

Untangling the positive and negative effects of shrubs on herbaceous vegetation in drylands

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Abstract Woody vegetation, as an ecosystem engineer, can modulate the landscape such that the levels of resources in its vicinity undergo positive and negative changes as far as the herbaceous vegetation is concerned. To better understand how these processes play out in a semi-arid ecosystem, we examined resource modulation by woody vegetation, and the response of herbaceous vegetation to that modulation, at a fine spatial scale. Experimental manipulations were employed to separate the positive and negative effects of water, light and seed dispersal in determining herbaceous species density and biomass in three

patch types within and adjacent to the shrub (core, periphery and open). We synthesized our results into a multilayered landscape diversity (MLLD) model. Woody vegetation creates distinct multilayered resource patches at its core and periphery which do not correspond to the dichotomous structural pattern of shrub canopy versus intershrub background. The combined effect of these multilayered resource patches had higher herbaceous species density (8.2 vs. 4.0 species 400 cm^{-2}) and herbaceous biomass (5.4 vs. 1.0 g 400 cm^{-2}) in the periphery than in the core (3-yr averages). The periphery's net positive effects are due to enhancement of soil properties (water infiltration depth of 11.1 cm at periphery vs. 8.1 cm at core), while the core's net negative effects are due to modulation of seed (seed abundance per seed trap of 44.2 at periphery vs. 3.0 at core) and light availability (PAR transmittance of 41.9 % at periphery vs. 16.5 % at core) by the shrub canopy. Thus, when examined at this fine spatial resolution, woody vegetation has both net positive and net negative effects on herbaceous vegetation. Analysis of our results by means of the MLLD model emphasizes the importance of examining the landscape at the spatial scale of the modulated resources and of recognizing different patch types and their differing effects on herbaceous vegetation.

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Introduction

Ecological studies have placed much emphasis on the effects of the environment on organisms; less emphasis has been placed on that of organisms on the environment (Wright and Jones 2006). Our understanding of the role of organisms in modulating their environment has been significantly advanced by recently introduced concepts, field studies and models; and especially by the influential concept of ecosystem engineers (Jones et al. 1994, 1997; Odling-Smee 1988; Wright and Jones 2006). Ecosystem engineers are organisms that modulate the availability of resources to other species by causing state changes in biotic or abiotic materials (Jones et al. 1994). Ecosystem engineers that modify the landscape by the processes of patch formation are defined as landscape modulators (Shachak et al. 2008).

Woody vegetation is a primary landscape modulator in terrestrial ecosystems (Callaway 1995); its presence often creates a two-phase mosaic of woody and open patches (Charley and West 1975; Aguiar and Sala 1999). Such mosaics cover about 40 % of terrestrial ecosystems (House et al. 2003) and therefore have significant environmental impacts (Perry 1998) by altering landscape diversity (Tongway and Valentin 2001) and species diversity (Maestre and Cortina 2005). In its role as a landscape modulator, woody vegetation modulates many resources differentially (Shachak et al. 2008), increasing levels of some while decreasing those of others, and thereby giving rise to a greatly modified pattern of resource patchiness (Wu et al. 1985; Gilad et al. 2007; Segoli et al. 2012). These different levels of resources can be conceptualized as multiple layers of resources that control the species assemblage and performance of herbaceous vegetation (Shachak et al. 2008).

It has been shown that the spatial extent of modulation can differ among resources modulated by the same organism (Callaway 1995; Moro et al. 1997; Drezner 2006; Caballero et al. 2008; Teste and Simard 2008; Bertiller et al. 2009; Yang et al. 2010; Segoli et al. 2012). Thus a single landscape modulator can simultaneously exert both positive and negative net effects on herbaceous vegetation at different spatial locations (Shmida and Whittaker 1981; Moro et al. 1997; Drezner 2006; Caballero et al. 2008; Teste and Simard 2008; Bertiller et al. 2009). However, manipulative experiments that create novel

combinations of resources in order to test mechanistic links between explanatory and response variables are rare (Ries et al. 2004; Barbier et al. 2008).

The present study was conducted at a semi-arid site of Israel, where the dominant shrub *Sarcopoterium spinosum* has a positive effect on its seedlings via water enrichment and negative effects via competition for light (Reisman-Berman 2007). However, *S. spinosum* dominance is attributed to its clonal reproduction ability (Reisman-Berman and Henkin 2007; Segoli et al. 2008). Our focus was on the effects that *S. spinosum* patches have on herbaceous vegetation, and at a fine spatial scale. We asked whether positive and negative effects have the same spatial extent or whether opposing modulated resources have different spatial extents, which can cause net positive effects in one location and net negative effects in another location. By combining observations and experimental manipulations, we examined the extent and magnitude of the effects of shrubs on water, light and seeds, and how these changes determine herbaceous species density and biomass.

