Received: 2 August 2016 | Revised: 27 October 2016 | Accepted: 3 November 2016
DOI 10.1002/eco.1806

WILEY

RESEARCH ARTICLE

Shifts in landscape ecohydrological structural–functional relationship driven by experimental manipulations and ecological interactions

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Abstract

Vegetation structure and patchiness are central controllers of ecohydrological function in semiarid regions. The feedback interactions between vegetation patchiness and water redistribution make semiarid ecosystems sensitive to state-shifts, where nonlinearities appear in the structure–function correlations. Hydrological connectivity of runoff sources is functionally important for source–sink interactions over a range of spatial scales and plays a key role in ecosystem state-shifts. Accordingly, the study of the functional responses of ecosystems to changes in connectivity is important for assessing the system's resilience in response to drivers of degradation. We used runoff data collected over 18 years in experimentally manipulated plots to study both the primary functional response to the manipulations and the changes in both structure and function over two decades. By comparing simultaneous changes in woody and herbaceous cover, biocrust cover and connectivity, and runoff yield, we examined the interactions among the different cover classes and assessed the functional consequences of these interactions. The manipulated changes in vegetation and biocrust cover caused large differences in runoff yields, with positive correlation between biocrust cover and runoff. However, changes in vegetation patterns reduced these differences, as the spread of herbaceous plant cover, at the expense of biocrust and woody cover, caused a shift in the cover–runoff relationship. The landscape was resilient to degradation due to rapid shrub growth in locations of high biocrust cover. On the other hand, a positive feedback of herbaceous plant cover replacing shrub cover caused a state-shift, likely driven by a combination of drought recurrence and cessation of grazing.

KEYWORDS

biocrust, functional connectivity, long-term study, overland runoff, semiarid rangeland, state shift, vegetation patterns

1 | INTRODUCTION

Understanding how vegetation structure and patterns affect ecosystem functions in drylands is central to rangeland science and management, where ecosystem functions directly support human livelihood (Aguiar, Paruelo, Sala, & Lauenroth, 1996; Reynolds et al., 2007; Reed et al., 2015). Primary production, the most critical ecosystem function, is controlled to a large part by climatic conditions during the growing season, especially rainfall amounts and distribution (Brookshire & Weaver, 2015; Hsu, Powell, & Adler, 2012). However, as the availability of water from precipitation for plant uptake is mediated by spatiotemporal soil moisture dynamics, the rainfall–productivity relationship is complex and scale dependent (Bisigato, Hardtke, & Francisco del Valle, 2013). Thus, although differences in annual precipitation may explain large-scale differences in productivity among sites along a rainfall gradient, or among years within a site (Golodets et al., 2015), smaller scale differences are governed by site conditions (Michaelides, Lister, Wainwright, & Parsons, 2009). The local controlling factors include topography, soil depth and structure, animal activity, and vegetation structure (Boeken & Orenstein, 2001; Gaitán et al., 2014; Katra, Lavee, & Sarah, 2008b; Katra, Lavee, & Sarah, 2008a; Svoray & Karnieli, 2011). Vegetation structure is defined here as the cover characteristics of different plant cover classes, differentiating between woody plants, herbaceous plants, and litter (Ruiz-Jaén & Aide, 2005). Spatial vegetation structure plays a crucial role in the rainfall–productivity relationship, because it controls both patterns of water redistribution and primary production, allowing for feedback processes to take place (D'Odorico, Caylor, Okin, & Scanlon, 2007; Gaitán et al., 2014; Thompson, Harman, Troch, Brooks, & Sivapalan, 2011).

Feedbacks between vegetation and water have been identified as drivers of vegetation pattern formation, interspecific plant interactions, and degradation processes in semiarid rangelands (D'Odorico, Bhattachan, Davis, Ravi, & Runyan, 2013; Meron, 2015; Wilcox et al., 2012). Semiarid ecosystems often experience long dry periods and short high-intensity rainstorms, conditions which allow for overland runoff on unvegetated surfaces (Rodriguez-Caballero, Canton, Lazaro, & Sole-Benet, 2014; Wei et al., 2014). Under such conditions, primary production is limited not only by precipitation amount but also by the rainfall–runoff ratio that can affect soil water storage (Hamerlynck, Scott, & Stone, 2012; Moreno-de las Heras, Saco, Willgoose, & Tongway, 2012). Accordingly, landscape structure and the patterns of runoff source and sink patches can control ecosystem functions such as productivity and water and nutrient cycling (Ludwig, Tongway, & Marsden, 1999; Schlesinger, Raikes, Hartley, & Cross, 1996). A positive feedback between vegetation reduction and resource leakiness is seen as a primary mechanism involved in dryland degradation and desertification and can lead to hysteretic behavior that limits recovery (D'Odorico et al., 2013; Kefi et al., 2007; Mayor et al., 2013). The risk of such processes is expected to increase under the predicted climate change, especially where anthropogenic disturbances such as overgrazing, clearing, or wood gathering take place (D'Odorico et al., 2013; Reynolds et al., 2007). However, the sensitivity of an ecosystem to any of these drivers depends on the resistance and resilience of the local plant community, which may either delay degradation or exacerbate it, depending on species-specific responses and community-level interactions (Maestre et al., 2009; Soliveres & Maestre, 2014).

The Northern Negev region in Israel has been under intense anthropogenic land use for several centuries, including seasonal grazing by sheep and goats, reducing vegetation cover and productivity (Leu, Mussery, & Budovsky, 2014). Also, cover of woody plants has been declining regionally following increasing aridity over the last two decades, with significant increases in mature shrub mortality (DeMalach, Kigel, Voet, & Ungar, 2014; Hoffman, de Falco, Yizhaq, & Boeken, 2016; Shoshany & Karnibad, 2015). Studies have shown that local plant communities in the northern edge of the Negev (mean annual rainfall ~280–330 mm), both herbaceous and woody, are resilient to perturbations and can recover from overgrazing and drought stress (DeMalach et al., 2014; Leu et al., 2014; Segoli, Ungar, & Shachak, 2008; Shafran-Nathan, Svoray, & Perevolotsky, 2013). In the more xeric central part of the Northern Negev (mean annual rainfall 150–200 mm), however, shrub cover has not recovered as in the more mesic zone, leaving much of the natural landscape with drastically low woody cover (Hoffman et al., 2016; Paz-Kagan, Panov, Shachak, Zaady, & Karnieli, 2014; Sher, Zaady, Ronen, & Nejidat, 2012). It has been suggested that these changes, driven by drought-induced shrub mortality, may cascade to severe degradation, or desertification, due to the important role shrub patches play as runoff sinks, which facilitate herbaceous plant productivity and diversity (Boeken & Shachak, 1994; Paz-Kagan et al., 2014; Shachak, 2011).

