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Geodiversity decreases shrub mortality and increases ecosystem tolerance to droughts and climate change

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ABSTRACT: Mass mortality of shrubs, especially the *Noaea mucronata* species, has been observed in the semi-arid Negev of Israel since the early twenty-first century. This has followed a long-term drought episode, and suggests a hysteresis-like effect. However, recent studies have revealed that the mortality has been varied across the region. Therefore, we assessed the depth and stoniness of the soil profile, in homogeneous and heterogeneous hillslopes. Then, we studied the volumetric moisture content during two consecutive growing seasons, in the topsoil of shrubby patches and of inter-shrub spaces in these hillslopes. The study shows that geodiversity – characterized by shallow soil, a high content of stones in the soil, and a high cover of rock fragment on the surface – reduced shrub mortality. This was attributed to the soil moisture content, which was considerably greater in the heterogeneous hillslopes, than that in the homogeneous hillslopes. It is proposed that the shallow soil halted the growth of herbaceous vegetation in the inter-shrub spaces of the heterogeneous hillslopes. Therefore, under rainstorms, this hillslope configuration results in considerable generation of overland water flow in the inter-shrub spaces. The water accumulates in the shrubby patches, allowing them to thrive, even during long-term dry episodes. In hillslopes with a deep soil layer, no stoniness in the soil profile, and no cover of rock fragments, the herbaceous vegetation is well developed, covering a considerable share of the inter-shrub spaces. This negates runoff formation and source–sink relations, limiting water availability for the shrubs, and resulting in their mass mortality. Despite no direct pastoral value for livestock, the shrubs play an important role in overall ecosystem functioning. This is due to their capacity to transect hydraulic connectivity, and negate ecosystem collapse. We propose a conceptual model for demonstrating the role played by geodiversity in alleviating drought stress in drylands. Copyright © 2018 John Wiley & Sons, Ltd.

KEYWORDS: climatic change; dryland ecosystems; land degradation; legacy effect; rock fragment position

Introduction

Geodiversity encompasses the natural range of physical components of ecosystems, including geological, geomorphological, and pedological (Silva *et al.*, 2013). So far, geodiversity has been mostly studied on large spatial scales, ranging between hillslopes, watersheds, and landforms (Serrano-Cañadas and Ruiz-Flaño, 2007; Jačková and Romportl, 2008; Thomas, 2012). It has been shown that geodiversity affects biodiversity, either directly or indirectly, determining both qualitative and quantitative aspects of the biotic components of ecosystems (Hjort *et al.*, 2015). Also, geodiversity regulates a wide range of goods and services, which are provided by the abiotic components of ecosystems (Gray, 2012). Among other impacts of geodiversity, the effect on hydraulic connectivity – characterized as the extent to which materials are redistributed within a landscape unit (Okin *et al.*, 2015) – is of particular importance for water-limited ecosystems.

A recent study from the semi-arid Negev region of southern Israel has shown that small-scale geodiversity has been generated by the uneven, spatially patterned distribution of livestock traffic on the hillslopes. This was reported to form networks of contour-like trampling routes, which are distinct from the remainder of the inter-shrub spaces. This small-scale geodiversity was reported to strengthen the spatial redistribution of water and associated dissolved and suspended materials on the hillslopes, resulting in the greater availability of these resources for vegetation (Stavi *et al.*, 2015). Another study highlighted the connections of one-decimeter-to-a-few-decimeters scale geodiversity, which regulates the surface hydrological processes and spatial patterning of vegetation (Stavi *et al.*, 2018). Recent modeling studies showed that small-scale geodiversity imposed by the stoniness of the soil alleviates water stress for shrubs, increasing their durability under decreased precipitation regimes (Yizhaq *et al.*, 2014; Yizhaq and Bel, 2016; Yizhaq *et al.*, 2017).

Mass mortality of shrubs across the semi-arid northern and western Negev has been reported since the early twenty-first century. This trend has been particularly prominent for the *Noaea mucronata* (Forssk.) Asch. & Schweinf, which is one of the predominant shrub species across the region. This has followed a prolonged drought period, questioning the tolerance of these shrublands to extremely dry episodes (Shachak, 2011; Sher *et al.*, 2012; Zaady *et al.*, 2012). The objective of this study was to assess the impact of geodiversity on shrubland functioning under the prolonged drought episode in these drylands. More precisely, our objective was to study the impact of geodiversity – as determined by the soil depth, stone cover, and rock fragment content – on the shrub vitality, pastoral productivity, and shrubland tolerance to long-term drought scenarios. It was hypothesized that either directly or indirectly, geodiversity has increased the spatial redistribution of the scarce water resource, increasing its availability for shrubs, and alleviating the impact of the prolonged drought, sustaining the functioning of these shrublands.

Materials and Methods

Regional settings

The study was implemented in the Long Term Ecological Research (LTER) station of the Sayeret Shaked Park, in the semi-arid north-western Negev of southern Israel (31°27′ N, 34°65′ E; 187 m above sea level [a.s.l.]: Figure 1). While the park covers an area of approximately 600 ha, the LTER station covers an area of ~ 20 ha, which has been surrounded by fence since the late 1990s to prevent livestock access. The region's lithology is comprised of chalk from Eocene and Plio-Pleistocene eolianites. The landform is dominated by rolling hills, with hillslope incline ranging between 3° and 6°. Soil is classified as loessial Calcic Xerosol, with a sandy loam to loamy sand texture (Singer, 2007). Depth and stoniness of soil, as well as rock fragment cover percentage, are highly varied.

Over the long run, mean daily temperatures in the warmest and coldest months have been 26 and 12°C, respectively, and mean cumulative annual precipitation has been ~ 250 mm (Bitan and Rubin, 1991). Yet, during the first decade of the twenty-first century, a sharp decrease in precipitation rates has occurred (Shachak, 2011), yielding a yearly average of ~ 165 mm only (Israel Meteorological Service website: http://www.ims.gov.il/ims/all_tahazit/).Simultaneously, since the early twenty-first century, a trend of mass mortality of shrubs has been observed, with particular high mortality rates among *Noaea mucronata*.

