

**IDEA AND  
PERSPECTIVE**

## Emerged or imposed: a theory on the role of physical templates and self-organisation for vegetation patchiness

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### Abstract

In this article, we develop a unifying framework for the understanding of spatial vegetation patterns in heterogeneous landscapes. While much recent research has focused on self-organised vegetation the prevailing view is still that biological patchiness is mostly due to top-down control by the physical landscape template, disturbances or predators. We suggest that vegetation patchiness in real landscapes is controlled both by the physical template and by self-organisation simultaneously, and introduce a conceptual model for the relative roles of the two mechanisms. The model considers four factors that control whether vegetation patchiness is emerged or imposed: soil patch size, plant size, resource input and resource availability. The last three factors determine the plant-patch size, and the plant-to-soil patch size ratio determines the impact of self-organisation, which becomes important when this ratio is sufficiently small. A field study and numerical simulations of a mathematical model support the conceptual model and give further insight by providing examples of self-organised and template-controlled vegetation patterns co-occurring in the same landscape. We conclude that real landscapes are generally mixtures of template-induced and self-organised patchiness. Patchiness variability increases due to source–sink resource relations, and decreases for species of larger patch sizes.

### Keywords

Drylands, landscape, patch size, patchiness, *Poa bulbosa* L., scale, self-organisation, template induced, vegetation pattern formation.

*Ecology Letters* (2013) 16: 127–139

### INTRODUCTION

Landscapes are networks of biotic and abiotic patches whose functional relationships control landscape and species diversity (Turner *et al.* 2001; Wiens *et al.* 2007) and thereby affect ecosystem function (Ludwig & Tongway 1997; de Blois *et al.* 2002; van der Valk & Warner 2009). The network of abiotic patches represents landscape heterogeneity induced by slow geological, geomorphological and pedological processes. This network creates the physical template for faster physical and biological processes, such as resource and organism flows, that drive biotic patch formation.

Two contrasting cases, representing top-down and bottom-up processes, can be envisioned for biotic patch formation: (1) biological patchiness dictated by the physical template (top-down) and (2) self-organised biological patchiness induced by local resource–biomass feedbacks (bottom-up) that occur even in the absence of a physical template (Valentin *et al.* 1999; Rietkerk *et al.* 2004; Deblauwe *et al.* 2008; Schmitz 2010). A typical example of the first case is rock–soil mosaics in water-limited landscapes, where bare bedrock patches cre-

ate run-off of water and nutrients that flow to adjacent soil patches. The resource-enriched soil patches provide favourable conditions for full vegetation coverage, leading to template-dictated vegetation patchiness (Greig-Smith 1979; Yair & Shachak 1982, 1987; Monger & Bestelmeyer 2006; Peters & Havstad 2006). Another form of template-induced vegetation patchiness occurs when the vegetation biomass follows the resource distribution pattern (e.g. nutrient-enriched soil patches or ‘islands of fertility’, Kershaw 1963; Aguiar & Sala 1999).

The second case – self-organised vegetation pattern formation – has been studied extensively in the last decade in the context of water-limited systems. Mathematical models (Lefever & Lejeune 1997; Klausmeier 1999; von Hardenberg *et al.* 2001; Rietkerk *et al.* 2002; Gilad *et al.* 2004; Borgogno *et al.* 2009) and field observations (Valentin *et al.* 1999; Becker & Getzin 2000; Tongway *et al.* 2001; Deblauwe *et al.* 2011) show that interactions among plants can form non-uniform vegetation patterns on plains and slopes even in homogeneous soil with no underlying physical template. These plant interactions are driven by positive local feedbacks between biomass and water, and between above-ground and below-ground biomass

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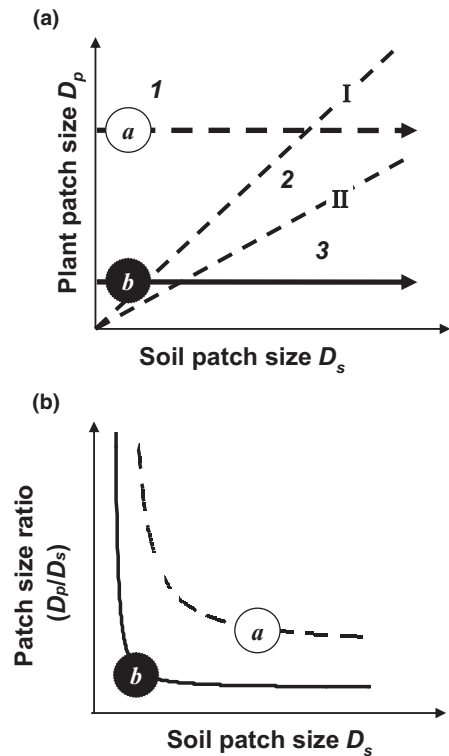
(Rietkerk *et al.* 2002; Gilad *et al.* 2004, 2007; Rietkerk & Van de Koppel 2008; Meron 2012). The feedbacks involve water transport towards growing patches, either by enhanced water run-off infiltration in the vegetated patch or by laterally extended root systems, which accelerate or 'activate' the patch growth and inhibit the growth in the patch surroundings. Short-range activation accompanied by long-range inhibition is a well-known pattern-formation mechanism (Gierer & Meinhardt 1972).

Observations of self-organised vegetation patchiness have been reported for arid and semi-arid landscapes worldwide (Tongway *et al.* 2001; Deblauwe *et al.* 2008). These observations are consistent with model predictions of five basic vegetation states along a decreasing rainfall gradient: uniform vegetation, vegetation cover interspersed by gaps of bare soil, vegetation stripes, spots and uniform bare soil (von Hardenberg *et al.* 2001; Rietkerk *et al.* 2004; Borgogno *et al.* 2009). The models further predict many additional patterned states, which are spatial mixtures of the basic states (Meron 2012).

Real landscapes, however, generally represent intermediate cases, where biological patchiness is affected both by source–sink relationships between abiotic and biotic patches and by local pattern-forming feedbacks (Schmitz 2010). The manner by which the physical template and self-organisation processes act in concert to shape vegetation patchiness has not been studied yet. As a first step towards closing this gap, we propose a conceptual model for vegetation patchiness in heterogeneous landscapes that links the structure and function of the physical template to self-organisation processes within the physical patchwork. We apply the conceptual model to a water-limited landscape where the physical template is a network of rock and soil patches. The space available for biological growth consists of the soil patches, and the vegetation comprises two species, *Sarcopoterium spinosum* and *Poa bulbosa*, that form large and small biomass patches respectively. Complementing the empirical studies by simulations of a mathematical model, we demonstrate that whether the vegetation patchiness is entirely constrained by the physical template or is a combined outcome of the physical template and self-organisation depends on the typical size of a plant-patch relative to the sizes of soil patches. Although we refer here to vegetation patchiness in water-limited rock–soil landscapes, we expect the theory to be applicable also to other contexts of biological patchiness in heterogeneous landscapes.

#### THEORETICAL FRAMEWORK: CONCEPTUAL MODEL OF TEMPLATE-BASED VS. SELF-ORGANISED VEGETATION PATTERN FORMATION

The model is based on the assumption that the development of vegetation patchiness in a heterogeneous landscape is affected by four main factors: (1) the spatial extents of the soil patches in which the plant species grows, (2) the physiological-genetical size of the plant species, (3) the precipitation regime and (4) the source–sink resource relationships between different patch types within the physical template. The last three factors together determine the 'typical patch size' of a given plant species when soil-patch size is not a limiting factor. Vegetation patch size is defined here with respect to the pattern that the species forms; the spot diameter in a spot pattern, the stripe width in a stripe pattern and the distance between nearby gaps in a gap pattern. The ratio of this size to the size of the soil patch in which the vegetation grows determines the prevailing mechanism of vegetation pattern formation, as we explain below and illustrate in



**Figure 1** Conceptual model of vegetation patchiness in heterogeneous landscapes. (a) Different mechanisms of vegetation patchiness in the plant-patch size  $D_p$  to soil-patch size  $D_s$  phase plane: patchiness dictated by the physical template (area 1,  $D_p > D_s$ ), patchiness affected by both the template and self-organisation (area 2,  $D_s \geq D_p$ ) and self-organised patchiness (area 3,  $D_s \gg D_p$ ). Diagonal lines I and II denote the decline from full vegetation cover  $\phi = 1$ , in area 1 to the typical cover,  $\phi_{pat} < 1$ , of a self-organised vegetation pattern in area 3. Horizontal lines represent plants with large ( $a$ ) and small ( $b$ ) typical patch sizes. (b) Transitions from template-induced (high  $D_p/D_s$ ) to self-organised (low  $D_p/D_s$ ) patchiness, as  $D_s$  increases, occur faster for smaller  $D_p$ .

