



# Transformation of shrublands to forests: The role of woody species as ecosystem engineers and landscape modulators



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## ABSTRACT

Trees in forests and shrubs in shrublands can be considered physical ecosystem engineers since they modify their environment by creating patches that differ in their ecosystem properties from un-engineered patches. The objective of this study was to evaluate the effects of replacing one functional group of woody species (shrubs) with another group (trees) that differs in its ecosystem engineering (EE) mode on soil and vegetation as emerging ecosystem properties in the northern Negev, Israel. The soil quality index (SQI) and the aboveground net primary productivity (ANPP) of herbaceous plants were used as emergent ecosystem properties for characterizing woody and non-woody patch states. The SQI integrates 14 physical, biological, and chemical soil properties, indicating the soil state in a patch. The ANPP of herbaceous plants was estimated as the annual plant biomass accumulation, indicating the vegetation state in a patch. Relationships between the SQI and ANPP properties in different patch states were calculated in terms of the magnitude (MG) and direction of the change ( $\theta$ ). The results show an overall conservation of the collective ecosystem properties on the landscape level, but an inversion in the ecosystem functions of the two patch types arising from the replacement of the woody EEs. A significant correlation between SQI and ANPP was found in the forest and shrubland system, with  $R^2 = 0.89$  and  $R^2 = 0.82$ , respectively. In the forest, higher SQI and herbaceous plant ANPP scores were found in the non-woody patches than in the tree understory with  $MG = 0.27$  and  $\theta = 214.61$ . The opposite trend existed in the shrubland where higher SQI and ANPP scores were found under the shrub canopy than in the non-woody patches with  $MG = 0.34$  and  $\theta = 43.65$ . The conclusions are: (1) the engineering properties induced by the dominant woody plants through patch formation are important in driving ecosystem modulation; (2) the SQI and ANPP trajectories represent the magnitude of change between patch type, and (3) SQI and ANPP are reliable emergent ecosystem properties for evaluating changes of patches formed by woody plants as EEs.

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## 1. Introduction

It is widely accepted among ecologists that certain organisms fundamentally modify, create, or define habitats by altering the ecosystem and landscape properties (Berke, 2010). For the past 20 years, these organisms have been formally defined as “ecosystem engineers” (EEs), reflecting a growing consensus that patch formation by organisms that affect other organism and ecosystem processes represents a fundamental class of ecological interaction occurring in most, if not all, ecosystems (e.g. Barker and Odling-Smee, 2014; Jones et al., 2006, 1997; Lawton and Jones, 1995; Pearce, 2011; Romero et al., 2014; Shachak et al., 2008). EEs' effects

on many other species occur in virtually all ecosystems because direct physical state changes, such as patch formation, control abiotic resources, and indirectly, the modulation of abiotic forces that, in turn, affect resource use and flows (Romero et al., 2014; Wright and Jones, 2006). The classification of EEs can be divided into four narrower functional categories reflecting four broad mechanisms by which ecosystem engineering occurs: structural engineers, bioturbators, chemical engineers, and light engineers (Berke, 2010). All these functions are associated with patch formation by woody plants.

Trees in a forest and shrubs in a shrubland can be considered physical EEs since they modify their environment by patch formation that changes the physical structures, the light regime, the water flow, and the redistribution of nutrients (e.g. Jones et al., 2006). The restoration of degraded ecosystems in drylands, aimed

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at land transformation, has usually involved the introduction of woody plants (Yelenik et al., 2015). We propose that in this type of restoration by humans, landscape modulation is created by woody plants functioning as EEs. The integration of EEs as agents of restoration was already suggested by Byers et al. (2006) who constructed a framework for restoring drylands by using EEs as system-state modifiers. In their framework, in the restoration process, the abiotic environment can be greatly modified by EEs that drive the transition between the alternative ecosystem states of a degraded and a restored landscape (Byers et al., 2006; Wright et al., 2004). The restoration of degraded semi-arid areas through the reintroduction of woody species has become increasingly important worldwide as a technique to protect against soil erosion and loss (Castillo et al., 1997), to combat desertification, to increase the supply of natural resources (Guevarat et al., 2003), and to provide space for recreation (Amir and Rechtman, 2006).

Prior to restoration, the landscape in the arid and semi-arid areas consisted of two small-scale patch type mosaics, made of scattered shrub patches embedded in a matrix of biological soil crust patches (biocrust) (e.g. Shachak et al., 2008; Shachak and Pickett, 1997). Shrubs in arid and semi-arid areas function as landscape modulators through patch formation (James et al., 2013), by constructing below and aboveground structures (Berke, 2010) that create resource-enriched patches (e.g. Segoli et al., 2008; Shachak et al., 1998). The biocrust functions as a source of water, sediments, nutrients, and seeds that flow from the crust and are absorbed by the shrub patches that function as a sink for the above resources (Eldridge and Greene, 1994). This “sink-source” functional relationship between the shrub and crust patches affects ecosystem processes, such as primary and secondary production, decomposition and nutrient cycling (Li et al., 2008), and can be attributed to the different modes of landscape modulation by the two EEs: biocrust organisms and shrubs. The spatial patterns of shrub patches in crusted areas, which are characterized by their size, shape, and spatial distribution (e.g. Noy-Meir, 1980), control several ecosystem and landscape processes: water infiltration into the soil and the number and size of water-enriched patches, nutrient cycling and the development of “islands of fertility,” organic matter flow across the landscape, productivity, biodiversity and biotic interactions.

We propose that the replacement of shrubs with trees will remodulate the landscape mosaic but will conserve a two-patch mosaic (Maestre and Cortina, 2004; Maestre et al., 2003). This is because trees construct more intensive canopy and root systems (a higher degree of structural engineering) than do the shrubs (Hernandez et al., 2015). Their higher leaf area index reduces surface radiation to a lower degree (light engineering) in comparison to shrubs and reduces the runoff generation and resource redistribution processes in the forest (Shachnovich et al., 2008). Trees in arid lands, in response to water limitation, form a spotted pattern (Martínez-García et al., 2013), thereby creating a two-phase mosaic landscape consisting of tree and non-woody open patches. In drylands, extensive land transformation occurs through replacing shrublands or grasslands with *Pinus halepensis* forests plantation (Bellot et al., 2004; Maestre and Cortina, 2004; Maestre et al., 2003). *P. halepensis* forests are constituted by one of the most important tree species in the Mediterranean region, one of the few that can thrive in semi-arid areas, covering more than 25,000 km<sup>2</sup> and dominating forest formations in semi-arid and dry sub-humid areas (Rotenberg and Yakir, 2010). Comparing the ecosystem properties of a two-phase mosaic in which shrubs are replaced with *P. halepensis* can enhance our understanding of the roles played by shrubs and trees in landscape modulation.

Changes in the ecosystem properties of landscape patches due to principal EE replacement can be assessed by two main indicators: the soil quality index (SQI) and herbaceous aboveground

net primary productivity (ANPP) (Paz-Kagan et al., 2014). The first indicator represents an emergent structural property that incorporates physical, chemical and biological processes (e.g. Andrews et al., 2002). The second indicator is an emergent functional property of ecosystems that integrates many community and population processes (Krausmann et al., 2013). In a recent study, we showed that the trajectories of these two indicators, in a phase plane, signify ecosystem state change (Paz-Kagan et al., 2014) and, therefore, can depict changes in patch properties. The detection of the change is done by using trajectories that are characterized by both the magnitude and the directions of the change. Trajectory studies enable us to address and compare the ecosystem consequences of patch modification in relation to patch formation by EEs.