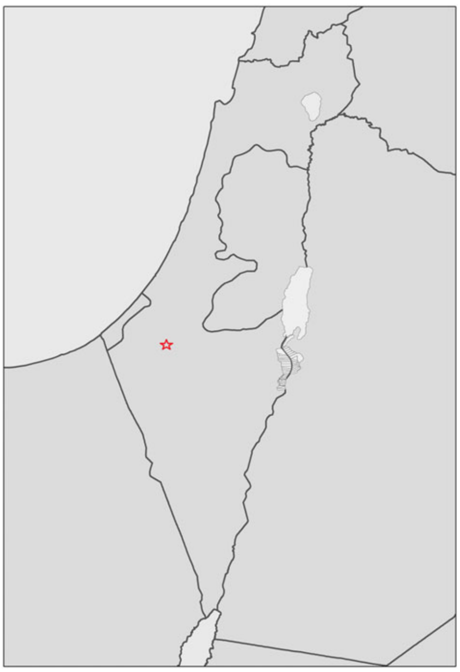

Figure 1. Map of Israel, with an indication of the study site. [Colour figure can be viewed at wileyonlinelibrary.com]

Preliminary observations across the park area revealed that perennial vegetation is comprised of a number of shrub and chamaephyte species. In addition to the *N. mucronata*, species of these life-forms include the *Deverra tortuosa* (Desf.) DC., *Helianthemum kahiricum* Delile, *Anabasis articulata* (Forssk.) Moq., *Echinops polyceras* Boiss., *Phagnalon rupestre* (L.) DC., *Thymelaea hirsuta* (L.) Endl., *Teucrium capitatum* L., *Ephedra aphylla* Forssk., and *Gypsophila capillaris* (Forssk.) C.Chr. In the wadis (ephemeral streams), *Lycium shawii* (Roem. & Schult.) is the dominant shrub species. Geophytes are also prevalent on the hillslopes, encompassing *Asphodelus ramosus* L., *Scilla hanburyi* Baker, *Moraea sisyrinchium* (L.) Ker-Gawler, *Gagea reticulata* (Pall.) Schult. & Schult.f., and *Anemone coronaria* L. Herbaceous vegetation includes a wide range of annuals and hemicryptophytes, of which the Stipa *capensis* Thunb. and *Avena sterilis* L. are the most dominant spices. Additional herbaceous vegetation species include the *Asphodelus tenuifolius* Cav., Poa *bulbosa* L., *Erodium crassifolium* L'Her. ex Aiton, *Senecio leucanthemifolius* subsp. vernalis Poir., *Erucaria rostrata* (Boiss.) Greuter & Burdet, *Calendula arvensis* L., *Trigonella arabica* Delile, and *Plantago ovata* Forssk.

Temperature and precipitation data for the rainy seasons between 1999/2000 and 2015/2016 were obtained from the meteorological station located at the Sayeret Shaked Park. However, due to several technical faults in the monitoring equipment during this period, only partial precipitation data was obtained for the rainy seasons between 2006/2007 and 2013/2014. In order to verify the validity of the data on a regional scale, precipitation data was also sought for an additional 11 meteorological stations across the north-western Negev, encompassing the nearest Gilat station (Ministry of Agriculture and Rural Development website: http://www.meteo.co.il/), and 10 stations (IsraelMeteorological Service website: http://www.ims.gov.il/ims/all_tahazit/) across the north-western Negev.

The study design and hillslopes survey

Fieldwork for the study was conducted between summer 2015 and summer 2017. In order to exclude disturbances imposed by livestock grazing, the study was confined to a land unit which has been fenced off since the late 1990s, providing an area of ~ 20 ha for the research. Surveying of this fenced land revealed the occurrence of hillslopes with a substantial rock fragment cover (Figure 2), and hillslopes with no rock fragment cover at all (Figure 3). Three hillslopes of each type were selected for the study, with a distance of at least 100 m between two adjacent hillslopes. In order to accurately represent the study region, it was decided to study the impact of hillslope type in 400 m^2 (20 m × 20 m) plots along the backslope geomorphic unit of each of these hillslopes. To negate aspect- and incline-related effects, all plots were delineated at a relatively similar azimuth (310° ± 29°) and slope (5° ± 0.5°).

Mapping of the plots was conducted in order to quantify the relative cover of the different components on the ground surface. This was implemented by the line-point intercept method (Herrick *et al.*, 2005), in which the type of cover was recorded

Figure 2. A typical stony hillslope in the study region. Note the plenty of shrubs/chamaephytes and the abundant rock fragment covering the ground surface. Picture taken by H. Yizhaq in spring 2017. [Colour figure can be viewed at wileyonlinelibrary.com]

Figure 3. A typical non-stony hillslope in the study region. Note the very dense cover of herbaceous vegetation, and the sparse (dead) shrubs. Picture taken by H. Yizhaq in spring 2017. [Colour figure can be viewed at wileyonlinelibrary.com]

at a 25-cm interval along a 20-m transect × three transects per plot (yielding a total of 240 reading points per plot). The transects were delineated in a parallel mode, and the lateral distance between each two adjacent transects was 10 m. The types of ground surface cover were tagged as alive shrub (and species), dead shrub (and species, as determined by the canopy's morphological features), herbaceous vegetation, partially-embedded rock fragment, loosely-resting rock fragment, exposed soil/biological crust, geophytes, rock exposure, and other (including all other types of cover, such as faunal perturbations, snail shells, etc.).

On-site measurements and monitoring

The soil depth was monitored in five randomly-selected spots per plot, by drilling with an auger down to the underlying bedrock layer. However, due to the intent to limit disturbance of the studied hillslopes (by avoiding the use of heavy machinery), drilling was limited to 100-cm depth. Therefore, in the event of a thicker soil layer, no further drilling was conducted beyond that depth.

Then, the soil stoniness (rock fragment content) was determined in five randomly-selected spots per plot. This was conducted by excavating an 8-l volume unit (20 cm × 20 cm × 20 cm quadrate), emptying this volume unit, and putting the excavated material in a plastic bag, which was taken to the laboratory for additional processing. In the event of thinner soil to the underlying bedrock, the quadrate's dimensions were modified accordingly in order to obtain an 8-l volume unit.

Starting at the beginning of the 2015/2016 rainy season (December 2015) and stretching until the end of the wet season (May 2016), a time-domain reflectometer (TDR) apparatus (with 3″ (7.6-cm) pins-length: Spectrum Technologies©, Aurora, IL) was utilized – at a frequency of once a month – for detecting the soil volumetric moisture content. The 3″ length for the TDR's pins was determined by the very shallow soil depth in some of the hillslopes, preventing the use of longer pins. The measurements were conducted in five randomly-selected shrubby patches and an additional five spots in the inter-shrub spaces per plot. Despite the minimal disturbance of the ground surface imposed by the TDR, each monthly set of measurements during the wet season was conducted in other, randomly-selected spots, in order to negate a cumulative effect of the apparatus on the readings. Similarly, TDR measurements were also implemented during the 2016/2017 rainy season (December 2016–May 2017).

For assessing the impact of hillslope type (i.e. heterogeneous versus homogeneous) on potential pastoral productivity, aboveground biomass of herbaceous vegetation was harvested in five quadrates of 20 cm × 20 cm which were randomly placed in the inter-shrub spaces of each plot. This was conducted – at a frequency of once a month – throughout the effective growing seasons, i.e. between January to May 2016, and between February to April 2017.

Laboratory analyses

For calibration of the winter-obtained TDR readings, representative soil cores (of 100 ml volume) were obtained and put in a drying oven to determine volumetric moisture content.