Here, we present a long-term study examining how experimental structural shifts change landscape functionality in terms of runoff leakiness and how the structure–function relationship changes over time. A structural-functional approach is very useful in studying dryland ecohydrology due to the multiple interactions between ecosystem structures and functions, especially where climate change and land use can drive detrimental and sometimes irreversible state transitions (Lopez, Cavallero, Brizuela, & Aguiar, 2011; Merino-Martin et al., 2012; Williams et al., 2016). By observing simultaneous changes in vegetation pattern and structure, we explore the effects of ecohydrological interactions on the structure–function relationship of the landscape, which is a critical step in predicting the ecosystem's functional responses to different environmental drivers (Turnbull et al., 2012; Wainwright, 2011; Williams et al., 2016). We describe the relationships among vegetation structure, patchiness, and runoff leakiness and examine how these relationships change through time, with the aim to elucidate the interactions that led to the observed changes in the ecohydrological structural–functional relationships. Consequently, we aim to assess the system's resistance and resilience in response to various drivers and the relative importance of the different cover classes for these emergent ecosystem properties.

2 | METHODS

2.1 | Study site

Park Shaked LTER station (31°17′ N, 34°37′ E, Figure 1) is located in the central Northern Negev, with a 25-year annual average of 165 mm of rainfall (range 80–280 mm; Boeken & Zaady, 2016). The soil is loessial with a sandy loam texture, ranging in depth from 10 cm to 1 m, with low organic matter content (~3%) situated in the top 5 cm (Eldridge, Zaady, & Shachak, 2000; Eldridge, Zaady, & Shachak, 2002; Stavi, Ungar, Lavee, & Sarah, 2008). The landscape is composed of gentle hills, with most slopes ranging from 6% to 10%. The slopes have sparse vegetation cover and are mostly covered by open space with biological soil crust (biocrust) covering the soil surface. The biocrust community comprises cyanobacteria (mostly *Microcoleus vaginatus* and *Nostoc* spp.), lichens, and—in partially shaded locations—mosses (Zaady, Karnieli, & Shachak, 2007). A dense biocrust cover requires more than a decade to develop, but early stage biocrust typically appears within a year or two on bare soils (Zaady et al., 2007; Zaady, Arbel, Barkai, & Sarig, 2013). In this work, the term biocrust refers to all stages of development, from apparently bare soil, common on disturbed soils, to a developed biocrust with a more diverse community. Biocrust forms a dense and hydrophobic surface layer, limiting infiltration and enhancing runoff during rainstorms, and is therefore a very effective runoff source (Eldridge et al., 2000).

Protection from grazing was implemented in part of the research site at establishment (in 1987), after which the vegetation cover increased over a decade to ~25–30% on the slopes (Boeken, 2008). Plant cover was mostly based in and around patches of sub-shrubs,

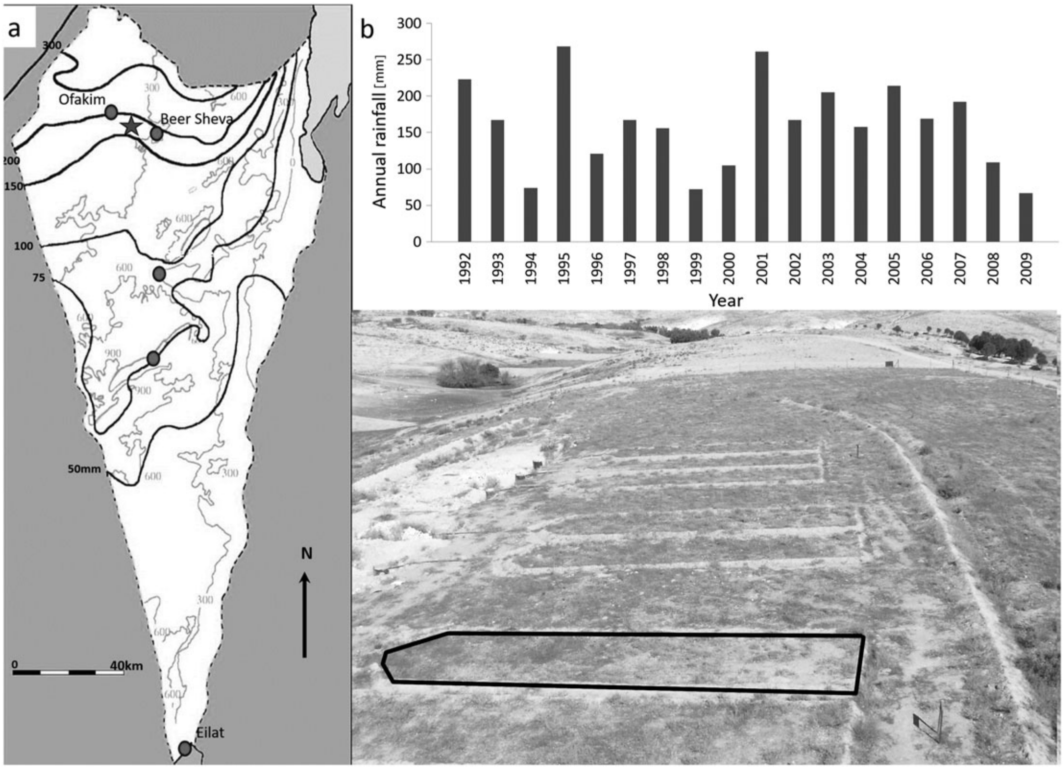

FIGURE 1 (a) Map of the Negev desert, Israel, with isohyets of the mean annual rainfall amounts across the region and the location of Park Shaked LTER (31°17′ N, 34°37′ E); (b) time-series of seasonal rainfall measured in Park Shaked LTER; and (c) a photograph of the experimental plots, taken January 2008, with a single plot delineated

mainly the species *Atractylis serratuloides* and *Noaea mucronata* on the slopes and *Thymelaea hirsuta* near the streambed (Sher et al., 2012; Linde, 2002; De Falco, 2013; Elbaz, 2012; Bos-Groenendijk, 2012). The vegetation on the slopes is a shrub-steppe with scattered shrub patches, increasing in density towards the foot of the slope (Buis, Veldkamp, Boeken, & van Breemen, 2009; De Falco, 2013). The exposed biocrust supports low densities of herbaceous annuals, whereas the shrub-dominated patches support denser herbaceous cover, due to a combination of runoff capture, improved soil and microclimatic conditions, and protection from herbivory (Boeken & Shachak, 1994; Noy-Meir, 1990; Wright, Jones, Boeken, & Shachak, 2006). The streambeds themselves are more densely vegetated, with high cover of annual plants and few shrubs (Osem, Perevolotsky, & Kigel, 2004; Svoray & Karnieli, 2011).

2.2 | Experimental setup

The experiment was established in 1991 with the aim of studying the effects of human-made disturbances on vegetation and biocrust dynamics and ecosystem functions (Zaady, Levacov, & Shachak, 2004; Zaady et al., 2013). Thirteen 4 m × 15 m plots were established on a west-facing hillslope of 6–7% slope angle. The manipulation treatments included removing the shrub canopies with a lawn-mower ("mowing", hereafter), spraying the plot with the herbicide Symazine ("herbicide"), and mechanical removal of the top 5 cm of the soil ("scraping"). The herbicide and mowing treatments were both carried out 2 years in a row and scraping only once. Three replication plots of each treatment were established, along with one un-manipulated plot ("control") near each treatment plot group. A fourth control plot, located near a treatment that was excluded, is included in the analysis. Each plot was surrounded on all sides with an earthen barrier that prevented overland flow from outside the plot, and the bottom of each plot had a metal runoff flume connected to a collection barrel. The water level was measured after each rainstorm, and the runoff amount was then converted to represent runoff depth (Arbel, 2009). The seasonal sum of those values was divided by the seasonal rainfall, measured using a meteorological station near the study site (Boeken & Zaady, 2016), to provide the runoff coefficient of each plot.