Scientific knowledge on both shrubland and *P. halepensis* forests and their replacement is extensive (e.g. Bellot et al., 2004; Maestre et al., 2004; Ruiz-Navarro et al., 2009). However, there is a need for studies that will evaluate the effects of replacement of shrubs with trees from an integrative perspective that links patch formation by woody plants, as a landscape modulator, with emergent ecosystem properties in the patch as a consequence of engineering. In the present paper, the response variables to patch formation, the SQI and the ANPP of herbaceous plants, were used as indicators of changes in patch properties. We hypothesize that the process of transforming shrubland into planted forest, by replacing the main woody engineer, will result in: (1) a reduction in SQ between patch type, since the trees will reengineer the soil (Ruiz-Navarro et al., 2009) and alter the resource-enriched patch formed by the shrub (Maestre et al., 2003, 2012); (2) a decrease in the ANPP of the herbaceous plants since the tree shading will suppress their growth (Maestre et al., 2004, 2003); and (3) a decrease in the contrast between the SQ and ANPP of the woody and open patches in the forest as compared to the shrubland due to more uniform redistribution processes of water and nutrients (Shachnovich et al., 2008); this result will exhibit a smaller magnitude of change. We assumed that the transition between the two alternative ecosystem states, shrubland and forest, could be quantified by the changes in the values of SQI and ANPP as a product of patch formation by shrubs and trees. This would support our comprehensive objective of elucidating the relationships between EEs' functional groups and patch formation. Specifically, the study aims at determining the long-term changes in ecosystem and landscape properties caused by replacing *Sarcopoterium spinosum* shrubs with *P. halepensis* trees using the SQI and the herbaceous plant ANPP as emergent ecosystem properties and their trajectories will induced modification of woody plants' patch formation.

## 2. Methods

### 2.1. Study site

The study area, named the Yatir Forest, is a long-term ecological research (LTER) site, located in the northern Negev Desert of Israel (35°03'E, 31°20'N, 650 m a.m.s.l.). Climatically, the site is situated in the transition belt between the semi-arid and the arid zones (Shachak and Groner, 2010). The research site receives a mean annual rainfall of 285 mm (Volcani et al., 2005). Precipitation occurs only during the wet season, from November to April. Average annual temperature is approximately 17 °C, with average maximum and minimum temperatures of 32 and 7 °C, respectively (Gelfand et al., 2009, 2012). The soil at the research site is shallow (20–40 cm) Aeolian origin loess with a silt–clay–loam texture (31% sand, 41% silt and 28% clay; density: 1.65 g cm<sup>3</sup>) overlying chalk and limestone bedrock (Raz-Yaseef et al., 2009). While the natural rocky hill slopes in the region are known to create flash floods, the

forested plantation reduces runoff dramatically, to less than 5% of rainfall (Shachnovich et al., 2008). Groundwater is deep (>300 m), reducing the possibility of groundwater recharge due to negative hydraulic conductivity or of water uptake by trees from the groundwater (Shachnovich et al., 2008).

The forest (Fig. 1) is approximately 2800 ha, predominantly comprising *P. halepensis* planted mainly in the 1960s. This forest is the largest planted forest in the semi-arid northern Negev Desert (Volcani et al., 2005). The *P. halepensis* tree density is about 300 trees/ha, mean tree height is about 10 m, and mean leaf area index (LAI) is about 1.5. There is no distinct organic horizon other than an occasional thin 1–3 cm plant litter layer (Grunzweig et al., 2003). The surrounding native vegetation is a two-phase mosaic dominated by the shrub *S. spinosum* with a total vegetation height of 0.30–0.50 m, embedded in a biological soil crust matrix. The areas of the patches in the forest are about 2.5–5 m<sup>2</sup> and in the shrubland about 1.5–3 m<sup>2</sup>. During the rainy season, herbaceous annuals and perennials are prominent in both patches (Sprintsin et al., 2009).

## 2.2. Experimental design and sampling

The experiment was performed in the Yatir Forest system and the adjacent natural shrubland. Each system is a patchwork of woody vegetation and non-woody open patches (with bare soil in the dry season and herbaceous plant cover in the wet season). The two-phase mosaic of woody vegetation patches interspersed with open patches is typical of semi-arid and arid areas in which a 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

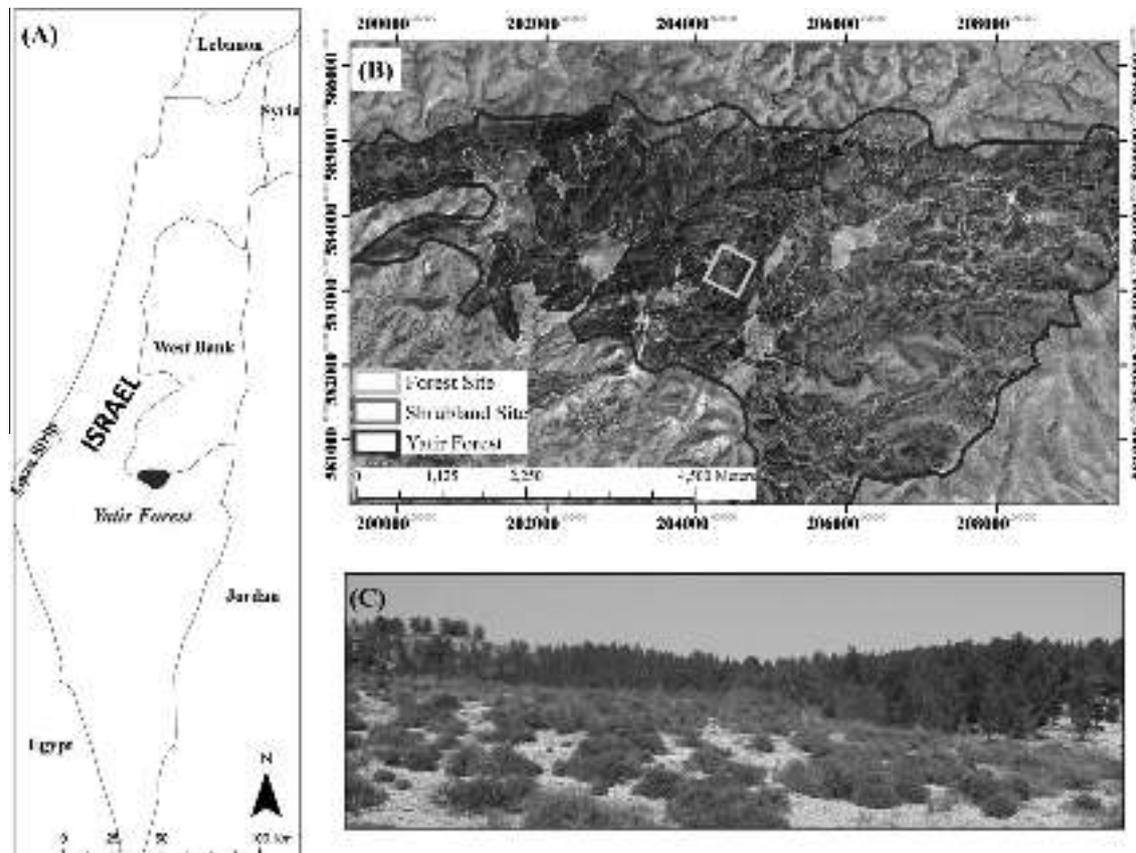
semi-arid areas (Segoli et al., 2008). Therefore, in this study, the sampling methodology proceeded according to the different patch mosaics in each system (Fig. 2). The sampling design included five replicates of 1 m<sup>2</sup>, randomly selected in each patch type. The sampling included: (1) ten replicates in the forest: five in the forest understory and five in the forest open patches; and (2) ten replicates in the adjacent shrubland: five under the shrubs and five in the biocrust patches ( $n = 20$  replicates of 1-m<sup>2</sup> quadrates). The comparisons were made between plots established in a matrix of patches over the same soil taxonomy, depth and slope in both sites and with similar orientations in order to have environmental factors that were as similar as possible.