The bags of the extracted mineral material were sieved through a 2000 μm sieve, where all finer material was excluded from the sample. Then, the remaining material was gently ground, for breaking down clods and macro-aggregates into < 2000 μm. The ground material was sieved again in order to exclude all fine material from the sample. Then, the remaining rock fragments were put in an 8-l beaker which was filled with water to its top, allowing a calculation of the volume of the rock fragments.

The herbaceous aboveground biomass samples harvested during the growing season were put in a drying oven set to 65°C for 48 h, in order to determine dry weight.

Statistical analysis

Analysis of variance (ANOVA) was conducted with the general linear model (GLM) procedure of SAS (SAS Institute, 1990) to study the effect of hillslope type (heterogeneous versus homogeneous) and microhabitat (shrubby patch versus inter-shrub space) on the soil moisture. Factors used in the model were hillslope type (1 df), plot within hillslope type (3 df; error term for plot), microhabitat (1 df), and the interaction of hillslope type × microhabitat (1 df). In the event of a statistically-significant interaction, an additional analysis of variance was conducted with the Slice command of the GLM procedure. Factors used in the model for the herbaceous vegetation aboveground biomass were: hillslope type (1 df), and plot within hillslope type (3 df; error term for plot). Separation of means was implemented by Tukey's HSD (Honestly Significant Difference) at a probability level of 0.05.

Results

Physical and biotic features

Meteorological data for the Sayeret Shaked Park over the years between 1999 and 2015 shows an average mean daily temperature of 19.9 ± 0.1°C. Annual cumulative precipitation between the rainy seasons of 1999/2000 and 2015/2016 shows a slightly increasing trend. Despite a weaker trend, an overall increase in precipitation during the same period was also observed for the 11 other meteorological stations across the north-western Negev (Figure 4). Monthly distribution and seasonal cumulative precipitation for the 2015/2016 and 2016/2017 rainy seasons are presented in Figure 5, revealing ~ 150% and 40%, respectively, of the inter-annual average (176 mm).

Soil was shallow (10.9 ± 1.5 cm depth) and heavily stony (34.2 ± 4.3% of volume) in the heterogeneous hillslopes, as opposed to a very thick soil layer (> 100 cm) and zero stoniness in the homogeneous hillslopes. On the ground surface of the heterogeneous hillslopes, mean rock fragment cover was found to be > 20%, of which a mean of over 80% was partially-embedded in soil. At the same time, not any cover of rock fragment was recorded for the homogeneous hillslopes. Also, bare soil, faunal perturbation, and geophytes were detected in the heterogeneous hillslopes only. Means of total cover of shrubby vegetation species and cover of alive shrubs in the heterogeneous hillslopes were ~ three-fold and ten-fold greater, respectively, than those in the homogeneous hillslopes. The number of shrubby vegetation species was six in the heterogeneous hillslopes, and two in the homogeneous hillslopes. At the same time, mean herbaceous vegetation cover in the homogeneous hillslopes was > 90%, and more than three-fold greater than that in the heterogeneous hillslopes (Table I).

Hillslope type effect on soil moisture regime and pastoral productivity

Moisture content of soil was found to be considerably affected by the hillslope type. For the 2015/2016 growing season, a sig-

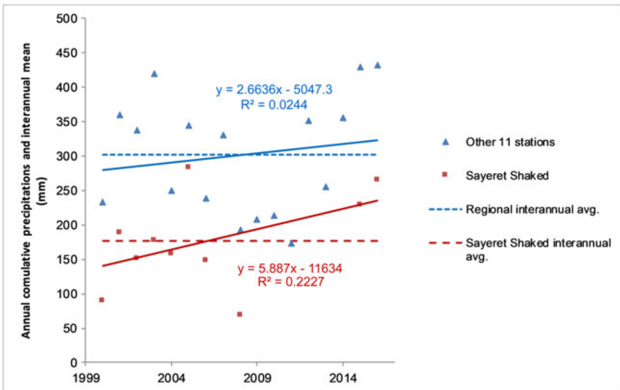

Figure 4. Annual cumulative precipitations (in millimeters) between the rainy seasons of 1999/2000 and 2015/2016 for the Sayert Shaked Park, and mean values for additional 11 meteorological stations across the semi-arid northern Negev. [Colour figure can be viewed at wileyonlinelibrary.com]

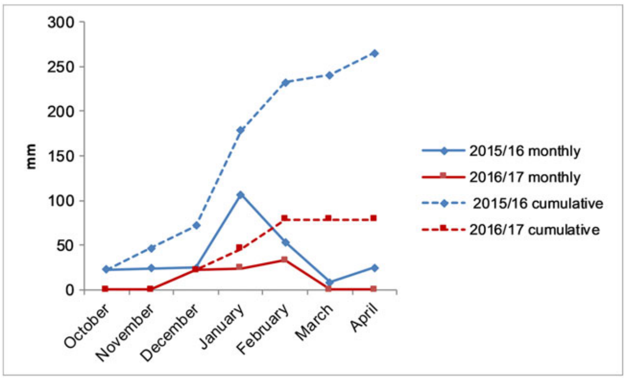

Figure 5. Monthly and seasonal cumulative precipitations (in millimeters) throughout the 2015/2016 and 2016/2017 rainy seasons (the Sayeret Shaked Park's meteorological station). [Colour figure can be viewed at wileyonlinelibrary.com]

Table I. Mean cover of physical and biotic features (%), by hillslope type

Hillslope type	Heterogeneous			Homogeneous		
Partially-embedded rock fragments			18.9 (1.1)			NA
Resting rock fragments			4.2 (0.7)			NA
Total rock fragments			23.1 (1.6)			NA
Exposed soil			18.8 (1.2)			NA
Faunal perturbation			1.4 (0.8)			NA
Geophytes			0.7 (0.3)			NA
Herbaceous vegetation			29.7 (2.0)			92.5 (1.1)
Shrubby vegetation	Alive	Dead	Total	Alive	Dead	Total
Noaea mucronata	12.1 (1.8)	0.8 (0.2)	12.9 (1.7)	0.3 (0.2)	5.3 (0.8)	5.6 (0.6)
Deverra tortuosa	0.3 (0.1)	NA	0.3 (0.1)	1.9 (1.6)	NA	1.9 (1.6)
Helianthemum kahiricum	7.8 (2.3)	0.6 (0.2)	8.4 (2.3)	NA	NA	NA
Echinops polyceras	1.5 (0.6)	NA	1.5 (0.6)	NA	NA	NA
Anabasis articulata	2.5 (1.7)	NA	2.5 (1.7)	NA	NA	NA
Phagnalon rupestre	0.7 (0.3)	NA	0.7 (0.3)	NA	NA	NA
Total shrubby vegetation	24.9 (4.0)	1.4 (0.2)	26.3 (4.1)	2.2 (1.8)	5.3 (0.8)	7.5 (1.1)
ToTotal cover			123.1 (7.4)			100.0 (0.0)

Note: NA, not available. Numbers within parentheses are standard error of the means. Total cover (in the heterogeneous hillslopes) is > 100% due to the line-point intercept method of a transect survey, allowing the record of more than one layer in the same spot.