2.3 | Vegetation structure and source-area connectivity

The data we used for vegetation structure and pattern analysis were from a time series of RGB photographs taken at low altitude (3–5 m) over the course of 23 years: 1993, 2008, and 2015. All photographs were taken during winter (January and February), limiting the effect of seasonal differences in phenology. For the assessment of source-area cover and connectivity, the photographs were converted into binary maps (1 for source, 0 for sink). One set of maps includes all inter-shrub pixels (biocrust and annuals) as source, based on manual digitization of all shrub canopies. A second set includes all biocrust pixels as source, based on a threshold conversion of only the red band using an image conversion and analysis program (ImageJ, Schneider, Rasband, & Eliceiri, 2012). Using these maps, we assessed plot-scale proportional cover of biocrust, shrub canopies, and herbaceous plants (including their litter). Changes in cover of shrubs and herbaceous plants over time were assessed by calculating differences in cover between years (Paz-Kagan et al., 2014).

To express the structure of the landscape in terms of runoff sources, we calculated each plot's representative downslope connectivity range, which is similar to the typical "flow length" used by Mayor (2008; 2013; see also, integral connectivity scale in Larsen, Choi, Nungesser, & Harvey, 2012). Studies in a wide range of dryland ecosystems have identified similar properties of the landscape as indicators of material flow rates and ecosystem state (Moreno-de las heras et al., 2012; Okin et al., 2015) .The connectivity range (α) was calculated based on McGlynn and Okin's method (2006), which takes into account the source area cover and the reduction in the probability to find connected source pixels as a function of increasing lag range. To allow comparison of connectivity values based on photographs with different original resolution, all binary maps were adjusted to a 10-cm resolution prior to calculations. All connectivity calculations were performed in Matlab (v. 2014, MathWorks Inc. MA, USA).

2.4 | Statistical analysis

The effect of manipulation treatment and year were tested for each cover class individually (shrubs, herbaceous plants, and biocrust) using two-way analysis of variance, following arcsine transformation of proportional cover values. Post hoc tests (Tukey's honestly significant difference) were used to find significant pairwise differences among treatments in each year and among the years within treatments.

The relationship between source-area connectivity and seasonal runoff coefficient was assessed using linear regression. The regression analyses were done for each year using the two sets of connectivity values (with biocrust or inter-shrub as source). Seasonal runoff yield data from the years 1993–1996 were compared with connectivity values attained in 1993, and runoff yield data from 2006–2009 to connectivity values from 2008. Runoff collection was discontinued after 2009 (Arbel, 2009).

Correlation analysis between connectivity range values of biocrust and inter-shrub was used to assess the similarity of shrub and herbaceous plant cover patterns in every year. We also used correlations to compare the simultaneous cover change between shrubs and herbaceous plants.

3 | RESULTS

3.1 | Immediate effects of treatment on cover

The treatments had significant effects on biocrust cover, $F(3, 12) = 19.02$, $p < .01$ (Figure 2a); shrub cover, $F(3, 12) = 24.85$, $p < .01$ (Figure 2b); herbaceous cover, $F(3, 12) = 9.96$, $p < .01$ (Figure 2c); and biocrust connectivity range α, $F(3, 12) = 9.58$, $p < .01$. Shrub cover in both mowing and scraping plots was significantly lower than the control plots directly following the manipulations. Compared with control plots, biocrust cover increased significantly due to scraping and decreased significantly due to mowing.

3.2 | Changes in cover through time

Biocrust cover decreased significantly between 1992 and 2015 in all treatments (Figure 2). Shrub cover also decreased though time in all plots except the scraping treatment, but with no statistical significance; in the scraping plots, shrub cover increased significantly between 1992 and 2008. Herbaceous cover increased significantly between 1992 and 2008 in the herbicide and mowing plots, whereas in the control plots, significant differences were only found between 1992 and 2015 and the scraping plots showed a nonsignificant increase. In 2008, only the mowing plots had significantly different cover proportions compared with the control, with lower biocrust and shrub cover and higher herbaceous cover.

Intershrub connectivity range (α) was positively correlated to biocrust connectivity range in 1992 ($R = .61$, $R^2 = .36$, $p = .03$). In contrast, the correlation between the two α values disappeared in 2008 and 2015 ($R = -.27$, $R^2 = .07$, $p = .37$, and $R = -.22$, $R^2 = .01$,

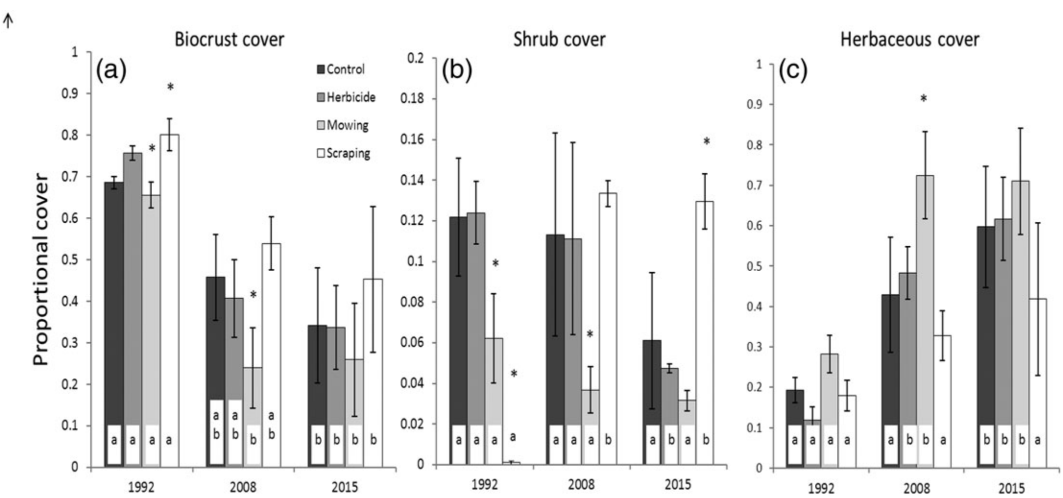

FIGURE 2 (a) Means and standard deviations of biocrust cover, (b) shrub cover, and (c) herbaceous cover by treatment and year. Asterisk signs mark significant differences ($p < .05$) from control within year. The letters within bars denote homogeneity groups between years within each treatment. All significance values were assessed using post hoc Tukey's honestly significant difference test

p = .42, respectively; See Fig. 3), signifying a spatial decoupling of herbaceous and shrub cover over the last two decades.

Additionally, analysis of cover change reveals that the changes in cover of shrubs and of herbaceous plants were not completely independent of each other. The cover changes of the two cover classes had a strong negative correlation in the 1992–2008 period (R = −.69, p = .01), and a weak negative correlation in the 2008–2015 period (R = −.30, p = .41).