## 2.3. Soil sampling, testing, and analysis

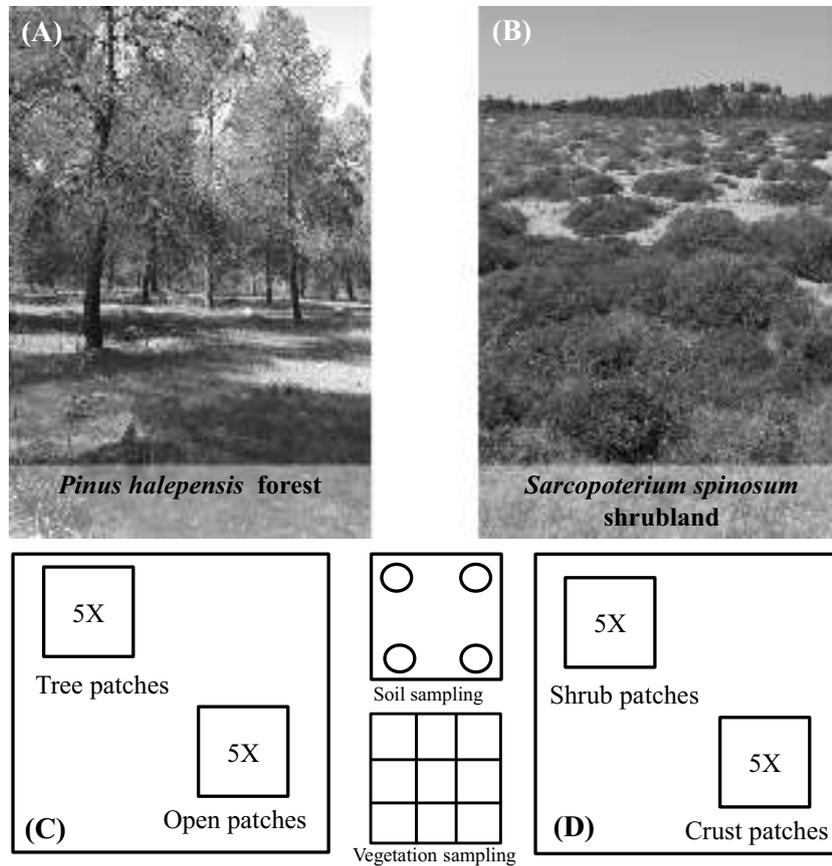
The measuring of the SQI included three main stages: (1) selecting the physical, biological, and chemical properties of the SQ; (2) using the transformation function to transform the SQ properties into a unitless score function; and (3) using the principal component analysis (PCA) to calculate the weight of the soil properties using an index (e.g. Idowu et al., 2008; Masto et al., 2008).

### 2.3.1. Sampling and testing of soil properties

Soil samples were collected from a depth of 0–0.15 m in late August 2011, at the peak of the dry season. The sampling was conducted following a stratified random method based on an experimental design as mentioned above ( $n = 20$  replicates of 1-m<sup>2</sup> quadrates). In each replicate, four soil samples of 700 gr were collected, for a total of 80 soil samples. All dry soil samples were transferred to the laboratory and were stored unopened until analysis. The Cornell Soil Health Test (CSHT) protocols were adopted



**Fig. 1.** The study areas with the sampling design of the shrubland and planted forest. (A) Israel schematic map with the location of the Yatir Forest study site; (B) orthophoto with 1-m resolution of the study sites; and (C) general view of the Yatir Forest: *P. halepensis* forest and the shrubland.



**Fig. 2.** (A) General view of the *P. halepensis* forest, demonstrating the tree understory patches and the open patches; (B) general view of the shrubland system showing the shrub patches and the biological soil crust patches; (C) sampling design of the forest system; and (D) sampling design of the shrubland system.

for analyzing 14 physical, biological, and chemical soil properties (Gugino et al., 2009). The physical properties included soil texture (fractions of clay, silt, and sand), aggregate stability (AGG), available water content (AWC), surface hardness (SH), and hydraulic conductivity (HC). The biological properties included soil organic matter (SOM), potential active carbon (PAC), and root health (RH). The chemical properties included pH, electric conductivity (EC), extractable phosphorus (P), extractable potassium (K), extractable ammonium ( $\text{NH}_4^+$ ), and extractable nitrate ( $\text{NO}_3^-$ ). All laboratory measurements were carried out with the CSHT's standards (Gugino et al., 2009). However, several modifications were introduced due to the specific management practices, the semi-arid climatic regions, and the available tools, including the following: (1) AGG was measured with an aggregate stability kit (Herrick, 2000); (2) AWC was measured by the soil moisture as water retention (Black, 1965); (3)  $\text{NH}_4^+$  and  $\text{NO}_3^-$  were measured using potassium chloride extracts (Stevenson, 2005); and (4) HC was measured by a mini-disk infiltrometer in the field (Ankeny et al., 1991). The soil texture is a result of the composition of the three fractions of clay, silt, and sand. Since texture is not a quality variable that change dues to management, it was not included in the SQI (Karlen et al., 1997).

### 2.3.2. Soil quality index

Evaluation of the SQI was carried out using the general approach of SQIs, involving scoring functions for each of the abovementioned soil properties (e.g. Andrews et al., 2004). The scoring functions were defined in a simple nonlinear polynomial framework. Each soil property was transformed through a scoring algorithm into a

unitless score (0–1) representing the associated level of function in that system so that the scores could be combined to form a single value (e.g. Andrews et al., 2002; Karlen et al., 1997). The success and usefulness of this method depended mainly on setting the appropriate critical limits for individual soil properties. Each soil property value was recorded by the different algorithms (scoring functions) to transform it into a unitless score ( $S_i$ ), using the following equations (Kinoshita et al., 2012; Masto et al., 2008, 2007):

$$S_{i_{mib}} = (1 + e^{-(b(x-a))})^{-1} \quad (1)$$

$$S_{i_{lib}} = (1 + e^{(b(x-a))})^{-1} \quad (2)$$

$$S_{i_{op}} = 1 \times e^{\left(\frac{-(x-a)^2}{b}\right)} \quad (3)$$

where  $x$  is the normally distributed soil property value,  $a$  is the baseline value of the soil property where the score equals 0.5 (inflection point) or the population mean, and  $b$  is the slope tangent of the baseline curve or  $2\sigma^{-2}$  of the population. Each scoring function (e.g. Idowu et al., 2009; Masto et al., 2008; Schindelbeck et al., 2008) has one the following general shape types: (1) more is better (*mib*): an upper asymptotic sigmoid curve (negative slope) that characterizes AGG, AWC, SOM, PAC,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , and K; (2) less is better (*lib*): a lower asymptote (positive slope) that characterizes RH and SH; and (3) optimum function (*op*): an optimum midpoint Gaussian function that characterizes pH, EC, P, and HC. All the soil property scores were integrated from the previous stage into a single additive index that quantified the SQI:

$$SQI = \sum_{i=1}^n PW_i \times S_i \quad (4)$$

where  $PWi$  is the PCA weighing factor. This value is considered to be an overall assessment of SQ, reflecting the management practice effects on soil function (Masto et al., 2008, 2007). To evaluate the index, the PCA statistical method was used. A PCA finds the combinations of the soil's transformed properties that describe major trends in the data. The index values ranged from 0 to 1 in which low values indicate poor soils, while high values indicate healthy soils (Gugino et al., 2009). Principal components (PCs) with eigenvalues higher than one that explained at least five percent of the variation of the data were examined (Andrews et al., 2002; Masto et al., 2008). Under a particular PC, only the variables with a high factor loading were retained for the SQI. High factor loading was defined as having an absolute value within 20 percent of the highest factor loading (Masto et al., 2008, 2007). When more than one variable was retained under a single PC, a multivariate correlation was employed to determine whether the variables could be considered redundant ( $R \geq 0.8$ ) and, therefore, eliminated from the SQI. Highly loaded factors that were not correlated were each considered important and, thus, retained in the SQI. Among well-correlated variables, the variable with the highest factor loading (absolute value) was chosen for the SQI. Each PC explained a certain amount of variance (percent) in the total dataset, and this percentage provided the weight for the variables chosen under a given PC.