nificantly greater mean volumetric soil moisture content in the heterogeneous hillslopes than that in the homogeneous hillslopes was recorded for December (39% greater in the heterogeneous than that in the homogeneous, $P < 0.0001$), January (13% greater in the heterogeneous than that in the homogeneous, $P = 0.0241$), and February (34% greater in the heterogeneous than that in the homogeneous, $P < 0.0001$), and then again, for April (19% greater in the heterogeneous than that in the homogeneous, $P = 0.0002$) and May (15% greater in the heterogeneous than that in the homogeneous, $P = 0.001$). During the 2016/2017 growing season, such an effect was recorded for December (30% greater in the heterogeneous hillslopes than that in the homogeneous, $P < 0.0001$), February (5% greater in the heterogeneous than that in the homogeneous, $P = 0.0417$), March (14% greater in the heterogeneous than that in the homogeneous, $P = 0.0181$), April (17% greater in the heterogeneous than that in the homogeneous, $P = 0.0011$) and May (32% greater in the heterogeneous than that in the homogeneous, $P < 0.0001$) (Figure 6).

Herbaceous aboveground biomass was significantly ($P = 0.0001$) and approximately three- to four-fold greater in the homogeneous hillslopes than that in the heterogeneous throughout each of the 2015/2016 and 2016/2017 growing seasons (Figure 7).

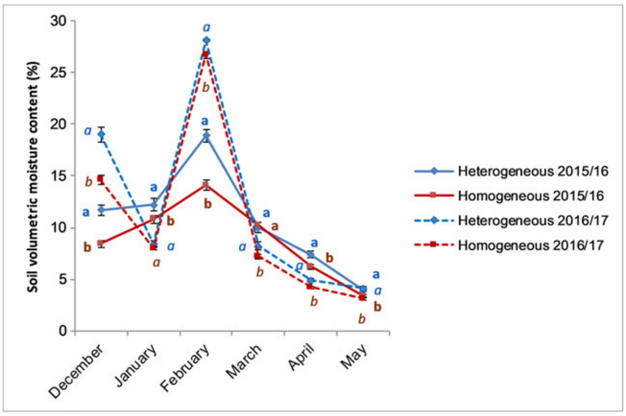

Figure 6. Mean soil's volumetric moisture content throughout the 2015/2016 and 2016/2017 rainy seasons, according to hillslope type. [Colour figure can be viewed at wileyonlinelibrary.com]

Microhabitat effect on soil moisture regime

For the 2015/2016 growing season, a significantly greater mean volumetric soil moisture content in the inter-shrub spaces than that in the shrubby patches was recorded for December 2015 (14% greater in the inter-shrub spaces than that in the shrubby patches, $P = 0.0288$), January 2016 (16% greater in the inter-shrub spaces than that in the shrubby patches, $P = 0.0076$), and February 2016 (21% greater in the inter-shrub spaces than that in the shrubby patches, $P < 0.0001$). In March and April, this trend was reversed, and the mean volumetric soil moisture content was marginally significantly ($P = 0.0951$ and 0.0516, respectively) and 8% and 9% greater for the shrubby patches that that for the inter-shrub spaces. No difference between the two microhabitats was recorded for May. For the entire 2016/2017 growing season, volumetric soil moisture content was similar between the two microhabitats (Figure 8).

Throughout the 2015/2016 growing season, the interaction between hillslope and microhabitat – which separately shows the mean and variability of volumetric soil moisture for each combination of type of microhabitat within type of hillslope – was significant for March and marginally significant for April. During the 2016/2017 growing season, this interaction was significant for December, April, and May. But for the last measurement, the greatest mean volumetric moisture content was recorded for the shrubby patches in the heterogeneous hillslopes (Table II).

Discussion

Hillslope-scale geodiversity

Our study suggests that a major limiting factor for herbaceous vegetation productivity in the heterogeneous hillslopes is the soil depth. This is consistent with previous studies, which reported that shallow soils limit the substrate's volume for herbaceous root growth and decrease water availability for these vegetations (Dyer and Rice, 1999; Shaxson and Barber, 2003; Reever Morghan *et al.*, 2007). Moreover, the shallower the soil depth is, the greater the share of soil moisture loss through evaporation (FAO, 2001), further depleting the soil–water content. Compared with herbaceous vegetation, many shrub species are known to cope much better with shallow, rocky soils,

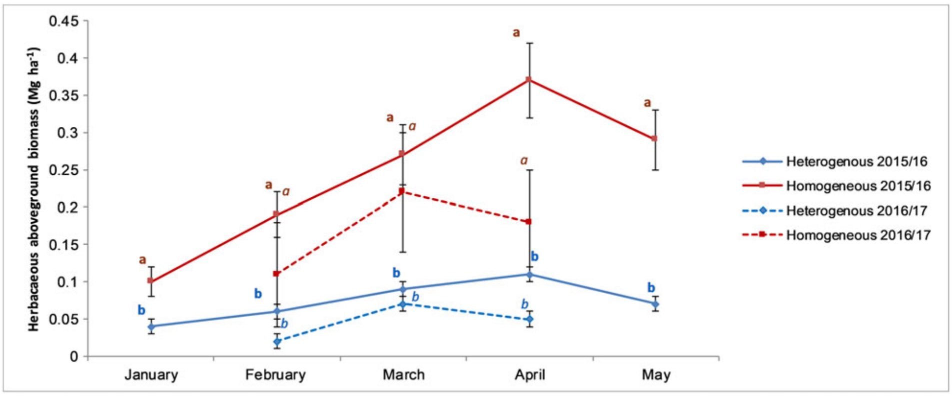

Figure 7. Mean herbaceous aboveground biomass throughout the 2015/2016 and 2016/2017 effective growing seasons, according to hillslope type. [Colour figure can be viewed at wileyonlinelibrary.com]

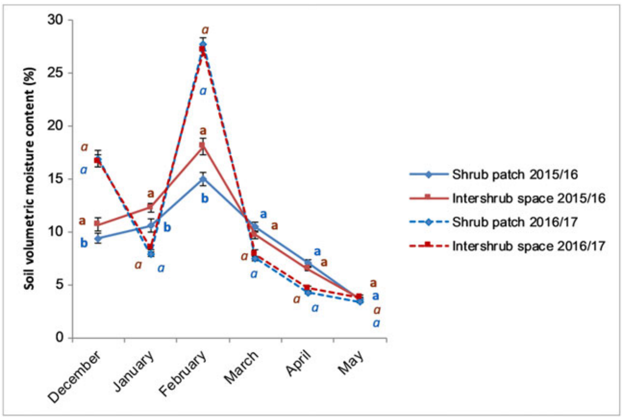

Figure 8. Mean soil's volumetric moisture content throughout the 2015/2016 and 2016/2017 rainy seasons, according to microhabitat. [Colour figure can be viewed at wileyonlinelibrary.com]

as their roots are defined with a high capability to penetrate rock cracks and fractures, obtaining moisture from deeper layers (Davis, 1977; Keely, 2000; Naveh and Carmel, 2004).