3.3 | Connectivity–leakiness relationship

The first years following manipulation showed a significantly positive relationship between biocrust cover, biocrust α, and runoff yield (Table 1). Initially, biocrust α outperformed cover as a predictor of the runoff yields. In 1996, 4 years after the cover photographs were taken, the connectivity–runoff relationship was no longer statistically significant, although still positive. In the later period (2006–2009, Table 1), runoff yield was again significantly and positively related to biocrust cover in all years except 2006 (169 mm rainfall, mostly in very large storms) but not to biocrust α. However, the slopes (β) of the relationship were much smaller than those in 1993–1995.

In contrast to biocrust, inter-shrub cover and connectivity did not predict runoff yields at all between 1993 and 1996, even though they were positively correlated with biocrust cover. Inter-shrub cover and α were poor predictors of runoff yield in 2006–2009 as well. In 2009, there was a significant negative correlation between inter-shrub cover and runoff yield. Because shrubs do not perform as runoff sources, we believe this result is spurious and represents the simultaneous decrease in shrub and biocrust cover and runoff yield, all of which were driven by an increase in herbaceous cover.

3.4 | Runoff change through time

Throughout the two decades of runoff collection, runoff coefficients diminished from 13–20% between 1993 and 2001 to 3–10% between 2002 and 2009 (Figure 4). The decline in the runoff coefficients was evident in all treatments, but was more pronounced in the herbicide and scraping manipulation plots, which by 2007 produced runoff less than, or equal to, the control plots. Seasonal rainfall was not discernibly lower in the later period (Figure 1), implying that the observed difference was due to changes in the state of the landscape, not in climate.

4 | DISCUSSION

4.1 | The functional role of vegetation structure and pattern

The immediate treatment effect on vegetation patterns drove an immediate change in landscape functioning, with runoff yields increasing with greater biocrust cover. This highlights the functional role of vegetation pattern in runoff leakiness at the plot scale, similar to other studies in drylands worldwide (Ludwig, Eager, Bastin, Chewings, & Liedloff, 2002; Mayor, Bautista, Small, Dixon, & Bello, 2008; Wainwright, 2011). The positive correlation was maintained throughout the entire observation period, even after biocrust cover shifted to significantly lower values and the differences among treatments were substantially reduced (Table 1; Figure 5a). Between 1992 and 2008, biocrust cover appears to have crossed a threshold between two phases of the cover–runoff relationship. Above the threshold, small differences in cover lead to large differences in runoff; below the threshold, the response of runoff is weaker (Figure 5a). Such shifts in structure–function relationships are the expected outcome of ecosystem state transitions (Lopez et al., 2011; Williams et al., 2016; Urgeghe, Breshears, Martens, & Beeson, 2010).

However, biocrust connectivity α was a worse predictor of runoff leakiness than the simpler cover measure, especially when runoff yields were low (2006–2009, Table 1). Furthermore, the range of values of biocrust α was similar in both periods, whereas both biocrust cover and runoff yields decreased significantly (Figure 5b). This finding indicates that our structural variable, α, is not a good indicator of leakiness at this scale, because a single value of α can be linked to a wide range of runoff coefficient values. More importantly, this discrepancy highlights the value of long-term observations of both structure and function, without which such unanticipated shifts remain unnoticed. The differences in performance of cover and connectivity as indicators of runoff leakiness may depend on several factors,

TABLE 1 Results from simple linear regressions of seasonal runoff coefficients against cover and against connectivity range (α) of biocrust and inter-shrub, as calculated from landscape photographs taken in 1992 (top) and 2008 (bottom). Reported values are the regression slope (β) and the coefficient of determination (R^2) from each linear regression; numbers in bold represent significant relationships (p < .05)

	1993		1994		1995		1996	
Spatial structure 1992	$\beta(SE)$	R^2	$\beta(SE)$	R^2	$\beta(SE)$	R^2	$\beta(SE)$	R^2
Biocrust cover	**0.58(0.17)**	**.50**	**1.04(0.24)**	**.64**	**0.93(0.25)**	**.56**	0.64(0.35)	.19
Biocrust α	**0.23(0.04)**	**.69**	**0.38(0.06)**	**.76**	**0.31(0.08)**	**.52**	0.22(0.13)	.18
Inter-shrub cover	0.06(0.31)	.00	0.22(0.54)	.01	0.10(0.48)	.00	−0.75(0.51)	.16
Inter-shrub α	0.01(0.04)	.09	0.03(0.07)	.02	0.03(0.07)	.02	−0.12(0.07)	.15
Spatial structure 2008	**2006**		**2007**		**2008**		**2009**	
	$\beta(SE)$	R^2	$\beta(SE)$	R^2	$\beta(SE)$	R^2	$\beta(SE)$	R^2
Biocrust cover	0.10(0.10)	.09	**0.06(0.02)**	**.38**	**0.11(0.03)**	**.42**	**0.19(0.06)**	**.46**
Biocrust α	0.11(0.06)	.25	0.03(0.01)	.31	0.05(0.03)	.22	0.07(0.05)	.16
Inter-shrub cover	−0.16(0.29)	.02	−0.10(0.07)	.14	−0.28(0.11)	.35	**−0.58(0.16)**	**.55**
Inter-shrub α	−0.01(0.04)	.00	−0.01(0.01)	.09	−0.02(0.02)	.20	**−0.06(0.02)**	**.39**

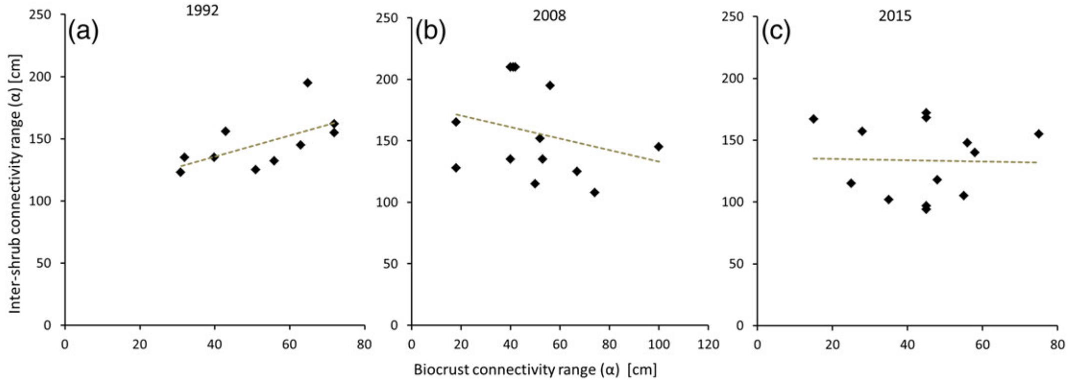

FIGURE 3 Scatterplot of inter-shrub α by biocrust α, as calculated from photos taken in 1993, 2008, and 2015. The dashed lines represent the linear relationship between the two variables