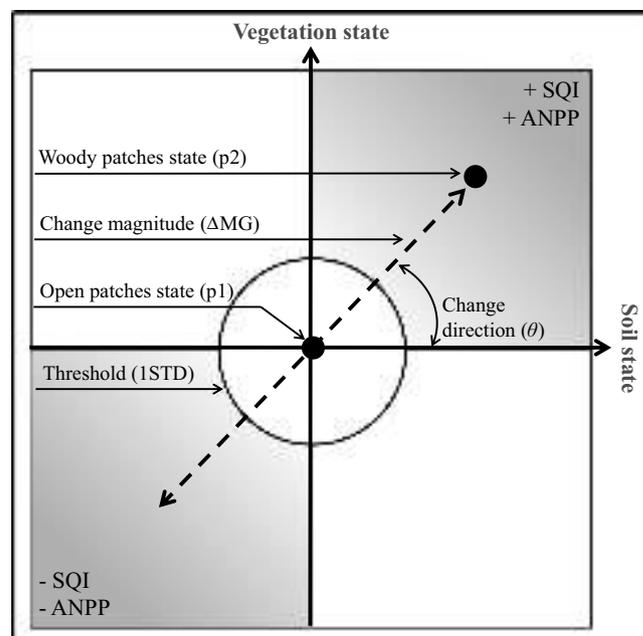
#### 2.4. Aboveground net primary production

The net primary production of herbaceous plants provides a comprehensive evaluation of the ecosystem state, including measures of changes in ecosystem state (e.g. Running and Coughl, 1988; TurHorst and Munguia, 2008). In the Negev, net primary herbaceous production can be determined by annual ANPP accumulation (Evenari et al., 1976). ANPP was estimated as the annual maximum plant biomass accumulation. Plant biomass was measured by quantifying the peak dry mass of plants per unit area in each patch type. Herbaceous biomass samples were collected twice during the peak of the growing season (April) in the years 2011 and 2012. The sampling was conducted using a stratified random method based on the experimental design. All the replicates were harvested in 0.33-m<sup>2</sup> sub-quadrates (nine repeated measurements for each quadrat); the total number of biomass samples was  $n = 180$  per year. The aboveground plant biomass was weighed, after a 48 h period of oven drying (75 °C). The ANPP values were calculated by the algorithm of the "more is better" upper asymptotic sigmoid curve (Eq. (1)). The transformation of ANPP enabled us to evaluate the relations between SQI and ANPP in the different ecosystems according to the landscape patches in the same units.

#### 2.5. Relation between SQI and ANPP

To evaluate the magnitude of the ecosystem state according to the landscape patch mosaic, due to the modification of ecosystem engineers, we used a change detection technique based on the trajectories of the two biophysical indicators, i.e., the scores of SQI and ANPP. Each measurement of these indicators is represented by a point in a two-dimensional phase space. It produces two outputs: change magnitude and change direction. As illustrated in Fig. 3, the magnitude of the change ( $\Delta MG$ ) is computed by the Euclidean distance of a vector between the indicators, the initial (reference) patch ( $P1$ : open patches) and the observation (target) patch ( $P2$ : woody patches as ecosystem engineers):

$$\Delta MG = \sqrt{(SQI_{1p1} - ANPP_{1p1})^2 + (SQI_{2p2} - ANPP_{2p2})^2} \quad (5)$$



**Fig. 3.** Conceptual scheme based on the soil quality index (SQI) and aboveground net primary productivity (ANPP) as indicators for quantifying ecosystem state change due to the modulation of ecosystem engineers according to the landscape mosaic. Dashed arrows indicate specific possible directions and magnitudes of state change in the landscape mosaic. The length of the arrow indicates the magnitude of change ( $\Delta MG$ ), and the slope angle ( $\theta$ ) represents the relative changes between the soil quality and productivity.  $p1$ : open patch as the initial state;  $p2$ : woody vegetation as the ecosystem modulator as the observed state; threshold represents significant differences between the initial state and the observed state. The threshold between the no-change and change was determined as one standard deviation (1STD) from the mean.

A threshold, in terms of one standard deviation from the mean of the change, is defined for the magnitude values to distinguish between changed and unchanged trends. The direction of the change is computed by the angle ( $\theta$ ) of the change vector (Eq. (6)):

$$\tan \theta = \frac{ANPP_{2p2} - ANPP_{1p1}}{SQI_{2p2} - SQI_{1p1}} \quad (6)$$

Due to its two output products, change magnitude and direction, this procedure enabled us to quantify the different trajectories for the two systems (forest and shrubland) according to the landscape patch mosaics and their ecosystem states.

#### 2.6. Statistical analyses

Analyses of variances for all variables were tested using: (1) a general linear model (GLM) analysis of random effect (nested analysis of variance (ANOVA)) (Zeger and Karim, 1991); and (2) a one-way ANOVA for the average of each replicate ( $n = 20$ ), and the separation of means was subjected to a Tukey test for significant differences and a normality test. A Pearson correlation coefficient analysis was conducted to identify relationships between the measured soil properties. The statistical analysis was performed with STATISTICA Version 11, 2014 software. The SQI calculation was performed in the MATLAB Version 7, 2011 software with a PLS toolbox (EIGENVECTOR research) and using Microsoft Excel packages. The SQ properties, SQIs, and primary productivity were tested for their level of significance at  $p \leq 0.05$  between patches.

### 3. Results

#### 3.1. Soil quality

The results of the SQ properties from the forest and the adjacent shrubland systems are shown in Table 1. The AGG, SOM, and PAC values were found to be significantly higher in the forest system than in the shrubland. The soil in the forest had a higher clay content, which indicates a higher ability to retain nutrients (higher cation exchange capacity) and to bind organic matter (Idowu et al., 2008), than in the biocrust areas of the shrubland. The results of the SQ properties under the canopy in both systems (forest and shrubland) exhibited significant increases in AGG, SOM, EC, and K.

Table 2 presents the Pearson correlation coefficients for the measured soil properties, with moderate and high correlations ( $R \geq 0.5$ ) marked in bold. The soil physical, biological, and chemical properties interact among themselves. The AGG and SOM show high Pearson correlations ( $R = 0.89$ ), as do AGG and EC ( $R = 0.79$ ). A high negative correlation was found between SH and HC ( $R = -0.74$ ;  $p < 0.01$ ).

##### 3.1.1. Soil property transformations

The radar diagrams in Fig. 4 are plots of the soil (selected) property transformation ratings of the soil functions by nonlinear scores of the different soil properties in the forest and shrubland systems (normalized 0–1) according to the landscape patch mosaic of the woody and open patches in the two systems. Lines crossing the axes represent the different soil patches. The lines lying at the periphery of the web have better SQ with reference to the particular function or soil property (axis), and lines toward the origin have low SQ. Fig. 4A shows the changes in all soil properties according to the landscape patch mosaic in the shrubland system, while Fig. 4B displays the results for the forest. The results show that in the shrubland, most of the biological, chemical, and physical properties are improved in the shrub patches. In the forest system, the tree canopy mainly reduced the chemical soil properties. The biological component did not change in either patch type in the forest system.

##### 3.1.2. Soil quality indices

The indices were developed from the results of the transformed scoring soil properties for the forest and shrubland systems. Only the significant differences in the soil properties between patch types were included in the PCAs. In the two systems, the RH did not show significant differences between patches; therefore, it wasn't included in the PCA (Table 1). The first three PCs that had eigenvalues  $>1$  were included in the PCA (cumulative variance 85.39%) (Table 3). The highly weighted variables under PC-1 were: AWC, SH, pH, EC,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , P, and K. The transformed data in PC-1 were not correlated among themselves and were all included in the PCA. Aggregation, SOM, and PAC had the highest weighted variables under PC-2. As AGG had a high correlation with SOM ( $R = 0.89$ ) under PC-2, it was not included in the SQI. The weight for AGG was determined to be factor loadings (Table 2). Hydraulic conductivity had the highest weighted variables under PC-3. Weights for selected variables were determined by the percentage of variation in the dataset explained by the first three PCs.

The SQI was calculated using a weighing factor for each scoring variable according to Eq. (4). The SQI results from the forest and the shrubland systems are presented in Fig. 5. In the *P. halepensis* forest, there was an improvement in the SQI in the forest open patches (score of 0.67) and a reduction in the tree understory (score of 0.62); however, the changes were not significant. In the shrubland, opposite trends were observed with significant improvement in the SQI occurring in the shrub patches (score of

0.76) and the reduction occurring in the open crust patches (score of 0.58) (Fig. 5). The changes in SQI were significant according to the landscape patch mosaic ( $F_{(3,76)} = 10.98$ ;  $p < 0.01$ ); significant differences were found at the patch scale between the forest and the shrubland and between the different patches in the shrubland.

