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Shrubs enhance resilience of a semi-arid ecosystem by engineering and regrowth

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ABSTRACT

Semi-arid ecosystems in the Mediterranean basin show a high degree of resilience, despite thousands of years of human disturbance. It has been suggested that this resilience is facilitated by a landscape structure that consists of woody vegetation and intershrub patches of crusted soil. We hypothesized that the woody vegetation patches have two main properties that increase the resilience of the ecosystem. The first property is the capability to accumulate water, and we hypothesized that this continues to function after anthropogenic disturbances to the shrubs. This was field-tested with a rainfall simulator by comparing the amounts of runoff and soil erosion generated by crusted intershrub patches, intact shrub patches, and disturbed shrub patches. The second property is the ability of the woody vegetation to recover after disturbances. This was tested by measuring the recovery rate of the woody vegetation, during 2 consecutive years after canopy removal. Intact and disturbed shrub patches generated similar amounts of runoff and soil erosion to one another, and much lower than crusted intershrub patches, and both kinds of shrub patches had deeper water infiltration. These results suggest that the accumulation of water under the shrub is due to surface and sub-surface soil properties, and not canopy properties. After anthropogenic removal of the woody vegetation canopy, most of the individuals regrew. These combined results suggest that the ecosystem can remain resilient to certain anthropogenic disturbances by virtue of ecosystem engineering and fast recovery by woody vegetation patches that act to conserve resources and to impede their leakage from the ecosystem.

KEY WORDS resilience; ecosystem engineering; runoff; infiltration; woody vegetation disturbance

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INTRODUCTION

Ecological resilience has been defined as the ability of an ecosystem to absorb disturbance and to reorganize while undergoing change, so as to retain essentially the same function, structure, identity, and feedbacks (Peterson *et al*., 1998). Resilience represents the degree to which a complex ecosystem can self-organize and return to a similar state to that which existed before the disturbance (Boesch, 2006).

Semi-arid ecosystems in the Mediterranean basin show a high degree of resilience despite thousands of years of human disturbance (Perevolotsky *et al*., 2005). It has been suggested that the resilience of semi-arid environments is related to their landscape structure: a two-phase mosaic of woody vegetation patches interspersed with open patches (Yizhaq *et al*., 2005). Two-phase mosaics are typical of ecosystems in which paucity of resources or competition with herbaceous vegetation prevents woody patches from covering the entire landscape, and such mosaics are a fundamental feature of most resource-limited semi-arid ecosystems (Ludwig and Tongway, 1997).

The modulation of the landscape to a two-phase mosaic is regulated by the ecosystem engineering function of woody vegetation (Jones *et al*., 1994, 1997), whereby resources are redistributed and, consequently, species composition and diversity are modified (Charley and West, 1975; Boeken and Shachak, 1998).

Positive feedbacks between woody vegetation growth and resource flows cause vegetation to form around accumulated resources (Gilad *et al*., 2004, 2007; Rietkerk *et al*., 2004). The resulting heterogeneity sustains higher overall species richness and biomass across the landscape than if resources were spread homogeneously (Noy-Meir, 1973). It appears that the size and configuration of woody vegetation at the landscape scale are also important to the maintenance of resources in semi-arid ecosystems (Loch, 2000).

In a functional semi-arid landscape characterized by a two-phase mosaic, the co-existence of shrubs and herbaceous vegetation represents a stable state that results from accumulation of water and nutrients under the shrubs (Ludwig *et al*., 1999; Caylor and Rodriguez-Iturbe, 2004). The resources are accumulated by mechanism(s) controlled by source-sink relations. The open (intershrub) patches are often covered by a biological crust of cyanobacteria, bacteria, algae, mosses, and lichens (Zaady *et al*., 1997), and the cyanobacteria

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excrete polysaccharides which bind the soil particles and create a tightly structured soil that reduces infiltration of water into the soil and generates runoff (Malam Issa *et al.*, 1999). In contrast, the soil under the woody vegetation does not have well-developed biological crusts; its surface comprises loose soil particles that facilitate water infiltration (Shachak *et al.*, 1999). The soil under the woody vegetation also has a higher content of organic matter than that in the intershrub patches, and this enhances its water-holding capacity (Daubenmire, 1959). Moreover, it has been shown that the macroporosity caused by roots and burrowing animals also promotes water infiltration (Joffre and Rambal, 1993; Wolfe and Nickling, 1996). The shrub canopy itself can also concentrate rainfall at the base of the plant by guiding raindrops down the stems and trunks (stem flow) (Crockford and Richardson, 2000). The interplay between woody vegetation and the soil crust plays an important role in determining the spatial pattern of runoff source (crust) and sink (shrub) areas (Cammeraat and Imeson, 1999; Valentin *et al.*, 1999; Wilcox *et al.*, 2003; Imeson and Prinsen, 2004; Ludwig *et al.*, 2005). The net effect is that the functional landscape is composed of water-enriched shrub patches and water-deprived intershrub patches. However, the generality of this statement cannot be taken for granted. In some semi-arid ecosystems, a higher infiltration rate under the shrub was related to the distance from its stem and not to the extent of the above-ground canopy (Dunkerley, 2000), and intershrub patches have been found to have higher infiltration rates than the shrub patches (Ravi *et al.*, 2007).

