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# 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.



## 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 by 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 $km^2$ 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 there 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 $cm^3$) 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