#### 3.2. Aboveground net primary productivity

The results of the ANPP of herbaceous plants (Fig. 6) in the forest and shrubland systems showed significant differences ( $F_{(3,177)} = 9.92$ ;  $p < 0.05$ ) between the patch types in the years 2010 and 2011. Significantly higher ANPP of herbaceous plants was found in the forest open patches in both years in comparison to the tree understory in the forest system (average of 81.3 and 139.5 mg/m<sup>2</sup>). In the adjacent shrubland, the opposite trend was found; significantly higher ANPP was found under the shrubs in both years in comparison to the biocrust area (average of 133.6 and 96.5 mg/m<sup>2</sup>). The effect of the woody vegetation on the ANPP shows a different trend. In the shrubland, the shrub patches had positive effects on the under-growing vegetation, while in the *P. halepensis* forest; the trees had a negative effect.

#### 3.3. Correlation between SQI and ANPP

The scatterplot of the SQI and ANPP scores of both systems are shown in Fig. 7. The results indicate a positive correlation between SQI and ANPP in the forest system, with  $R^2 = 0.89$ ;  $p \leq 0.01$ , and in the shrubland, with  $R^2 = 0.82$ ;  $p \leq 0.01$ . Additionally, we calculated the magnitude and the direction of the change (Fig. 7). In this study, different effects caused by the EEs in the woody patches were found. In the forest system, the magnitude of the change vector analysis (CVA) showed a magnitude of  $MG = 0.27$  and an angle of  $\theta = 214.61^\circ$ . This represents the reduction in the SQI and ANPP indicators caused by the ecosystem engineers in the woody patches. On the other hand, in the shrubland, the magnitude was  $MG = 0.34$  with an angle  $\theta = 43.65^\circ$ . This represents the improvement in the SQI and ANPP indicators caused by the shrub woody patches as an ecosystem engineer. The magnitude of the CVA from the open patch in the shrubland to the open patches in the forest was 0.17 with an angle of  $\theta = 61.45^\circ$ .

### 4. Discussion

In this study, we evaluated land transformation from shrubland to forest using an EE paradigm (Berke, 2010; Byers et al., 2006). In essence, we viewed land transformation, from shrubland to forest, as a replacement of woody EEs that modulate the landscape by forming patches exhibiting different ecosystem properties. The creation of different patch type properties, as shown by the SQI and ANPP values resulting from woody species replacement, indicates engineering. If only the physical variables determine patch properties, without engineering, we would expect that the SQI values, for example, would be generally similar in all patch types. This is because the soil in the study site is loess whose sources are desert dust depositions that are poorly developed (Tsoar and Pye, 1987). If patchiness cannot be explained as driven by the physical substrate, the alternative explanation is modulation of the substrate by the biota, i.e., engineering (Romero et al., 2014; Sanders et al., 2014). This implies that our results emerge from different modes of engineering between the shrubs and the trees as patch-forming agents. The results of the different SQI and ANPP values in the shrub and tree patches raise the questions: (1) how do different modes of landscape modulation by woody species as EEs create different patch properties in terms of ecosystem

**Table 1**  
Soil quality properties for the afforested and shrubland systems according to the landscape mosaics of the following patches: forest open patches, shrubland under the shrub, and shrubland open patches. Statistics include average value, standard deviation, and significant differences between patch types (small superscript letters). Values with different letters are significantly different ( $p < 0.05$ ).

Treatments	Sand (%)	Silt (%)	Clay (%)	AGG (1–6)	AWC (m/m)	SH (psi)	HC (mm/h)	SOM (%)	PAC (mg/l)	RH (1–9)	pH	EC ( $\mu\text{S}/\text{cm}$ )	N ( $\text{NH}_4$ ) (mg/kg)	N ( $\text{NO}_3$ ) (mg/kg)	P (mg/kg)	K (mg/l)
Forest understory	35.82 ± 4.15 <sup>b</sup>	43.78 ± 1.92 <sup>b</sup>	20.4 ± 3.58 <sup>a</sup>	3.92 ± 0.1 <sup>a</sup>	1.65 ± 0.22 <sup>a</sup>	300.8 ± 4.17 <sup>c</sup>	0.136 ± 0.07 <sup>ab</sup>	11.18 ± 1.81 <sup>a</sup>	821.06 ± 25.68 <sup>a</sup>	2.43 ± 0.53 <sup>a</sup>	7.82 ± 0.19 <sup>a</sup>	0.86 ± 0.12 <sup>a</sup>	12.02 ± 1.87 <sup>a</sup>	14.71 ± 11.08 <sup>a</sup>	6.09 ± 0.73 <sup>b</sup>	10.65 ± 1.18 <sup>a</sup>
Forest open patches	41.02 ± 2.22 <sup>a</sup>	41.58 ± 2.92 <sup>b</sup>	17.4 ± 1.95 <sup>a</sup>	3.2 ± 0.12 <sup>b</sup>	0.99 ± 0.13 <sup>b</sup>	286.13 ± 8.79 <sup>d</sup>	0.14 ± 0.06 <sup>a</sup>	8.38 ± 1.16 <sup>b</sup>	750 ± 26.81 <sup>a</sup>	3.06 ± 0.24 <sup>a</sup>	7.68 ± 0.04 <sup>a</sup>	0.63 ± 0.02 <sup>b</sup>	12.88 ± 3.4 <sup>a</sup>	10.39 ± 1.74 <sup>a</sup>	8.23 ± 1.09 <sup>a</sup>	7.62 ± 0.55 <sup>b</sup>
Shrubland under the shrub patches	33.42 ± 1.224 <sup>b</sup>	49.38 ± 1.09 <sup>a</sup>	17.2 ± 1.923 <sup>a</sup>	2.43 ± 0.39 <sup>c</sup>	1.171 ± 0.115 <sup>b</sup>	316.15 ± 5.83 <sup>b</sup>	0.107 ± 0.049 <sup>ab</sup>	6.23 ± 0.72 <sup>c</sup>	658.44 ± 71.82 <sup>b</sup>	1.56 ± 0.91 <sup>a</sup>	7.13 ± 0.04 <sup>c</sup>	0.82 ± 0.15 <sup>a</sup>	18.61 ± 5.05 <sup>a</sup>	9.42 ± 3.54 <sup>a</sup>	9.51 ± 0.75 <sup>a</sup>	11.31 ± 2.32 <sup>a</sup>
Shrubland open patches	35.42 ± 2.65 <sup>b</sup>	49.58 ± 1.23 <sup>a</sup>	15 ± 2.6 <sup>b</sup>	1.18 ± 0.06 <sup>d</sup>	0.91 ± 0.18 <sup>b</sup>	336.15 ± 6.73 <sup>a</sup>	0.094 ± 0.04 <sup>b</sup>	4.24 ± 0.4 <sup>d</sup>	339.61 ± 102.7 <sup>c</sup>	2.67 ± 0.67 <sup>a</sup>	7.41 ± 0.081 <sup>b</sup>	0.37 ± 0.05 <sup>c</sup>	6.97 ± 1.14 <sup>b</sup>	3.79 ± 0.64 <sup>b</sup>	6.88 ± 0.73 <sup>ab</sup>	5.76 ± 1.13 <sup>b</sup>
$p < \alpha$	<0.05	<0.05	<0.01	<0.01	<0.01	<0.05	<0.01	<0.01	<0.05	NS	<0.05	<0.01	<0.01	<0.01	<0.05	<0.01

AGG: aggregation; AWC: available water content; SH: surface hardness (penetration); HC: hydraulic conductivity (infiltration); SOM: soil organic matter; PAC: potential active carbon; RH: root health; EC: electrical conductivity;  $\text{NH}_4$ : ammonium;  $\text{NO}_3$ : nitrate; K: potassium; P: phosphorus; NS: no significant differences.

properties?; and (2) how do patch properties induced by woody species affect landscape functions?

To address the above questions, we: (1) discuss the mechanisms that shrubs and trees use as patch-formation agents; (2) compare the ecosystem properties of patches modulated by shrubs and trees; and (3) discuss the relationships between the shrub- and tree-modulated patches and the open patches that together determine the landscape mosaic.