Severe disturbance to shrubs in a two-phase mosaic may cause a state change that leads to a dysfunctional (desertified) landscape, and which ultimately results in a landscape with diminished water, nutrients, and productivity (D'Odorico *et al.*, 2005). Dysfunctional landscapes caused by shrub removal promote leakage of soil, water, and nutrients from the system (Deangelis *et al.*, 1989; Williams and Gascoigne, 2003). Resilience in a two-phase mosaic prevents the ecosystem changing from a functional to a dysfunctional state, and the transition from the latter to the former depends on rehabilitation of the shrubs and restoration of the two-phase mosaic.

Dryland studies provide numerous examples of the transition from functional to dysfunctional states through the effects of natural and anthropogenic disturbances on ecological processes (Buffington and Herbel, 1965; Shachak *et al.*, 1999; von Hardenberg *et al.*, 2001). Water is the main limiting resource for biological processes in drylands; therefore, the transition from functional to dysfunctional states is linked to processes that control rainwater redistribution via runoff generation and the infiltration of moisture into the soil (Yair and Shachak, 1982).

The Negev Desert of Israel is a good example of state transition in semi-arid landscapes and, therefore, a good subject for study. Human disturbances such as the removal of the canopy of woody plants for firewood and livestock browsing have been common in the Negev for the past few thousand years (Perevolotsky and Seligman, 1998). Shachak *et al.* (1998) showed that some areas of the Negev Desert dominated by *Noaea mucronata* have undergone desertification and leakage of resources from the system. While these shrubs do accumulate water and nutrients, they do not regrow after removal of the above-ground canopy (Oren, 2001). In our study site, the two-phase mosaic has persisted as a functional landscape which suggests that the system is resilient. We hypothesized that a cornerstone of this resilience is the recovery capability of the shrubs, and their control over the hydraulic system after disturbance. To test this hypothesis we selected a two-phase mosaic composed of the dwarf shrub, prickly burnet, *Sarcopoterium spinosum*, which is very common in the northern Negev (Litav and Orshan, 1971; Perevolotsky *et al.*, 2001; Osem *et al.*, 2002). We studied the effects of intact as well as canopy-removed shrubs on the hydraulic regime, and the relationship between hydraulic regime and the recovery rate of shrubs. Since different shrub species affect the hydraulic regime differently and have different re-sprouting strategies, it is important to use the same system with the same shrubs when studying the combined effect of these factors.

Our specific hypothesis was that resilience of the system derives from two properties of *S. spinosum*: its ability to function as an ecosystem engineer that accumulates water, and its strong capability for recovery, following disturbance. The aspect of the hypothesis relating to water accumulation springs from studies that showed how shrubs in the northern Negev Desert create water-enriched patches (Eldridge, 1998; Valentin and d'Herbes, 1999). The recovery capability aspect arises from studies of the biology of *S. spinosum* (Litav and Orshan, 1971; Perevolotsky *et al.*, 2001), which demonstrated a clonal reproduction mode in the Mediterranean rangelands, which allows for re-sprouting after canopy disturbance. This trait is specific to *S. spinosum* among the dwarf shrubs in the area (Litav and Orshan, 1971). To test our hypothesis regarding the hydraulic role of *S. spinosum*, we carried out a field experiment using rainfall simulation. To test the recovery aspect, we removed the canopy of *S. spinosum* shrubs and measured their recovery rate.

The overall objectives of our study were: (1) to determine the role of *S. spinosum* in maintaining semi-arid ecosystem resilience; (2) to generalize on the role of shrubs in dryland stabilization; and (3) to incorporate the concept of resilience into ecosystem-based management of semi-arid lands (Carpenter *et al.*, 2001; Boesch, 2006; Byers *et al.*, 2006).

METHODS

Study area

The study area is located in the northern Negev of Israel (31°21′52″N, 34°49′46″E), at the Lehavim Long-Term Ecological Research (LTER) site. The site is in the semi-arid transition zone between the Mediterranean and the arid climatic zones. Average annual precipitation is 305 mm, with a range of 78–540 mm (1953–1996). Precipitation occurs from December to March. Average daily temperatures range from 10 °C in winter to 25 °C in summer (Baram, 1996).