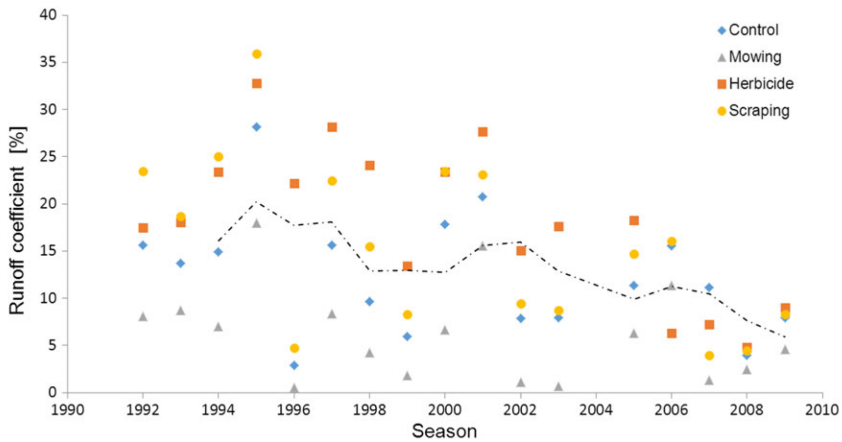

FIGURE 4 Time series of the mean seasonal runoff coefficients for each treatment and a three-year running average of all plots combined (dashed line)

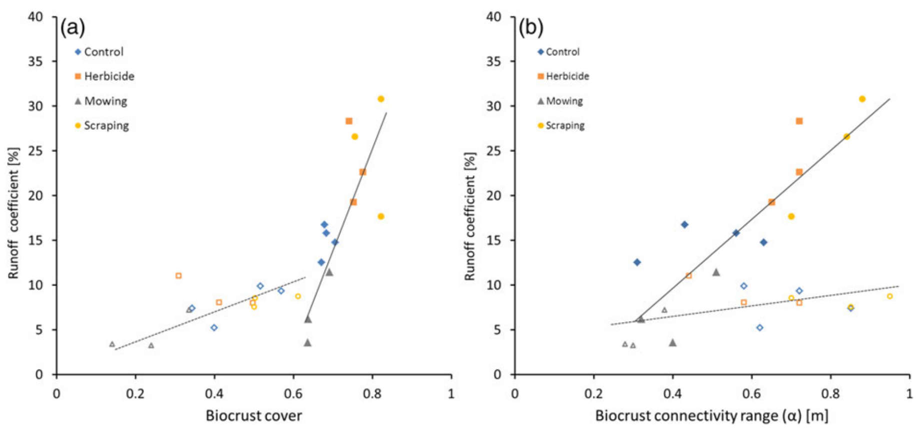

FIGURE 5 (a) Scatterplots of the seasonal runoff coefficient against the biocrust cover and (b) inter-shrub cover, measured per plot, for the seasons 1994 (full symbols) and 2008 (hollow symbols). Runoff values of 1994 are compared with cover measured in 1992 and runoff of 2008 to cover measured in 2008. Least-square regression lines are presented, with full lines for 1994 and dashed lines for 2008 runoff coefficients (statistics in Table 1)

including rainfall intensity, scale of measurement, and edaphic properties, stressing the value of examining a combination of metrics (Lazaro, Calvo-Cases, Lazaro, & Molina, 2015; Wainwright et al., 2011). Connectivity may be a more effective indicator at the scale of slopes and watersheds, due to the nonlinear effects of scale on runoff rates, complex topography and heterogeneity, and the critical role of the slope-channel interface (Jenerette, Barron-Gafford, Guswa, McDonnell, & Villegas, 2012; Rodriguez-Caballero et al., 2014; Thompson et al., 2011).

Although previous studies in this site have identified shrub patches as the prominent runoff sinks (Buis et al., 2010; Shachak, Sachs, & Moshe, 1998), our results show neither shrub cover nor inter-shrub connectivity as important in controlling runoff yield. However, overall vegetation cover, including both shrubs and herbaceous vegetation, did control runoff throughout the experiment. Herbaceous vegetation was—at the beginning of the experiment—tightly linked to shrub cover (Boeken & Orenstein, 2001), but was decoupled from shrubs later on (Figure 3). We attribute this decoupling to a combination of two drivers: the first is the cessation of grazing allowing dense herbaceous growth in the inter-shrub (Golodets & Boeken, 2006; Noy-Meir, 1990); the second is widespread mortality of mature shrubs caused by successive drought years (Hoffman et al., 2016; Sher et al., 2012).

Accordingly, we propose that the main ecohydrological role of shrubs is patch creation and maintenance, which is critical under livestock grazing, but loses its importance after herbaceous and shrub cover are decoupled (Guardiola-Clararnonte et al., 2011). Thus, although the direct effect of the shrubs during rainfall is limited to interception of the rainfall itself (Hoffman, Yizhaq, & Boeken, 2013), whatever effects shrub cover has on runoff movement are indirect, via their facilitation of herbaceous plants. These effects are mediated by ground cover and soil structures that control the sink function, such as porosity and hydrophobicity, which are strongly influenced by herbaceous biomass (both green and senescent; Boeken & Orenstein, 2001; Hoffman et al., 2013). Consequently, the decoupling of herbaceous and shrub cover drove the reorganization of infiltration patterns and runoff paths, resulting in the observed shift in the structural–functional relationships. This process has been shown experimentally at smaller scale in our study site (Boeken & Orenstein, 2001) and at larger scales in other ecosystems (Ludwig et al., 1999).

4.2 | Recovery trajectory

All experimental treatments created a disturbance to the vegetation structure by changing the absolute and relative cover of the different cover classes. The scraping treatment eliminated shrub cover entirely, but the vegetation in the scraped plots fully recovered by 2008, resembling the initial condition of the control plots. Initially, the herbicide application mostly affected herbaceous cover (Zaady et al., 2004), which recovered by 2008 and even overcompensated (Figure 2). The mowing treatment, however, reduced both shrub and biocrust cover while increasing herbaceous cover—as a specific consequence of the method, spreading the mound's soil and litter cover onto the biocrust—but the plots did not return to their pre-treatment structure. Instead, the effect of the disturbance was amplified through time, with herbaceous cover increasing further at the expense of the shrub and biocrust cover. Other studies have shown that the biocrust can lose its structure and function when covered by dense litter or soil (Boeken & Orenstein, 2001; Buis et al., 2010), a process we believe took place in the mowed plots.

We suggest that the differences in recovery trajectories are due to ecohydrological interactions among the cover classes and the resulting feedbacks (Turnbull et al., 2012). A negative feedback took place between shrubs and biocrust, as high biocrust cover resulting from scraping increased shrub growth due to the extra runoff water, allowing rapid shrub recovery (Eldridge et al., 2002; Espigares, Merino-Martin, Moreno-de las Heras, & Nicolau, 2013). However, in the mowing treatment, the large increase in herbaceous cover suppressed shrub growth by reducing runoff to the shrubs, thus creating a positive feedback that enhanced the original treatment effect (Urgeghe & Bautista, 2015). Likely, a similar but slower process drove the changes observed in the control and herbicide plots, where a reduction in runoff yields coincided with the decoupling of herbaceous plants from shrub cover. This positive feedback interaction further enhanced drought stress and mortality for the shrubs (Espigares et al., 2013; Guardiola-Clararnonte et al., 2011; Urgeghe & Bautista, 2015). This could partly explain the negative correlation between cover changes of shrubs and herbaceous plants over the observed period and act as a mechanism destabilizing the patchy shrub-steppe state under some conditions (Cingolani et al., 2014; Turnbull et al., 2012).