#### 4.1. Mechanisms of biotic patch formation

We propose that the end products of landscape modulation by woody species are the result of several properties: (1) the mechanisms used by the EEs for patch formation, (2) the ecosystem properties of the modulated patch, and (3) the interactions of the modulated patch with other patches in the landscape mosaic. Our results show that the replacement of shrubs with trees was accompanied by an inversion in the ecosystem functions of open and under-canopy patches. The differences in the SQI and ANPP scores and trajectories (Fig. 7), which represent changes in the essential collective emergent ecosystem properties, occurred on the patch level, which indicates the strong effect of EE replacement on patch properties. We attribute the inversion of patch ecosystem functions to the mechanisms of patch formation by shrubs and trees. Berke (2010) suggested four broad mechanisms by which EEs modulate their environment: (1) structural engineers that create durable structural features in their surroundings; (2) bio-turbator engineers that disturb and mix materials in their surroundings usually by burrowing and excavation; (3) chemical engineers that modify the chemistry of the modulated site, either by moving or depositing materials; and (4) light engineers that alter the local patterns of light transmission, changing the intensity of light in nearby locations by casting shade or causing light scattering. We discuss patch formation by shrubs and trees and their effects on emergent ecosystem properties in terms of Berke (2010) classification. We suggest adding to this classification a new class of hydro-engineers that modulate the pattern and intensity of the water flow between woody and open patches (Shachnovich et al., 2008). Water flow between woody and open patches effect redistribution processes and there engineering mode.

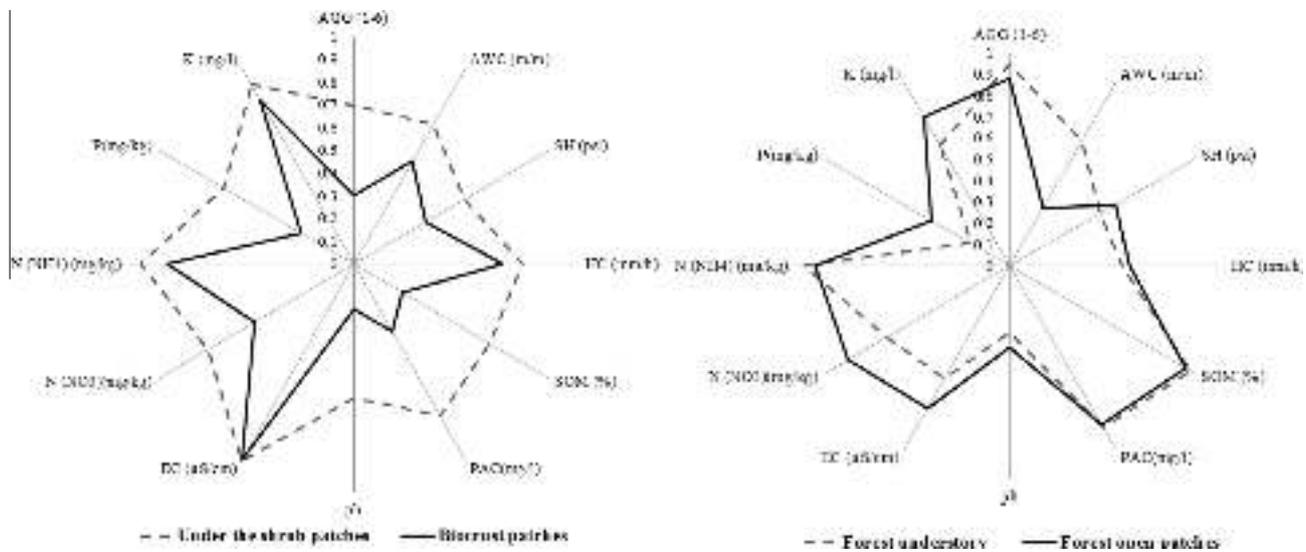
Shrubs in arid ecosystems are landscape modulators that form distinct patches that are structured by a network of mechanisms that include structural, hydrological, light and chemical engineering (Shachak et al., 2008). As structural engineers, the shrubs construct below and aboveground structures and create resource-enriched patches. In the case of the shrub, the aboveground patch structure controls the hydro-engineering function that redistributes the rainfall water by intercepting runoff, reducing its energy and transforming surface runoff into soil moisture (Segoli et al., 2008, 2012). The hydro-engineering is followed by chemical engineering resulting from the deposition of mineral and organic materials carried by the runoff water (Eldridge et al., 2002). The web of aboveground engineering drives a chain of belowground physical, chemical, and biological processes affecting all components of SQ (Figs. 4 and 5).

We explain the trees' reorganization in patch structure through their function as structural, hydrological, chemical and light engineers. Trees are characterized by having a more intensive canopy structure than shrubs, which increases their light engineering strength and modifies their mode of hydro-engineering. The high aboveground biomass and the architecture of trees reduce the energy of the rain drops (Raz-Yaseef et al., 2009; Yaseef et al., 2010) and surface runoff production (Yaseef et al., 2010), thus preventing water leakage from the system (Schindelbeck et al., 2008). Other studies have also explained the reduction in the ANPP of

**Table 2**  
Pearson correlation coefficients for the measured soil quality properties in the desertified shrubland and the forest. Bold numbers indicate significant differences with  $R \geq 0.5$  and  $p \leq 0.05$  (\*) and highly significant differences with  $R \geq 0.8$  and  $p \leq 0.01$  (\*\*).

Soil quality properties	Sand (%)	Silt (%)	Clay (%)	AGG (1–6)	AWC (m/m)	HC (mm/h)	SH (psi)	SOM (%)	PAC (mg/l)	EC ( $\mu\text{S}/\text{cm}$ )	pH	N ( $\text{NH}_4^+$ ) (mg/kg)	N ( $\text{NO}_3^-$ ) (mg/kg)	P (mg/kg)	K (mg/l)
Sand (%)	1.00														
Silt (%)	<b>-0.66*</b>	1.00													
Clay (%)	-0.46	-0.36	1.00												
AGG (1–6)	0.17	<b>-0.65*</b>	<b>0.56*</b>	1.00											
AWC (m/m)	-0.28	0.00	0.35	0.28	1.00										
HC (mm/h)	-0.18	-0.14	0.39	0.30	0.38	1.00									
SH (psi)	-0.09	0.37	-0.32	-0.48	0.02	<b>-0.74*</b>	1.00								
SOM (%)	0.01	<b>-0.62*</b>	<b>0.72*</b>	<b>0.89**</b>	0.45	0.31	-0.44	1.00							
PAC (mg/l)	0.23	-0.49	0.30	0.71*	0.02	0.22	-0.21	<b>0.53*</b>	1.00						
EC ( $\mu\text{S}/\text{m}$ )	-0.07	-0.36	<b>0.51*</b>	<b>0.79**</b>	0.19	0.22	-0.31	<b>0.74*</b>	<b>0.69*</b>	1.00					
pH	0.29	<b>-0.69*</b>	0.46	<b>0.59*</b>	0.45	0.26	-0.48	<b>0.69*</b>	0.17	0.28	1.00				
N ( $\text{NH}_4^+$ ) (mg/kg)	0.07	-0.42	0.42	0.49	-0.25	-0.06	-0.06	0.38	<b>0.56*</b>	0.43	0.09	1.00			
N ( $\text{NO}_3^-$ ) (mg/kg)	<b>0.56*</b>	<b>-0.64*</b>	0.07	<b>0.60*</b>	0.04	-0.10	-0.12	0.37	<b>0.53*</b>	0.42	0.37	<b>0.58*</b>	1.00		
P (mg/kg)	0.34	-0.29	-0.08	-0.02	-0.25	-0.27	0.21	-0.17	0.14	-0.16	-0.06	0.45	<b>0.58*</b>	1.00	
K (mg/l)	-0.07	-0.11	0.22	0.48	-0.08	-0.10	-0.25	0.44	0.37	<b>0.69*</b>	0.14	0.21	0.23	-0.18	1.00

AGG: aggregation; AWC: available water content; HC: hydraulic conductivity (infiltration); SH: surface hardness (penetration); SOM: soil organic matter; PAC: potential active carbon; EC: electrical conductivity;  $\text{NH}_4^+$ : ammonium;  $\text{NO}_3^-$ : nitrate. P: phosphorus; K: potassium.