The area is characterized by hilly slopes composed of Eocene limestone and chalk, with altitudes of 350–500 m a.s.l. The landscape is a shrubland dominated by *S. spinosum* and organized spatially as a two-phase mosaic of shrub patches and open soil patches. The areal cover of *S. spinosum* tends to be greatest on northwest-facing hillsides, where coverage is typically about 40% (Arnon, 2005). The herbaceous vegetation develops mostly in the open soil patches and persists for 3–5 months after the first rains, depending on the amount and distribution of the precipitation (Giladi *et al.*, 2007). On the hillsides, peak standing biomass of herbaceous vegetation in the intershrub zone is strongly related to rainfall, and exceeds 100 g m^{-2} under average rainfall (Ungar *et al.*, 1999). The area is grazed by flocks of approximately 800 Awassi sheep and 200 goats. The nutritional requirements of the animals are completely met by the vegetation during the green season; an indication that the environment is not degraded.

Soil

The soil is a brown lithosol with eolian loess. The most detailed study of the soil at the study site was conducted recently by Stavi (2008). The bulk density of the soil under the canopy of *S. spinosum* shrubs was significantly lower than that of the three elements of the intershrub zone, which were examined (flock trampling routes, rock fragment clusters, and the remainder of the intershrub), for both sampling depths examined (0–2 and 5–10 cm). For the shallower sampling depth (summer sampling), soil bulk density at the shrub patch was 1·42 g cm^{-3} and ranged from 1·49 to 1·57 g cm^{-3} for the above three intershrub cover elements. The organic carbon content of the soil was significantly higher for the shrub patch (28·7 g kg^{-1}) than for the intershrub elements (16·6–21·8 g kg^{-1}; 0–2 cm sampling depth; summer). The effect of cover element on the aggregate size distribution of the soil depended on factors such as sampling season, hillside aspect, and animal presence. Overall, content of the >8000 μm fraction tended to be lowest, and content of the 1000–5000 μm fraction tended to be highest, at the shrub patch.

Study organism

S. spinosum (L.) Spach (Rosaceae) is a dwarf shrub, dominant in the eastern Mediterranean shrublands (Litav and Orshan, 1971); it forms monospecific patches that contain one or several individual shrubs (Reisman-Berman *et al.*, 2006), and the process of patch formation has been studied by several authors (Litav and Orshan, 1971; Seligman and Henkin, 2000; Perevolotsky *et al.*, 2001; Reisman-Berman, 2004). The process is initiated by the germination of *S. spinosum* seeds. However, their development is suppressed by shade and they compete poorly with herbaceous vegetation. Seedlings of *S. spinosum* suffer high mortality (up to 90%) in the first year, but almost no mortality between the second and eighth year. Between the first and second year, the seedlings barely increase their shoot biomass, and most of their growth is allocated to the root system, especially to the taproot. This strategy presumably enables the plant to access soil moisture deeper in the ground, which is available for longer periods. After 5 years, *S. spinosum* grows adventitious roots that can disconnect and become separate shrubs. It has been suggested that at this stage the shrub starts to modify its environment (Reisman-Berman, 2004). Estimation of the longevity of clonal shrubs is difficult since the ramet that founded the patch might have disappeared, leaving a new, genetically identical younger ramet. In other words, the patch persists even though there is turnover of the ramets (Reisman-Berman *et al.*, 2006). The oldest *S. spinosum* ramet reported was 34 years (Seligman and Henkin, 2003). A mature patch of *S. spinosum* forms a slight mound under its canopy (Stavi *et al.*, 2008).

S. spinosum patches are prone to disturbances, mainly browsing by domestic animals and canopy removal for firewood. In the Mediterranean rangelands, *S. spinosum* recovers mostly by re-sprouting and vegetative regeneration after a disturbance such as removal of the above-ground canopy or fire (Litav and Orshan, 1971; Perevolotsky *et al.*, 2001).

Experimental design

We conducted two experiments: (1) irrigation of *S. spinosum* patches in order to understand the relationships among rainfall, *S. spinosum* as an ecosystem engineer, and soil moisture; and (2) canopy removal from *S. spinosum* patches in order to monitor their recovery. The patches used in each of the experiments comprised several individuals that formed a continuous canopy (Reisman-Berman, 2004).

Experiment 1: simulated rainfall

Ten similar, mature patches of *S. spinosum*, of approximately 70 × 70 cm^2 in size and surrounded by an open intershrub area at least 60 cm in width, were randomly selected along the shoulder of a northwest-facing hillside. Areas of 1 m^2, each centred on one of these shrub patches, were delineated as the experimental plots. The 10 plots were randomly allocated to 2 treatments: 5 shrub patches were left intact (Intact treatment), and 5 had their canopies removed at ground level (Removed treatment). The shrub canopy in the Intact and Removed treatments covered most of the plot. In the vicinity of these plots, we delineated five additional plots of 1 m^2, each comprising an open intershrub patch covered with crusted soil (Crust treatment). The slope angle of each experimental plot was recorded.

