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ECOLOGICAL AND MICRO-TOPOGRAPHICAL IMPACT OF *MESSOR EBENINUS* AND *MESSOR ARENARIUS* ANTS ON ARID LOESS RANGELANDS OF THE NORTHERN NEGEV

ABSTRACT. Improper land management, such as over-grazing in arid areas, has negative effects on the local ecosystems for both the short and the long term time periods. An effective rehabilitation scheme requires human interference by introducing ecosystem engineering organisms together with activities that encourage the spreading and the reproduction of the local plant and animal species. Most of the former studies in arid lands focused on shrubs as engineering species, and much less on other organisms. The major focus of this study was on assessing the impact of *Messor ebeninus* and *M. arenarius* on the micro-topographic patterns of arid areas using unique spatial statistical tools designed solely for this purpose. As a case study, the nests' sizes and their distribution were compared between two adjacent shrublands with similar geographic outlines during 2008 and 2015. One of the shrublands was moderately grazed for the last 20 years (at the far past it was exposed to over-grazing), while the other one is still exposed to over-grazing. The results collected in 2014 at the shrublands and at the adjacent loess area demonstrate the spatial ecosystem ability of the *Messor sp.* to engineer and beneficially modify their environment by enlarging the water conserving area, increasing the soil fertility and vegetative productivity, and finally accelerating the whole area rehabilitation.

KEY WORDS: *Messor ebeninus* and *Messor arenarius*, Micro-topographic impacts, Ecosystem engineers, Rangeland management temporal changes, Shrub' patches vs. ants' nests

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INTRODUCTION

Overgrazing has negative effect on the ecological system of the Northern Negev [Olsvig-Whittaker et al. 2006], and other arid areas all over the globe [Belsy 1992]. This negative impact has been demonstrated by decrease in flora and fauna biodiversity [Leu et al. 2014], damage of soil properties [Greenwood and McKenzie 2001], change in the micro-topographic structures (shape, size and distribution of different landscape patches) [Steinberger et al. 1992; Pablo and Martin 2006], and in some cases, even damage to the macro-topographic structures (sheet erosion, rills and gullies formation) [Hoffmann et al. 2014]. In extreme cases, such as at wide parts of the Northern Negev, the area rehabilitation cannot rely solely on natural processes. Therefore human interference including drastic change of the land management is required [Aronson et al. 1993].

The so far used management for rehabilitation of over-grazed¹ areas is based on the complete enclosure of a given area and prevention of any grazing at it for several years [Asefaet al. 2003]. Although such management policy has its ecological advantages, it also has crucial drawbacks associated with its long term application such as high costs, and the dependency of the local population on grazing as the main income resource [Sidahmed 1996].

An alternative approach that allows accelerating the natural rehabilitation processes is based on introduction of biological ecosystem engineers [Byers et al. 2006]. Ecosystem engineers were defined by Jones [1994] as: «Organisms which create modify or destruct habitat and directly or indirectly influence on the availability of resources for other species by generating physical changes in biotic and abiotic parameters». The 'ecosystem engineer' based approach was studied mainly on plants with an emphasis on shrubs [Sarah 2002] and less on other taxonomic groups

such as isopods [Shachak and Jones 1995], porcupines [Wilby and Shachak 2004] and ruminants herds [Greenwood and McKenzie 2001; Stavi et al. 2009]. While many studies stressed the effect of ants on the areal flora seedbank [Wilby et al. 2001], nest fertility [Cammaraat et al. 2002], and even local insect population [Offenberg 2015], none of them took into account their spatial patterns such as spreading, correlation to the other areal bio-patches (for example, shrub), and the effects of changes in area management on these patterns.

Former observations of our group at the continuously over grazed areas all over the Negev revealed death of shrubs, and lack of new shrub establishment due to consecutive dry years. While in general no significant change was observed in ant nests number and size, some of them did demonstrate an increase in size. Additionally, the nests' herbaceous cover, both of the abandoned and the active ones, was higher and more productive than that of the surrounding area.