**Fig. 4.** Radar plot of soil quality index scoring normalized between 0 and 1: (A) a shrubland with different patches (under the shrub, biocrust patches); and (B) a *P. halepensis* forest with different patches (forest understory, forest open patches).

herbaceous plants in the understory of *P. halepensis* forests as a hydro-engineering result from precipitation interception by the tree canopy and belowground competition for soil moisture and nutrients (Maestre et al., 2003, 2012). In addition to hydro-engineering, chemical engineering that resulted in the pine trees' allelopathic effects, influencing the germination and establishment of the understory vegetation, has been studied (e.g. Fernandez et al., 2006).

In relation to belowground patch formation, root traits play a major role in shaping soil properties using a variety of mechanisms. As a major part of belowground structural engineering, their morphological traits, such as root length, density and diameter, strongly influence soil physical properties (Gyssels et al., 2005; Tisdall and Oades, 1982). Other architectural root traits, such as branching, affect water flow in the soil while functioning as hydrological engineers. In addition, root exudation is another root trait that can be classified as a chemical engineer having a strong impact on SQ, by constructing soil aggregates (Tisdall and Oades, 1982) that modulate soil physical properties. We attribute the differences in the belowground patch properties between shrubs and trees to differences in structural engineering by their root systems.

In *S. spinosum*, root architecture is funnel-shaped, which enhances hydro-engineering through concentrating the runoff water and creating high soil moisture in the patch (Segoli et al., 2008). In *P. halepensis*, the root branching is mainly horizontal, which diffuses the water across the landscape, creating lower soil moisture content in the tree patches than in the shrub patches (Maestre and Cortina, 2004; Querejeta et al., 2001). Another type of chemical engineering by woody species that affects the chemical component of SQ is the degree and type of mycorrhizal infection, which impact soil physical and biological composition (Hallett et al., 2009). Unfortunately, no data is available on the differences between mycorrhizal infections in *S. spinosum* and *P. halepensis*.

4.2. Re-engineering of patch properties

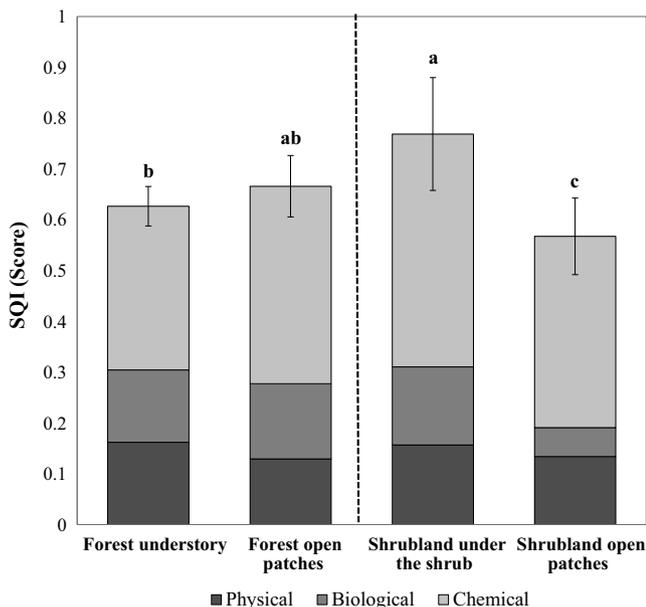
We hypothesize that the process of transforming shrubland into planted forest, by replacing the main woody engineer, will result in a modulation in SQ and a decrease in the ANPP of the herbaceous plants. For the pre-replacement patch mosaic, we found that the shrub patches are higher in physical, biological, and chemical scores, and are significantly higher in total SQI (score of 0.76) than

**Table 3**

Results of principal component analysis (PCA) of soil properties in the desertified shrubland and the forest. Bold and underlined values indicate the soil properties that were included in the index. Bold values indicate the soil properties that weren't included in the index.

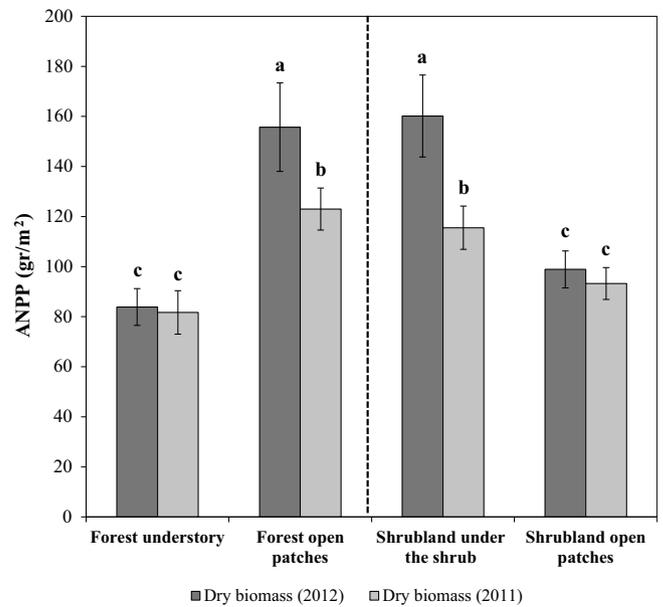
	Scores on PC 1 (46.72%)	Scores on PC 2 (24.22%)	Scores on PC 3 (14.44%)	Scores on PC 4 (9.95%)
Eigenvalue	3.74	1.94	1.16	0.79
Variance	46.72	24.22	14.44	9.95
Cumulative variance	46.72	70.94	85.39	95.34
<i>Soil quality</i>				
AGG (1–6)	–0.88	<b>5.92</b>	0.01	–2.31
RW (m/m)	<b>6.03</b>	–4.49	3.35	1.15
SH (psi)	<b>–7.07</b>	–0.56	–5.63	–1.47
HC (mm/h)	0.72	<b>–3.42</b>	<b>–5.84</b>	1.02
SOM (%)	–0.49	<b>7.29</b>	1.01	1.02
PAC (ml/kg)	0.48	<b>4.69</b>	0.69	3.13
pH	<b>7.05</b>	–4.39	–1.34	3.44
EC ( $\mu\text{S}/\text{cm}$ )	<b>2.83</b>	0.95	–3.43	–0.54
N ( $\text{NH}_4^+$ ) (mg/kg)	<b>–10.1</b>	–2.28	1.47	–2.89
N ( $\text{NO}_3^-$ ) (mg/kg)	<b>6.73</b>	1.93	2.44	–1.17
Phosphorus (mg/kg)	<b>–9.25</b>	–3.54	5.06	–5.55
Potassium (mg/l)	<b>3.96</b>	–2.1	2.23	3.505

AGG: aggregation; AWC: available water content; SH: surface hardness (penetration); HC: hydraulic conductivity (infiltration); SOM: soil organic matter; PAC: potential active carbon; EC: electrical conductivity;  $\text{NH}_4^+$ : ammonium;  $\text{NO}_3^-$ : nitrate, P: phosphorus; K: potassium.



**Fig. 5.** Soil quality index (SQI) in the *P. halepensis* forest and shrubland according to the physical, chemical, and biological scoring transformed data.