The rainfall simulator described by Morin *et al.* (1967) was used to irrigate the plots. The advantage of this system is its ability to sprinkle a known quantity of rainfall without relying on the unpredictable natural rainfall. However, this system is limited to a small number of replicates due to high costs and time requirements. This tractor-mounted device is designed to deliver raindrops at a constant rate and of similar drop-size distribution to that of natural raindrops, i.e. 2·5 mm average diameter and kinetic energy delivery rate of 30 kJ m^{-2} min^{-1}. The simulator sprays water from a nozzle at a height of 2 m and distributes the drops homogeneously over an area of 2 m^2. Since this area is larger than that of the experimental plots, a 5-cm high concrete barrier was erected along the three upslope sides of the perimeter of the plots to prevent any inflow of runoff. A flume was constructed along the down-slope edge of each plot in order to collect any runoff generated within the plots. This liquid was pumped into bottles.

The plots were irrigated towards the end of the dry summer period, prior to the first winter rains, during 20–26 September 2005. There was a small but significant difference in gravimetric soil moisture content at the end of the dry summer period between the crust (1·9%) and under the shrub (3·9%) (Segoli, unpublished data). Each simulation lasted 30 min at a rainfall intensity of 40 mm h^{-1}. The runoff was collected and its volume recorded every minute.

Twenty-four hours after the plots were irrigated, three trenches were dug parallel to the direction of the runoff flow at distances of approximately 20, 50, and 80 cm from the side of the plot. A pickaxe and spade were used to excavate the soil, rocks, and stones. Roots were severed with cutters as needed. The trenches were at least 5 cm deeper than the depth of soil-moisture infiltration. The trenches were at least 15 cm wide and their sides were straightened with a spade. The moisture infiltration depth, which was readily visible, was recorded every 5 cm along each trench and was averaged for each trench.

The runoff samples were taken to the laboratory, dried at 105 °C, and the sediments were weighed to determine soil erosion. When runoff generation was small, the sediments collected during several 1-min intervals were pooled. Technical problems with the pump that collected the runoff forced us to exclude from the analysis one plot each of the Intact and the Removed treatments, and two plots of the Crust treatment.

Experiment 2: regrowth

An experimental plot of 1000 m^2 was established on each of four northwest-facing hillsides. Following a survey of the shrub patches, ten patches in each plot were randomly selected and their above-ground canopies were removed (canopy removal treatment) in December 2004. For each patch, two measurements were recorded: the number of *S. spinosum* individuals and their locations within the patch. An individual shrub was defined as a single stem or a cluster of stems that rose from the ground and was clearly separated from other stems. In addition, the shrub canopies were brought to the laboratory, dried, and weighed for biomass determination. After 1 year (in December 2005), the numbers of individuals that re-sprouted from the stems were recorded, and the number of new rhizome-sprouted individuals was recorded. The above-ground regrowth of each individual was removed and taken to the laboratory to be dried and weighed. The numbers of re-sprouting stems and rhizome-sprouting individuals were counted again in December 2006, 2 years after the initial cutting treatment and 1 year after the re-cutting.

Statistical analysis

The total volume of runoff generated (R_T), the volume of runoff during the last, i.e. 30th min of irrigation (R_{30}), and the total weight of soil eroded were subjected to one-way analysis of variance (ANOVA). The infiltration depth was subjected to a nested one-way ANOVA, with trench nested within plots. The means were separated with Tukey's Honestly Significant Difference test. To correct for non-homogeneity of variances, a reciprocal transformation was applied to the runoff and infiltration data and a logarithmic transformation was applied to the soil erosion data (Zar, 1999).

RESULTS

The average slope of the simulated rainfall plots was 13°, and there was no correlation between this and any of the other measurements that were recorded.

Simulated rainfall experiment

Runoff. In treatments Intact and Removed, runoff generation was low and constant throughout the 30-min experiment (Figure 1). However, in treatment Crust, runoff was low for the first 6 min and then increased in a curvilinear fashion. Of the total of 20 l of irrigation applied to each 1-m^2 patch, mean totals (± SD) of 0·17 ± 0·07, 0·44 ± 0·53, and 5·62 ± 1·54 l of runoff (including sediment) were recovered in treatments Intact, Removed, and Crust, respectively. ANOVA showed that treatment was a highly significant factor in the total volume of runoff (R_T) ($F_{(2,8)} = 11{\cdot}72$, $P = 0{\cdot}004$) and in the runoff volume generated during the last minute of the experiment (R_{30}) ($F_{(2,8)} = 54{\cdot}87$, $P < 0{\cdot}001$). There was no significant difference between treatments Intact and Removed for either R_T ($P = 0{\cdot}544$) or R_{30} ($P = 0{\cdot}861$), but both R_T and R_{30} were significantly ($P < 0{\cdot}01$ and $P < 0{\cdot}001$, respectively) greater for treatment Crust than for treatments Intact and Removed. Shrub size was similar in all Intact and Removed patches and no correlation was found between size of shrub patch and total runoff generated.

