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Multi-stability of model and real dryland ecosystems through spatial self-organization

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15Spatial self-organization of dryland vegetation constitutes one of the 16 most promising indicators for an ecosystem's proximity to desertifi-17cation. This insight is based on studies of reaction-diffusion mod-18 els that reproduce visual characteristics of vegetation patterns ob-19 served on aerial photographs. However, until now the development 20of reliable early warning systems has been hampered by the lack 21of more in-depth comparisons between model predictions and real 22ecosystem patterns. In this paper, we combined topographical data, 23(remotely sensed) optical data and in-situ biomass measurements 24 from two sites in Somalia to generate a multi-level description of 25dryland vegetation patterns. We performed an in-depth comparison 26between these observed vegetation pattern characteristics and pre-27dictions made by the extended-Klausmeier model for dryland vegeta-28tion patterning. Consistent with model predictions, we found that for 29a given topography, there is multi-stability of ecosystem states with 30 different pattern wavenumbers. Furthermore, observations corrob-31 orated model predictions regarding the relationships between pat-32tern wavenumber, total biomass and maximum biomass. In contrast, 33model predictions regarding the role of slope angles were not corrob-34orated by the empirical data, suggesting that inclusion of small-scale 35topographical heterogeneity is a promising avenue for future model 36development. Our findings suggest that patterned dryland ecosys-37tems may be more resilient to environmental change than previously 38 anticipated, but this enhanced resilience crucially depends on the 39adaptive capacity of vegetation patterns.

41 vegetation patterns | spatial self-organization | Busse balloon | arid 42 ecosystems | ecosystem resilience

44key aim of ecological modeling is to generate an under-45A standing of the mechanisms driving observed patterns (1). 46 A significant challenge in this pursuit, however, is that mul-47tiple alternative processes may generate the same emergent 48outcome (1-4), a phenomenon also referred to as equifinal-49 ity (5, 6). As a result, modeling efforts may reveal that a 50particular ecological pattern can be explained by a suite of 51alternative driver mechanisms. Therefore, a match between a 52pattern simulated with a mechanistic model and a pattern ob-53served in a real ecosystem may only constitute limited support 54for the modeled mechanism being its true driver (2, 5, 6). 55

Pattern-oriented modeling (2, 7) aims to address the challenge of equifinality of alternative model formulations. In this approach, model assessment is based on the degree to which the output corresponds to observed patterns. A distinction is made between strong and weak patterns. Strong patterns are the dominant emergent features a model should reproduce, such as the cycles within predator and prey population sizes, or a spatial distribution of vegetation patches (6, 7). Weak patterns are typically qualitative relationships, such as the existence of a population over a specific timespan, or a positive association between one state variable and another (6, 7). Rather than comparing model output to a single strong pattern, additional comparisons to multiple weak patterns, at different scales or levels of organization, provide more power to model validation and selection procedures (2, 6, 7).

A specific type of ecological patterns that has received considerable attention is regular spatial patterning of sessile biota (8). On flat terrain, the reported patterns are gaps, labyrinths, and spots (9, 10). On sloping grounds banded patterns form, their regular spacing enabling a description of the characteristic band-inter-band period and wavenumber. Evidence is accumulating that these patterns are self-organized, meaning that the larger-scale patterning is driven by internal ecosystem processes operating at smaller scales (8, 11). The crucial component in this self-organization process is a long-range negative effect of biota on itself, either directly or through modulation of resource availability. In cases where this long-range negative feedback is coupled to a locally positive feedback, the mechanism creating pattern formation may be linked to the existence of alternative stable states, as well

Significance Statement

Today, vast areas of drylands in semi-arid climates face the dangers of desertification. To understand the driving mechanisms behind this effect, many theoretical models have been created. These models provide insight in the resilience of dryland ecosystems. However, until now, comparisons with reality were merely visual. In this article, a systematic comparison has been performed using data on wavenumber, biomass and migration speed of vegetation patterns in Somalia. In agreement with reaction-diffusion models, a wide distribution of regular pattern wavenumbers has been found in the data. This highlights the potential for extrapolating predictions of those models to real ecosystems, including those that elucidate how spatial self-organization of vegetation enhances ecosystem resilience.

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125as the possibility of so-called catastrophic shifts between these 126states (11). This phenomenon has been most prominently 127studied in (semi-)arid ecosystems, where decreases in resource 128availability or increases in grazing pressure may trigger catas-129trophic shifts from vegetated states to desert states without 130vegetation (12-14). In this context, the formation of regu-131lar spatial vegetation patterns may indicate proximity to a 132threshold of catastrophic change (11).