The effect of the soil's rock fragment content on water availability for vegetation is still under debate. On the one hand, the decrease in net volume of soil, concordant with the increase in the volume of rock fragments, allows smaller water storage in a certain gross volume of substrate (Chow *et al.*, 2007). On the other hand, depending on the rock fragments' size and overall volume of stoniness, stones in the soil profile could improve the soil–water status, particularly by allowing water film to cover their surfaces, increasing availability of water for vegetation (El Boushi, 1969).

The stony cover of the ground surface, which – in the heterogeneous hillslopes – was found to be dominated by partially-embedded rock fragments, is assumed to increase water overland flow in the inter-shrub spaces. This is consistent with previous studies, which reported that partially-embedded rock fragments increase the sealing of the ground surface (Poesen *et al.*, 1990; Dunkerley, 1995), decreasing water infiltration capacity, and increasing overland flow (Lavee and Poesen, 1991; Valentin, 1994). It seems that in the heterogeneous hillslopes, the decreased infiltration and increased runoff in the inter-shrub spaces, further hindering the development of herbaceous vegetation. At the same time, rock fragments resting loosely on the ground surface – which were also found in the heterogeneous hillslopes, though to a lesser extent – increase infiltration rates, and therefore, decrease runoff generation (Poesen *et al.*, 1990). Regardless, depending on their species composition, biological crusts developed in the inter-shrub spaces might increase or decrease infiltration, with the respective decreased or increased runoff generation (Eldridge *et al.*, 2000).

Despite the adverse effects of the limited soil depth and high cover of partially-embedded rock fragments, the generally greater mean soil moisture content in the heterogeneous hillslopes than that in the homogeneous hillslopes during this two-year study, could be attributed to the processes taking place in the inter-shrub spaces of the homogeneous hillslopes. These processes include: (1) interception of raindrops by the dense aboveground biomass of herbaceous vegetation, being either senescence (at the beginning of the rainy season) or fresh (starting mid-rainy season onward); and (2) the loss of soil–water through transpiration by the fresh herbaceous vegetation between the mid-rainy season and end of the rainy season. This is consistent with studies which stressed the regulation of soil moisture through interception (Uijlenhoet and Sempere Torres, 2006) and transpiration (e.g. Rodriguez-Iturbe *et al.*, 1999) by herbaceous vegetation.

Also, despite not being available for vegetation uptake, since hygroscopic moisture content is positively affected by the physical quality of soil (Stavi *et al.*, 2015), its greater mean value in the heterogeneous hillslopes at the end of the growing season (May) of this two-year study, suggest better soil conditions than those in the homogeneous hillslopes.

Table II. Effect of the interaction hillslope-type × microhabitat on volumetric moisture content (%)

Date *P* value	March 2016 **0.0139**	April 2016 0.0516	December 2016 **0.0082**	April 2017 **0.006**	May 2017 **0.0369**
Heterogeneous hillslope × shrub patch	11.0 a (0.8)	8.0 a (0.4)	20.1 a (0.7)	5.3 a (0.3)	3.7 b (0.2)
Heterogeneous hillslope × inter-shrub space	8.9 b (0.3)	6.8 b (0.3)	17.9 ab (1.1)	4.4 b (0.2)	4.5 a (0.4)
Homogeneous hillslope × shrub patch	10.1 ab (0.4)	6.2 b (0.2)	13.6 c (0.6)	4.3 b (0.1)	3.2 b (0.1)
Homogeneous hillslope × inter-shrub space	10.4 ab (0.4)	6.2 b (0.3)	15.5 bc (0.3)	4.1 b (0.1)	3.1 b (0.1)

Notes: Bold typeface *P* value indicates a significant effect. Means within the same column followed by a different letter differ at the 0.05 probability level according to Tukey's Honestly Significant Difference (HSD) test. Numbers within parentheses are standard error of the means.

Geo-ecosystem functioning

Over the long run, 'normal' precipitation regimes across the north-western Negev region have formed a relatively stable vegetation community (Shachak, 2011; Sher *et al.*, 2012; Zaady *et al.*, 2012). Even though the assessment of species diversity and richness was not the focus of this study, our results show a considerable impact of hillslope type on density and composition of the shrubby vegetation. It is suggested that in the heterogeneous hillslopes, the little cover of herbaceous vegetation in the inter-shrub spaces has allowed – under medium to strong rainstorms – the generation of overland water flow, which has then accumulated in the shrubby patches. Over time, the abundance of water in the patches has allowed the shrubby vegetation to thrive, encompassing a relatively wide composition of species that have taken advantage of these favorable conditions. Further, as previously shown for other shrublands, the spatial redistribution of water increases the accumulation of dissolved and suspended materials in the shrubby patches, increasing their pools of organic and mineral resources, and improving their soil quality (Stavi *et al.*, 2009). This concurs with previous studies (Puigdefábregas, 2005; Lesschen *et al.*, 2009; Merino-Martín *et al.*, 2012), which reported the occurrence of source–sink relations in drylands, sustaining patchy and multi-species vegetation patterns, of which woody species play a central role in the ecosystem functioning.

At the same time, it is proposed that in the homogeneous hillslopes, the dense herbaceous vegetation cover has resulted in the emergence of some processes which, altogether, decrease the generation of water runoff in the inter-shrub spaces. These processes include: (1) raindrop interception by the dense herbaceous vegetation's shoot (see: Uijlenhoet and Sempere Torres, 2006), with the resultant negated splash impact, mechanical crust formation, soil surface sealing, and water ponding (see: Zhou *et al.*, 2013); (2) the improvement of the surface soil's physical quality through macro-aggregate formation and stability, increased macro-porosity, and tunneling by roots (see: Abu, 2013); and (3) the increased roughness of the ground surface (see: Liu *et al.*, 2010). Moreover, in these deep-soil hillslopes, the herbaceous vegetation seems to compete with the shrubs for moisture which is stored in the relatively deep soil layers. Yet, under 'normal' precipitation scenarios, the raindrops falling directly on the shrubby patches have provided them with adequate quantities of water, allowing them to survive. Nonetheless, this limited water availability allowed for the establishment of a relatively small cover of shrubs, which have encompassed a relatively limited composition of species that can cope with such unfavorable conditions.

The dramatic precipitation decrease and the long-term drought episode since the turn of the century have induced the mass mortality of shrubs (Shachak, 2011; Zaady *et al.*, 2012). Nevertheless, our results show that the mass mortality has been unevenly distributed, and that the extent to which the ecosystem has faced these stresses has been determined by the type of hillslope. In the homogeneous hillslopes, the smaller quantities of rains have not reached the minimum level required to sustain the survival of many of the shrubs, resulting in their mass mortality. At the same time, in the heterogeneous hillslopes, even the considerably smaller quantities of runoff water that accumulate in the shrubby patches, still succeed in sustaining a large part of them. Therefore, the obtained results accord with the study hypothesis.

