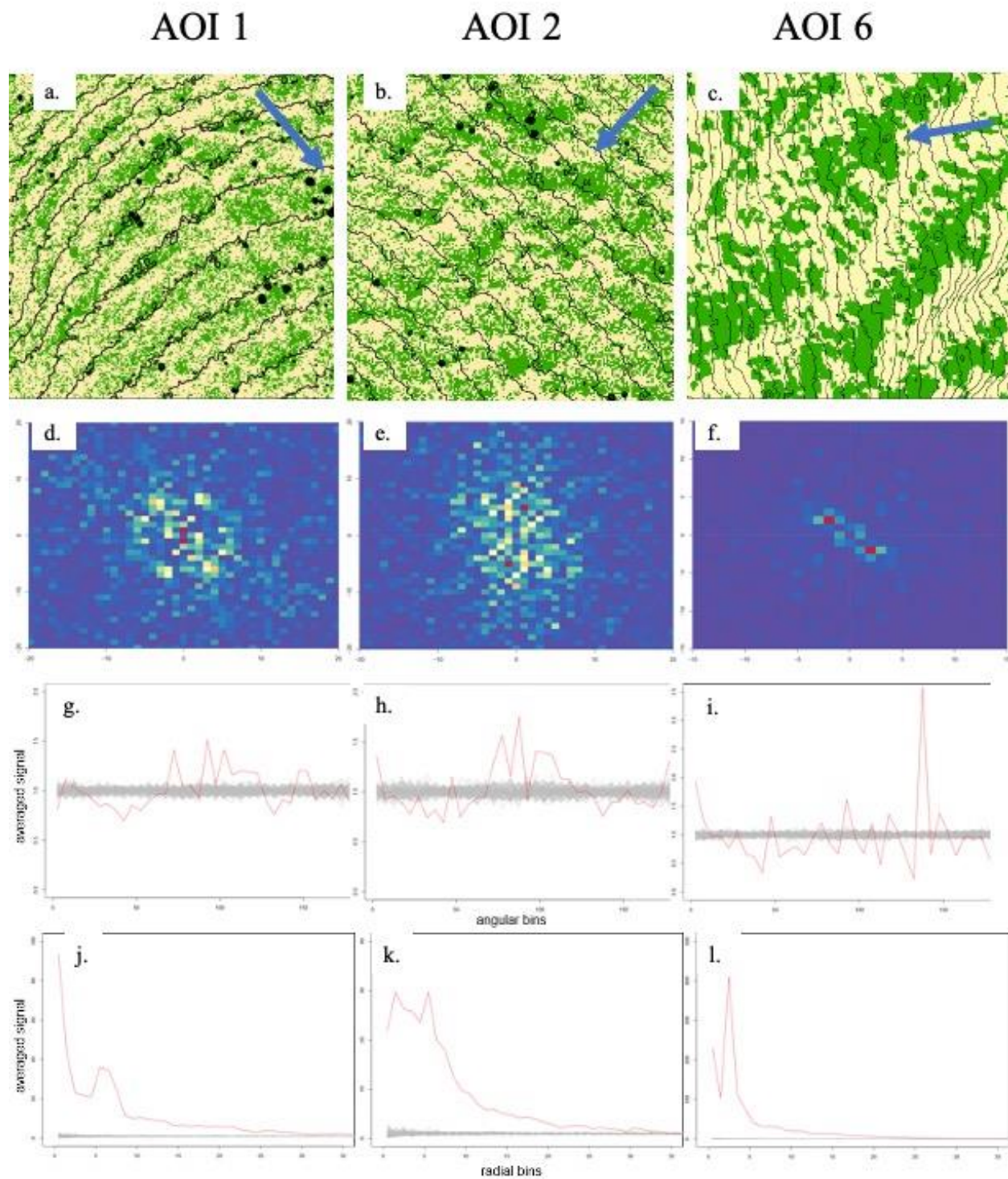
Fig. 8 Inputs and outputs for the Fourier Transforms for the clipped areas of AOI 1, 2 and 6 (First, Second and Third columns, respectively). (A-C) Orthomosaic imagery of vegetation (color scaled to green) in relation to slope contours of 10cm (red lines). Blue arrows indicate the general direction of water flow, pointing towards lower elevations. (D-F) Periodograms for each AOI showing the amplitude of observed

waves at every wavelength and direction. Warmer colors indicate a stronger signal at that specific wavelength and direction. (G-I) The strength of signal given from each angular bin (red line) in comparison to those of 100 randomly scrambled patterns (grey lines). Areas where the red line is notably different from the grey lines indicate the patterns at those orientations are non-random. (J-L) The strength of signal given from each radial bin (red line) in comparison to those of 100 randomly scrambled patterns (grey lines). Areas where the red line is notably different from the grey lines indicate the patterns at those wavelengths are non-random.