We tested three hypotheses regarding the effects of woody vegetation on resources and herbaceous vegetation in the semi-arid ecosystem. (1) The spatial extent and magnitude of landscape modulation by *S. spinosum* will differ among various resources, creating distinct patch types with different resource combinations. (2) The specific combination of resources will determine the herbaceous species density and biomass. (3) Canopy removal will reduce the spatial extent and magnitude of landscape modulation by *S. spinosum* and consequently will affect the herbaceous vegetation.

Materials and methods

Study area

The various experiments described below were all conducted in the same study area, located in the northern Negev of Israel (31°21'52"N, 34°49'46"E), at the Lehavim LTER and Bedouin Demonstration Farm (350–500 m a.s.l, on limestone and chalk substrate). Average annual precipitation is about 300 mm, with a range of 78–540 mm (1953–2007). Precipitation occurs mostly from December to March. Average daily temperatures range from 10 °C in winter to

25 °C in summer (Baram 1996). The landscape is a shrubland organized spatially as a two-phase mosaic of shrub and open soil patches. Various shrub species are present, of which *S. spinosum* is by far the most prevalent. There is a diverse community of herbaceous species (mainly annuals), which persist for 3–5 months after the first rains, depending on the amount and distribution of the precipitation (Giladi et al. 2007). This region has been subjected to domestic grazing (mainly by sheep and goats) for thousands of years (Perevolotsky and Seligman 1998). Since the research station was established in 1980, the area has been grazed by flocks of approximately 800 Awassi sheep and 200 Mamber goats.

Study organism

Sarcopoterium spinosum (L.) Spach (Rosaceae) was the focal woody species in each experiment. This is a dwarf shrub, dominant in the eastern Mediterranean shrublands (Litav and Orshan 1971), that forms monospecific patches that contain one or several individual shrubs (Reisman-Berman et al. 2006). The process of patch formation has been intensively studied (Litav and Orshan 1971; Seligman and Henkin 2000; Perevolotsky et al. 2001; Reisman-Berman 2004; Reisman-Berman and Henkin 2007; Segoli et al. 2008). *S. spinosum* patches are prone to disturbances, mainly through browsing by domestic animals and canopy removal for firewood. In the Mediterranean rangelands, *S. spinosum* recovers from such disturbances 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; Segoli et al. 2008).

Patch types

Based on Arnon et al. (2007), we defined three patch types in each experiment. Two of these patch types were associated with the shrub patches: the core, whose boundary was a line 10 cm inside the canopy drip line; and the periphery, which was a 20-cm-wide strip extending from 10 cm inside the canopy drip line to 10 cm outside it. The third patch type was the open, defined as an intershrub matrix with boundaries no closer than 10 cm from a canopy drip line.

Water infiltration

In this first experiment, we reanalyzed the infiltration data of Segoli et al. (2008) in order to differentiate between core and periphery with respect to water conditions. Briefly, runoff, soil erosion and water infiltration depth were determined for intershrub patches, intact shrub patches, and canopy-removed shrub patches in a rainfall simulator experiment conducted in September 2005. There were five replicates for each patch type. A rainfall intensity of 40 mm h⁻¹ was applied for 30 min. Twenty-four hours after the plots were irrigated, three trenches were dug parallel to the direction of the runoff flow in each patch. The trenches were at least 5 cm deeper than the depth of soil-moisture infiltration. The moisture infiltration depth, which was readily visible, was recorded every 5 cm along each trench. In the current analysis we subdivided the infiltration depth that was recorded in the dug trenches, into core and upslope periphery. We present the original results of the open patch for reference.

Photosynthetically active radiation (PAR)

In this second experiment, the PAR near ground level was measured and compared between the three patch types. We used a portable Radiation Ceptometer (SunLink, Decagon Devices, Inc., Pullman, WA, USA). Measurements were conducted once a month, from November 2006 through April 2007, with three measurement periods on each day of measurements: morning (10:00–11:00), midday (12:30–13:30) and afternoon (14:30–15:30). During each measurement period PAR was measured at five patches of *S. spinosum* with intact canopy. There were four measurements per patch, one per each cardinal direction. For each measurement, the probe was partially inserted under the shrub canopy, close to ground level and spanning the three patch types. The length of insertion varied somewhat with the dimensions of the shrub and was recorded. Reference measurements were interspersed among the patch measurements with the probe held approximately 1 m above ground level. For each patch measurement, the PAR recorded by each sensor of the probe was converted to transmittance by dividing it by the mean entire-probe PAR of the reference measurement that was closest in time.