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134There is a long tradition in the scientific literature of explaining regular spatial patterning with reaction-diffusion 135models (15-17). In line with this work, a variety of 136reaction-diffusion models has been applied to investigate self-137138organization in (semi-)arid ecosystems (9, 10, 18, 19). Despite 139the broad support for the findings obtained with these models and their implications for (semi-)arid ecosystem functioning, 140comparisons of model results with empirical data have mainly 141142been limited to comparison of a single strong pattern, namely the spatial distribution of vegetation patches. Until now, the 143few studies considering additional weak patterns have shown 144that reaction-diffusion model simulations successfully repro-145146duce associations between pattern shape and aridity, and associations between pattern shape and slope of the terrain (20). 147148In addition, models that account for sloped terrain also seem 149to capture the observed migration of the location of banded patterns in uphill direction (21). Despite these promising 150agreements between model results and empirical data, a more 151152systematic comparison between model results and data, based on multiple patterns at different levels of organization (2, 7), 153154was still lacking.

Advanced model analyses that have recently been applied 156to ecological models have yielded a number of findings which, 157when confronted with high quality remote sensing products, 158makes a more systematic comparison possible. More specifi-159cally, recent theoretical studies have shown that for a given 160161environmental condition (i.e. a given parameter combination), not a single ecosystem state, but multiple ecosystem states 162with patterns spanning a range of wavenumbers may be stable, 163hence observable (22–24). The range of observable patterns, 164165across a range of environmental conditions forms a bounded region in (parameter, wavenumber)-space. This region is referred 166 to as the Busse balloon, after F.H. Busse, who studied similar 167phenomena in the field of fluid dynamics (25). Although the 168169patterned ecosystem states in the Busse balloon are defined by 170their wavenumber, other properties, like migration speed and 171spatially averaged biomass, have also been studied (26) and are suggested to depend on the position of a system within 172173the Busse balloon. These theoretical findings provide multiple additional weak patterns that can be compared to empirical 174data, providing opportunities for more powerful tests of the 175176validity of the developed reaction-diffusion models to describe 177dryland ecosystems.

The aim of this study was to confront theoretical findings 179regarding pattern wavenumber, biomass and migration speed 180181 with the same pattern properties derived from aerial imagery and remote sensing products of banded vegetation patterns 182in the Horn of Africa, a location with prominent undisturbed 183presence of vegetation pattern formation. Hence, a multi-184level comparison between theory and data in line with the 185pattern-oriented modeling approach was conducted (2, 6, 7). 186

1. Theory

188A. Model description. Multiple reaction-diffusion models of 189dryland vegetation dynamics include a mechanism in which 190vegetation acts as an ecosystem engineer, locally increasing 191 the influx of available water (9, 10, 18, 19). Despite the differ-192ent nuances between these models, a number of predictions 193can be robustly derived from these frameworks. One of the 194simplest of these ecosystem models - and the archetype con-195sidered in this article - is an extended version of the dryland 196ecosystem model by Klausmeier (18, 22), which we will refer 197 to as the extended-Klausmeier model. This model describes 198the interaction between water, w, and plant biomass, n. A 199non-dimensional version of this model is used for the purposes 200 of this article. A dimensional version of the model and the 201 physical meaning of its parameters can be found in SI 1. The 202 model is given by the following equations 203

$$\begin{cases} \frac{\partial w}{\partial t} &= e \frac{\partial^2 w}{\partial x^2} + \frac{\partial (vw)}{\partial x} + a - w - wn^2, \qquad 204\\ \frac{\partial n}{\partial t} &= \frac{\partial^2 n}{\partial t} - mn + wn^2. \qquad [1.1] 205 \end{cases}$$

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$$\left(\begin{array}{c} \frac{\partial n}{\partial t} &= \frac{\partial^2 n}{\partial x^2} - mn + wn^2. \end{array}\right)$$

207The reaction terms model the change in water as a combined 208effect of rainfall (+a), evaporation (-w) and uptake by plants 209 $(-wn^2)$. The change of plant biomass comes from mortality 210(-mn) and plant growth $(+wn^2)$. Dispersion by plants is 211modeled as diffusion and the movement of water as a combined 212effect of diffusion and advection. The latter is due to gradients 213in the terrain, which are proportional to the slope parameter 214v. 215