On average, about 30% of the rainfall was collected as runoff in treatment Crust which was almost 20 times more than in the treatments with *S. spinosum*. The observed difference in runoff between the Crust and Intact treatments was not unexpected, and was consistent with the source-sink relations attributed to intershrub and shrub patches of many semi-arid environments. However,

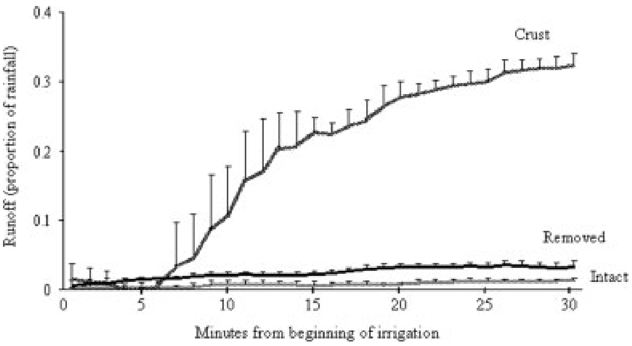

Figure 1. Runoff generated in the various treatments (Crust: intershrub crust without *S. spinosum*; Intact: intact *S. spinosum* patch; Removed: canopy-removed *S. spinosum* patch). Vertical bars denote the standard deviation of the mean.

the reasons for the lack of runoff from the canopy-removed patch are not trivial and will be discussed in the next section.

Water infiltration. A typical transect of water infiltration depth after rainfall simulation in the Intact treatment is shown in Figure 2. The waterfront outside the soil volume containing the main root system was shallow and horizontal, whereas within this volume it followed the root system profile. This pattern was not altered by the removal of the shrub canopy prior to the rainfall simulation (Removed treatment), whereas in the Crust treatment the entire front was shallow and horizontal.

The mean (± SD) water infiltration depths were 10·0 ± 3·2, 8·1 ± 1·8, and 5·5 ± 1·2 cm for treatments Intact, Removed, and Crust, respectively. ANOVA of water infiltration depth showed that treatment was a highly significant ($F_{(2,9)} = 81{\cdot}85$, $P < 0{\cdot}001$) factor. The water infiltration depth was shallower in the Crust treatment than in the Intact and Removed treatments ($P < 0{\cdot}001$, $P < 0{\cdot}001$, respectively), and the latter two treatments did not differ significantly ($P = 0{\cdot}43$) (Figure 3).

As might be expected, opposite rankings of the three treatments with respect to water infiltration and runoff were found (Figures 1, 3); when more runoff is generated, there is less water left to infiltrate into the soil. Areas containing intact or canopy-removed shrubs acted as sinks for water, whereas those covered by crusts acted as sources.

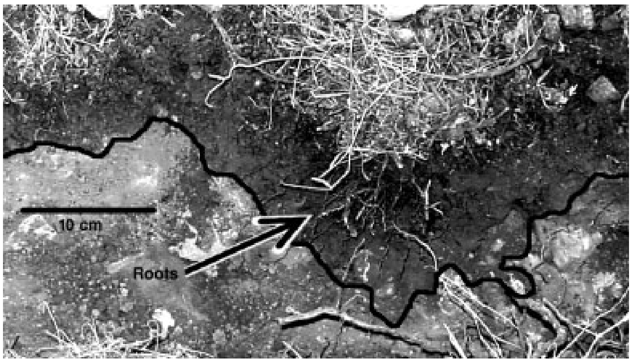

Figure 2. Side view photograph of a trench dug in an Intact treatment plot showing the depth of water infiltration (irregular black line) after rainfall simulation. The deepest infiltration of soil moisture is under the root system of *S. spinosum*.

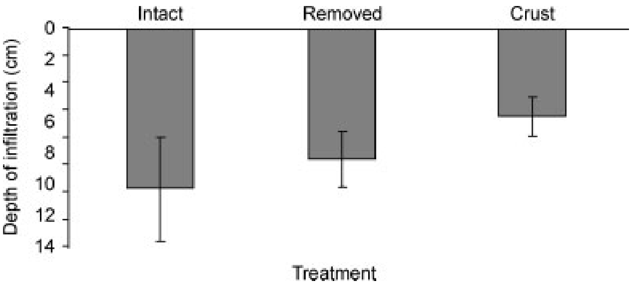

Figure 3. Infiltration depth of soil moisture into the soil after 30 min of rainfall simulation in the three treatments (Crust: intershrub crust without *S. spinosum*; Intact: intact *S. spinosum* patch; Removed: canopy-removed *S. spinosum* patch). Vertical bars denote the standard deviation of the mean.

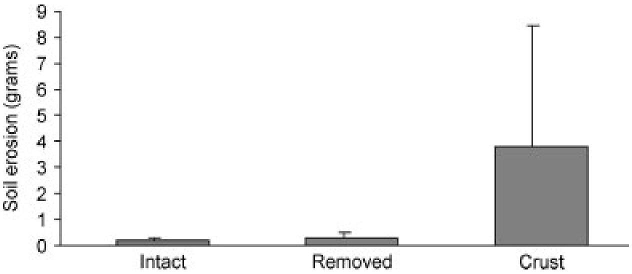

Figure 4. Total soil erosion (in grams) collected during the rainfall simulation in the three treatments (Crust: intershrub crust without *S. spinosum*; Intact: intact *S. spinosum* patch; Removed: canopy-removed *S. spinosum* patch). Vertical bars denote the standard deviation of the mean.