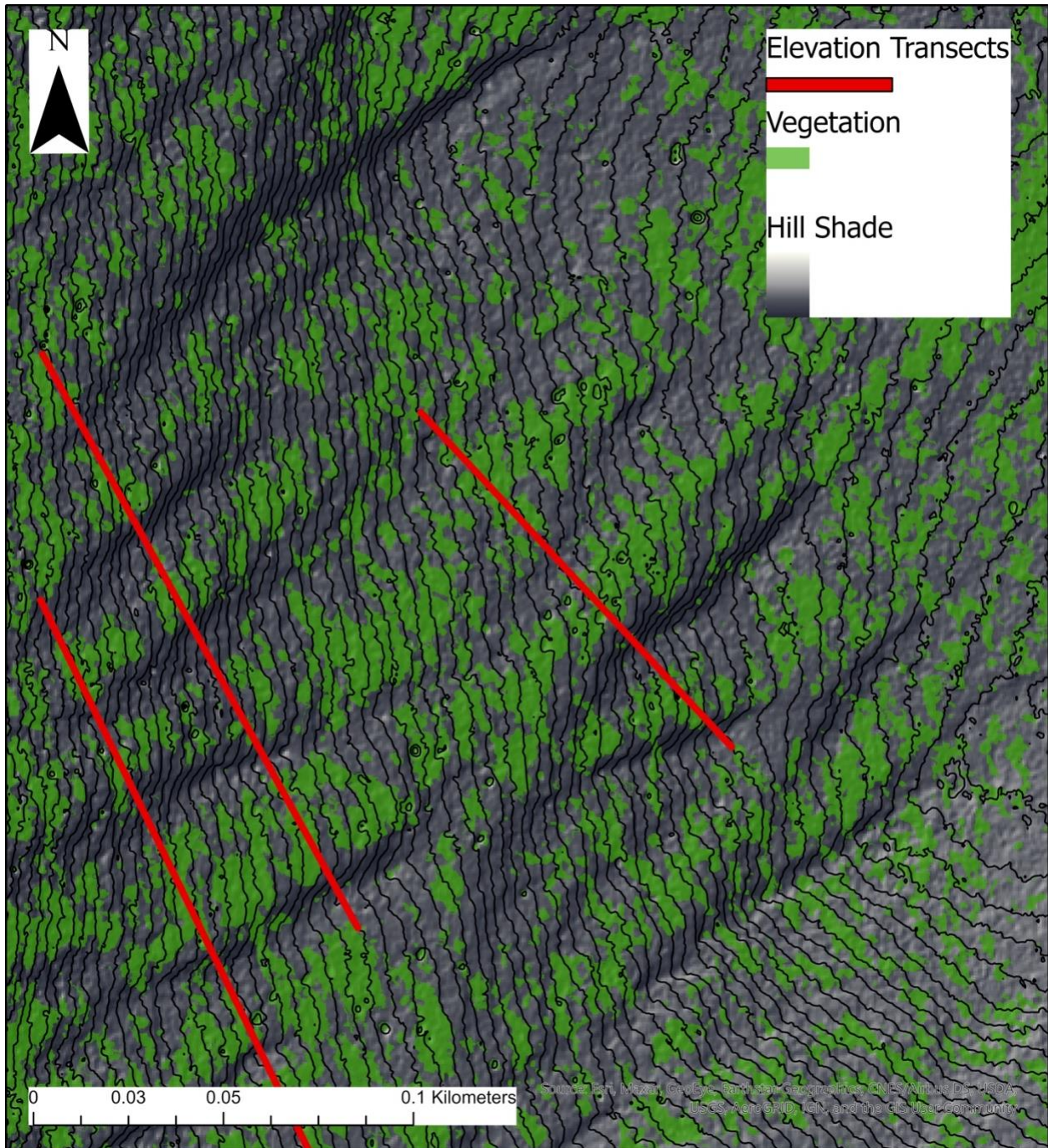
Fig. 9 Areas of classified vegetation at AOI6 in green over the underlying terrain, which has been hillshaded (black to white) with the sun oriented directly south at 15 degrees above the horizon. Black areas indicate north-facing slopes, while lighter areas indicate south-facing slopes and areas of no slope (predominantly in the upper right). Red lines indicate transects where points were sampled every 0.5m for lagged correlation analysis. Comparisons between vegetation location and the hill shade reveal where vegetation organizes within the series of ridges and valleys in AOI6.