Figs 1 and 2. We first study vegetation patchiness as a function of the soil-patch size assuming a fixed water availability (Fig. 1a, b). We then take into account the additional effect of water redistribution by the physical template through source–sink relationships (Fig. 2a, b).

#### Soil-patch–plant-patch size relationship

Assuming a fixed water input to a soil patch, we ask how vegetation coverage is affected by the plant- to soil-patch size ratio (Fig. 1a). When the typical plant-patch size,  $D_p$  is larger or about the size  $D_s$  of a soil patch, the soil patch will be fully covered (for simplicity, we consider  $D_s$  to be the diameter of a circular soil patch). If that is the case for all soil patches in the landscape, the spatial organisation will be dictated by the physical template. In the plane spanned by  $D_s$  and  $D_p$ , this behaviour is limited to the area for which  $D_p \geq D_s$  (area 1 in Fig. 1a). When the typical plant-patch size is much smaller than the size of a soil patch,  $D_p \ll D_s$ , the plants will interact and self-organise to form a vegetation pattern. At the landscape level, the vegetation will still follow the physical template by occupying the network of soil patches, but within soil patches, the vegetation pattern will show self-organisation into a patterned state. This behaviour is limited to area 3 in Fig. 1a. An intermediate regime of the plant-patch size relative to the soil-patch size exists in which soil patches

are partially covered by vegetation, but are too small to hold a sufficiently large number of interacting plants for a vegetation pattern to develop (area 2 in Fig. 1a).

To better characterise the three areas, let us denote by  $\phi$  the fraction of area covered by vegetation within a soil patch, and by  $\phi_{pat}$  the maximal area fraction that can be covered by vegetation, given the conditions of water availability and their associated vegetation patterns. We expect  $\phi_{pat}$  to gradually increase with water availability, except for threshold values at which pattern transitions take place (e.g. from a spot pattern to a stripe pattern), where  $\phi_{pat}$  is expected to change more sharply. Area 1 is then characterised by  $\phi = 1$  (fully covered soil patches). It extends up to transition line I, where  $\phi$  begins declining. Area 2 is characterised by  $\phi_{pat} < \phi < 1$ , and extends up to transition line II, where  $\phi$  approaches the value  $\phi_{pat}$ . Area 3 is characterised by  $\phi = \phi_{pat}$ .

The convergence of transition lines I and II at the origin reflects the increased probability to find self-organised patterns as the plant-patch size gets smaller. Thus, a plant species with a sufficiently small patch size ( $b$  in Fig. 1a) will develop self-organised patterns within most of the soil patches in the landscape, while a species with a large patch size ( $a$  in Fig. 1a) will uniformly cover most of the soil patches. In other words, while the vegetation patchiness associated with species  $b$  is mostly due to self-organisation, the patchiness associated with species  $a$  is mostly dictated by the physical template.

Another view of this effect is illustrated in Fig. 1b, which shows the dependence of the ratio  $D_p/D_s$  on  $D_s$  for species  $a$  and  $b$ . This ratio quantifies the degree to which vegetation patchiness follows the physical template; high values correspond to template-dictated patchiness, whereas low values correspond to self-organised patchiness. Species with small plant-patch sizes ( $b$ ) shift quickly from template-dictated patchiness to self-organised patchiness as the soil-patch size increases, whereas species with large plant-patch sizes ( $a$ ) shift much more gradually.

**Resource availability**

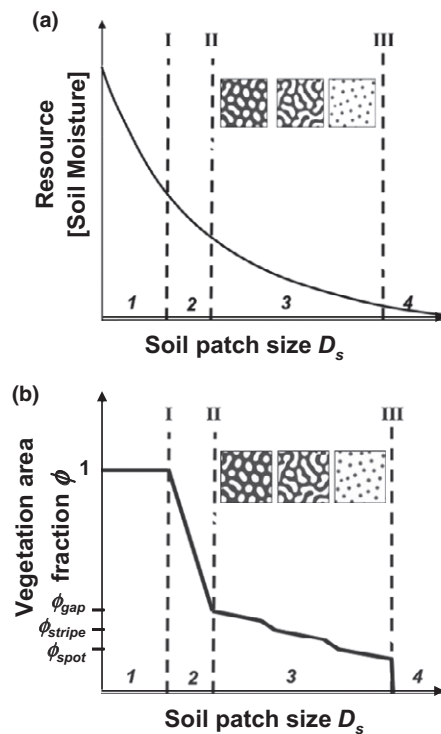
The typical patch size of a plant species increases with water availability. Increased precipitation will therefore result in more fully covered soil patches and fewer soil patches showing self-organised patchiness. At sufficiently high precipitation, we may expect the patchiness to completely follow the pattern dictated by the template. Water availability in the space available for growth, however, is also determined by the source–sink relationships within the physical template, e.g. between rock and soil patches. Specifically, the redistribution of incoming rainfall in a rock–soil landscape will result in a differential increase of the water content in soil patches, with small patches having soil–water content significantly higher than large patches as Fig. 2a illustrates.<sup>1</sup> This differential water availability increases landscape variability as we now explain.

Consider the extreme case of a precipitation regime that is too low for any form of vegetation to grow in a homogeneous landscape totally covered by soil. In a patchwork of soil and rock, large soil patches may remain bare because of insufficient run-off water input (area 4 in Fig. 2a). In smaller soil patches, rainfall plus run-off may supply sufficient water to support vegetation patterns (area 3 in

Fig. 2a). Very small soil patches may even be fully covered. This will be the case when the typical plant-patch size exceeds the soil-patch size because of the high water content in small soil patches. Fig. 2b illustrates this vegetation variability in a schematic graph of the vegetation area fraction  $\phi$  in a soil patch as a function of the soil-patch size, taking into account the possible appearance of different vegetation patterns in soil patches of different sizes.

We conclude that dry heterogeneous landscapes characterised by wide distributions of soil-patch sizes can be highly variable, showing big bare patches along with intermediate patches with various forms of self-organised vegetation (patterns of spots, stripes, gaps and mixtures thereof), as well as fully covered small patches. As the precipitation rate increases, this variability decreases; the typical plant-patch size increases, more soil patches become fully covered and larger, partially covered patches exhibit patterns typical of more favourable conditions, e.g. gaps and stripes rather than spots. At sufficiently high precipitation, for which the plant-patch size exceeds the largest soil patch, the vegetation patchiness follows the physical template with all soil patches fully covered by vegetation.

Landscape variability can also change with the type of plant species considered. While a species with a small typical patch size (e.g. small herbs) will exhibit a highly variable landscape with soil patches



**Figure 2** The effect of resource redistribution on vegetation patchiness in heterogeneous landscapes. (a) Source–sink resource relationships within the physical template result in a decreasing water content in soil patches of increasing sizes. Accordingly, larger soil patches exhibit vegetation patchiness characteristic of drier areas with a possible transition (line III) to a bare-soil state (area 4) at sufficiently large soil patches. (b) Changes in vegetation patchiness with increasing  $D_s$ , as reflected by vegetation cover  $\phi$  within a soil patch.

<sup>1</sup>It is easy to show that the dependence of the soil moisture per unit ground area on the soil-patch size  $D_s$ , shown in Fig. 2a, should scale like  $D_s^{-2}$ . The total rainfall amount per unit time in a domain of size  $L$  is  $PL^2$ , where  $P$  is the precipitation rate. Suppose that this domain consists of a soil patch of size  $D_s$ , or area  $\pi D_s^2/4$ , surrounded by a rocky patch. The overland water flow from the rocky patch to the soil patch increases the total water inflow to the soil patch to  $PL^2$ . This leads to a water inflow per unit area of  $4PL^2/\pi D_s^2$ .