Seed dispersal

It has been shown that the canopy of *S. spinosum* acts as a barrier that reduces the seed rain arriving at the core below that arriving at the open (Giladi et al. 2007). In addition, it was found that seed rain in the core of shrubs whose canopy had been removed was higher than that in the core of intact shrubs (Giladi et al. 2007). In this third experiment, we tested the effect of the canopy of *S. spinosum* on seed dispersal, while eliminating local within-patch seed production and taking into account short-range dispersal. Ten mature *S. spinosum* patches were randomly chosen, and an open patch of matching size was designated adjacent to each shrub patch. In order to eliminate local within-patch dispersal we removed all seed-producing vegetation beneath and 30 cm beyond the shrub canopies, and from areas of similar dimensions in the open patches. One seed trap was placed in the core of each shrub patch and a second in its east-facing periphery. Correspondingly, one seed trap was placed in the center of each open patch and a second near its edge. Each seed trap consisted of a 9-cm-diameter Petri dish filled with fine sand and embedded in the soil with its rim at ground level (Giladi et al. 2007). Seeds were collected twice a month between May and November 2007. At each collection date the sand from each trap was sifted through a 560- μm sieve, the seeds and dispersal units were bagged, and the sand was returned immediately to the Petri dish. The material collected from the seed traps was brought to the laboratory and identified under a microscope. Seed abundance data (excluding *S. spinosum* seeds) were accumulated across all dates for each seed trap.

Herbaceous vegetation

In this fourth experiment, we chose four west-facing slopes in November 2004 and on each slope established four adjacent plots, each of 1,000 m². Plot dimensions were (25 × 40 m) or (20 × 50 m), with the long side oriented perpendicular to the contours of the hillside. Two plots in each slope were randomly allocated to an intact canopy treatment and two to a canopy removed treatment. In December 2004 (following the marking of focal patches as described below) the entire canopies of all shrubs in the plots designated for canopy removal were cut near ground level and removed from the plot. This time of year

follows seed dispersal of the previous growing season, and precedes herbaceous growth of the next one. Regrowth from these shrubs was cut in December of 2005 and of 2006. The cutting of the regrowth eliminated the shade and seed barrier effects of the shrub canopy.

In each of the experimental plots 15–20 mature patches of *S. spinosum* with closed canopies measuring at least 60 cm in diameter were randomly chosen and designated as focal patches. Such patches usually contained more than one *S. spinosum* individual (Reisman-Berman 2004; Segoli et al. 2008). A similar number of open (intershrub) patches were randomly chosen in each plot, and designated as focal open; they varied in size, according to the patterns of woody vegetation, but were at least 70 cm in diameter. The locations of the focal shrub and focal open patches were mapped and marked in the field prior to any manipulation, based on the canopy drip lines of the focal shrubs and the borders of the focal open patches. Once delineated, the original boundary of each focal patch was used to define that patch for the duration of the experiment.

In order to provide a quantitative estimate of the landscape-level extent of the three patch types, a GIS-based analysis was conducted of an orthophoto image of one of the 1,000-m² experimental plots. Following separation of woody and non-woody cover, a 20-cm buffer, centered on the boundary of each patch, was created to represent the periphery. The relative cover of the three patch types was found to be 40 % for core, 30 % for periphery, and 30 % for open.

Herbaceous vegetation sampling

The herbaceous vegetation was characterized in terms of standing aboveground biomass and number of species per sampling unit. We refer to the latter as species density based on the terminology of Gotelli and Colwell (2001) and Magurran (2005). Herbaceous biomass and species density were sampled in the core, open and periphery sections of the focal patches during the peak growing seasons (March–April) of 2005, 2006 and 2007. For both measures, randomly placed sampling quadrats of (20 × 20 cm) were used in the core and open patch types, and quadrats of (10 × 40 cm) in the periphery. Herbaceous biomass was sampled separately at the peak of the growing season: all standing herbaceous biomass in the

biomass sampling quadrats was cut with scissors and bagged, and the location was marked to avoid re-sampling in subsequent years. Cut material was dried at 60 °C for 24 h and weighed. Herbaceous species density—the number of herbaceous species per quadrat (400 cm²)—was determined by recording all plants at the species level (Feinbrun-Dothan et al. 1991). The numbers of sampled quadrats are given in Table S1 (Supplementary material).

In order to differentiate between shade and other effects of the shrub canopy, we erected one shade net in each of the eight removed canopy plots. Each net covered a (1 × 2 m) area containing three adjacent patch types: core, periphery and open. The nets intercepted approximately 90 % of the incident PAR, similar to values measured under the canopy of *S. spinosum* in the study area (Reisman-Berman 2007). The shade nets were erected during 2005—after seed dispersal from herbaceous vegetation produced in the 2004 season and before the start of the 2006 herbaceous growing season. Herbaceous species density and biomass were sampled as described above during the peak growing season (March) of 2006. The numbers of sampled quadrats are given in Table S1 (Supplementary material).

Statistical analysis

Results of the water infiltration depth experiment were subjected to a nested two-way ANOVA. In the radiation experiment, the PAR data were averaged for each patch type in the various shrub patches, with time of day, month and cardinal direction pooled, and were subjected to one-way ANOVA. For the seed dispersal experiment, seed abundance data were subjected to the unequal variance *t* test, because of violation of homoscedasticity (Zar 1999). Biomass and species density data from the herbaceous vegetation experiment were subjected to two-way ANOVA (adjusted for unequal sample sizes, where appropriate). Shade net was considered as an additional canopy removal treatment in the second season. Tukey–Kramer hsd tests were used for post hoc comparisons. When data violated ANOVA assumptions, an appropriate transformation was applied to the data (Conover and Iman 1981; Zar 1999). All statistical analyses were conducted with the STATISTICA 7.0 software (StatSoft Inc., Tulsa, OK, USA).