4.3 | Resilience of vegetation to disturbance

The local plant community recovered from the disturbance treatments, exhibiting high resilience to biomass removal, even one as extreme as the scraping treatment. As other studies in the region show, ecosystem engineering shrubs carry a significant role in this demonstrated resilience by their ability to regrow or resprout in bare locations and to concentrate resources under their canopies (Bos-Groenendijk, 2012; Elbaz, 2012). However, the patchy shrub-steppe structure is not stable in all cases, as the continued decline in shrub cover demonstrates. Loss of the ecosystem engineer shrub populations under the combined effects of climate change and protection against grazing may affect ecosystem structure and dynamics (Boeken & Shachak, 1994). Although the emergent structure of extensive herbaceous cover and decreasing shrub cover may still maintain high primary production rates, its stability and drought resistance may be lower, and the effects on plant species diversity are likely negative (Hoffman et al., 2016; Ruppert et al., 2015, but see Shafran-Nathan et al., 2013).

REFERENCES

Aguiar, M. R., Paruelo, J. M., Sala, O. E., & Lauenroth, W. K. (1996). Ecosystem responses to changes in plant functional type composition: An example from the Patagonian steppe. *Journal of Vegetation Science*, *7*, 381–390. doi:10.2307/3236281

Arbel, S. (2009). Rainfall-runoff relationship under different management practices on loessial slopes in a semi-arid region (in Hebrew). MSc thesis in Geography and Environmental Science. Haifa University. Haifa, Israel.

Bisigato, J. A., Hardtke, L., & Francisco del Valle, H. (2013). Soil as a capacitor: Considering soil water content improves temporal models of productivity. *Journal of Arid Environments*, *98*, 88–92. doi:10.1016/j.jaridenv.2013.08.004

Boeken, B. (2008). Park Shaked LTER-Ma'arag station: research and education activities 1991–2008. Israel LTER Network (Ma'arag).

Boeken, B., & Orenstein, D. (2001). The effect of plant litter on ecosystem properties in a Mediterranean semi-arid shrubland. *Journal of Vegetation Science*, *12*. doi:10.2307/3236870

Boeken, B., & Shachak, M. (1994). Desert plant communities in human-made patches—implications for management. *Ecological Applications*, *4*, 702–716.

Boeken B, Zaady, E. (2016). Daily meteorological data from Park Shaked LTER station 1999–2016. Retrieved from http://www.bgu.ac.il/desert_agriculture/PSKmeteo-web/PSK99-16daily.htm

Bos-Groenendijk G. 2012. Development and composition of shrub communities in the northern Negev desert of Israel. MsC thesis in

Nature Conservation and Plant Ecology. Wageningen University. Wageningen, The Netherlands.

Brookshire, E. N. J., & Weaver, T. (2015). Long-term decline in grassland productivity driven by increasing dryness. *Nature Communications*, *6*, 7148. doi:10.1038/ncomms8148

Buis, E., Temme, A. J. A. M., Veldkamp, A., Boeken, B., Jongmans, A. G., van Breemen, N., & Schoorl, J. M. (2010). Shrub mound formation and stability on semi-arid slopes in the Northern Negev Desert of Israel: A field and simulation study. *Geoderma*, *156*, 363–371. doi:10.1016/j.geoderma.2010.03.005

Buis, E., Veldkamp, A., Boeken, B., & van Breemen, N. (2009). Controls on plant functional surface cover types along a precipitation gradient in the Negev Desert of Israel. *Journal of Arid Environments*, *73*, 82–90. doi:10.1016/j.jaridenv.2008.09.008

Cingolani, A. M., Vaieretti, M. V., Giorgis, M. A., Poca, M., Tecco, P. A., & Gurvich, D. E. (2014). Can livestock grazing maintain landscape diversity and stability in an ecosystem that evolved with wild herbivores? *Perspectives in Plant Ecology, Evolution and Systematics*, *16*, 143–153. doi:10.1016/j.ppees.2014.04.002

De Falco N. 2013. Degradation of *Noaea mucronata* patches: Shrub mortality and landscape structure. MsC thesis in Desert Studies. Ben-Gurion University of the Negev. Beer-Sheva, Israel.

DeMalach, N., Kigel, J., Voet, H., & Ungar, E. D. (2014). Are semiarid shrubs resilient to drought and grazing? Differences and similarities among species and habitats in a long-term study. *Journal of Arid Environments*, *102*, 1–8. doi:10.1016/j.jaridenv.2013.10.016

D'Odorico, P., Bhattachan, A., Davis, K. F., Ravi, S., & Runyan, C. W. (2013). Global desertification: Drivers and feedbacks. *Advances in Water Resources*, *51*, 326–344. doi:10.1016/j.advwatres.2012.01.013

D'Odorico, P., Caylor, K., Okin, G. S., & Scanlon, T. M. (2007). On soil moisture–vegetation feedbacks and their possible effects on the dynamics of dryland ecosystems. *Journal of Geophysical Research – Biogeosciences*, *112*, G04010. doi:10.1029/2006JG000379

Elbaz S. (2012). Atractylis serratuloides establishment and its role in patch formation in Northern Negev shrubland. MsC thesis in Desert Studies. Ben-Gurion University of the Negev. Beer-Sheva, Israel.

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

Eldridge, D. J., Zaady, E., & Shachak, M. (2002). Microphytic crusts, shrub patches and water harvesting in the Negev Desert: The Shikim system. *Landscape Ecology*, *17*, 587–597. doi:10.1023/A:1021575503284

Espigares, T., Merino-Martin, L., Moreno-de las Heras, M., & Nicolau, J. (2013). Intensity of ecohydrological interactions in reclaimed Mediterranean slopes: Effects of run-off redistribution on plant performance. *Ecohydrology*, *6*, 836–844. doi:10.1002/eco.1307

Gaitán, J. J., Oliva, G. E., Bran, D. E., Maestre, F. T., Aguiar, M. R., Jobbágy, E. G., … Massara, V. (2014). Vegetation structure is as important as climate for explaining ecosystem function across Patagonian rangelands. *Journal of Ecology*, *102*, 1419–1428. doi:10.1111/1365-2745.12273

Golodets, C., & Boeken, B. (2006). Moderate sheep grazing in semiarid shrubland alters small-scale soil surface structure and patch properties. *Catena*, *65*, 285–291. doi:10.1016/j.catena.2005.12.005

Golodets, C., Sternberg, M., Kigel, J., Boeken, B., Henkin, Z., Seligman, N. G., & Ungar, E. D. (2015). Climate change scenarios of herbaceous production along an aridity gradient: Vulnerability increases with aridity. *Oecologia*, *177*, 971–979. doi:10.1007/s00442-015-3234-5

Guardiola-Claramonte, M., Troch, P. A., Breshears, D. D., Huxman, T. E., Switanek, M. B., Durcik, M., & Cobb, N. S. (2011). Decreased streamflow in semi-arid basins following drought-induced tree die-off: A counter-intuitive and indirect climate impact on hydrology. *Journal of Hydrology*, *406*, 225–233. doi:10.1016/j.jhydrol.2011.06.017