The term 'harvester ants' group is related to species which consume seeds as their main feeding resource. The ants collect the seeds and store them in nests, which they built at the communal chambers. In arid areas they have an important role as seeds dispersal agents for 'myrmecochorous' plant species, while in case of other plant species they serve as seeds predators [Arnan et al. 2012]. One of the interesting phenomena related to harvester ants is their colony spreading into new locations and establishment of 'daughter' nests. Locating to the new colony (daughter nest) is done by two parallel mechanisms. The first mechanism is patrolling in which the nest's queen appoints patrollers to evaluate viability of the soil in a given plot for the daughter nest by digging 'experimental holes'. The collection of these holes is defined as a 'patrolling route' [Gordon 1987]. The second mechanism is a 'Nuptial flight' in which young virgin queens from the source nest are carried by the wind and those that find adequate places, build new colonies and nests [Hoelldobler, 1976].

¹ This term will be used in the text for areas that were exposed to unrestricted grazing and that have observable decrease in annuals cover, and/or their degradation along the years.

While in general these mechanisms are clear, many behavioral questions' mainly regarding the data transmission of the patrollers' findings to the young queens and its role in their final decision for colony location' remain unanswered. Many studies were carried out regarding behavioral, chemical, and physical patterns of the harvester ants [Cammaraat et al. 2002]. Additive studies were implemented regarding their local effect on plant species [Brown and Human 1997]. Nevertheless, there are still wide gaps regarding their spatial impact on fertility and productivity of agricultural fields.

Specifically, the objective of this study was to define the spatial impacts of harvester ants on grazing lands under different 'field conditions' (drought, different rangeland management, etc.). We chose as a research site area in the northern Negev as it has dominant rangeland use [Ginguld et al. 1997] with large presence of the *Messor ebeninus* and *M. arenarius* harvester ants (the most wide spread ant species among the 23 species that are known in Israel) [Steinberger et al. 1992; Ofer 2000]. Due to the fact that the wide part of the northern Negev is defined as 'shrubland' (Shachak et al. 1998), comparisons of the nests distribution were implemented on shrub patches and the respective inter-patch area (matrix).

TOOLS AND METHODS

Site of study

The research took place in Chiran area (East-West: 34°59'04"E, North-South: 31°19'34"N), North of Hura Bedouin settlement, and South of Yatir forest, Northern Negev, Israel. The area has hilly topography (250 m ASL). The soil is Sand-Clay [USDA 1999].

Climatically, the area is located in the transition zone between the arid and semi-arid regions with annual mean precipitation of 150 and 250 mm originating from winter rains (November-April) and convective storms [Goldreich 2003]. The rains are characterized by high inconsistency with

regard to their amounts, locations and intensities [Ward et al. 2000].

The temperatures at the cold season (December-February) are 8.1 -19.2°C, while those of the hot one (June-August) are 21-34°C (Data from Israel Meteorological Services).

This research is an episode of the much larger long term study on arid shrublands at the area, started at 2006 and that continues till this day. The core of the study was implemented between 2008 and 2010. Although the rain amounts were similar between 2008 and 2009, 155 and 159 mm year⁻¹ respectively, due to the lack of homogeneous rain spreading, 2009 was considered as the drought year, as opposed to 2008. In 2010 the precipitation amounts were 237 mm per year (IMS).

Ecologically most of the area is defined as steppe and rocky shrubland [Goldets and Boeken 2004; Stavi et al. 2009] which has been exposed for decades to unrestricted and intensive grazing accompanied by a decrease in floral cover and enhanced land degradation [Olsvig-Whittaker et al. 2006]. The intensive grazing has led to low perennials cover (60-700 shrubs per hectare) and massive soil erosion phenomena [Lin et al. 2010].

Between the years 1992 and 1994 several family farms were established by authorized farmers with the objective of decreasing the soil erosion, and land rehabilitation by implementing sustainable grazing management illumination of grazing at annuals germination stage, reduced in annuals growth and spread grazing at the dry season [Swanson 2008]. As a result a gradual rehabilitation was observed with regard to the soil fertility, whereas the surrounding overgrazed area continued to experience a dramatic decrease of the vegetation cover together with soil erosion acceleration along the years.