**Table 1** Landscape patchwork characteristics at the Lehavim LTER site. Patchwork characteristics of north- and west-facing slopes are compared. Transects along these slopes were used to measure the frequency and composition of patch transitions ( $\pm$  SE); the proportions of the slopes covered by each patch type (Rock, Soil and Shrub); and mean length of each patch type

Spatial measure	North slope ( $n = 8$ ) Mean ( $\pm$ SE)	West slope ( $n = 4$ ) Mean ( $\pm$ SE)
Total transition frequency (Transitions $m^{-1}$ )		
Proportion	0.619 (0.036)	0.594 (0.067)
Rock–Soil transition	0.054 (0.012)	0.392 (0.042)
Soil–Rock transition	0.081 (0.014)	0.350 (0.046)
Rock–Shrub transition	0.062 (0.013)	0.032 (0.032)
Shrub–Rock transition	0.035 (0.012)	0.052 (0.038)
Soil–Shrub transition	0.369 (0.019)	0.097 (0.016)
Shrub–Soil transition	0.399 (0.018)	0.077 (0.014)
Rock cover	0.079 (0.016)	0.283 (0.023)
Soil cover	0.634 (0.02)	0.615 (0.05)
Shrub cover	0.286 (0.011)	0.102 (0.03)
Average Rock patch length (cm)	109.828 (11.735)	110.427 (13.216)
Range	10–550 ( $n = 58$ )	15–930 ( $n = 82$ )
Average Soil patch length (cm)	222.5 (15.304)	223.75 (21.159)
Range	15–1580 ( $n = 228$ )	30–1080 ( $n = 88$ )
Average Shrub patch length (cm)	106.018 (4.806)	130.2 (14.808)
Range	15–450 ( $n = 216$ )	30–310 ( $n = 25$ )

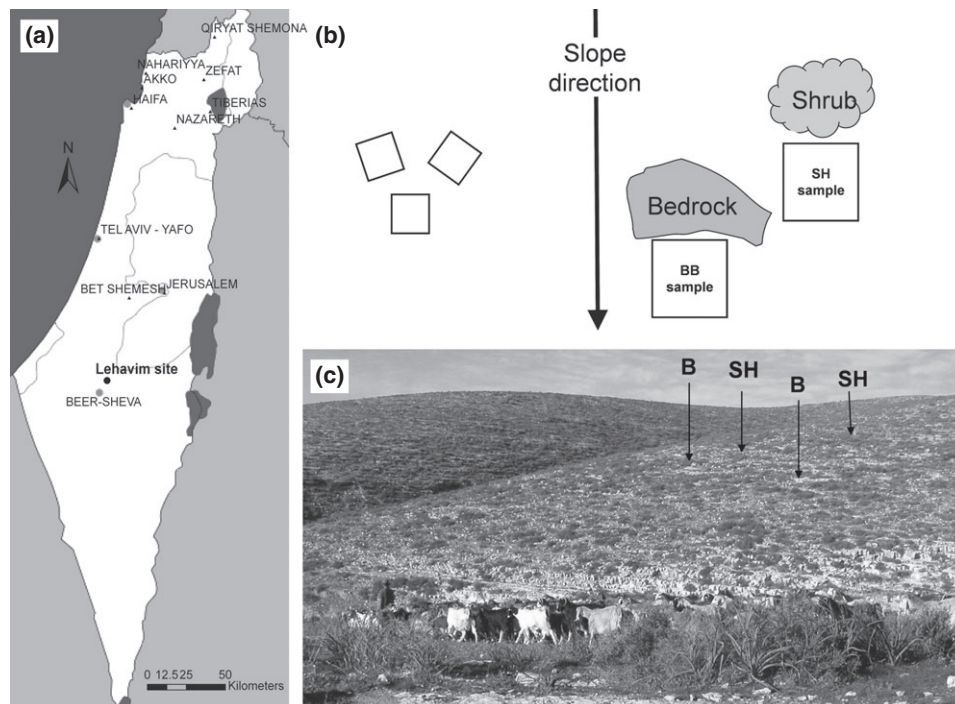
exhibiting all or most types of vegetation states, a larger species (shrub or tree), whose typical patch size exceeds the sizes of a wider range of soil patches, will exhibit lower landscape variability. Moreover, large soil patches, partially covered by the larger species, may tend to exhibit patterns characteristic of arid landscapes, such as

spots rather than gaps, because of the lower soil–water content in large soil patches.

### Testing the conceptual model

We present empirical studies and complementary mathematical-model studies to test the predictions of the conceptual model on the significance of source–sink relations and plant-patch size for vegetation patchiness in water-limited heterogeneous landscapes. The empirical studies were conducted in a semi-arid landscape in the Northern Negev (Lehavim LTER station), where the physical template consists of soil and rock patches with average soil-patch size of 4.5  $m^2$  (Table 1). We investigated the patchiness of two common species, *S. spinosum* and *P. bulbosa*. *Sarcopoterium spinosum* represents a large patch-size shrub with a typical patch area of 1.3  $m^2$  (Table 1), whereas *P. bulbosa* represents a small tussock grass whose genet area size varies between 10 and 100  $cm^2$ . While soil patches typically contain a single or a few *S. spinosum* patches, dozens of *P. bulbosa* patches (thousands of individuals) fit in an average soil patch (Table 1). In earlier laboratory experiments, we demonstrated that competition over limited water supply among individual ramets within a single *P. bulbosa* patch caused biomass spatial patterning (Sheffer *et al.* 2007, 2011). We thus assume that *P. bulbosa* patchiness reflect self-organisation.

Besides representing large patch-size plants, *S. spinosum* shrubs also play an important role in redistributing the soil water available to *P. bulbosa*. While rock patches act as run-off water sources that enrich soil patches, the shrub patches act as run-off sinks, by absorbing run-off (Segoli *et al.* 2008), and thereby counteract the effect of the rock patches.



**Figure 3** (a) Lehavim LTER study site in the map of Israel; (b) Study design. Two types of sampling quadrats measured along the north and west slopes of the study site. Groups of three interspersed small quadrats (50  $\times$  50 cm) sampled along the elevation gradient of the slopes (to the left); and large (100  $\times$  100 cm) quadrats sampled downslope and adjacent to bare bedrock (BB) and shrubs (SH) (c) Picture of the north slope. Arrows indicate examples of *Sarcopoterium spinosum* SH and bedrock (b).

We used simulations of a mathematical model to explain the two extreme cases of the shrub and grass patterns in the field, as well as to test the entire set of behaviours predicted by the conceptual model. The mathematical-model studies were conducted using the Gilad *et al.* (2004, 2007) model for self-organised vegetation patchiness in water-limited systems. The model has been successfully applied to a wide range of problems, including vegetation patterns and pattern transitions along environmental-stress gradients (Gilad *et al.* 2004, 2007), mechanisms of vegetation-ring formation (Sheffer *et al.* 2007, 2011), plants as ecosystem engineers (Gilad *et al.* 2004, 2007), the appearance of scale-free vegetation patterns (von Hardenberg *et al.* 2010) and others (Meron 2011, 2012). The model not only captures the main mechanisms of vegetation pattern formation but also the overland water flow in a heterogeneous environment. It is therefore capable of representing the source–sink relationships within the physical template and their impact on plant-patch size. These model properties allow the study of the interplay between template-dictated patchiness and self-organised patchiness for various plant species and physical templates.

## MATERIAL AND METHODS

### Study area

The LTER Lehavim Station (Fig. 3a), is located in the Goral Hills (31°25' N 34°48' E) at an altitude of 350–500 m a.s.l, in the Northern Negev of Israel. The climate is semi-arid, with winter rainfall (December–March). Average annual precipitation is 300 mm (Baram 1996). Annual precipitation was 195 and 190 mm in the two research years (2002–2004). Average daily temperatures range from 10 °C in winter to 25 °C in summer (Baram 1996). Soils were loamy textured, of a brown desert skeletal type that develops on Eocene limestone, dolomite and chalk (Ravikovitch 1981). Vegetation in the study area corresponded to the Irano–Turanian phytogeographical region (Zohary 1973). The landscape is a shrubland dominated by *S. spinosum* and organised spatially as a patch mosaic of rock, shrub and open soil patches (Fig. 3c). Shrubs cover most of the interrock soil patches leaving some soil patches open (Segoli *et al.* 2008). Open soil patches are typically covered by herbaceous vegetation, mostly dominated by *P. bulbosa*.

### Study species

*Sarcopoterium spinosum* (L.) Spach is a clonal dwarf shrub forming monospecific biomass patches that contain one to several individuals (Reisman-Berman *et al.* 2006). *Sarcopoterium spinosum* communities dominate a wide spectrum of habitats in the Middle East, including the batha vegetation of the Mediterranean coast, the semi-steppic plant aggregates of the hinterlands and the Grecian phrygana (Zohary 1973; Chiesura Lorenzoni & Lorenzoni 1977). Its distribution ranges from Sardinia, Italy to south Israel (Proctor 1968). This low shrub is dominant in the eastern Mediterranean and semi-arid shrublands in Israel (Litav & Orshan 1971). In Mediterranean rangelands, *S. spinosum* shows a great ability to persist and expand, mostly by resprouting and vegetative regeneration, even at high disturbance such as browsing by domestic animals, canopy removal for firewood or fire (Litav & Orshan 1971; Seligman & Henkin 2002).

*Poa bulbosa* L. is a small clonal geophytic-perennial winter-growing grass, common in rangelands on poor shallow soils. It is widely dis-

tributed in the Mediterranean and adjoining phytogeographical regions, central and north Europe, the central parts of Asia (Feinbrun-Dotan 1986) and an expanding invasive grass in North America. *Poa bulbosa* forms small tufts (3 to 20 cm diameter) of genets composed of many interacting small ramets (3–500) (Ofir & Dorenfeld 1992). The individuals within a genet population are distinct, with autonomous and genetically identical ramets. *Poa bulbosa* clones are formed by vegetative reproduction of a sprouting seed or bulb usually from vegetative propagation (vivipary) or from occasional flowering (Ofir 1986).