Results

Water infiltration

Removal treatment and patch type (core and periphery) showed no significant effect on water infiltration depth (two-way ANOVA; $F_{(1, 16)} = 1.79$, $P = 0.200$; two-way ANOVA; $F_{(1, 16)} = 0.09$, $P = 0.771$; respectively). However, there was a slight trend towards deeper infiltration depth in the intact periphery than in the intact core (Fig. 1).

Photosynthetically active radiation (PAR)

Patch type had significant effects on PAR (one-way ANOVA; $F_{(2,21)} = 83.53$, $P < 0.001$): PAR differed significantly among the three patch types and was ranked in descending order, open > periphery > core (Fig. 2).

Seed dispersal

The shrub canopy affected seed abundance (Fig. 3), which was significantly lower in the core than in the periphery of the shrub patch but not in the corresponding locations in the open patch (*t* test with unequal variances; $t_{(9,10)} = 4.62$, $P = 0.001$; *t* test with unequal variances; $t_{(9,96)} = 1.82$, $P = 0.099$; respectively). The core had significantly lower seed abundance than the corresponding location in the open patch but there was no significant difference between seed abundance in the periphery and its corresponding location in the open patch (*t* test with unequal

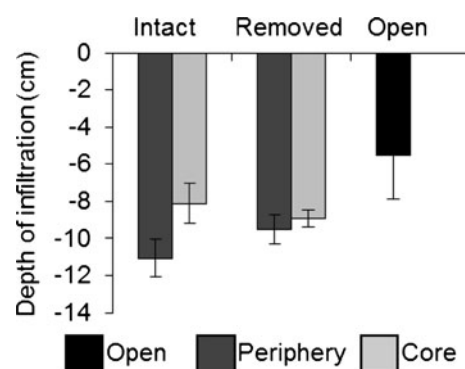


Fig. 1 Water infiltration depth into the soil after 30-minute rainfall simulation in the various treatments and patch types. Original open patch values are given for reference (Segoli et al. 2008). Data are represented as means \pm SE

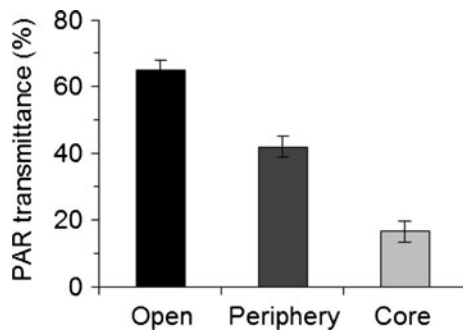


Fig. 2 Percentage transmittance of photosynthetically active radiation (PAR) in the various patch types. Data are represented as means \pm SE

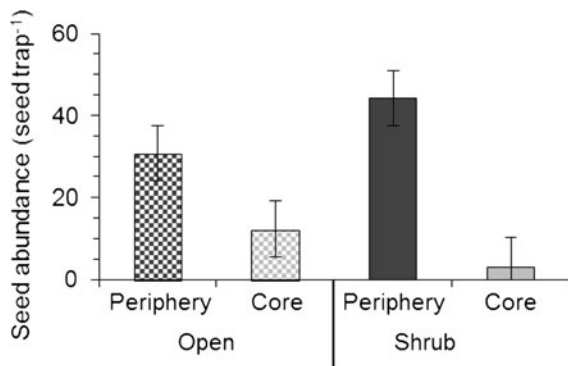


Fig. 3 Seed abundance during May–November 2007 in the periphery and core, and in the corresponding locations in the open patch (see text for details). Data are represented as means \pm SE

variances; $t_{(10,53)} = 3.93$, $P = 0.003$; t test; $t_{(18)} = -1.02$, $P = 0.322$; respectively).

Herbaceous vegetation biomass

In the first growing season following shrub canopy removal (2005), removal treatment, patch type and their interaction had significant effects on herbaceous vegetation biomass (“biomass” hereafter) (log-transformed data; two-way ANOVA; $F_{(1, 30)} = 22.57$, $P < 0.001$; $F_{(2, 30)} = 87.27$, $P < 0.001$; $F_{(2, 30)} = 3.75$, $P = 0.035$; respectively). For both the intact and removed treatments the periphery had significantly higher biomass than the open, which in turn had significantly higher biomass than the core in the intact