B. Theoretical outcomes.

B.1. Multi-stability of patterned states. Reaction-advection-218 diffusion equations in general – and the extended-Klausmeier 219model in particular – exhibit a vast variety of spatial 220patterns (27, 28). However, not all feasible patterns are 221 stable solutions of these models. Which patterned states 222are stable (hence, observable) depends on the combina-223tion of the model parameters. For regular patterns, the 224concept of the Busse balloon can help to illustrate this 225dependency (25). A Busse balloon is a model dependent 226shape in the (*parameter*, *wavenumber*)-space that indicates all 227 combinations of parameter and wavenumber that represent 228 stable solutions of the model. If, for a given set of model 229parameters, a wavenumber k lies within the Busse balloon, 230then regular patterns with wavenumber k are observable. So, 231in measurements, all (non-transient) patterns are expected to 232be present in the Busse balloon. 233

Typically, the Busse balloon is a high-dimensional struc-234ture due to the number of parameters in a system. Therefore, 235usually, only one parameter is varied when a Busse balloon is 236visualized. This produces a 2D-slice of the full Busse balloon. 237 In the context of desertification research, the straightforward 238choice would be to vary the rainfall (23). However, mean 239annual rainfall was relatively constant in our study sites dur-240ing the observation period considered. Instead, topography 241(i.e. the slope gradient) comprised the main source of envi-242 ronmental variation within our study areas. Thus, relevant 243 theoretical predictions for our study sites can be generated 244 by varying the slope parameter v (while keeping rainfall con-245stant). Here, we present two of such 2D-Busse balloon slices 246for the extended-Klausmeier model (Figure 1), which were 247constructed by tracking the boundary of the Busse balloon 248



267Fig. 1. (slope,wavenumber)-Busse balloon slices for the extended-Klausmeier model 268for two different values of the rainfall parameter a. A banded pattern solution to the extended-Klausmeier model with slope v and wavenumber k is stable if the 269(v, k)-combination lies inside the Busse balloon. This indicates that a wide spread of 270(v, k)-combinations yields stable banded patterns. The latter are therefore expected 271for a broad range of wavenumbers – and not for specific (v, k)-choices only. The 272shape of a Busse balloon can change between models and between parameter values. 273This is illustrated in the figures which were computed for different a-values 274

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using numerical continuation methods (23, 24, 29, 30). The shaded region in these figures indicates the combinations of pattern wavenumber k and slope v for which stable solutions exist. Thus, a specific slope v does not lead to one specific pattern. In fact, the model shows multi-stability; a given slope v can sustain a continuous range of wavenumbers k. A similar spread in wavenumbers is expected in the real system.

Though the Busse balloon indicates which patterns might 283be observed, it does not specify the likelihood of finding a 284certain pattern with specific wavenumber k within this range. 285Recent numerical studies suggest that the (entire) history of en-286vironmental changes is relevant in the selection process (26, 31). 287To understand these hysteretic dynamics, it is vital to acknowl-288edge that model patterns do not change their wavenumber 289290unless they have to (23, 30): if an environmental change forces 291 the system outside of the Busse balloon, the current pattern has become unstable, and will need to adapt into a new pat-292tern that is again stable – thus part of the Busse balloon. 293During this (fast) adaption, only part of the vegetation bands 294are lost, while the remaining bands increases in size; these 295adaptions thus have limited effect on the total biomass in 296the system (23). Hence multiple wavenumber adaptations are 297expected to occur after each other that will, gradually, lead to 298 a complete desertification of the system (23). Precisely which 299 wavenumber k gets selected at each of these destabilizations 300 is difficult to predict, though, for low noise levels, a prefer-301 ence for an approximate period doubling is expected, i.e. the 302wavenumber gets halved (23). 303

Numerical simulations help to get an insight in the kind of wavenumber distribution one ought to expect in observations. To illustrate the typical spread in wavenumber, a total of 200 simulations on a flat terrain (v = 0) were run, where the rainfall parameter was slowly decreased from a = 3 to a = 0.5. The initial configurations for these runs were chosen randomly, but close to the equilibrium state of uniform biomass before



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Fig. 2. Histogram demonstrating a spread in wavenumber (*k*) at the end of 200 simulations of the extended-Klausmeier model on a flat terrain (v = 0) with model parameters e = 500 and m = 0.45. These simulations had a random initial configuration close to a stable fully vegetated state. A climate change was simulated by decreasing the rainfall parameter *a* linearly from 3 to 0.5 over the course of 10^5 time unit, causing several pattern selections and corresponding changes in wavenumber.

the onset of patterns (between 90% and 110% of the uniform vegetated equilibrium state). At the end of each simulation – after several pattern selections – the wavenumber of the remaining pattern was measured. This gives a snapshot of the wavenumber distribution, similar to the snapshots acquired from observations. Note that a similar experiment was done before, albeit on a much smaller scale (30). The histogram of the resulting wavenumbers is shown in Figure 2. It shows a substantial spread, which goes from a wavenumber of 0.08 to 0.16 (a difference of 100%).