Soil erosion. The mean (±SD) total masses of soil recovered from 1-m^2 patches were 0·21 ± 0·09, 0·56 ± 0·61, and 3·83 ± 4·64 g, in treatments Intact, Removed, and Crust, respectively. ANOVA showed that treatment was a significant ($F_{(2,8)} = 7{\cdot}12$, $P = 0{\cdot}017$) factor in total soil erosion. The Crust treatment resulted in more soil erosion than the Intact and Removed treatments ($P = 0{\cdot}02$, $P = 0{\cdot}03$, respectively), but there was no significant ($P = 0{\cdot}95$) difference between the quantities of soil eroded in the latter two treatments (Figure 4).

Regrowth experiment

The average (± SD) number of *S. spinosum* individuals per patch at the time of canopy removal was 14 ± 6, and the dry matter biomass of the canopy of the whole patch was 1748 ± 536 g. After 1 year, over 50% of individuals re-sprouted from the stem, and an additional 18% of the original individuals sprouted from the rhizome (Figure 5). This regrowth constituted 4·9 ± 3·33% and 3·23 ± 1·75% of the original canopy biomass within 1 year of the first and second removals, respectively.

Although anthropogenic canopy removal usually occurs at intervals of many years since they are not re-cut until they are large enough to be useful, we found similar trends after the second consecutive year of canopy removal (Figure 5). The number of individuals that re-sprouted from the rhizome did not differ significantly between the years (separate variance *t*-test:

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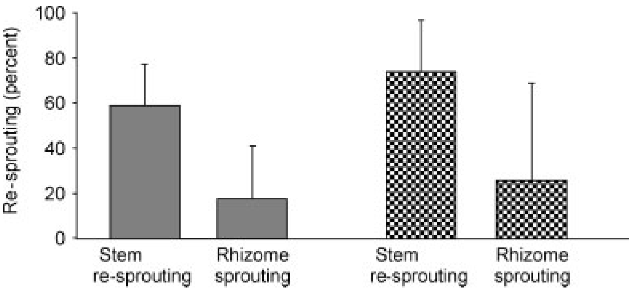

Figure 5. Percentages of initial numbers of individuals that showed stem re-sprouting and rhizome sprouting 1 year after the initial canopy removal (solid), and 1 year after the re-cutting (checkered). Vertical bars show the standard deviation of the mean.

$t_{(43\cdot47)} = -0\cdot92$, $P = 0\cdot36$). Re-sprouting from the stem was significantly greater following the second removal than the first ($t_{(68)} = -3\cdot11$, $P < 0\cdot01$).

DISCUSSION

A better understanding of the drivers of state transition in ecosystems is a focus of current ecological studies; it is especially important where human disturbances cause a transition from desirable to undesirable ecological states (Lechmere-Oertel *et al*., 2005). Desertification is a state transition from a functional to a dysfunctional landscape, from the human perspective (Hellden, 1988). It has been suggested by Schlesinger *et al.* (1990) that grazing can cause a semi-arid ecosystem to undergo a deterioratory shift from grassland to shrubland. Thus, the current state of the shrubland studied here could be interpreted as degraded relative to a natural, undisturbed grassland. But it is certainly less degraded than a desertified system of homogeneous crust, and the two-phase mosaic is the desirable state compared to the homogeneous crusted state. Many semi-arid shrublands show state transitions from functional to desertified structures, which involve changes from a two-phase mosaic composed of woody and open patches to a homogeneous crusted surface (Shachak *et al*., 1998). This transition results in water, soil, and nutrient losses that exacerbate aridity (Lechmere-Oertel *et al*., 2005).

The causes of state changes in semi-arid shrublands and their consequences in terms of ecosystem processes are known (Whitford, 2002). However, we still lack understanding of the factors associated with system resilience to state changes. Resilience is a feature of stability normally associated with the rate of decay of a perturbation within a system and the time needed for components to return to their original state (Deangelis *et al*., 1989; Neubert and Caswell, 1997). In a two-phase mosaic, resilience is the time shrub patches need to restore the landscape mosaic after disturbances such as browsing, biomass removal, or fire.

We selected a resilient semi-arid shrubland dominated by *S. spinosum*, which has persisted in a two-phase mosaic state in spite of several thousand years of human disturbances (Perevolotsky and Seligman, 1998). This selection was expected to provide insight into the relationships between shrub traits and system resilience. We hypothesized that the restoration of the structure and function of *S. spinosum* progresses faster than the change of the system to a homogeneous crusted state. Our results suggest that two traits of *S. spinosum*—engineering of the soil environment and regrowth from cut stems or by rhizome sprouting—maintain the two-phase mosaic after disturbances.