Hamerlynck, E. P., Scott, R. L., & Stone, J. J. (2012). Soil moisture and ecosystem function responses of desert grassland varying in vegetative cover to a saturating precipitation pulse. *Ecohydrology*, *5*, 297–305. doi:10.1002/eco.214

Hoffman, O., Yizhaq, H., & Boeken, B. (2013). Small-scale effects of annual and woody vegetation on sediment displacement under field conditions. *Catena*, *109*, 157–163. doi:10.1016/j.catena.2013.04.003

Hoffman, O., de Falco, N., Yizhaq, H., & Boeken, B. (2016). Annual plant diversity decreases across scales following widespread ecosystem engineer shrub mortality. *Journal of Vegetation Science*, *27*, 578–586. doi:10.1111/jvs.12372

Hsu, J. S., Powell, J., & Adler, P. B. (2012). Sensitivity of mean annual primary production to precipitation. *Global Change Biology*, *18*, 2246–2255. doi:10.1111/j.1365-2486.2012.02687.x

Jenerette, G. D., Barron-Gafford, G. A., Guswa, A. J., McDonnell, J. J., & Villegas, J. C. (2012). Organization of complexity in water limited ecohydrology. *Ecohyrdrology*, *5*, 184–199. doi:10.1002/eco.217

Katra, I., Lavee, H., & Sarah, P. (2008a). Rainfall distribution around shrubs: Eco-geomorphic implications for arid hillslopes. *Geomorphology*, *95*, 544–548. doi:10.1016/j.geomorph.2007.05.016

Katra, I., Lavee, H., & Sarah, P. (2008b). The effect of rock fragment size and position on topsoil moisture on arid and semi-arid hillslopes. *Catena*, *72*, 49–55. doi:10.1016/j.catena.2007.04.001

Larsen, L. G., Choi, J., Nungesser, M. K., & Harvey, J. W. (2012). Directional connectivity in hydrology and ecology. *Ecological Applications*, *22*, 2204–2220. doi:10.1890/11-1948.1

Lazaro, R., Calvo-Cases, A., Lazaro, A., & Molina, I. (2015). Effective run-off flow length over biological soil crusts on silty loam soils in drylands. *Hydrological Processes*, *29*, 2534–2544.

Kefi, S., Rietkerk, M., Alados, C. L., Pueyo, Y., Papanastasis, V. P., ElAich, A., & de Ruiter, P. C. (2007). Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. *Nature*, *449*, 213–2U5. doi:10.1038/nature06111

Leu, S., Mussery, A. M., & Budovsky, A. (2014). The effects of long time conservation of heavily grazed shrubland: A case study in the Northern Negev, Israel. *Environmental Management*, *54*, 309–319. doi:10.1007/s00267-014-0286-y

Linde L. (2002). The role of Thymelaea hirsuta shrubs in water flow on slopes in the Negev Desert of Israel. MsC Thesis. University of Leipzig, Germany.

Lopez, D. R., Cavallero, L., Brizuela, M. A., & Aguiar, M. R. (2011). Ecosystemic structural–functional approach of the state and transition model. *Applied Vegetation Science*, *14*, 6–16. doi:10.1111/j.1654-109X.2010.01095.x

Ludwig, J. A., Tongway, D. J., & Marsden, S. G. (1999). Stripes, strands or stipples: Modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena*, *37*, 257–273. doi:10.1016/S0341-8162(98)00067-8

Ludwig, J. A., Eager, R. W., Bastin, G. N., Chewings, V. H., & Liedloff, A. C. (2002). A leakiness index for assessing landscape function using remote sensing. *Landscape Ecology*, *17*, 157–171. doi:10.1023/A:1016579010499

Maestre, F. T., Bowker, M. A., Puche, M. D., Belen Hinojosa, M., Martinez, I., Garcia-Palacios, P., … Escudero, A. (2009). Shrub encroachment can reverse desertification in semi-arid Mediterranean grasslands. *Ecology Letters*, *12*, 930–941. doi:10.1111/j.1461-0248.2009.01352.x

Mayor, A. G., Bautista, S., Small, E. E., Dixon, M., & Bello, J. (2008). Measurement of the connectivity of runoff source areas as determined by vegetation pattern and topography: A tool for assessing potential water and soil losses in drylands. *Water Resources Research*, *44*, W10423. doi:10.1029/2007WR006367

Mayor, A. G., Kefi, S., Bautista, S., Rodriguez, F., Carteni, F., & Rietkerk, M. (2013). Feedbacks between vegetation pattern and resource loss dramatically decrease ecosystem resilience and restoration potential in a simple dryland model. *Landscape Ecology*, *28*, 931–942. doi:10.1007/s10980-013-9870-4ER

Merino-Martin, L., Breshears, D. D., Moreno-de las Heras, M., Villegas, J. C., Perez-Domingo, S., Espigares, T., & Nicolau, J. M. (2012). Ecohydrological source-sink interrelationships between vegetation patches and soil hydrological properties along a disturbance gradient reveal a restoration threshold. *Restoration Ecology*, *20*, 360–368. doi:10.1111/j.1526-100X.2011.00776.x

Meron, E. (2015). Pattern formation—A missing link in the study of ecosystem response to environmental changes. *Mathematical Biosciences*, *271*, 1–18. doi:10.1016/j.mbs.2015.10.015

Michaelides, K., Lister, D., Wainwright, J., & Parsons, A. J. (2009). Vegetation controls on small-scale runoff and erosion dynamics in a degrading dryland environment. *Hydrological Processes*, *23*, 1617–1630. doi:10.1002/hyp.7293

Moreno-de las Heras, M., Saco, P. M., Willgoose, G. R., & Tongway, D. J. (2012). Variations in hydrological connectivity of Australian semiarid landscapes indicate abrupt changes in rainfall-use efficiency of vegetation. *Journal of Geophysical Research – Biogeosciences*, *117*, G03009. doi:10.1029/2011JG001839

Noy-Meir, I. (1990). Responses of two semi arid rangeland communities to protection form grazing. *Israel Journal of Botany*, *39*, 431–442.

Okin, G. S., Moreno-de las Heras, M., Saco, P. M., Throop, H. L., Vivoni, E. R., Parsons, A. J., … Peters, D. P. C. (2015). Connectivity in dryland landscapes: Shifting concepts of spatial interactions. *Frontiers in Ecology and the Environment*, *13*, 20–27. doi:10.1890/140163ER

Osem, Y., Perevolotsky, A., & Kigel, J. (2004). Site productivity and plant size explain the response of annual species to grazing exclusion in a Mediterranean semi-arid rangeland. *Journal of Ecology*, *92*, 297–309. doi:10.1111/j.0022-0477.2004.00859.x

Paz-Kagan, T., Panov, N., Shachak, M., Zaady, E., & Karnieli, A. (2014). Structural changes of desertified and managed shrubland landscapes in response to drought: Spectral, spatial and temporal analyses. *Remote Sensing*, *6*, 8134–8164. doi:10.3390/rs6098134

Reed, M. S., Stringer, L. C., Dougill, A. J., Perkins, J. S., Atlhopheng, J. R., Mulale, K., & Favretto, N. (2015). Reorienting land degradation towards sustainable land management: Linking sustainable livelihoods with ecosystem services in rangeland systems. *Journal of Environmental Management*, *151*, 472–485. doi:10.1016/j.jenvman.2014.11.010