B.2. Biomass & migration speed. Besides a wavenumber, each 338 ecosystem state also has a specific biomass and a specific 339pattern migration speed. The biomass of regular patterned 340states has been studied using numerical simulations (23) and 341 more general formulas have been derived for small-wavenumber 342patterns (32). Both indicate that the biomass (per unit area) 343 is positively correlated with both the wavenumber k of the 344 pattern and the slope parameter v (23); see also Figure 3a. 345This has a physical interpretation: both steeper slopes and 346higher wavenumbers (lower wavelengths) reduce the time it 347 takes for water to reach vegetation bands, and thereby reduce 348 water losses during the transportation process. As a result, the 349vegetation will be able to harvest water from the uphill inter-350 bands more effectively. The biomass per wavelength is also of 351interest. The same studies indicate that the band biomass (per 352wavelength) is increased when the wavenumber k is decreased 353and when the slope v is increased. Hence, vegetation bands 354 are expected to have more biomass when other vegetation is 355farther away, because of the larger (upslope) inter-band area 356water can be collected from. 357

The theoretical predictions for migration speed (of a pat-358 tern's location) are a bit more subtle. For terrains with a con-359 stant slope, numerical simulations have been done (33, 34) and 360 general formulas have been determined for small-wavenumber 361 patterns (32, 35). In these idealized limit cases, migration 362speed is negatively correlated with wavenumber k and posi-363 tively correlated with slope v. However, beyond these ideal-364 izations, numerical computations show the contour lines are 365 slightly humped, see Figure 3b. This indicates a (slightly) 366 negative correlation between speed and slope v for large slopes. 367368

C. Testable predictions. The theoretical findings in this section lead to predictions that can be confronted with the field 371 data. First of all, the model possesses a Busse balloon, which 372



391Fig. 3. (slope, wavenumber)-Busse balloon slices for the extended Klausmeier model392that include contours for the total biomass (per area) B (a) and the migration speed393c (b). Biomass (per area) is positively correlated with both wavenumber k and394slope v; the migration speed is negatively correlated with the wavenumber k. Model395

397 should lead to a wide spread in observable pattern wavenum-398bers (Figures 1 and 2). Moreover, biomass and migration 399speed are affected by pattern wavenumber. The biomass (per 400 unit area) is expected to be positively correlated with both 401the wavenumber and the slope of the terrain (Figure 3a). 402Migration speed is expected to decrease as a function of pat-403tern wavenumber; the effect of slope on the migration speed 404is context-specific, as it can be either positive or negative 405depending on the specific topographical and environmental 406 conditions (Figure 3b). 407

$\frac{408}{409}$ 2. Data acquisition & processing

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For this comparison study, two sites were selected in Somalia. 410The first one $(8^{\circ}0'14'' \text{ to } 8^{\circ}15'11''\text{N}; 47^{\circ}11'54'' \text{ to } 47^{\circ}31'4''\text{E})$ 411is located in the Haud pastoral region, which will be referred 412to as the 'Haud' site. The other site $(9^{\circ}18'49'' \text{ to } 9^{\circ}34'34''\text{N};$ 413 $48^{\circ}8'15''$ to $48^{\circ}43'15''E$) is located in the Sool-Plateau pastoral 414area and will be called the 'Sool' site. Both sites mainly exhibit 415banded vegetation and have ground slopes ranging from zero 416417to one percent. Vegetation mainly constitutes of perennial 418 grasses, which typically have an average life time of one to 419seven years (36-38). A more detailed description of these sites 420can be found in SI 2; a map with the location of these sites along with the mean annual rainfall in these areas is shown in 421Figure S1. 422