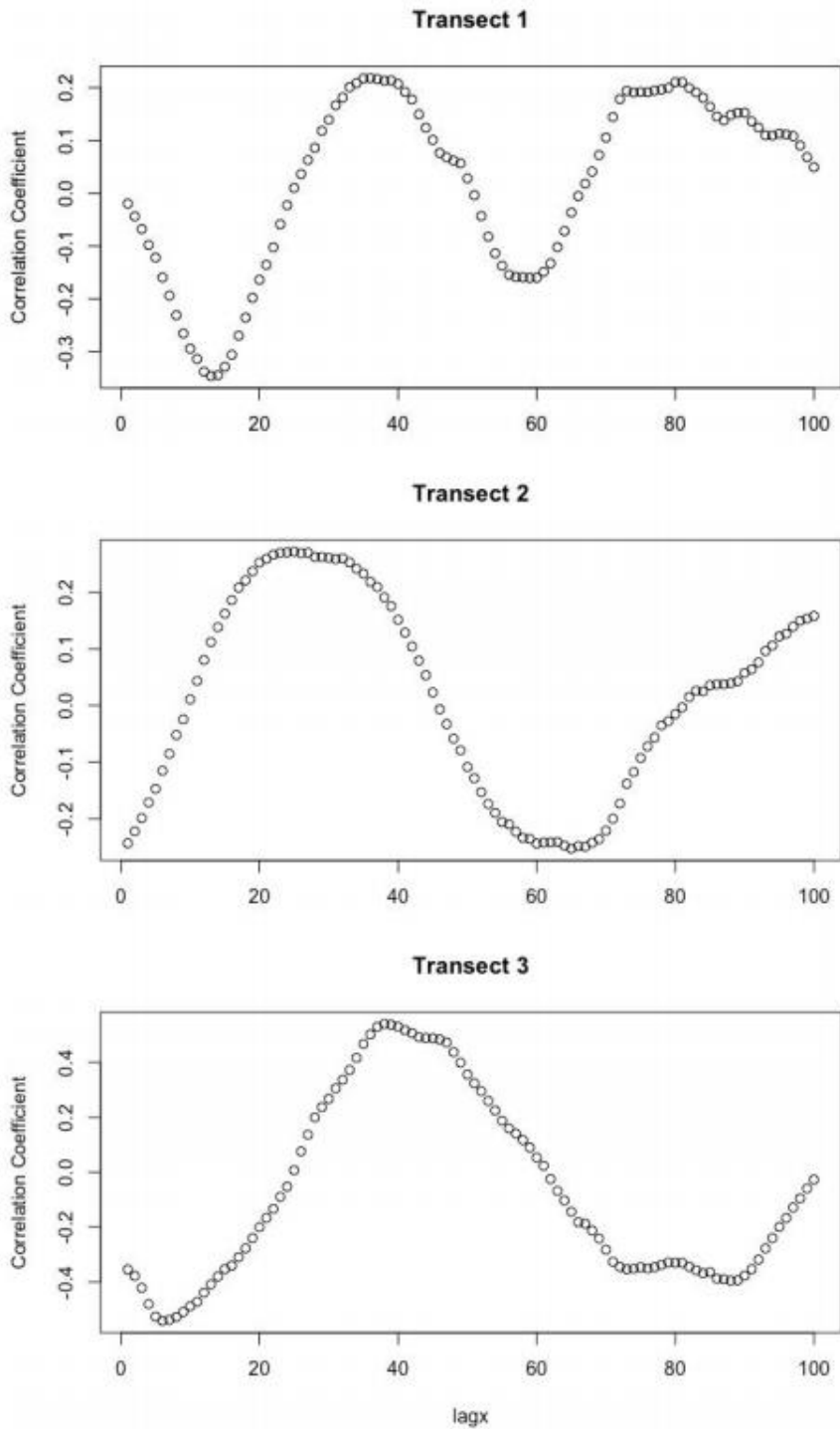
Fig. 10 Lagged correlations of the vegetation orthomosaics (higher values indicate vegetation presence) to the relief of the slope (positive values indicate ridges while negative values indicate valleys) along three transects moving South perpendicular to the series of banded vegetation at AOI6. Correlation Coefficients calculated at points collected every 0.5 meters.

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