Ecosystem engineering and resilience

The rain-simulation experiment demonstrated the ability of *S. spinosum* to accumulate water and reduce runoff. The accumulation of water could not be attributed to plant–soil hydraulic pressure gradients induced by the root system, because of the short time interval between irrigation and measurement of the soil-moisture depth. Nor, it should be stressed, could it be attributed to some direct effect of the shrub canopy, because no difference was found between intact shrub patches and those that had their canopies removed, in their ability to accumulate water. However, there was a small trend of deeper infiltration under the Intact treatment compared to the Removed treatment, which could indicate a small stem-flow effect. The fact that shrub patches with intact and removed canopies showed similar hydrological patterns suggests that infiltration processes are primarily related to the effects of the root system on soil structure. We suggest that the ability of the soil under the shrub patch to absorb almost all the water that reaches it arises from modulation of the soil structure by the shrub. This is supported by other research at the study site, which found lower soil penetration resistance and lower bulk density under the shrub compared to the crust patches (Stavi, 2008; Stavi *et al*., 2008) Such soil properties under the shrub are expected to increase water infiltration (Hillel, 2004).

Physical state modulation is a trait of organisms that function as ecosystem engineers (Jones *et al*., 1994, 1997). We hypothesize that *S. spinosum* acts as an ecosystem engineer by enabling the accumulation of water and, with that water, soil and nutrients. This engineering conserves these resources and prevents their leakage from the system. Thus *S. spinosum*, in its function as an ecosystem engineer, plays a central role in conserving water in a two-phase mosaic landscape.

In addition, our experiments showed that runoff carries more soil particles from the crust than from the shrub patches and, therefore, we would expect soil particles to be deposited under the shrub (Shachak and Lovett, 1998). Since soil particles contain nutrients, this process of accretion also accumulates nutrients under the shrub. The loose soil and nutrients that are deposited under the shrub further increase soil-water infiltration.

In addition to conserving resources at the landscape scale, the engineering effects of *S. spinosum* create a strong contrast in soil-moisture content between the components of the two-phase mosaic: shrub patches and crusted intershrub patches. The resulting spatial heterogeneity sustains a greater species richness and higher biomass across the landscape than would be the case if resources were spread homogeneously (Noy-Meir, 1973).

Our present experiment was carried out on the patch scale. However, in the light of a recent mathematical model of shrubs as ecosystem engineers (Gilad *et al*., 2004, 2007), we can further extrapolate the function of *S. spinosum* to the landscape level. The model predicts that in water-limited systems positive feedbacks between water and biomass result in resource accumulation under the shrubs, and self-organization of the woody vegetation into patterns such as spots, bands, labyrinths, and holes. Our empirical field study helps to translate the abstract mathematical representation of a positive feedback loop into a physical and measurable entity. We suggest that modulation of the soil by the enhancement of macroporosity drives a positive feedback between *S. spinosum* and water: As macropores are formed, water accumulates and thereby enhances biomass growth which, in turn, increases macropore density. We further suggest that at the landscape level the configuration of *S. spinosum* in the form of vegetation patterns is a fundamental aspect of resource conservation in the two-phase mosaic. We see two emergent properties driven by *S. spinosum* in its role as an ecosystem engineer. The first is soil-moisture heterogeneity at the patch level, i.e. water-enriched shrub patches contrasted with water-deprived crust patches. The second is the vegetation pattern on the landscape level, which preserves resources and prevents their leakage.

Regrowth and resilience

Resilience of a two-phase shrubland mosaic is related to the rate at which the shrub recovers from perturbations and resumes its function as a patch that accumulates and conserves resources. The time needed to return from disturbance to full functionality must be shorter than the time it takes for cyanobacteria and mosses to colonize a disturbed shrub patch (Oren, 2001). Our regrowth experiment with *S. spinosum* showed that two attributes promote a short return time: biomass regrowth from the stems and rhizome sprouting. After 1 year, over 50% of *S. spinosum* individuals regrew, an additional 18% exhibited rhizome sprouting, and about 5% of the original biomass regenerated. After a severe disturbance represented by 2 consecutive years of cutting, 41% of the individuals survived and 26% of the rhizomes sprouted.

Semi-arid woody species can be characterized, according to their response to disturbances, either as re-sprouters or as non-re-sprouters that re-establish from seed (Vesk *et al*., 2004). Hodgkinson (1998) found that re-sprouters survived a disturbance such as fire, whereas non-re-sprouters did not. Shrubs that are re-sprouters have long life spans (Bond and Midgley, 2001), and their populations can tolerate long periods without recruitment. In addition, their return time to pre-disturbance conditions is shorter than that of non-re-sprouters (Calvo *et al*., 2002). There is probably a trade-off between allocating energy and nutrients for bud production, which enables re-sprouting on the one hand and other types of biomass production on the other. However, allocation to bud production for re-sprouting is advantageous in disturbed environments, where re-establishment from seed is a slow process (Vesk and Westoby, 2004). In the case of *S. spinosum*, the probability of recovery and patch re-establishment by re-sprouting is high because patches are usually composed of several individuals (Reisman-Berman, 2004). We found that a typical *S. spinosum* patch contains an average of 14 ± 6 individuals. Rapid regrowth of several individual shrubs after removal of the above-ground canopy enables the shrub patch to recover from the disturbance without 'losing' its pre-disturbance, engineering-modified soil environment. Furthermore, such a soil environment enhances regrowth by increasing the availability of water for re-sprouting and biomass production.