### Field methods

#### Physical template and *S. spinosum* landscape patterns

We sampled the patch mosaic structure of the landscape at a north and a west slope of the study site. We measured the proportion of the three main patch types: Rock, Soil and Shrub using eight 100-m (north slope) and four 80-m (west slope)-long transects, spaced 10 and 5 m apart respectively. We calculated the mean size of each patch type according to the length measured along the axis of the transect line, length proportion among patch types and the frequency of transitions from one patch type to another (e.g. rock–shrub, rock–soil and soil–shrub) along each transect. We used the data to analyse *S. spinosum* pattern across the slopes and the shrub density in soil patches.

#### *Poa bulbosa* patterns

We studied the multiclone patterns of *P. bulbosa* in Lehavim during two consecutive rainy seasons (February–March 2003 and 2004).

*Poa bulbosa* patterns along the slopes. In the first season, the aim was to investigate the diversity of multiclone patterns and identify *P. bulbosa* patterns along elevation gradients. For this purpose twenty-four 50 × 50-cm quadrats were sampled every 20 m along two 60-m transects on north- and west-facing slopes (2 slopes × 4 positions along each transect × 3 replicates located at random in each position interspersed enough to assure independence, Fig. 3b). The multiclone biomass pattern of *P. bulbosa* was sampled in the quadrats. The spatial distribution of *P. bulbosa* was measured in the plots as follows: (1) photography from c. 2-m height for image analysis; images were acquired after excluding all other plant species in each quadrat; (2) above-ground green biomass was clipped, collected, oven dried at 60 °C for 3 days and weighed.

*Poa bulbosa* patterns and run-off water redistribution. The aim of the second season of research was to test how patterns of *P. bulbosa* are affected by surface run-off water from rock patches and shrub patches. We selected an area with many soil patches containing *P. bulbosa* on the north-facing slope (10–20°) that was sampled the previous season. Twenty soil patches were randomly selected. We sampled the pattern of *P. bulbosa* in sites downslope and adjacent to *S. spinosum* shrubs and to bedrock (Fig. 3b). Our rationale was that on soil patches downslope of shrubs, little or no run-off water contributed to the soil patch as *S. spinosum* shrubs absorb all the run-off generated upslope (Segoli *et al.* 2008). However, downslope of rocky patches, there is a relatively high amount of run-off water generated and it is absorbed by the soil patch and available to *P. bulbosa* (Yair & Shachak 1987). We measured *P. bulbosa* pattern in these patches using a 1 × 1-m quadrat and the same method detailed for the first season.

**Table 2** Landscape spatial indices computed for vegetation pattern analyses

Index	Function	Meaning
Patch density (PDN)	$PDN[m^{-2}] = n/A_p$ $n$ – Number of patches $A_p$ – Total plot area ( $m^2$ )	$PDN > 0$ , The upper bound is constrained by grain size. Equivalent to the number of patches
Proportion of vegetation cover ( $\varphi$ )	$\varphi = \frac{\sum_{i=1}^n A_i}{A_p}$ $A_i$ – Area of patch $i$	$0 < \varphi < 1$ Equivalent to the total Area covered by vegetation
Perimeter to area (PAR)	$PAR[m^{-1}] = \frac{\sum_{i=1}^n p_i}{\sum_{i=1}^n A_i}$ $p_i$ – Perimeter of patch $i$	$PAR > 0$ , without limit $PAR \rightarrow 0$ in regular shapes, $PAR > 0$ as shape complexity increases. Measure of patchiness complexity
Total biomass	$B[mg]$ - Collected dry matter	
Biomass Density	$BD[g \cdot m^{-2}] = \frac{B}{\sum_{i=1}^n A_i}$	Average biomass produced per unit of plant cover area in the entire plot

### Image processing and pattern analysis

The high-resolution images (Tiff  $2272 \times 1074$  pixels) of the plots that we photographed were processed and analysed with geographical information system (GIS) tools using ERDAS IMAGINE 8.7 (ERDAS Inc., GA, USA), ArcView GIS Release 9 software (ESRI, CA, USA) and the MATLAB version 6.5 image-processing toolbox (The MathWorks, MA, USA). The images were geometrically and geographically corrected with the global coordinates of Lehavim and Transverse-Mercator projection, and the sampling quadrat area was clipped. *Poa bulbosa* plant patches were manually digitised to a polygon cover layer. Polygon layers were exported back to image format and saved as binary images. Image-size resolution ranged according to camera altitude. Thus, we rescaled all images to the average size of  $275 \times 275$  pixels for  $50 \times 50$ -cm plots and  $550 \times 550$  pixels for  $100 \times 100$ -cm plots (1.8-mm pixel size).

We computed three spatial pattern indices for each image (Table 2). Indices of Patch Density (PDN), Proportion of Vegetation Cover ( $\varphi$ ) and Perimeter to Area Ratio (PAR) were computed for the binary image of each plot. The collected biomass was used to determine Total Biomass ( $B$ ) per quadrat and biomass Density (Table 2). We used the combination of different indices to characterise different aspects of the *P. bulbosa* multiclone patterns (Turner *et al.* 2001; Li & Wu 2004). Computation was done using MATLAB 6.5. Spatial indices were adopted from FRAGSTATS (McGarigal *et al.* 2002) and adapted for the binary landscapes of vegetation vs. soil matrix.

### Statistical analysis

The effect of position within the landscape mosaic on *P. bulbosa* pattern was analysed for each index separately. Differences in indices among plots (1) along elevation gradients, (2) on north and west slopes and (3) in patches downslope to a shrub (SH) vs. downslope of bare bedrock (BB) were tested using one-way analysis of variance (ANOVA) for normally distributed indices or nonparametric Kruskal–Wallis tests for non-normally distributed variables. Proportion of

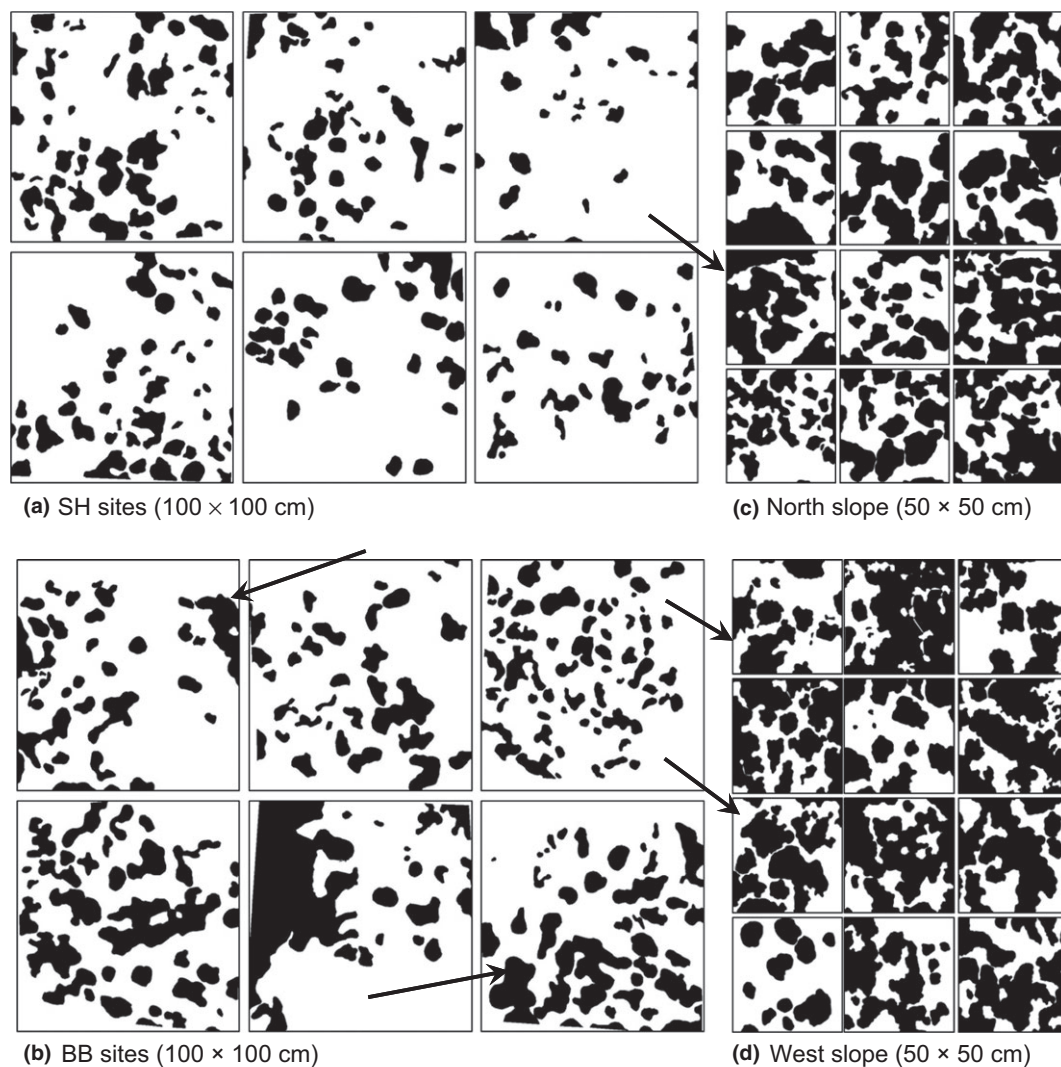
cover index  $\varphi$  was arcsine transformed to improve normal distribution. For the statistical comparison of spatial indices between  $50 \times 50$ -cm and  $100 \times 100$ -cm plots, we divided the large plots into four  $50 \times 50$ -cm subplot images and used an average of the four recomputed indices for the four images compiling the large quadrat image.