Two plots located inside the representative shrublands were chosen, each having 15X15m area, 25% rockiness, south aspect and similar vegetation composition based

mainly of shrubs from Irano-Turanian and Saharo-Aribian biogeographical origins, and *Sarcopoterium spinosum* from Mediterraneanone [Yair and Danin 1980]. The moderately grazed plots was located inside Yatir family farm, while the over-grazed one was located 200m east, outside of all family farms. It has to be stressed that the definition of area as 'over-grazed' was based on several observations, measurements and data from the local farmers with regard to the state of vegetation cover and soil erosion prior to the study. The soil state findings were compared to the data and the definitions of Olsvig-Whittaker et al. [2006]. Complementary observations were collected in 2014 from additional site. This site, which will be defined along the text as 'wadi Atir, is located in the south part of Eshtamoa basin (part of which has been defined by the local population as wadi Atir), 7 km southeast from the main site of 0.4 ha size. In the past, the site and its surroundings suffered from massive soil erosion, but from 2012 it is under rehabilitation processes due to constructions of topographic soil structures along its streambeds- called 'limans' [Prinz and Malik 2002]. Parts of the remaining areas were tilled and sowed with winter cereals and rain-fed, while other sections were fenced and were left unmanaged in order to serve as control plots for agricultural research. The closeness of the differently managed plots allowed continuous assessment of ants' settlement in them [Mor-Musser and Leu 2012].

Patches analysis

In order to accumulate Folgarait [1998] finding on the effect of ants on ecosystem functioning, we tested unique methodology which based on field work and lab analyses.

Patch definition and documentation at field.

Arid shrublands are defined as composed of scattered shrubs and other perennials that are located on micro-topographic patches surrounded by matrix [Goldets and Boeken 2004]. In our primary observation all over the Negev, we noticed

the similarity of the micro-topographic patterns of the landscape patches which included presence of ant nests and perennials and their visual difference from the surroundings. For this study we examined the effects of the nests and perennials using the same methodologies as did Steinberger et al. [1992]. In order to analyze the different landscape patches in comparison to the surroundings, at both sites we defined the patches' patterns as follows:

- a. Loose area with unique micro-topographic predominant patterns as compared to the surrounding area (raised or lowered).
- b. Area without soil disturbances caused by human or fauna activities (for example, rodents diggings), except ants activity.
- c. Area which includes nests, perennials (shrubs, geophytes, hemicryptophytes and perennial herbs) and several annuals which were documented in literature as having noticeable impact on their ecosystem [Lacey et al. 1989].

Note. In stand-alone case, the 'nests' size, was defined based on the total area of its mounds (composed from reflected ants entrance holes) and reflected dumps [Rissing, 1986]. Nests with additional bio-groups were treated based on their total patch area. Due to research limitations the *Messor ebeninus* and *M. arenarius* nests were documented altogether, although their ants different foraging characters [Avgar et al. 2008].

Division of the patches' biogenic components into study groups.

In order to define the interactions between the nests and the biogenic activity inside the patches, the studied organisms inside the patches were divided conceptually into three groups: 'shrubs' (including *Thymelea hirsuta*, *Pituranthos triradiatus*, *Noaea mucronata*, and *Sarcopoterium spinosum*), 'perennial herbs' (*Asphodelus ramosus*, *Echinops adenocaulos* and *Centaurea hyalolepis*) and 'ants'. The nests activity (or abundance) was defined based on ants' entrance observations at the time of

study based on Gordon and Kulig [1996] principles. Patches which contain the same 'examined group', were defined along the text as 'sub-plot'. The matrix, which represents the area between the patches, was also defined as sub-plot.

Size and distribution analyses of the patches.

The longitudinal and lateral axes of the different patches and ants' nests were measured, and their areas were calculated based on elliptic shape form [Mailleux et al. 2003]. Specifically, the sizes of the nests were determined based on the ants' external activities (location of entrance holes, soil dumps, litter dumps etc.). Based on Gustafson [1998] findings, we implemented unique analysis methodology for the composite patches (those that include more than one of the examined groups). Each composite patch was analyzed as several separate ones. Each of them contained one examined group having the size of the whole source patch. For example, source patch (area with axes of 0.5 and 0.6 m) which included ant nest and *Noaea mucronata*, was treated as two elliptic patches with size of 0.24m², one with 'shrubs' and the other with 'nests'. The mean of the allocated patches sizes per each sub-plot was used to assess the impact of the 'examined groups' on the area micro-topography' and as result on the whole ecosystem parameters by assuming that higher value represents bigger influence [Mor-Musser et al. 2013]. Importantly, for the calculations, the number of individuals from examined groups was not taken into account, only their appearance was valid. Using this type of analysis, we defined additional factor per each 'examined group' termed 'allocated heterogeneity' that expresses the number of different groups in the studied patch. For example, in patch with ants' nests and *Echinops adenocaulos* perennial herb, the 'nests' and 'perennial herbs' groups got the value '2' for 'allocated heterogeneity' parameter, while in patch with *Thymelea hirsuta* shrub value of '1' was allocated per the 'shrubs' group. Afterwards, per each 'examined group', the ratio between composite appearances ('allocated heterogeneity' equal or above '2') and the total ones was calculated.