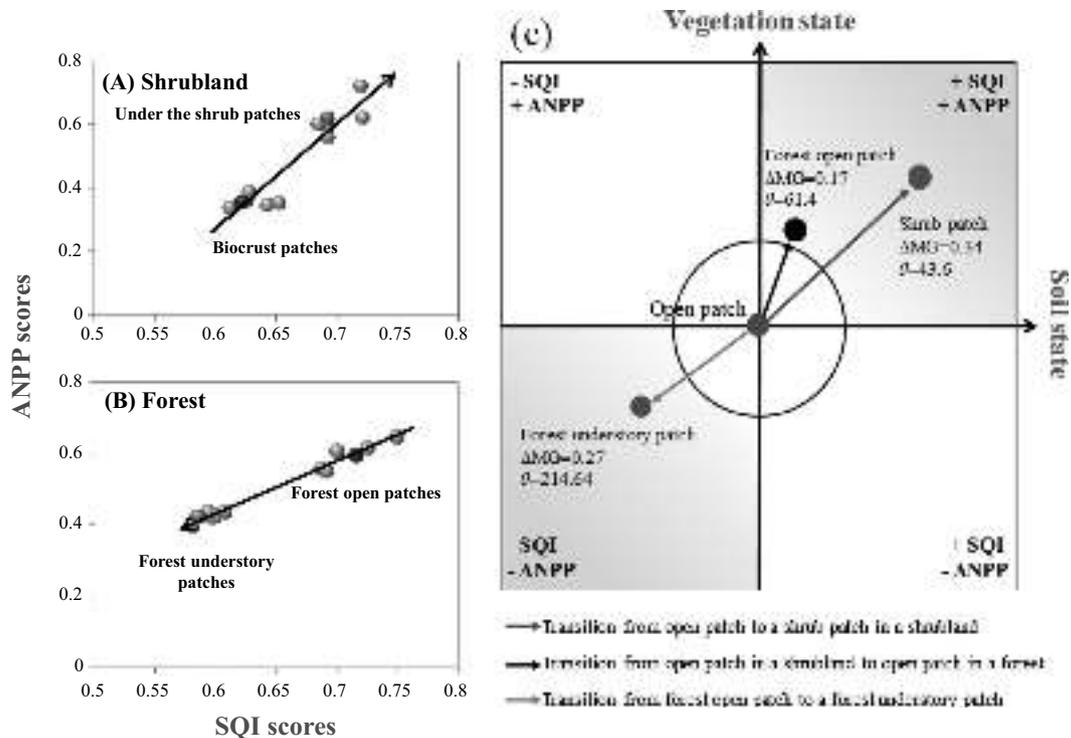
the open crust patches (score of 0.58). We attribute these results to the shrubs' engineering modes as described in the previous section. The web of engineering that transformed a crusted uniform landscape into a non-uniform two-patch mosaic also affects primary production (Fig. 6). We found significantly higher ANPP of herbaceous plants under the shrubs ( $133.6 \text{ mg}/\text{m}^2$ ) than in the biocrust ( $96.5 \text{ mg}/\text{m}^2$ ). Mathematical modeling demonstrates that feedbacks between woody vegetation and resource flows cause the formation of a resource-enriched patch with higher vegetation



**Fig. 6.** The results of the aboveground net primary productivity in the *P. halepensis* forest and shrubland according to the landscape mosaic, average biomass measurements, and standard deviations for the years 2011–2012. Small letters represent significant differences between patches in the different years and between the two systems.

production (Gilad et al., 2004; Rietkerk et al., 2004). We attribute the higher ANPP of the herbaceous plants in the shrub patch to a shrub-soil feedback initiated by the web of structural, chemical and hydrological engineering, terminating in high ANPP (Figs. 5 and 6). We propose that the positive relationships between SQI and ANPP (Fig. 7) also indicate the possibility of below-aboveground feedback relationships, resulting from the cascading effect of shrub canopy and root structural systems, that produce a web of light, chemical and hydrological engineering (Gilad et al., 2004). Therefore, SQI and ANPP trajectories, (Fig. 7), signify the overall ecosystem effects of shrubs as ecosystem engineers. The trajectories, as indicators of the cascading effect of the web of engineering initiated by shrubs, can also indicate a set of ecosystem processes, such as secondary production, decomposition and nutrient cycling, in shrub patches (Li et al., 2008).

The changes in the SQI and ANPP scores and trajectories, in relation to open and under canopy patches, when trees replaced the shrubs, suggest that trees represent a different mode of engineering. We found that the planted forest has higher SQI scores in the open patches than in the understory (scores of 0.67 and 0.62, respectively); however, the difference wasn't significant. In the shrubland, the SQI scores were significantly higher in the shrub patches than in the crusted patches (scores of 0.76 and 0.58, respectively) (Fig. 5). The trees re-engineered the soil properties of the previous two-phase mosaic in two ways: (1) increasing the SQI scores of the open patches; and (2) decreasing the contrast between the SQI of the woody and open patches as our third hypothesis suggested. In relation to the ANPP of herbaceous plants, the trees reversed the performances of the two patch types; higher ANPP scores were found in the open patches than in the tree understory, while in the shrubland, the opposite trend prevailed (Fig. 6). This is in accordance with our hypotheses that the trees re-engineer the soil and modulate the resource-enriched patch formed by the shrub, and decrease the ANPP of the herbaceous plants. However, we did not expect that the trees would reverse the performances of the two patch types (open and under canopy) in terms of ecosystem properties due to re-engineering.



**Fig. 7.** (A) Scatterplot of soil quality index scoring and aboveground net primary productivity scoring in the shrubland system; (B) scatterplot of soil quality index scoring and aboveground net primary productivity scoring in the forest system; and (C) ecosystem state according to the landscape structure of woody engineers and open patches evaluated by soil quality and aboveground net primary productivity. The arrows point to the direction of change from the open to the woody patches, the length of the arrow indicates the magnitude of change ( $\Delta MQ$ ), and slope angle ( $\theta$ ) represents the relative changes in the vegetation and soil states.

#### 4.3. Implications of re-engineering

We propose that in the human-dominant era (Anthropocene), woody species replacement, along with its consequences for ecosystem and landscape processes, will become a common phenomenon driven by global changes and land transformation. There is already evidence that global changes are causing species reshuffling, including species replacement (e.g. Lenoir et al., 2008; Wookey et al., 2009). Processes of global change may introduce new woody species with new engineering traits into the landscape, which would have consequences for below and aboveground engineering processes related to patch formation and its ecosystem properties, such as SQI and ANPP, and landscape processes, such as source-sink relationships.

Climate and land-use change could impact organisms' engineering traits that regulate patch formation via individual plant responses (plasticity) and community-level responses (species replacement). In turn, these responses via new engineering modes, for example, alternation of SQ, may induce new ecosystem properties in the patch, such as changes in ANPP. Thus, the development of frameworks, based on woody engineer replacement, can improve our understanding of landscape-level responses, in terms of patch formation, to global changes. The reorganization of engineering traits by species replacement, resulting from global changes, may induce shifts in patch-mosaic ecosystem properties, which affect both individual patch function and landscape properties as demonstrated in our study. We also propose that global change phenomena can substantially impact a suite of engineering traits due to the replacement of woody species with cascading effects on patch-based ecosystem processes. Therefore, ecosystem-engineering-based approaches offer a potential framework for elucidating the complexity of ecological responses to global changes and their consequences for regulating landscape and ecosystem processes.

In addition to contributing to the understanding of global changes and their effects on landscape and ecosystem processes, the EE framework is an important tool with which to cope with land transformation's ecological consequences, in general, and those of landscape restoration, in particular. Land transformation, by definition, implies species replacements that, in many cases, include engineering species. We believe that, in essence, the methodology used in this paper is applicable for studying land transformations that involve EE substitution. An engineering framework is also relevant for ecological restoration projects. Consideration of the engineering effect of planted woody vegetation in restoration could assist in predicting the end results of the restoration effort.

#### 5. Conclusions

Our specific conclusions are as follows: (1) the transformation of shrublands to forests, driven by the replacement of the principal EEs (shrubs with trees), results in a new patch mosaic with a new set of ecosystem properties indicated by the SQI and the herbaceous plant ANPP scores; (2) the SQI and the herbaceous plant ANPP scores are emergent ecosystem properties resulting from a web of engineering mechanisms that induce a chain of ecological processes initiated by trees as a landscape modulator by patch formation and terminated by SQI and ANPP as ecosystem properties; (3) the trajectories of the SQI and ANPP scores indicate the magnitude and the direction of changes in the patch state in a transformed landscape; and (4) changes in the SQI and ANPP scores and their trajectories during landscape transition are a result of different ecosystem engineering mechanisms of patch formation. In general, we conclude that a conceptual framework based on woody engineer replacement can improve our understanding of ecosystem level responses to land transformation driven by restoration efforts.

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