We analysed spatial indices for 14 of twenty  $1\text{-m}^2$  plots measured (six SH and eight BB plots) due to image-processing limitations such as extreme topographies or partial image cover. For the analysis of Total Biomass and Biomass Density, we used 19 of 20 measurements (one plot was excluded as an outlier because its total biomass was outside of the 0.95 confidence interval, as it had an exceptionally large number of *P. bulbosa* flowers compared with all other replications). We used JMP version 4 SAS software (SAS Institute, NC, USA) for all statistical analyses.

### Mathematical model

We studied vegetation patchiness in the presence of a physical template using the Gilad *et al.* (2004, 2007) model, spatially modulating the surface-water infiltration rate to account for a heterogeneous landscape. The model consists of three state variables representing above-ground biomass  $B(r,t)$ , soil–water content  $W(r,t)$  and surface water  $H(r,t)$ , where  $r = (x,y)$  are spatial coordinates and  $t$  is time. The state variables satisfy a system of partial differential equations that capture pattern-forming feedbacks and source–sink relations as we briefly discuss below. The model contains various parameters that characterise environmental conditions and quantify species traits. Parameters that describe the environment include the precipitation rate  $P$ , those describing the soil include the infiltration rate  $I$ , the infiltration contrast  $f$  (see below) and the surface-water transport coefficient  $D_{Hs}$  and those describing plant traits include the lateral root-to-shoot ratio  $E$  (see below), the seed dispersal coefficient  $D_B$  and the lateral root-zone size<sup>2</sup>  $S_0$ . For a fuller account of the model and all the parameters it contains, the reader is referred to earlier publications (Gilad *et al.* 2007; von Hardenberg *et al.* 2010; Meron 2011).

<sup>2</sup>The length  $S_0$  represents the root-zone size in the lateral ( $x,y$ ) plane of a seedling. In the case of no root feedback, i.e.  $E = 0$ , it also represents the lateral root-zone size of a mature plant whose roots extend vertically into the soil.



**Figure 4** Examples of binary images of the patterns of *Poa bulbosa* L. biomass (in black) found at the different sampling sites at Lehavim, Israel: in the north-facing slope in (a) 1-m<sup>2</sup> plots downslope of *Sarcopoterium spinosum* shrub (SH plots); and (b) 1-m<sup>2</sup> plots downslope of bedrock (BB plots); and in (c) 50 × 50-cm plots at random positions along elevation gradients in the North-facing slope; and (d) 50 × 50-cm plots at random positions along elevation gradients in the west-facing slopes (three plots from each elevation). Arrows indicate examples where we assume that the large *P. bulbosa* patches are a result of clumping of two or more clones.

One pattern-forming feedback included in the model is a positive feedback between above-ground and below-ground biomass mediated by water uptake (hereafter the ‘root feedback’). As a plant grows, its root-zone extends to new soil regions. As a result, the amount of water available to the plant increases and the plant can grow even further. The strength of this feedback is controlled by parameter  $E$  that provides a measure for the lateral root-to-shoot size ratio. Clonal plants whose lateral root-zone size is very small, such as *P. bulbosa*, are modelled by setting  $E = 0$ .

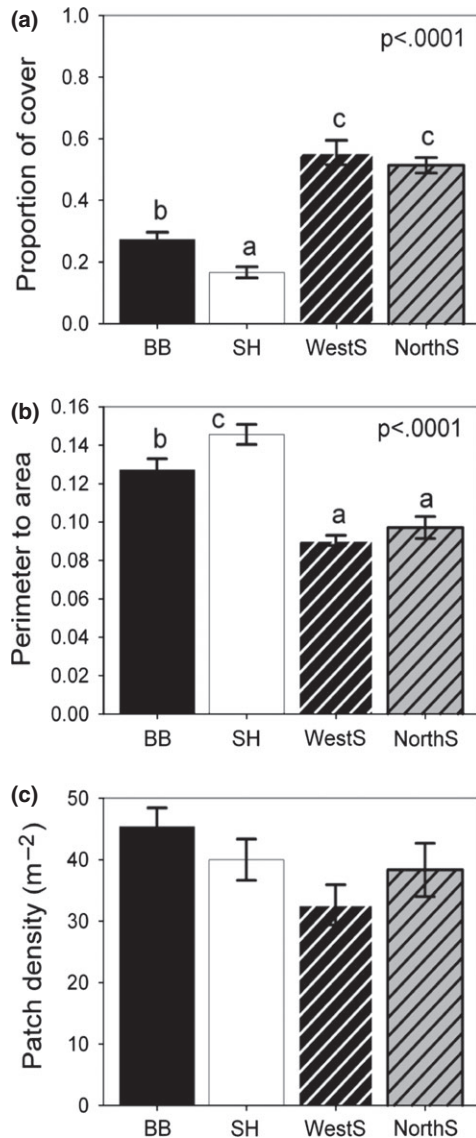
A second pattern-forming feedback in the model is a positive feedback between above-ground biomass and soil water (hereafter the ‘infiltration feedback’). Vegetation patches in drylands are generally surrounded either by bare soil or rocky patches. Bare soil is often covered by biological and physical soil crusts that reduce the infiltration rate of surface water into the soil relative to the infiltration rate in vegetation patches (Eldridge *et al.* 2000; Sela *et al.* 2012). Rocky patches do not infiltrate surface water at all. As a consequence, vegetation patches act as sinks for run-off water generated

by their crusted or rocky neighbourhoods. This accelerates their growth, sharpens the infiltration contrast and increase even further the soil moisture in the vegetation patch. The strength of this feedback is controlled by an infiltration parameter  $0 \leq f \leq 1$  that represents the infiltration contrast between bare and vegetated areas. The smaller  $f$ , the higher the infiltration contrast. In rock patches, we set infiltration rate  $I$  to zero.

We use the Gilad *et al.* (2007) model to test two main predictions of the conceptual model: (1) the possible increase of patchiness variability by source–sink relations in a landscape of variable soil-patch sizes and (2) the decreased variability and the appearance of arid-like patchiness for plants of larger patch sizes. To test these predictions, we conducted numerical simulations of the model equations on a series of five squared domains of area  $L^2$  each for four plant species of increasing patch sizes. Each domain contains a circular subdomain at its centre within which the infiltration rate is non-zero and biomass dependent. In the surrounding area, the infiltration rate is set to zero to model a rock patch. The domains

for each plant species differ in the size of the circular soil patches they contain. The soil-patch areas successively increase by a factor of 1.2. The four species  $n = 1, \dots, 4$  are distinguished by their  $S_0$  and  $D_B$  values:  $S_{0n} = c_n S_0$ ,  $D_{Bn} = c_n^2 D_B$ , where  $c_1 = 1$ ,  $c_2 = 3$ ,  $c_3 = 5$ ,  $c_4 = 8$ . With this choice, the plant-patch sizes increase by approximately a factor  $c_n$ .

In all simulations, we used the same domain size  $L$  and model parameters (including the precipitation  $P$ ). We further omitted the root feedback by choosing  $E = 0$ , and used the limit of fast overland water flow relative to water infiltration into the soil, which we practically achieved by setting  $D_H = \infty$ .



**Figure 5** Comparison of pattern indices (mean  $\pm$  SE) of *Poa bulbosa* at the Lehavim LTER (a) *Proportion of Vegetation cover*  $\phi$ , (b) *Perimeter to Area* ratio, and (c) *Patch Density*. Comparisons show plots downslope from bare bedrock (BB patch,  $n = 32$ ), downslope from a shrub (SH patch,  $n = 24$ ), along an elevation gradient in a west-facing slope (WestS,  $n = 12$ ) and a north-facing slope (NorthS,  $n = 12$ ). An average of the four  $50 \times 50$ -cm plots that compile each  $1\text{-m}^2$  BB and SS plot were used for the comparison with West and North slopes plots. Letters indicate significant differences among groups by ANOVA and post-hoc Tukey–Kramer tests ( $P = 0.05$ ).