S. spinosum exhibits a set of traits of stable patches that accumulate resources and prevent their leakage from the landscape. The patches persist through time, despite disturbances and continuous turnover of individual plants. The life span of *S. spinosum* individuals is about 25 years, whereas *S. spinosum* patches may persist for hundreds of years (Reisman-Berman, 2004). This phenomenon maintains the stability of the two-phase mosaic in spite of individual turnover. The properties of *S. spinosum* as an ecosystem engineer, in conjunction with its recovery-enhancing trait of re-sprouting of several individuals within a patch, promote system resilience. This prevents a transition from a two-phase mosaic to a dysfunctional landscape, which may lead to desertification.

Shrub traits and resilience

Knowledge of the traits of *S. spinosum* provides insight into the processes necessary to develop and maintain a functional semi-arid landscape in the face of disturbances. Development of such a functional landscape implies development of a two-phase mosaic comprising resource-enriched shrub patches and open patches which together prevent leakage of resources from the ecosystem (Aguiar and Sala, 1999). During ecosystem development, the transition from a homogeneous landscape to a two-phase mosaic is accompanied by changes in the flow of water, soil, and nutrients, and resource accumulation. *S. spinosum* changes resource flow by modulating soil hydraulic properties and shortening the flow distance. This ecosystem engineering is beneficial to *S. spinosum* as well as to other plant species that utilize the resources available in the enriched patch (Arnon, 2005). Generalization from the *S. spinosum* case study implies that modulation of the environment by shrubs that change the flow of resources and conserve them is essential for the functioning of a two-phase mosaic. Mathematical modelling of the development of a two-phase mosaic through vegetation pattern formation also shows that changes in water infiltration caused by biomass patches constitute a key factor that leads to local accumulation of soil moisture under and around biomass patches (Gilad *et al.*, 2004, 2007). The general conclusion is that for a transition from a leaky one-phase state consisting of crusted soil to a state that conserves resources, shrubs should possess ecosystem engineering traits that enable them to accumulate resources by modulating their immediate environment. However, development of a two-phase mosaic by a shrub does not ensure shrub-patch stability. Resilience of a two-phase mosaic depends on the sustainability of the shrub patch, i.e. its ability to persist and to retain its functionality in the face of individual shrub mortality and disturbances. It is difficult to attain shrub-patch sustainability, because semi-arid shrublands exhibit co-existence of two stable states (Gunderson *et al.*, 2002). One of these—a one-phase system—develops when the entire soil surface is covered with biotic crust whose properties entail low productivity and diversity, and high leakage of resources. The other is a two-phase mosaic of shrub patches and crust patches whose properties entail relatively high productivity and diversity and low leakage of resources from the landscape. In semi-arid shrublands, humans should aim at maintaining a two-phase mosaic in order to conserve soil, water, and nutrients.

In *S. spinosum* the recovery-promoting attributes of maintaining patch hydraulic properties in conjunction with re-sprouting enables it to overcome three main types of disturbance—browsing, canopy removal, and fire—and may account for the large areas covered by this species. Because of the many types and unpredictable nature of disturbances in semi-arid shrublands, shrubs require a diversity of traits to cope with disturbed conditions (Williams and Saunders, 2005). We suggest that the main such traits are engineering-capability properties related to resource accumulation, and biological properties that enable recovery.

There are areas of the Negev Desert where the dominant shrubs accumulate water and nutrients, but do not regrow after canopy removal (Shachak *et al.*, 1998; Oren, 2001). These areas are prone to desertification (Shachak *et al.*, 1998). Our study area is more resistant to desertification because of water accumulation and regrowth of *S. spinosum*. This indicates that both water accumulation and regrowth are needed for system resilience and maintenance of a functional ecosystem.

Implications for management

In general, management, in order to achieve the desired landscape state, presents a major challenge (Grumbine, 1994). However, in the case of a two-phase mosaic, the desired stable state is recognizable and manageable: Management must aim to preserve or restore the shrub component of the system. Dysfunctional shrublands may not necessarily return spontaneously to their desired two-phase mosaic state, because both the desirable and undesirable states are stable (Meron *et al.*, 2004). In a system based on shrubs that exhibit properties like those of *S. spinosum*, the system itself can switch from a homogeneous to a two-phase state. However, where the shrubs do not have the necessary traits, management intervention is essential (Shachak *et al.*, 1998). As a substitute for the trait of water accumulation, humans can dig furrows that prevent leakage from the system (Boeken and Shachak, 1994) and in the absence of re-sprouting, they can sow seeds to enhance regrowth.

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