Also, the results show that the effect of hillslope-type geodiversity has somewhat overshadowed the effect of microhabitat on the soil–water status. This was demonstrated by the consistent trend of mean volumetric soil moisture content in the heterogeneous hillslopes, which was generally (except for March 2016 and January 2017) greater than that in the homogeneous hillslopes, as opposed to the smaller and apparently random effect of microhabitat on the soil moisture. This trend was relatively similar in the two studied years, despite the large difference in precipitation regime between them.

The importance of geodiversity for shrubland tolerance under prolonged drought scenarios

Worsening climatic conditions, including ~ 1°C increase in mean annual temperatures and ~ 25% decrease in mean annual precipitation across the Israeli Negev between 1970 and 2002, led to an increase in the regional aridity index (precipitation/evapo-transpiration: P/ETP ratio) from *c.* 0.16 to 0.11 (Kafle and Bruins, 2009). Several observations since the early twenty-first century have revealed the mass mortality of shrubs across the north-western Negev (Sher *et al.*, 2012), with a particularly prominent trend for the predominant *N. mucronata* species (Shachak, 2011; Zaady *et al.*, 2012). Yet, as shown in this study, the mass mortality of shrubs has been confined to homogeneous hillslopes. Regardless, our data suggests that despite the trend of slightly increasing precipitation rates across the region since the beginning of the twenty-first century, the shrubland ecosystem in the homogeneous hillslopes has reached an irreversible state of degradation, negating the restoration of the shrubby vegetation. To some extent, this is consistent with Anderegg *et al.* (2015), who reported for the world's dryland forests a 'legacy effect', or hysteresis, after severe droughts, expressed by a long delay in vegetation recovery following the cessation of drought episodes. The hysteresis effect also consists with the concept of catastrophic regime shift, which was developed in mathematical models of vegetation patterns in water-limited ecosystems (Zelnik *et al.*, 2013; Meron, 2015).

Despite being mostly non-edible by livestock, the shrubs have a crucial role in ecosystem functioning through the transecting of hydraulic connectivity, decreasing overland flow generation and soil erosion at the hillslope level, and controlling land degradation (Stavi *et al.*, 2009). Yet, the high density of herbaceous plants in the homogeneous hillslopes could have led to the erroneous conclusion that this vegetation lifeform successfully copes with long-term increased aridity. Moreover, it could have led to the misperception that pastoral productivity has not been degraded in this type of hillslope. However, the large productivity of herbaceous vegetation in the homogeneous hillslopes has been enabled due to the long-term (> 15 years) exclusion of livestock access to the LTER Sayeret Shaked Park. It is assumed that if livestock access would have been allowed, the herbaceous vegetation cover in this type of hillslope would have considerably decreased. This would have resulted in the lessened recycling of organic materials, reduced roughness of the ground surface, and increased raindrop splash impact and water ponding.

A conceptual model is proposed, demonstrating the geo-ecosystem functioning in terms of herbaceous vegetation cover, potential runoff coefficient, ecosystem self-organization, and shrubby vegetation cover under homogeneous versus heterogeneous hillslopes. The conceptual model shows that considering livestock exclusion, a kind of (dynamic) equilibrium is maintained under each of the two types of hillslopes. However, once livestock grazing is allowed on the homogeneous hillslopes, the pastoral productivity considerably shrinks, and hillslope level's hydraulic connectivity and soil erosion are accelerated. At the same time, these processes are generally

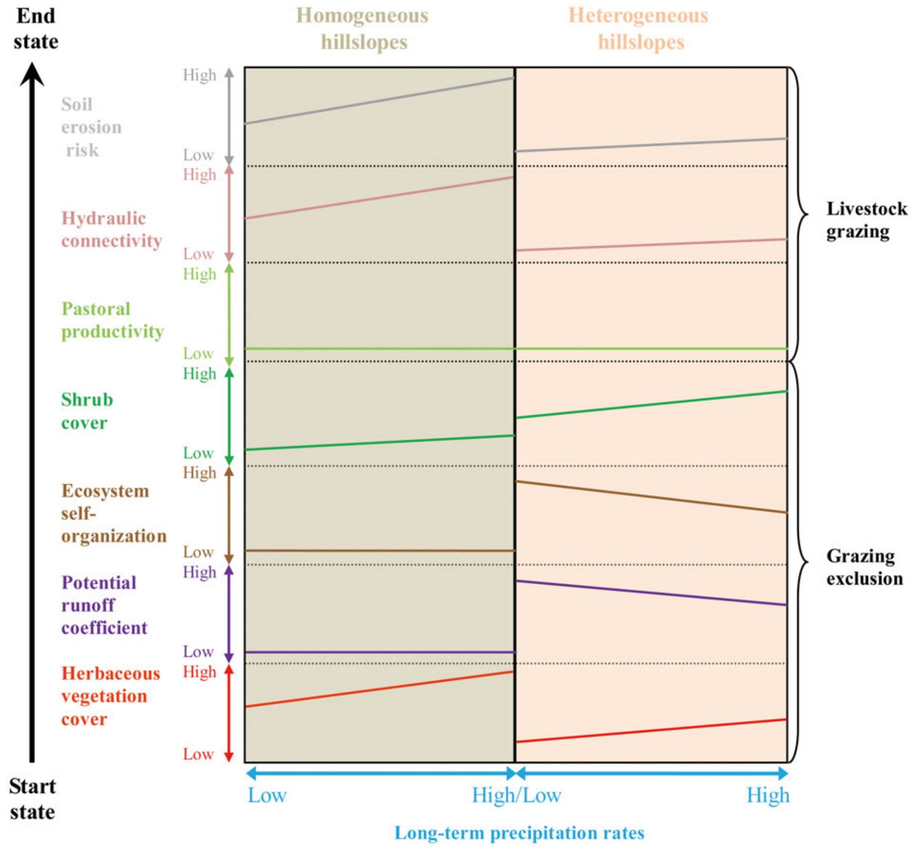

Figure 9. Conceptual model, demonstrating the herbaceous vegetation cover, runoff ratio, self-organization, shrubby vegetation cover, hydraulic connectivity, and soil erosion risk under the homogeneous versus heterogeneous hillslope types. [Colour figure can be viewed at wileyonlinelibrary.com]

mitigated in the heterogeneous hillslopes, by their natural geodiversity (Figure 9).