Defining the correlations between the nests development and shrubs growth

One indication for the reciprocal impacts between the ants and plant development is analysis of their sizes in combined patches [Gustafson, 1998].

For this propose we chose the *Thymelea hirsuta* which is one of the most widespread shrub species at the site of study. We noticed that in most *Thymelea h.* patches there were ants' nests. For examining the correlation between the *Thymelea h.* growth and the nest development, we compared the *Thymelea h.* canopy and nest sizes (only in patches containing stand-alone *Thymelea h.*). Additional comparisons were done in patches containing groups of *Thymelea h.* by comparing their number and the nest sizes [Rico-Gray and Oliveira 2007].

Herbaceous productivity analysis. The most representative parameter for identifying degradation or rehabilitation process in arid areas is the herbaceous productivity [Lin et al. 2010]. For measuring the herbaceous productivity, the herbaceous samples were harvested randomly at March 2010 using 20X30cm iron frames from sub-plots containing stand-alone 'examined group' (five replicates per each sub-plot). The samples were dried in 60°C per 48h according to the protocols of Sava [1994]. The values were expressed as Kg per m². It has to be stressed that the samples from the nests were taken from their edges in order to minimize the damage [Wagner and Jones 2006]. In addition to the comparisons of the average herbaceous productivity between the different sub-plots, the obtained values were used for estimating the contribution of the nests and shrub 'examined groups' to the herbaceous productivity of the whole shrubland by subtracting the obtained matrix herbaceous biomass from the examined group ones and multiplying the results by their coverage ratio. Here we bring calculation example for the 'shrubs' defined group. The calculation was carried out in the same manner for the nests. The equations which were developed based on Wagner et al. (2004) findings, were as follows:

$$ShrubsAr_{HerbBM.Contribution} = (Shrubs_{HerbBM} - Matrix_{HerbBM}) * Shrubs_{Coverage} * 10$$

$ShrubsAr_{HerbBM.Contribution}$ - The herbaceous biomass contribution of the 'shrubs' (compared to the hypothetical state of an area composed of matrix without patches) [Ton ha⁻¹]

$Shrubs_{HerbBM}$ - The average herbaceous biomass of the 'shrubs' per area unit [Kg m⁻²]

$Matrix_{HerbBM}$ - The average herbaceous biomass of the matrix per area unit [Kg m⁻²]

$Shrubs_{Coverage}$ - The partial coverage of the shrubs' patches from the entire area.

'10' is for units matching

Soil properties analyses. In order to assess the effects of *Messor ebeninus* and *M. arenarius* on soil nest [Dosta'let et al. 2005] describe on *Lasius flavus* ants, at April 2009 soil samples of 0.5Kg were collected from the moderately grazed plot. All samples were taken from the 20 cm thick upper soil layer which represents the root zone of the most annuals [Schenk and Jackson 2002]. The samples were transferred to Gilat Field Services Lab for nutrient analyses, based on their importance to ecosystem fertility including Soil Organic Carbon, N_{total} and P-PO₃ [Zaady et al., 2001]. Additionally to these analyses, two parameters reflecting the water absorption and holding capacities were analyzed in the different sub-plots, including field capacity and infiltration schemes [Rico-Gray and Oliveira 2007]. All factors were measured with four replicate sper each sub-plot, based on Sava [1994] protocols. The obtained values were also used for estimating the contribution of the nests and shrub patches to the whole mineral content of the shrubland. This was achieved by subtracting the matrix values from those of the sub-plots and multiplying the results by their coverage rate as follows from the Potassium content measurement example:

samples were of half litter volume and dried overnight at 105°C)[Sava 1994].

In order to obtain a more comprehensive view on the impact of the nests on the water balance of arid ecosystem, a set of infiltration measurements were taken from wadi Atir site in bare, *Messor abensis* nests, and *Anabasis setifera* patches (the most common shrub species at the site of study). The measurements were implemented using Decagon® mini-disk infiltrometer for duration of six minutes [Decagon, 2012].

Statistics analyses. Confidence analyses between the different plots with regard to the herbaceous biomass, patch sizes, nutrients concentrations, etc. were implemented using ANOVA test. The correlations between the nests sizes and *Thymelea h.* growth were analyzed by linear regression. For both types of analyses we used JMP® ver. 5.0 (α=0.05).