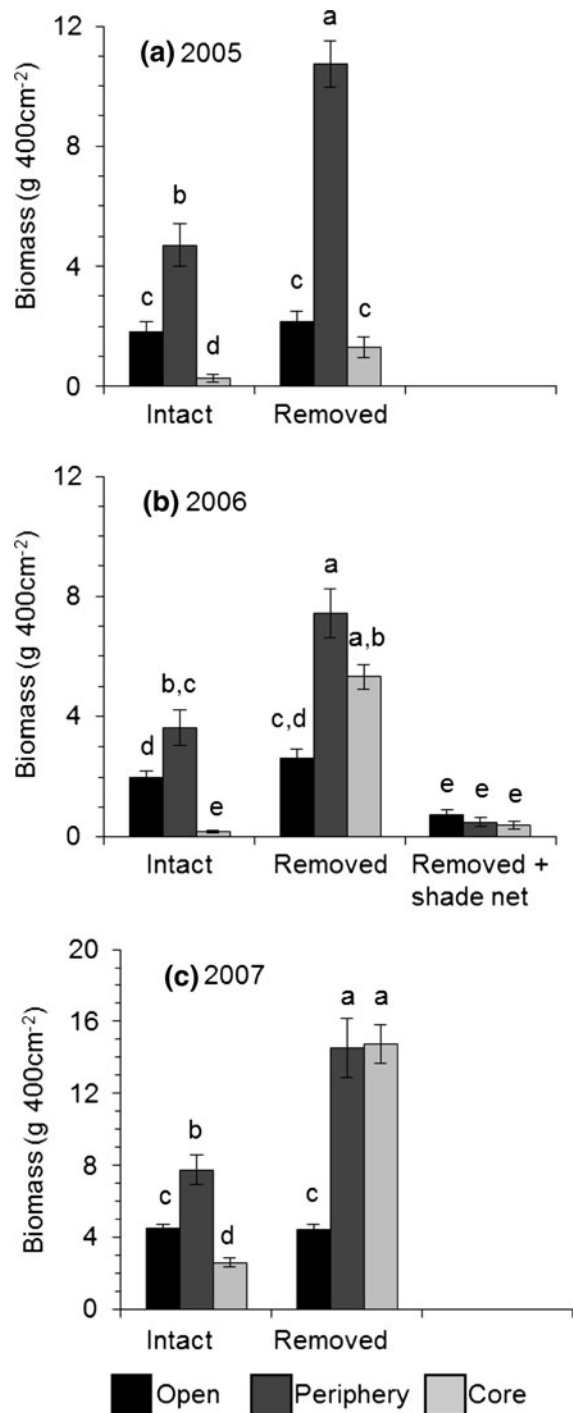


Fig. 4 Herbaceous biomass in the various treatments and patch types. Letters denote significant differences. Data are represented as means \pm SE

treatment (Fig. 4a). Removal of the canopy increased biomass in the core and periphery (Fig. 4a).

In the second growing season (2006), removal treatment, patch type and their interaction again had significant effects on biomass (rank transformed data; two-way ANOVA; $F_{(2, 142)} = 122.09$, $P < 0.001$; $F_{(2, 142)} = 11.74$, $P < 0.001$; $F_{(4, 142)} = 25.52$, $P < 0.001$; respectively). In the intact treatment, biomass differed significantly among the three patch types and was ranked in descending order: periphery > open > core (Fig. 4b). In the removed treatment, biomass in the core did not differ from that in the periphery, and biomass in the open was significantly lower than that in the other two patch types (Fig. 4b). Removal of the canopy increased biomass in the periphery and core, although the effect in the latter was greater (Fig. 4b). The combination of shade with shrub canopy removal reduced the biomass in all patch types to a level similar to that of the intact core (Fig. 4b).

In the third growing season following shrub canopy removal (2007), removal treatment, patch type and the interaction between removal treatment and patch type had significant effects on biomass (log-transformed data; two-way ANOVA; $F_{(1,247)} = 104.13$, $P < 0.001$; $F_{(2,247)} = 51.78$, $P < 0.001$; $F_{(2,247)} = 60.52$, $P < 0.001$; respectively). In the intact treatment, biomass differed significantly among the three patch types and was ranked in descending order, periphery > open > core (Fig. 4c). Removal of the canopy increased biomass in the core and periphery (Fig. 4c). In the removed treatment, biomass in the core did not differ from that in the periphery, and biomass in the open was significantly lower than that in the other two patch types (Fig. 4c).

Herbaceous vegetation species density

In the growing season of 2005, which followed the initial shrub canopy removal in December 2004, patch type and its interaction with removal treatment had significant effects on species density (square-root-transformed data; two-way ANOVA; $F_{(2, 268)} = 92.49$, $P < 0.001$; $F_{(2, 268)} = 3.36$, $P = 0.036$). In both intact and removed treatments, species density differed significantly among the three patch types, and was ranked in the order periphery > open > core (Fig. 5a).