Reynolds, J. F., Stafford Smith, D. M., Lambin, E. F., Turner, B. L., Mortimore, M., Batterbury, S. P. J., … Walker, B. (2007). Global desertification: Building a science for dryland development. *Science*, *316*, 847–851. doi:10.1126/science.1131634

Rodriguez-Caballero, E., Canton, Y., Lazaro, R., & Sole-Benet, A. (2014). Cross-scale interactions between surface components and rainfall properties. Non-linearities in the hydrological and erosive behavior of semiarid catchments. *Journal of Hydrology*, *517*, 815–825. doi:10.1016/j.jhydrol.2014.06.018

Ruiz-Jaén, M. C., & Aide, T. M. (2005). Vegetation structure, species diversity, and ecosystem processes as measures of restoration success. *Forest Ecology and Management*, *218*, 159–173. doi:10.1016/j.foreco.2005.07.008

Ruppert, J. C., Harmoney, K., Henkin, Z., Snyman, H. A., Sternberg, M., Willms, W., & Linstaedter, A. (2015). Quantifying drylands' drought resistance and recovery: The importance of drought intensity, dominant life history and grazing regime. *Global Change Biology*, *21*, 1258–1270. doi:10.1111/gcb.12777ER

Schlesinger, W. H., Raikes, J. A., Hartley, A. E., & Cross, A. F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology (Washington D C)*, *77*, 364–374. doi:10.2307/2265615

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675. doi:10.1038/nmeth.2089

Segoli, M., Ungar, E. D., & Shachak, M. (2008). Shrubs enhance resilience of a semi-arid ecosystem by engineering and regrowth. *Ecohydrology*, *1*, 330–339. doi:10.1002/eco.21

Shachak, M., Sachs, M., & Moshe, I. (1998). Ecosystem management of desertified shrublands in Israel. *Ecosystems*, *1*, 475–483. doi:10.1007/s100219900043

Shachak, M. (2011). Ecological networks: Northern Negev ecosystems as a model. *Ecology and Environment*, *2*, 18–29 (in Hebrew).

Shafran-Nathan, R., Svoray, T., & Perevolotsky, A. (2013). The resilience of annual vegetation primary production subjected to different climate change scenarios. *Climatic Change*, *118*, 227–243. doi:10.1007/s10584-012-0614-2

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. doi:10.1016/j.ejsobi.2012.09.002

Shoshany, M., & Karnibad, L. (2015). Remote sensing of shrubland drying in the South-East Mediterranean, 1995–2010: Water-use-efficiency-based mapping of biomass change. *Remote Sensing*, *7*, 2283–2301. doi:10.3390/rs70302283

Soliveres, S., & Maestre, F. T. (2014). Plant–plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies. *Perspectives in Plant Ecology, Evolution and Systematics*, *16*, 154–163. doi:10.1016/j.ppees.2014.04.001

Stavi, I., Ungar, E. D., Lavee, H., & Sarah, P. (2008). Grazing-induced spatial variability of soil bulk density and content of moisture, organic carbon and calcium carbonate in a semi-arid rangeland. *Catena*, *75*, 288–296. doi:10.1016/j.catena.2008.07.007

Svoray, T., & Karnieli, A. (2011). Rainfall, topography and primary production relationships in a semiarid ecosystem. *Ecohydrology*, *4*, 56–66. doi:10.1002/eco.123

Thompson, S. E., Harman, C. J., Troch, P. A., Brooks, P. D., & Sivapalan, M. (2011). Spatial scale dependence of ecohydrologically mediated water balance partitioning: A synthesis framework for catchment ecohydrology. *Water Resources Research*, *47*, W00J03. doi:10.1029/2010WR009998

Turnbull, L., Wilcox, B. P., Belnap, J., Ravi, S., D'Odorico, P., Childers, D., … Sankey, T. (2012). Understanding the role of ecohydrological feedbacks in ecosystem state change in drylands. *Ecohydrology*, *5*, 174–183. doi:10.1002/eco.265

Urgeghe, A. M., & Bautista, S. (2015). Size and connectivity of upslope run-off-source areas modulate the performance of woody plants in Mediterranean drylands. *Ecohydrology*, *8*, 1292–1303. doi:10.1002/eco.1582

Urgeghe, A. M., Breshears, D. D., Martens, S. N., & Beeson, P. C. (2010). Redistribution of runoff among vegetation patch types: On ecohydrological optimality of herbaceous capture of run-on. *Rangeland Ecology & Management*, *63*, 497–504. doi:10.2111/REM-D-09-00185.1

Wainwright, J., Turnbull, L., Ibrahim, T. G., Lexartza-Artza, I., Thornton, S. F., & Brazier, R. E. (2011). Linking environmental régimes, space and time: Interpretations of structural and functional connectivity. *Geomorphology*, *126*, 387–404. doi:10.1016/j.geomorph.2010.07.027

Wei, W., Jia, F., Yang, L., Chen, L., Zhang, H., & Yu, Y. (2014). Effects of surficial condition and rainfall intensity on runoff in a loess hilly area, China. *Journal of Hydrology*, *513*, 115–126. doi:10.1016/j.jhydrol.2014.03.022

Wilcox, B. P., Turnbull, L., Young, M. H., Williams, C. J., Ravi, S., Seyfried, M. S., … Wainwright, J. (2012). Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. *Ecohydrology*, *5*, 160–173. doi:10.1002/eco.247

Williams, C. J., Pierson, F. B., Spaeth, K. E., Brown, J. R., Al-Hamdan, O. Z., Weltz, M. A., … Nichols, M. H. (2016). Incorporating hydrologic data and ecohydrologic relationships into ecological site descriptions. *Rangeland Ecology & Management*, *69*, 4–19. doi:10.1016/j.rama.2015.10.001

Wright, J. P., Jones, C. G., Boeken, B., & Shachak, M. (2006). Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology*, *94*, 815–824. doi:10.1111/j.1365-2745.2006.01132.x

Zaady, E., Arbel, S., Barkai, D., & Sarig, S. (2013). Long-term impact of agricultural practices on biological soil crusts and their hydrological processes in a semiarid landscape. *Journal of Arid Environments*, *90*, 5–11. doi:10.1016/j.jaridenv.2012.10.021

Zaady, E., Karnieli, A., & Shachak, M. (2007). Applying a field spectroscopy technique for assessing successional trends of biological soil crusts in a semi-arid environment. *Journal of Arid Environments*, *70*, 463–477. doi:10.1016/j.jaridenv.2007.01.004

Zaady, E., Levacov, R., & Shachak, M. (2004). Application of the herbicide, simazine, and its effect on soil surface parameters and vegetation in a patchy desert landscape. *Arid Land Research and Management*, *18*, 397–410. doi:10.1080/15324980490497483

How to cite this article: Hoffman O, Yizhaq H, Boeken B. Shifts in landscape ecohydrological structural–functional relationship driven by experimental manipulations and ecological interactions. *Ecohydrology*. 2016;e1806. doi:10.1002/eco.1806