## RESULTS

### Empirical studies

The landscape of the study site is heterogeneous (Table 1). The slopes differed in the proportion of distinct physical patches and in the frequency of transitions between patches. The west-facing slope was characterised by more soil–rock transitions, whereas in the north-facing slope, there were more soil–shrub transitions (Table 1). However, typical lengths of each of these patches along the hill slope were similar among the different slopes. Mean soil-patch length was  $c$  twice the size of shrub and rock patches. The soil patches typically contained two to six individual *S. spinosum* shrubs, and were either completely covered by shrub patches (area 1 in Fig. 1a) or partially covered (area 2). They were too small to support self-organised shrub patterns (area 3). By contrast, each soil patch contained a large number of *P. bulbosa* clones (thousands of individual ramets).

Qualitative and quantitative spatial analysis of *P. bulbosa* showed a variety of patterns in the study site. Spatial-pattern indices of *P. bulbosa* distribution displayed high heterogeneity and no significant correlation to elevation or slope in the  $50 \times 50$ -cm scale of observation (results not shown). We found a diversity of multiclone patterns ranging from spots to gaps. We found different patterns in close proximity (within few metres of distance) on the slope scale (Fig. 4c, d). We infer from these results that *P. bulbosa* spatial patterns are influenced by processes acting at a length scale smaller than the spatial extent of the slope, and apparently are associated with conditions in the soil patch. These results motivated a more scrutinised examination of *P. bulbosa* patterns during the second season.

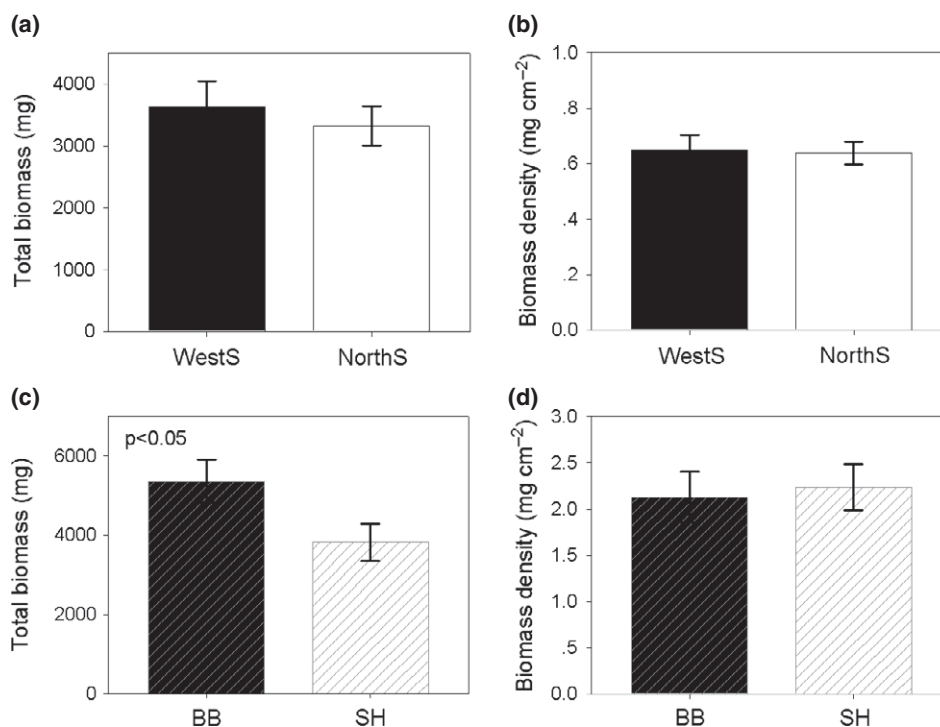
We qualitatively and quantitatively compared biomass patterns of *P. bulbosa* in soil patches located downslope of either BB or SH. Examples of *P. bulbosa* patterns at the different locations are shown in Fig. 4a, b. *Poa bulbosa* patches of intermediate size can be seen qualitatively in all of these plots representing typical clone sizes of different ages. However, in BB plots, much like in the  $50 \times 50$ -cm samples, we observed larger plant patches (Fig. 4b–d respectively), whereas in the SH plots the plant biomass pattern consists mainly of smaller single genet spot patches interspersed by larger areas of bare soil (Fig. 4a).

**Table 3** Comparison of *Poa bulbosa* organisation among soil patch types. Shown are comparisons (mean  $\pm$  SE) of spatial indices between plots downslope from bedrock (BB patch,  $n = 8$ ) and downslope from a shrub (SH patch,  $n = 6$ ). Indices were compared using one-way Analysis of Variance (ANOVA) and  $t$ -test, or a nonparametric Wilcoxon/Kruskal–Wallis test (indicated by KW)

Spatial index	BB plots	SH plots	P-value
Average number of patches/plot	36.625 (4.110)	34.833 (3.833)	(no $p$ )
Patch density (PDN) [# /plot]	0.04 (0.004)	0.038 (0.004)	0.7829
Proportion of vegetation cover (PVC)	0.273 (0.027)	0.161 (0.02)	0.0034**
Perimeter-to-area ratio (PAR) [ $m^{-1}$ ]	0.111 (0.009)	0.135 (0.005)	0.0575
Circumscribing circle (CIR)	0.455 (0.013)	0.431 (0.014)	0.2496
Mean patch perimeter to area [ $m^{-1}$ ]	1.479 (0.596)	0.408 (0.029)	0.0142*
Mean elongation of patches (KW)	0.0468 (0.036)	0.002 (0)	0.0142*
<i>Analysis of all the patches in all plots</i>			
Mean patch area [ $cm^2$ ] (KW)	22.468 (297.7)	14.37 (88.4)	0.0259**
Mean major axis length (cm) (KW)	6.598 (2.834)	5.497 (1.876)	0.0201*
Mean minor axis length (cm) (KW)	3.723 (1.474)	3.234 (1.082)	0.0412*
Number of patches	293	209	

\*, \*\* indicate  $P < 0.05$  and  $0.01$  respectively





**Figure 6** Comparison of standing *P. bulbosa* biomass from four sites at Lehavim LTER (mean  $\pm$  SE). (a) and (b); Comparison of Total Biomass (mg) and Biomass Density ( $\text{mg cm}^{-2}$ ) between plots on a west-facing slope (WestS,  $n = 12$ ) and a north-facing slope (NorthS,  $n = 12$ ). (c) and (d): comparison of plots downslope from bedrock (BB patch,  $n = 10$  and 8 respectively) and plots downslope from a shrub (SH patch,  $n = 9$  and 6 respectively).

Quantitative pattern analysis showed that the proportion  $\phi$  of *P. bulbosa* cover (Fig. 5a) was higher and PAR, (Fig. 5b) was significantly lower ( $P < 0.0001$  one-way ANOVA for both) in the  $50 \times 50$ -cm samples that were sampled along the soil–rock slopes (West and North slope), compared with subsamples of the same size from soil patches in the rock–shrub patch mosaic of the northern slope (BB and SH). In all the plots, however, PDN, (Fig. 5c) was similar among these landscape positions. This combination of indices reflects the differences in the *P. bulbosa* pattern states found at different conditions of soil patches within the rock–soil–shrub patch mosaic. The main difference is between spot patterns found in soil patches in the shrub–rock–soil mosaic (Fig. 4a, b) and the higher diversity of patterns (spots, stripes and even gaps) found in soil patches along soil–rock slopes with no shrubs (Fig. 4c, d). Soil patches in a soil–rock slope (e.g. the west-facing slope) receive higher run-off input in comparison with soil patches in a rock–soil–shrub mosaic (e.g. the north-facing slope) in which more run-off is absorbed by the shrubs.