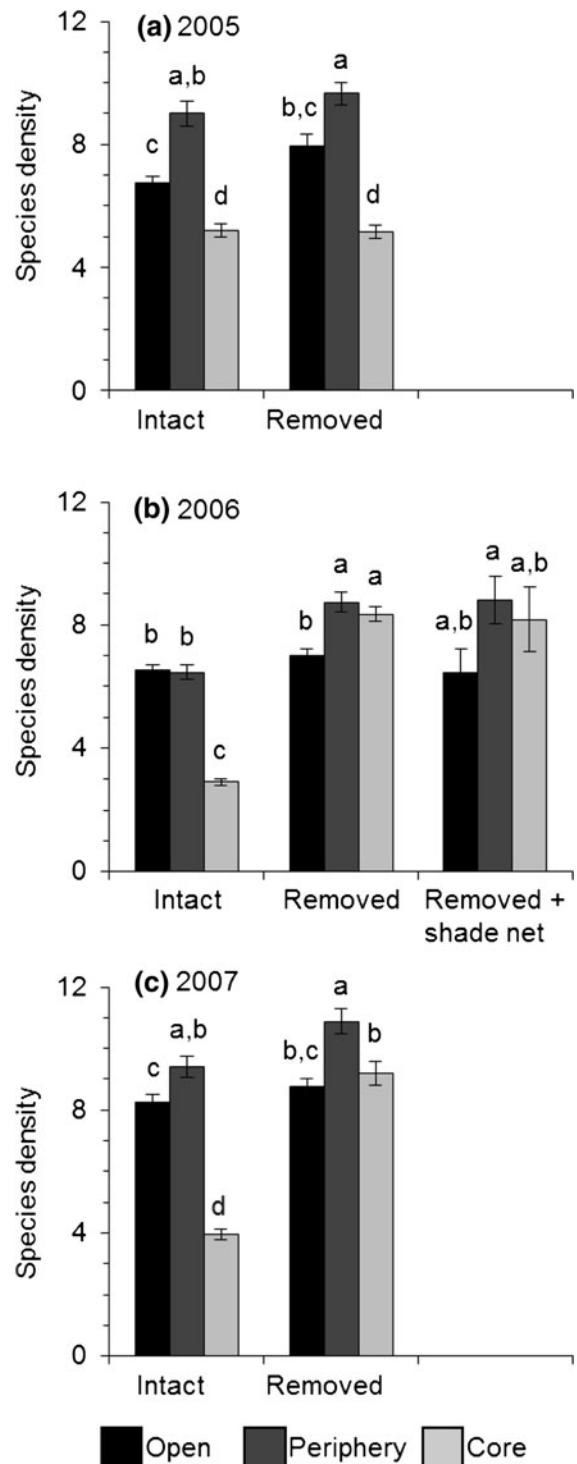


Fig. 5 Herbaceous species density per 400-cm² sample in the various treatments and patch types. Letters denote significant differences. Data are represented as means \pm SE

In the second growing season (2006), by which time two rounds of shrub canopy removal had been implemented, removal treatment, patch type and their interaction had significant effects on species density (rank transformed data; two-way ANOVA; $F_{(2, 564)} = 131.40$, $P < 0.001$; $F_{(2, 564)} = 10.21$, $P < 0.001$; $F_{(4, 564)} = 37.20$, $P < 0.001$; respectively). In the intact treatment, the core still had the lowest species density, but the periphery and open patch types did not differ (Fig. 5b). However, in the removed treatment, species density in the core was as great as that in the periphery, and that in the open was lowest. Removal of the canopy increased species density in the core and periphery (Fig. 5b). The combination of shade with shrub canopy removal had no significant effect on the species density in any patch type, compared with the effect of canopy removal alone (Fig. 5b).

In the third growing season (2007), following three rounds of shrub canopy removal, the effects of removal treatment, patch type and their interaction on species density were again significant (rank transformed data; two-way ANOVA; $F_{(1, 404)} = 99.34$, $P < 0.001$; $F_{(2, 404)} = 72.36$, $P < 0.001$; $F_{(2, 404)} = 32.18$, $P < 0.001$; respectively). In the intact treatment, species density differed significantly among the three patch types and was ranked in the descending order, periphery > open > core (Fig. 5c). In the removed treatment, species density in the core equaled that in the open, and that in the periphery was the greatest of the three patch types (Fig. 5c).

Discussion

A landscape modulator has been defined as an ecosystem engineer that modifies its environment through patch formation (Shachak et al. 2008). Our experimental studies on woody–herbaceous relations in a semi-arid ecosystem sought to explore whether the negative and positive effects of our model landscape modulator—*S. spinosum*—on herbaceous vegetation are spatially uniform, or whether the effects were spatially heterogeneous within and immediately adjacent to the woody vegetation patch. Our results provide strong evidence that the effects are spatially heterogeneous.

We used the concept of MLLD, proposed by Shachak et al. (2008), as a tool to assist in the interpretation of our results. A landscape modulator impacts biodiversity via processes related to the creation of diverse resource patches having differing spatial patterns. Resource levels vary in differing manners, with some increasing and others decreasing (Malkinson and Tielbörger 2010). This process of resource modulation by the landscape modulator creates a new and finer-scale resource patchiness that can be conceptualized as multiple layers of resources, and these in turn affect species assemblages (Shachak et al. 2008). Each modified resource layer could have different effects on the species assemblage, and the net result of the interactions between the multilayered resources would be a specific species assemblage and its associated biomass production.