423To study the pattern properties in these study areas, each site was divided into square windows (of size $750m \times 750m$ for 424the Haud site and of size $1010m \times 1010m$ for the Sool site). 425426As has been done in previous studies, the type of pattern (e.g. bare soil, banded vegetation), along with its wavenumber, was 427 428 determined using spectral analysis (20, 39–41). Only those 429windows were kept that exhibited banded vegetation with a wavenumber that could be determined with enough certainty 430(i.e. between 0.4 and 2.5 cycles per 100m). Moreover, windows 431with a too large curvature were ignored, because the theoretical 432predictions only apply to terrains with a constant slope. To 433obtain data on the migration speed of the banded vegetation, 434



 Fig. 4. Frequency distribution of banded patterns as function of ground slope and wavenumber (number of cycles per 100m) for the Haud site (a) and Sool site (b). The distribution on the right indicates the relative frequency of banded vegetation with corresponding wavenumber. The color gradient indicates the amount of windows (N).
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a cross-spectral analysis was performed, along the lines of previous studies (21, 42, 43). A more in-depth explanation of these processing steps can be found in SI 4.

466The topographical data used in this article were derived 467from the ALOS World 3D (AW3D) digital raster elevation 468 model; biomass data for the Haud site have been retrieved 469from a recently made map on (above-ground) biomass of 470African savannahs and woodlands (44) (no reliable data for 471the Sool site was available). Finally, optical data were acquired 472from various sources: three multispectral WorldView-2 images 473were mosaicked and used as reference for the Haud site; a 474 panchromatic Ikonos 'Geo' Imagery was acquired for the same 475site. For the Sool site, six WorldView-2 images were used and 476a panchromatic SPOT4 image preprocessed to level 2A was 477used as reference layer (©Cnes 2004 – Spot Image distribution). 478Moreover, two $7\mu m$ digitized panchromatic declassified Corona 479spy satellite image, national intelligence reconnaissance system, 480 available from the USGS were obtained for the Haud and the 481 Sool sites. More information about these data sets can be 482found in SI 3. 483

3. Results

Empirical Busse balloon. The most prominent pattern prop- 486 erty studied in this article is the pattern wavenumber, which 487was derived from aerial imagery. The resulting distribution of 488 wavenumbers is reported in Figure 4. These figures show the 489number of windows that have a particular slope-wavenumber 490 combination. Also given is the relative frequency that indi- 491 cates the spread of wavenumbers across all windows. This 492 data displays banded vegetation with wavenumbers roughly 493between 0.4 and 2.0 cycles per 100m. Importantly, this large 494 spread is present for all of the ground slope values which had 495a representative sample size and could not be explained by 496

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512 **Fig. 5.** Biomass distribution per area (a) and per period (b) as a function of ground 513 slope and wavenumber (cycles per 100m) for the Haud site. The color gradient 514 indicates the amount of biomass measured for a particular (slope, wavenumber)-515

517present heterogeneities in elevation or rainfall. This shows 518that for a given environmental condition not a single wavenum-519ber pattern, but rather multiple patterns spanning a sizable 520range of wavenumbers are observable. Additionally, measure-521ments used to determine the migration speed show barely any 522changes in wavenumber over the scope of 39 years (consistent 523with (43)), indicating that these patterns are in fact quite 524stable. Therefore, the observations are in agreement with the 525existence of a Busse balloon in the real ecosystem. 526

527Biomass and migration speed. The processed biomass data 528for the Haud site is shown in Figure 5. In Figure 5a the rela-529tion between biomass per area (in $t ha^{-1}$) is plotted against 530the ground slope and the wavenumber. From the same data 531the biomass per period is computed – which is biomass per 532area divided by the window's wavenumber. The resulting plot 533is given in Figure 5b. The measurements of biomass show 534agreement with theoretical predictions of model studies; in 535both, the total biomass increases (all slopes: r = 0.80, n = 714, 536P < 0.001; linear regression) and the biomass per period de-537creases when the wavenumber increases (all slopes: r = -0.30, 538n = 714, P < 0.001; linear regression). However, a more 539in-depth inspection reveals disagreements. For one, the effect 540of ground slope is not strongly present in the data, though its 541effect is clear in the extended-Klausmeier model (Figure 3a). 542Additionally, the more refined details of wavenumber depen-543dence also differ (it is concave in the theoretical model and 544convex in the real-life data).

The migration speed is plotted in Figure 6 for both the Haud and the Sool sites. These measurements show an increase in speed when the wavenumber decreases (Haud: r = -0.65, n = 104, P < 0.001; Sool: r = -0.67, n = 79, P < 0.001; linear regression), corroborating theoretical predictions (see Figure 3b).