On the north-facing slope, we found that the proportion  $\phi$  of *P. bulbosa* cover was higher in BB than in SH plots (Fig. 5a, Table 3). The PAR index was slightly higher in SH plots with less plant cover ( $P = 0.057$ , Table 3, Fig. 5b). A comparison between SH and BB patterns shows that the density of biomass patches (PDN) as well as the average number of patches per plot were similar in both cases (Fig. 5c, Table 3). Perimeter-to-area ratio was negatively correlated to the proportion of cover (linear regression slope =  $-2.5$ ,  $r^2 = 0.54$ ,  $P = 0.0028$ ,  $n = 14$ ). Proportion of cover may increase by an expansion of existing patch areas and/or by the addition of

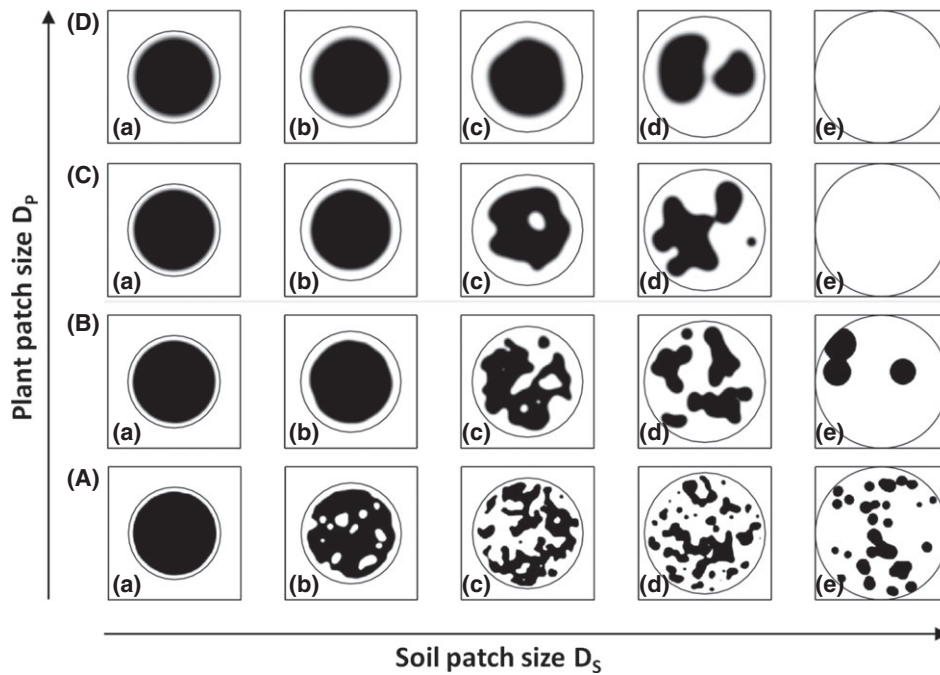
more patches with similar area size. A negative correlation between  $\phi$  and PAR is true only in the first case and not in the latter, which indicates that the BB plots were characterised by an increase in spot areas. *Poa bulbosa* patch density was similar in BB and SH plots, but the patches were larger in BB than in SH plots. Biomass patches in BB plots were larger in total area and in both major and minor axes length, more elongated and exhibited a more complex shape i.e. higher patch perimeter-to-area ratio (Table 3). Thus, SH plots displayed a spot pattern, whereas in BB plots, we found a more complex spot-stripe shape, and the patterns along elevation gradients consisted of more complex maze<sup>3</sup> and gap patterns (see examples in Fig. 4c, d).

Total above-ground biomass of *P. bulbosa* (per plot) was similar in West and North slopes (Fig. 6a), but was higher in BB than in SH plots (Fig. 6c,  $P = 0.036$  one-way ANOVA). Biomass density ( $\text{mg cm}^{-2}$ ) was similar in both sets compared (West and North slopes, Fig. 6b, BB and SH plots Fig. 6d), indicating that total biomass density was an outcome of higher cover, i.e. larger plant patches in BB plots. Average productivity per *P. bulbosa* ramet did not differ among landscape positions, although they grew under distinct soil moisture conditions. A complete comparison is not possible due to the difference in sampling time.

### Model studies

Results of model simulations for various relative sizes of soil patches and plant patches are shown in Fig. 7. Figure 7A shows the effect of decreasing soil patch size on the patchiness of a species

<sup>3</sup>We use the term 'maze' to denote labyrinth-like patterns that lack a characteristic length, and reserve the term 'labyrinth' to describe patterns that do have a characteristic length – the width of the stripes that make the labyrinthine pattern. Maze patterns, which are intermediate to spot and gap patterns, tend to appear (and replace labyrinthine patterns) when the competition for water becomes global (von Hardenberg *et al.* 2010).



**Figure 7** Vegetation patchiness in rock–soil domains of increasing soil-patch size (a–e, successively increasing in area by a factor 1.2) and increasing plant-patch size (A–D), obtained as solutions of the Gilad *et al.* (2007) model. The circles represent soil patches that act as sinks for run-off produced by the surrounding rock areas. Small plant-patch sizes lead to highly variable self-organised patchiness (A). As plant-patch size increases, the patchiness becomes more template dictated (B, C, and D). Parameters:  $P = 310 \text{ (kg m}^{-2}\text{) year}^{-1}$ ,  $K = 1 \text{ kg m}^{-2}$ ,  $Q = 0.05 \text{ kg m}^{-2}$ ,  $M = 6 \text{ year}^{-1}$ ,  $A = 40 \text{ year}^{-1}$ ,  $N = 6 \text{ year}^{-1}$ ,  $E = 0$ ,  $\lambda = 0.064 \text{ (kg m}^{-2}\text{) year}^{-1}$ ,  $\Gamma = 8 \text{ (kg m}^{-2}\text{) year}^{-1}$ ,  $R = 0.95$ ,  $f = 0.1$ ,  $S_0 = 0.05$ ,  $D_W = 0.0625 \text{ m}^2 \text{ year}^{-1}$ ,  $D_H = \infty$ ,  $D_B = 6.25 \cdot 10^{-4} \text{ m}^2 \text{ year}^{-1}$ ,  $L = 16 \text{ m}$ . The root-zone sizes and the seed dispersal coefficients are scaled as  $S_{0n} = c_n S_0$  and  $D_{Bn} = c_n^2 D_B$ , with  $c_n = 1, 3, 5, 8$  for species  $n = 1 \dots 4$  (rows A–D).

with a small plant-patch size. A large soil patch surrounded by a small rock patch (panel Ae) receives little run-off and remains relatively dry. If  $P$  is not too small for any vegetation form to grow, such a soil patch supports vegetation spot patterns typical of homogeneous arid landscapes. A smaller soil patch receives more run-off and shows maze patterns characteristic of homogeneous semi-arid landscapes (panels Ac,d), while a yet smaller soil patch is wet enough to support a gap pattern often observed in dry–subhumid landscapes (panel Ab). A sufficiently small soil patch is not water limited and shows uniform vegetation coverage (panel Aa). These results are in line with the first prediction of the conceptual model: increased patchiness variability by source–sink relations in a landscape of variable soil-patch sizes.

Figure 7B–D show the effects of increasing plant-patch size. The variability of vegetation patchiness decreases as more soil patches become fully covered by vegetation (panels Ba,b,Ca,b and Da,b) or completely bare (panels Ce, and De). In addition, soil patches that do support patchy vegetation of species with large plant-patch sizes show vegetation patterns characteristic of dry landscapes such as spots (panel Dd). These results are in line with the second prediction of the conceptual model: decreased variability and the appearance of arid-like patchiness for plants of larger patch sizes.

The suite of patterns generated by the model simulations (Fig. 7) support the conceptual model as presented in Fig. 1a. Looking at the locations of these patterned states in the phase plane spanned by the soil-patch and plant-patch sizes, one can identify the transitions between the three areas depicted in Fig. 1a (lines I and II): self-organised patchiness (right bottom corner of the figure), patchiness

controlled by both self-organisation and physical template and patchiness solely controlled by the physical template (upper left corner).

## DISCUSSION

We put forth a theoretical framework that links vegetation patchiness to a pre-existing physical template consisting of rock and soil patches interrelated by resource flows. According to the theory, the actual realisations of vegetation patchiness are highly dependent on the relative sizes of vegetation and soil patches. We studied these size relations empirically, using field experiments, and theoretically, simulating a mathematical model for water-limited vegetation. We discuss the results of these studies below, and address the following questions: How can the theory be tested? How general is it?

### Empirical studies

The empirical studies focused on two plant species, *S. spinosum* shrub and *P. bulbosa* grass, that give rise to small and large vegetation patches under the same environmental conditions. The observed shrub patterns supported the predictions for a plant species whose patch size is of the same order of magnitude as the largest soil patch in the landscape. As a consequence, its above-ground biological patchiness in the studied slopes was highly constrained by the physical template and showed high similarity to the soil patchiness (areas 1 and 2 in Fig. 1a).

The observed grass patterns combined with the differences found in pattern indices and total biomass supported the predictions for a plant species whose patch size is small enough to produce a highly

variable patchiness ranging from bare soil to spot, maze and gap patterns. These vegetation states appear to be qualitatively homologous to the basic states predicted by mathematical models (Borgogno *et al.* 2009) and observed in the field (Deblauwe *et al.* 2008), except that they coexist in the same landscape. Using the conceptual model, we attribute this high variability to the differential water content within soil patches of different sizes, induced by the source–sink rock–soil relationships (Fig. 2a). This differential water content not only allows for different vegetation states, it also stretches the axis of plant-to-soil patch ratio  $D_p/D_s$ , by increasing the typical plant-patch size in smaller soil patches, thereby allowing for a wider range of vegetation coverage forms (Fig. 2b).