Of course, this study has some limitations. For example, the competition between the shrubby and herbaceous vegetation for the limited water resource shown in this study would not necessarily apply in ecosystems where a kind of facilitation occurs between the two life forms (Iyengar *et al.*, 2017). Particularly, these relations might not apply in ecosystems where hydraulic lifting by woody plants (see: Munoz *et al.*, 2008) could increase the availability of water for herbaceous vegetation. Also, we acknowledge the fact that the shrubs' tolerance to drought is affected by their physiological properties. For example, species-specific adaptation mechanisms to water stress conditions, such as the regulation of stomata opening time, and more. That way, non-adaptation of the *N. mucronata* can explain the mass mortality of this species across the study region, whereas other shrub species showed better durability to prolonged droughts. Regardless, results of this study highlight the crucial role of geodiversity in preventing the collapse of water-limited ecosystems under prolonged drought scenarios. The increased uncertainty of the regional and global climate, as foreseen by many climatic modeling studies (Christensen *et al.*, 2011; Curry, 2011; Collins *et al.*, 2013), emphasize the need for extensive research of the interrelations between terrestrial geodiversity and ecological sustainability under aggravated water-stressed conditions.

Conclusions

Mass mortality of shrubs has occurred in the semi-arid Negev region, along with a consecutive, long-term drought episode. This study showed that the mass mortality has been confined to hillslopes defined with little geodiversity, while in high-geodiversity hillslopes, the shrubby vegetation has continued to thrive under the increased aridity conditions. It is proposed that the hillslope geodiversity has improved the tolerance of shrubs to dryness, alleviating their vulnerability to prolonged drought scenarios and climatic changes. Despite little palatability by livestock, the important role played by shrubs in decreasing hydraulic connectivity and sustaining rangeland functioning, makes them a crucial component of drylands. Over the long run, the mass mortality of shrubs could lead to the degradation and collapse of extensive shrubland ecosystems.

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References

Abu ST. 2013. Evaluating long-term impact of land use on selected soil physical quality indicators. *Soil Research* **51**: 471–476. https://doi.org/10.1071/SR12360

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD, Shevliakova E, William AP, Wolf A, Ziaco E, Pacala S. 2015. Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* **349**: 528–532. https://doi.org/10.1126/science.aab1833

Bitan A, Rubin S. 1991. *Climatic Atlas of Israel for Physical and Environmental Planning and Design*. Department of Geography, Tel Aviv

University: Tel Aviv Israel Meteorological Service, Ministry of Transport: Bet Dagan.

Chow TL, Rees HW, Monteith JO, Toner P, Lavoie J. 2007. Effects of coarse fragment content on soil physical properties, soil erosion and potato production. *Canadian Journal of Soil Science* **87**: 565–577.

Christensen OB, Goodess CM, Harris I, Watkiss P. 2011. European and global climate change projections: discussion of climate change model outputs, scenarios and uncertainty in the EC RTD Climate Cost Project. In *The Climate Cost Project. Final Report. Volume 1: Europe*, Watkiss P (ed). Stockholm Environment Institute: Stockholm http://www.climatecost.cc/images/Policy_brief_1_Projections_05_lowres.pdf

Collins M, Knutti R, Arblaster J, Dufresne JL, Fichefet T, Friedlingstein P, Gao X, Gutowski WJ, Johns T, Krinner G, Shongwe M, Tebaldi C, Weaver AJ, Wehner M. 2013. Long-term climate change: projections, commitments and irreversibility. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to The Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds). Cambridge University Press: Cambridge http://www.climatechange2013.org/images/report/WG1AR5_Chapter12_FINAL.pdf

Curry M. 2011. Reasoning about climate uncertainty. *Climatic Change* **108**: 723–732. https://doi.org/10.1007/s10584-011-0180-z

Davis EA. 1977. Root system of shrub live oak in relation to water yield by chaparral. In *Proceedings of the meetings of the Arizona Section of the American Water Resources Association and the Hydrology Section of the Arizona Academy of Science*, Las Vegas, NV; 241–248. http://arizona.openrepository.com/arizona/bitstream/10150/300998/1/hwr_07-241-248.pdf

Dyer AR, Rice KJ. 1999. Effects of competition on resource availability and growth of a California bunchgrass. *Ecology* **80**: 2697–2710.

Dunkerley DL. 1995. Surface stone cover on desert hillslopes – parametrizing characteristics relevant to infiltration and surface runoff. *Earth Surface Processes and Landforms* **20**: 207–218. https://doi.org/10.1002/esp.203290200303

El Boushi IM. 1969. Water-retention characteristics of coarse rock particles. *Journal of Hydrology* **8**: 431–441.

Eldridge DJ, Zaady E, Shachak M. 2000. Infiltration through three contrasting biological soil crusts in patterned landscapes in the Negev, Israel. *Catena* **40**: 323–336. https://doi.org/10.1016/S0341-8162(00)00082-5

Food and Agriculture Organization of the United Nations (FAO). 2001. *Conservation of natural resources for sustainable agriculture*. FAO: Rome http://www.fao.org/ag/ca/training_materials/cd27-english/sm/soil_moisture.pdf

Gray M. 2012. Valuing geodiversity in an 'ecosystem services' context. *Scottish Geographical Journal* **128**: 177–194. https://doi.org/10.1080/14702541.2012.72585

Herrick JE, Van Zee JW, Havstad KM, Burkett LM, Whitford WG. 2005. *Monitoring Manual for Grassland, Shrubland and Savanna Ecosystems – Volume I: Quick Start*, Vol. **15**. USDA-ARS Jornada Experimental Range: Las Cruces, NM http://www.fwspubs.org/doi/suppl/10.3996/052014-JFWM-039/suppl_file/052014-jfwm-039r1-s04.pdf?code=ufws-site

Hjort J, Gordon JE, Gray M, Hunter ML. 2015. Why geodiversity matters in valuing nature's stage. *Conservation Biology* **29**: 630–639. https://doi.org/10.1111/cobi.12510

Jačková J, Romportl D. 2008. The relationship between geodiversity and habitat richness in Šumava National Park and Křivoklátsko PLA (Czech Republic): a quantitative analysis approach. *Journal of Landscape Ecology* **1**: 23–38.

Kafle HK, Bruins HJ. 2009. Climatic trends in Israel 1970–2002: warmer and increasing aridity inland. *Climatic Change* **96**: 63–77. https://doi.org/10.1007/s10584-009-9578-2

Keely JE. 2000. Chaparral. In *North America Terrestrial Vegetation*, Barbour MG, Billing WD (eds), 2nd edn. Cambridge University Press: Cambridge; 203–254.

Lavee H, Poesen JWA. 1991. Overland flow generation and continuity on stone-covered soil surfaces. *Hydrological Processes* **5**: 35–360. https://doi.org/10.1002/hyp.3360050403

Lesschen JP, Schoorl JM, Cammeraat LH. 2009. Modelling runoff and erosion for a semi-arid catchment using a multi-scale approach based on hydrological connectivity. *Geomorphology* **109**: 174–183. https://doi.org/10.1016/j.geomorph.2009.02.030

Iyengar SB, Bagchi S, Barua D, Mishra C, Sankaran M. 2017. A dominant dwarf shrub increases diversity of herbaceous plant communities in a Trans-Himalayan rangeland. *Plant Ecology* **218**: 843–854. https://doi.org/10.1007/s11258-017-0734-x

Liu G, Tian FX, Warrington DN, Zheng SQ, Zhang Q. 2010. Efficacy of grass for mitigating runoff and erosion from an artificial earthen road. *Transactions of the ASABE* **53**: 119–125. https://doi.org/10.13031/2013.29509

Merino-Martín L, Moreno-de las Heras M, Pérez-Domingo S, Espigares T, Nicolau JM. 2012. Hydrological heterogeneity in Mediterranean reclaimed slopes: runoff and sediment yield at the patch and slope scales along a gradient of overland flow. *Hydrology and Earth System Sciences* **16**: 1305–1320. https://doi.org/10.5194/hess-16-1305-2012

Meron E. 2015. *Nonlinear Physics of Ecosystems*. CRC Press: Boca Raton, FL; 344.