Our results show that *S. spinosum* modulates the landscape by increasing water while reducing radiation and seed availability in its core. However, the same resource layers are modulated differently in its periphery. A complementary study also found that soil nutrients are modulated differently in the core and periphery of *S. spinosum* (Segoli et al. 2012). This creates distinct multilayered resource patches at the core and periphery of the shrub, which, along with the open (intershrub) patch type, generate a three-patch-type classification that does not follow the dichotomous structural pattern of the shrub canopy. This supports our first hypothesis and emphasizes the importance of examining the effect of landscape modulators at the spatial scale at which the modulated resources vary (Breshears and Barnes 1999; Barbier et al. 2008; Bar Massada et al. 2008; Li et al. 2010).

The specific combination of resource layers led to net positive effects on herbaceous vegetation in the periphery and net negative effects in the core (Figs. 4, 5), supporting our second hypothesis. Previous studies documented similar herbaceous responses in the center and edge of woody vegetation patches (Dickie et al. 2005; Caballero et al. 2008; Li et al. 2010). This small-scale spatial separation is important for understanding the semi-arid ecosystem functioning. Although the periphery accounts for only 30 % of the landscape, it contains 47 % of the landscape biomass (unpublished data). Therefore, studies that

sample only the open and core could possibly overlook up to 50 % of the productivity of the system.

Our results demonstrate that water infiltrates 48 % deeper in the intact core than in the open (Fig. 1). This is consistent with findings from the same study site that the gravimetric water content of soil sampled in the spring at the core was 35 % higher than that sampled in the open (Stavi et al. 2008). Thus water infiltration appears to be a good proxy for water availability in this ecosystem (Bergkamp et al. 1999). However, we cannot disentangle the effects of water and soil nutrients: modulation of these by *S. spinosum* showed similar trends (Segoli et al. 2012). So the net positive effects on herbaceous vegetation observed in the periphery are due to modulation of soil properties, while net negative effects prevail in the core because radiation and seed dispersal are modulated by the canopy.

Few studies manipulated the modulation effects of woody vegetation in order to understand the underlying positive and negative mechanistic effects controlling herbaceous vegetation (but see Holzapfel and Mahall 1999; Maestre et al. 2003; Dickie et al. 2005; Teste and Simard 2008). Although previous studies examined the effects of water, nutrients, shade and seed limitation, to our best knowledge, no study has spatially separated these mechanisms in the field (but see Weedon and Facelli 2008; Segoli et al. 2012).

A model is needed that can examine different levels and spatial extents of modulated resources and how they influence different measures of plant performance (Maestre et al. 2005; Brooker et al. 2008). We synthesized our results in a graphical representation of the MLLD model (Fig. 6) in order to disentangle the effects of water (possibly linked with nutrients), radiation and seeds on herbaceous biomass and species density.

Biomass and species density are lower in the removed open (Fig. 6fVI, gVI) than in the removed core (Fig. 6fIV, gIV). The only resource that differs between these two patch types is water, suggesting that the limiting factor for herbaceous vegetation in the open is water availability. This is further supported by the higher biomass and species density in the intact periphery (Fig. 6fII, gII) than in the intact open (Fig. 6fI, gI). Relative to the removed core, the addition of shade reduced herbaceous biomass but did not affect species density (Fig. 6fIV, fIX, gIV,

gIX). This can be attributed to a change (reduction) in radiation (Fig. 6dIV, dIX) but not in availability of water (Fig. 6cIV, cIX) or seeds (Fig. 6eIV, eIX). Relative to the intact core, canopy removal plus shade increased species density (Fig. 6gIII, gIX) but did not affect herbaceous biomass (Fig. 6fIII, fIX), which can be attributed to increased seed availability in the absence of the canopy barrier (Fig. 6eIII, eIX).

The MLLD model suggests that the net negative effect of the woody patch on the herbaceous community in the core is imposed via two pathways: radiation controls the herbaceous biomass, whereas the canopy acts as a seed barrier that controls species density. The hypothesis that biomass and species density are affected via different pathways is further supported by the differences between the observed effects in the first and second years, respectively. Canopy removal increased biomass already in the first year (Fig. 4), which supports our inference that biomass is limited by radiation. Canopy removal increased species density only from the second year (Fig. 5). Since the removal of the shrub canopy was performed after the seed dispersal of the previous growing season, this supports our inference that species density is limited by seed availability. However, it is important to note that although we found different effects of shade and seed limitation there are feedbacks between these factors. Less biomass causes the herbaceous vegetation to produce less seeds and less seeds can affect the amount of biomass produced (Li et al. 2010).