$\frac{552}{553}$ 4. Discussion

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Leading ecological frameworks emphasize the potential role of regular spatial vegetation patterns as indicators for proximity to catastrophic ecosystem shifts (11, 45). In these frameworks, however, mono-stability of patterns is implicitly assumed, suggesting that for a given environmental condition there is only



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Fig. 6. Observed (average) migration speed of vegetation bands in the Haud (a) and the Sool (b) sites over the course of 39 years as a function of ground slope and wavenumber (cycles per 100m). The colour gradient indicates the migration speed for a particular (*slope*, *wavenumber*)-combination. The sign indicates the direction of migration relative to the slope, with positive and negative values indicating upslope and downslope migration respectively.

one stable vegetated state, i.e. a single pattern with a specific wavelength (11, 45). Subsequent theoretical insights have challenged this view, highlighting the possibility of multi-stability of patterns, bounded by the so-called Busse balloon. In this study, we provide the first empirical evidence corroborating the existence of a Busse balloon for stable vegetation patterns in dryland ecosystems. Specifically, our two study sites in Somalia revealed the sustained (i.e. over a 39-year period) co-occurrence of banded vegetation with wavenumbers varying over a substantial range. Our findings have major implications for the way in which vegetation patterns indicate ecosystem resilience and mediate ecosystem responses to environmental change.

593Specifically, the existence of a Busse balloon implies that 594an ecosystem's resilience can no longer merely be defined by 595the magnitude of environmental change it can cope with (46). 596 In these systems there is not one tipping point, but a cascade 597 of destabilizations - indicated by the boundary of the Busse 598balloon. When environmental changes push a patterned ecosys-599tem beyond the boundary of the Busse balloon, a wavelength 600 adaptation occurs, and typically part of the vegetation patches 601 are lost, while the remaining patches grow in size. The extent 602 of these adaptations depends on the rate of environmental 603 change (23, 26, 47, 48). Moreover, human activities or natural 604 variations can cause local disturbances, diminishing the regu-605 larity of ecosystem patterns. The recovery process from such 606 disturbances may involve a rearrangement of patches in the 607 landscape (23, 32). Again, the extent to which such recovery is 608 possible depends on the rate of environmental change that the 609 ecosystem is exposed to (47). Hence, the existence of a Busse 610 balloon of stable dryland vegetation patterns suggests that 611 adaptability of patches to changing environmental conditions 612 provides a more comprehensive indicator for the ecosystem's 613 resilience than the shape of the pattern itself, as suggested 614 in current leading frameworks (11, 45). Future studies in 615this direction should provide a more thorough understanding 616 of what determines the spatial rearrangement of vegetation 617 patches resulting from disturbances, environmental changes 618 and spatial heterogeneities in the landscape. 619

The pattern-oriented modeling approach was mainly devel- 620

621 oped to aid model development and design, but the approach 622 can also be used to evaluate the success of existing models to 623 explain multiple strong and weak patterns observed (7). This 624 so-called 'reverse pattern-oriented modeling' approach (7)625was used in the current study. Such systematic comparisons 626 between model predictions and empirical data can be part of 627 an iterative process toward further model improvement (5, 6). In this context, it is interesting to note the discrepancy that we 628629 observed between model predictions and field measurements of 630 the influence of the ground slope on pattern migration speeds. 631 Because topography critically changes the distribution of wa-632 ter within ecosystems, it also alters the migration speed of 633patterns. Therefore, future model developments should relax 634 the assumption of uniform slopes, and examine the effects of 635 more complex topographies for dryland ecosystem dynamics. 636

637 Since their appearance on aerial photographs in the 638 1950s (49), the origin of regular vegetation patterns in dryland 639 ecosystems has been a topic of fascination within the scientific 640 community. The study of these patterns through reaction-641 diffusion modeling subsequently highlighted the importance of 642 these patterns for the functioning of dryland ecosystems, and 643

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their response to environmental change. The recent increase 683 684 in the availability of optical and topographical data provides 685 unprecedented opportunities to confront model predictions with empirical data (6, 31). In this study, we combined these 686data sources with in-situ measurements of biomass, enabling 687 the comparison of multiple pattern characteristics of Soma-688 689 lia drylands with predictions derived from reaction-diffusion 690 modeling. The empirical evidence corroborates theories of 691 multi-stability of patterned vegetation states, improving our 692 understanding of these systems' resilience to environmental 693 change. In addition, our results call for more detailed inves-694 tigations of the role of small-scale topographic variability in pattern formation and migration, to be undertaken in future 695 696 studies.

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