Munoz MR, Squeo FA, Leon MF, Tracol Y, Gutierrez JR. 2008. Hydraulic lift in three shrub species from the Chilean coastal desert. *Journal of Arid Environments* **72**: 624–632. https://doi.org/10.1016/j.jaridenv.2007.09.006

Naveh Z, Carmel Y. 2004. The evolution of cultural Mediterranean landscape in Israel as affected by fire, grazing, and human activities. In *Evolutionary Theory and Processes: Modern Horizons*, Wasser SP (ed). Springer: Dordrecht; 337–410.

Okin GS, Moreno-de las Heras M, Saco PM, Throop HL, Vivoni ER, Parsons AJ, Wainwright J, Peters DPC. 2015. Connectivity in dryland landscapes: shifting concepts of spatial interactions. *Frontiers in Ecology and the Environment* **13**: 20–27. https://doi.org/10.1890/140163

Poesen J, Ingelmo-Sanchez F, Mucher H. 1990. The hydrological response of soil surfaces to rainfall as affected by cover and position of rock fragments in the top layer. *Earth Surface Processes and Landforms* **15**: 653–671. https://doi.org/10.1002/esp.3290150707

Puigdefábregas J. 2005. The role of vegetation patterns in structuring runoff and sediment fluxes in drylands. *Earth Surface Processes and Landforms* **30**: 133–147. https://doi.org/10.1002/esp.1181

Reever Morghan KJ, Corbin JD, Gerlach J. 2007. Water relations. In *California Grasslands – Ecology and Management*, Stromberg M, Corbin J, D'Antonio C (eds). University of California Press: Oakland, CA; 87–93.

Rodriguez-Iturbe I, D'Odorico P, Porporato A, Ridolfi L. 1999. On the spatial and temporal links between vegetation, climate, and soil moisture. *Water Resources Research* **35**: 3709–3722. https://doi.org/10.1029/1999WR900255

SAS Institute. 1990. *SAS/STAT User's Guide. Version 6*, 4th edn. SAS Institute: Cary, NC.

Serrano-Cañadas E, Ruiz-Flaño P. 2007. Geodiversity: concept, assessment and territorial application. The case of Tiermes-Caracena (Soria). *Boletín de la Asociación de Geógrafos Españoles* **45**: 389–393.

Shachak M. 2011. Ecological textures: ecological systems in the northern Negev as a model. *Ecology and Environment* **1**: 18–29 (in Hebrew).

Shaxson F, Barber R. 2003. *Optimizing Soil Moisture for Plant Production – The Significance of Soil Porosity. FAO Soil Bulletin 79*. Food and Agriculture Organization of the United Nations (FAO): Rome ftp://ftp.fao.org/agl/agll/docs/sb79.pdf

Sher Y, Zaady E, Ronen Z, Nejidat A. 2012. Nitrification activity and levels of inorganic nitrogen in soils of a semi-arid ecosystem following a drought-induced shrub death. *European Journal of Soil Biology* **53**: 86–93. https://doi.org/10.1016/j.ejsobi.2012.09.002

Singer A. 2007. *The Soils of Israel*. Springer Verlag: Berlin; 306.

Silva JP, Pereira DI, Aguiara AM, Rodrigues C. 2013. Geodiversity assessment of the Xingu drainage basin. *Journal of Maps* **9**: 245–262. https://doi.org/10.1080/17445647.2013.775085

Stavi I, Lavee H, Ungar ED, Sarah P. 2009. Eco-geomorphic feedbacks in semi-arid rangelands: a review. *Pedosphere* **19**: 217–229. https://doi.org/10.1016/S1002-0160(09)60111-9

Stavi I, Shem-Tov R, Chocron M, Yizhaq H. 2015. Geodiversity, self-organization, and health of three-phase semi-arid rangeland ecosystems, in the Israeli Negev. *Geomorphology* **234**: 11–18. https://doi.org/10.1016/j.geomorph.2015.01.004

Stavi I, Rachmilevitch S, Yizhaq H. 2018. Small-scale geodiversity regulates functioning, connectivity, and productivity of shrubby, semi-arid rangelands. *Land Degradation & Development* **29**(2): 205–209. https://doi.org/10.1002/ldr.2469

Thomas MF. 2012. Geodiversity and landscape sensitivity: a geomorphological perspective. *Scottish Geographical Journal* **128**: 195–201. https://doi.org/10.1080/14702541.2012.725863

Uijlenhoet R, Sempere Torres D. 2006. Measurement and parameterization of rainfall microstructure. *Journal of Hydrology* **328**: 1–7. https://doi.org/10.1016/j.jhydrol.2005.11.038

Valentin C. 1994. Surface sealing as affected by various rock fragment covers in west Africa. *Catena* **23**: 87–89. https://doi.org/10.1016/0341-8162(94)90055-8

Yizhaq H, Sela S, Svoray T, Assouline S, Bel G. 2014. Effects of heterogeneous soil–water diffusivity on vegetation pattern formation. *Water Resources Research* **50**: 5743–5758. https://doi.org/10.1002/2014WR015362

Yizhaq H, Bel G. 2016. Effects of quenched disorder on critical transitions in pattern-forming systems. *New Journal of Physics* **18**: 023004. https://doi.org/10.1088/1367-2630/18/2/023004

Yizhaq H, Stavi I, Shachak M, Bel G. 2017. Geodiversity increases ecosystem durability to prolonged droughts. *Ecological Complexity* **31**: 96–103. https://doi.org/10.1016/j.ecocom.2017.06.002

Zaady E, Shir Y, Ronen Z, Nujedat A. 2012. The effect of consecutive drought in the northern Negev on soil characteristics and plant mortality. *Ecology and Environment* **3**: 44–52 (in Hebrew).

Zelnik Y, Kinsat S, Yizhaq Y, Bell G, Meron E. 2013. Regime shifts in models of dryland vegetation. *Philosophical Transactions of the Royal Society A* **371**: 20120358. https://doi.org/10.1098/rsta.2012.0358

Zhou H, Peng XH, Darboux F. 2013. Effect of rainfall kinetic energy on crust formation and interrill erosion of an Ultisol in subtropical China. *Vadoze Zone Journal* **12**(4). https://doi.org/10.2136/vzj2013.01.0010