By recognizing and quantifying the modulation of various resources and its spatial extent, and by portraying this information graphically in the MLLD model, we were able to depict an intricate landscape that is composed of patches that differ in their combinations of resource levels. This informs us as to the functionally relevant division of the landscape into patch types. The MLLD model revealed that different resource combinations can have varying effects on specific herbaceous traits, such as biomass and species density. We would therefore expect the degree of MLLD to control the herbaceous diversity in the landscape. Our model demonstrated this process by distinguishing between the periphery and core patch types, and by considering separately biomass and species density when examining the response of the herbaceous vegetation to the multilayered landscape diversity.

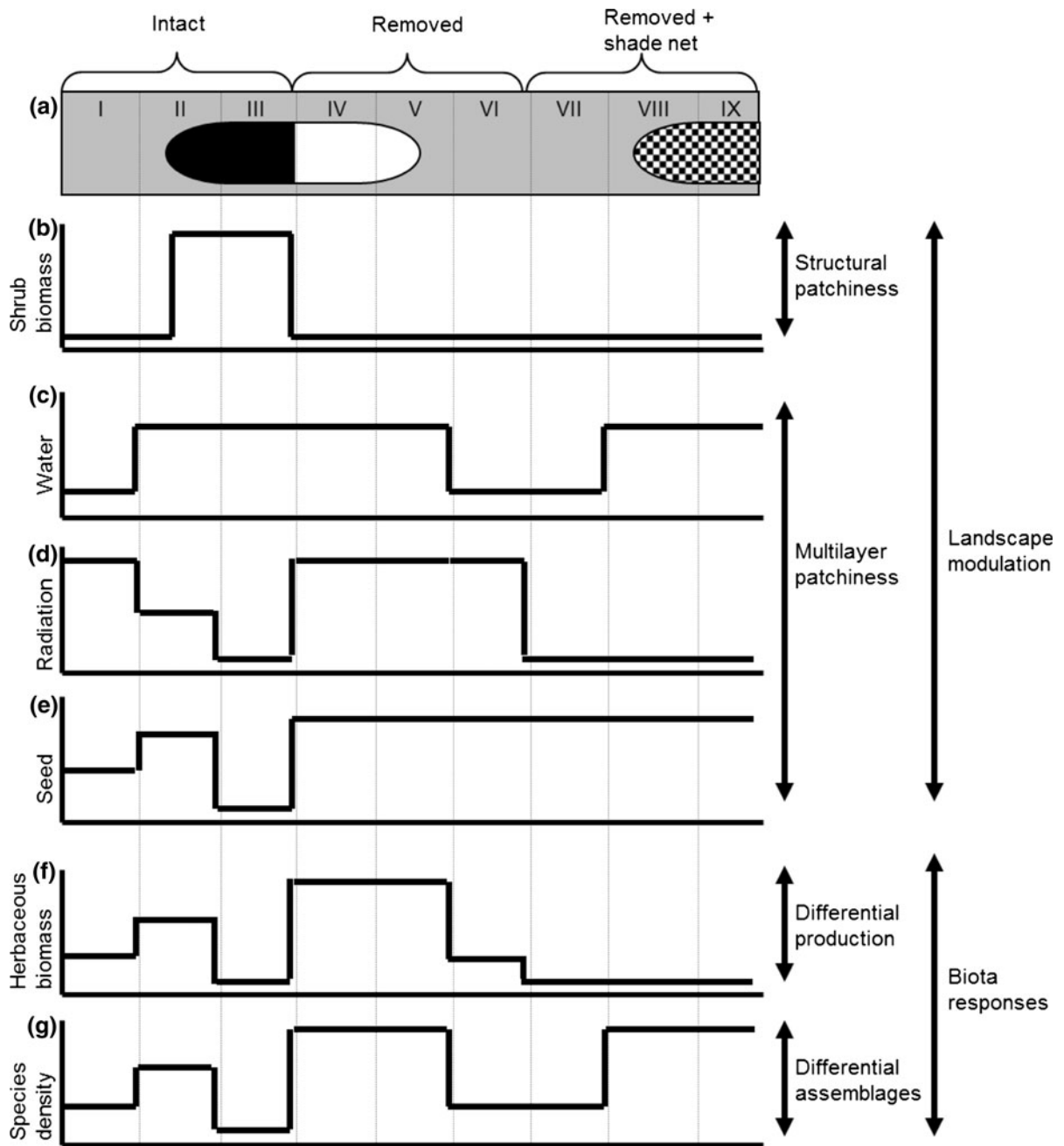


Fig. 6 A conceptual model of the effects of woody vegetation on the biomass and species distribution of herbaceous vegetation in a semi-arid ecosystem (MLLD model). **a** Schematic spatial representation of a landscape with open (intershrub) matrix (grey), woody vegetation (black), canopy removed woody vegetation (white) and canopy removed woody vegetation with addition of shade (checkered). **b** The shrub canopy

creates a distinct border that delineates the presence or absence of shrub biomass and defines the structural patchiness of the landscape. **c–e** Multiple layer resource patchiness induced by modulation by the shrub with respect to **c** water, **d** radiation and **e** seed availability. **f–g** Biotic responses to the modulated resources with respect to **f** biomass and **g** species density of herbaceous vegetation

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