The shrub species *S. spinosum* not only plays the role of a species with a large plant-patch size but also provides another test of the conceptual model by reducing run-off towards soil patches in which *P. bulbosa* grow. According to the model, in the absence of source–sink relations, the variability of *P. bulbosa* patchiness should be lower. Indeed, the prevailing pattern in the shrub–rock–soil mosaics was spots (Fig. 4a, b), whereas *P. bulbosa* patterns in the rock–soil mosaics with no shrubs included spot, maze and gap patterns (Fig. 4c, d).

### Model studies

The model studies complement the field studies in two respects: (1) they provide a better account of the rock to soil source–sink relations within the physical patchwork and their impact on self-organised patchiness and (2) they allow studying the intermediate range of plant-patch sizes between the two extremes represented by *S. spinosum* and *P. bulbosa*.

By capturing the dynamics of overland water flow and linking the increased soil–water content in soil patches of decreasing sizes to the sequence of basic vegetation patterns (spots, maze, gaps, uniform), the model studies achieve two goals. First, they support the prediction of the conceptual model that source–sink relationships in a non-uniform physical patchwork of soil and rock patches can increase the variety of vegetation patterns that can be observed in a given landscape. By negation, they also account for the proposed role of shrubs in reducing the variety of *P. bulbosa* patchiness; by eliminating run-off, the shrubs even out the water content in soil patches of different sizes and thereby reduce the variability of *P. bulbosa* patchiness. Furthermore, the exploration of intermediate plant-patch sizes reveals a gradual decrease in patchiness variability as the plant-patch size increases, in line with the conceptual model; more soil patches become uniformly vegetated, whereas others show patterns typical of dry landscapes or are completely bare.

The exploration of different soil-patch sizes, for a given plant-patch size, suggests a narrow transition range between self-organised and template-imposed patchiness, corresponding to area 2 in Fig. 1a. Detailed simulations at smaller increments of patch-size ratios can resolve this range and provide numerical thresholds at which vegetation patchiness becomes entirely template induced (line I in Fig. 1a) or self-organised (line II). A deeper understanding of these thresholds calls for a mathematical analysis of the model equations on finite domains.

The model results presented in Fig. 7 were obtained for fast surface-water flow relative to infiltration and in the absence of the root feedback. These conditions lead to global competition and the formation of wide patch-size distributions at intermediate levels of

water stress, as the maze patterns shown in Fig. 7Ac,d indicate (von Hardenberg *et al.* 2010). These conditions were chosen to simulate small clonal plants capable of showing vegetation patchiness in small plots, such as *P. bulbosa*. The lateral root expansion for such species is very small, and the time scale associated with run-off flow is very short compared with the infiltration time because of the small plot sizes.

Switching on the root feedback ( $E > 0$ ) will narrow down the vegetation-patch size distribution and lead to nearly periodic patterns of spots, stripes (labyrinth) and gaps (insets in Fig. 2a, b) within soil patches of sufficient size (von Hardenberg *et al.* 2010). Slowing down the surface-water flow will introduce a soil–water gradient towards the soil-patch centre. This may result in a vegetation ring near the boundary of the soil patch (as a result of high run-off infiltration at the rock–soil boundary) and vegetation spots inside, a patch form characteristic of dryer environments.

### Different forms of patchiness variability: a further test of the theory

Water-limited landscapes with large homogeneous areas can show a wide variety of vegetation patterns. The variability of these patterns is the result of the five basic patterned vegetation states and the bistability ranges between any consecutive pair of states. These bistability ranges give rise to a multitude of disordered stable states that can be viewed as spatial mixtures of the two alternative stable basic states, e.g. scattered spots in bare soil, or a spatial mixture of spots and stripe fragments (Meron 2012). This fairly high variability is still limited in the sense that all plant patches have a characteristic length – the diameter of a spot, the width of a stripe or the diameter of a gap. Pattern variability will increase when conditions of global competition develop, e.g. fast overland flow relative to infiltration, and produce patterns lacking any characteristic length (von Hardenberg *et al.* 2010; Fig. 7Ac, d).

Vegetation patchiness induced by source–sink relations in rock–soil mosaics present a yet higher degree of patchiness variability. When the competition for water is local, the most variable patterns that can emerge in homogeneous landscapes are spatial mixtures of two consecutive basic states. In the presence of a source–sink rock–soil template, the most variable patterns can involve all five basic states and spatial mixtures thereof, spatially coexisting at different soil patches within the same landscape. When the competition is global, a similar conclusion holds. In homogeneous landscapes, the most variable patchiness is formed by maze patterns (Fig. 7Ac, d). In rock–soil landscapes, the patchiness can involve in addition spot and gap patterns characterised by narrow patch-size distributions (Kéfi *et al.* 2011, Fig. 7Ae, b). Last, the variability of vegetation patchiness will increase even more by the coexistence of different plant species, each with its typical patch-size, within a given soil patch.

The different degrees of patchiness variability can be used to test the proposed theory. Landscapes exhibiting either spot, or stripe or gap patterns, or spatial mixtures of at most two consecutive patterned states, all indicate the existence of fairly homogeneous areas (Becker & Getzin 2000; Tongway *et al.* 2001; Deblauwe *et al.* 2008; Barbier *et al.* 2010). By contrast, landscapes that exhibit all or most of these patterns imply the existence of an underlying rock–soil physical template. Verifying in the field, the existence of such a template can corroborate the theory.

## Generality of the theory

The theoretical framework has been presented in the context of vegetation patchiness in a heterogeneous landscape consisting of rock–soil mosaics. Such mosaics are characteristic of terrestrial ecosystems with rock being the basic matrix of earth surface and soil being the product of rock-weathering processes (Chapin *et al.* 2011). Rock–soil mosaics are therefore inherent elements of terrestrial landscapes. The combination of pedological and geomorphological processes creates various forms of rock–soil mosaics that span a wide range of spatial scales (Gerrard 1995). Our field case study represents the low edge of this range, with soil and rock patch sizes of the order of 1 m. Watersheds in extreme deserts represent the high edge of the range. These ecosystems consist of soil planes, a few hundreds of metres big that are embedded within rocky mountain ridges and maintain source–sink relations with them. Inflows of water and nutrients from the rocky mountains along with strong pattern-forming feedbacks can result in self-organised patchiness of trees and shrubs within the soil planes.

The theoretical framework may be applicable or extendable to other ecological contexts where different factors (e.g. stream-lines, peat mounds, coral reefs and disturbances) constrain the space available for biomass growth or resource (e.g. water, nutrient, energy) availability. Possible examples of such contexts are vegetation patterns in peatlands (Eppinga *et al.* 2009), wetlands (van der Valk & Warner 2009), plankton patchiness (Medvinsky *et al.* 2002) mussel-bed patterns (van de Koppel *et al.* 2008) and wave regeneration of forest trees (Satō & Iwasa 1993).

## CONCLUSIONS

We presented here a theoretical framework for vegetation patterns in heterogeneous landscapes that integrates two disparate views: patchiness dictated by a pre-existing rock–soil template and self-organised patchiness driven by plant interactions through positive biomass–resource feedbacks. The framework highlights two aspects of vegetation patchiness: (1) the relation between the size of a soil patch, and the size of a plant patch and (2) the dependence of the plant-patch size on genetic species constraints and on resource availability. The two aspects are coupled through source–sink resource relations within the rock–soil template; the smaller the soil patch, the more resources it receives and the larger the plant patches it can grow. When the plant-patch size exceeds the size of the biggest soil patch in the landscape, the vegetation patchiness is template dictated. When the smallest soil patch is large in comparison with the plant-patch size, the patchiness is self-organised.

Our framework explains the intermediate cases between these two extremes, which are more common in nature. We explored these complex intermediate cases empirically, using two plant species, and theoretically, using a spatially explicit mathematical model. The main findings of these explorations are: (1) vegetation patchiness in any landscape is likely to be a mixture of patchiness induced by the physical template and by self-organisation, (2) source–sink resource relations increase patchiness variability by allowing all forms of vegetation patterns to coexist in the same landscape and (3) species of larger patch sizes are associated with decreased variability and the appearance of arid-like patchiness.

## ACKNOWLEDGEMENTS

This study was supported by the Israel Science Foundation, Grant No. 780/01, by the James S. McDonnell Foundation and by the EU-ARI programme at the Blaustein Institute for Desert Research. We would like to thank Adi B., Niv, Noga, Sonja, Yael S., Gal, Marina, Diana, Hofesh, Sol, Guy, Dikla and Ziv for their help in the experimental work and data analysis; and Sol Brand and Bert Boeken. Finally, we thank the editor and three anonymous referees for their insightful comments and for helping us improve this manuscript.

## AUTHORSHIP

ES designed and performed the empirical research and analysed data, MS designed the study, JvH, HY and EM performed the modelling work, ES, MS, JvH and EM contributed to developing the conceptual model and ES, MS and EM wrote the manuscript.

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Editor, Bernd Blasius

Manuscript received 31 August 2012

First decision made 27 September 2012

Manuscript accepted 6 October 2012