RESULTS

The quantitative analysis of 2008 and 2009 findings strengthened the trends observed from the preliminary observations. The nests were much widely distributed in moderately

$$Nest_{P.Contribution} = ((Nests_{(P)} - Matrix_{(P)}) * Nests_{Coverage}) * 0.2 * 1.2 * 10$$

$Nest_{P.Contribution}$ - The nests contribution to the Potassium amount of the root zone of the shrubland [Kg ha⁻¹]

$Nests_{(P)}$ - The average Potassium concentration per nest volume unit [Kg m⁻³]

$Matrix_{(P)}$ - The average Potassium concentration per matrix volume unit [Kg m⁻³]

$Nests_{Coverage}$ - The relative cover of the nests from the whole area (expressed as decimal fraction). '0.2' represents the root zone of the annuals [m]

'1.2' represents the Bulk density [Kg per m⁻³]

'10' is for units matching

Note. The specific weigh per volume was calculated by averaging the drought weight of five samples with known volume (the

grazed shrubland than at the other patches. Our findings regarding the coverage of the nests in the moderately grazed area at 2009 were similar to the preliminary observations

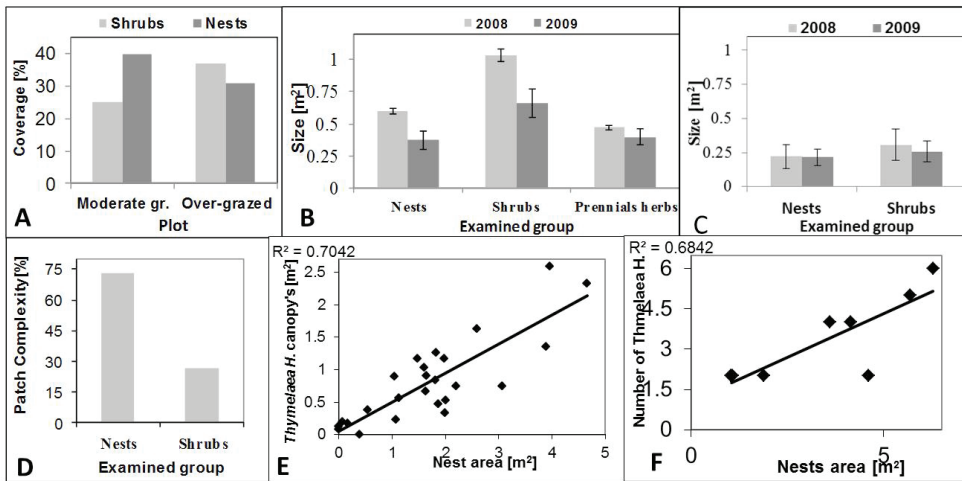


Fig. 1. The spatial impact of the different patches on micro topographic patterns of the ecosystem.

A. The coverage of 'nests' and 'shrubs' sub-plots in the moderate and over-grazed plots at 2009; B. The sizes of the different sub-plots in the moderate grazed plot at spring 2008 and 2009; C. The 'shrubs' and 'nests' sub-plots in the over grazed site at spring 2008 and 2009; D. The percentage of the 'complex' patches with relation to each 'examined group' at 2009; E. The effect of nests size on *Thymelaea hirsutae* canopy size; F. The effect of nests' size on the number of *Thymelaea hirsutae* shrubs.

Thin lines on columns represent +/- Standard errors.

*The number of patches containing herbaceous perennials was negligible in the overgrazed plot, so it is not presented

(Fig. 1A). There was almost 50% higher distribution of the nests than the calculated value for the shrub patches (40 and 30%, respectively). Additionally, the calculated nests sizes were much higher as compared to the 'perennials herbs' sub-plots in 2008 (in 2009 due to the drought there was a decrease in all patches with regard to the size as compared to 2008, but still the decrease in the nests size was lower than that at the shrub' patches, Fig. 1B). In the over-grazed site both nests and shrub patches maintained their sizes between the years (Fig. 1C). The ants' contribution to the biodiversity is evident from Fig 1D, whereas 75% of the nests appeared in complex patches as compared to only 25% in case of the shrubs. Positive correlation was found between the nest size and canopy area and between the number of *Thymelaea hirsutae* shrubs (Fig 1E and 1F).

The annuals characteristics at the different sub-plots

Visual observations revealed that opposed to the diverse range of annuals in the 'shrubs'

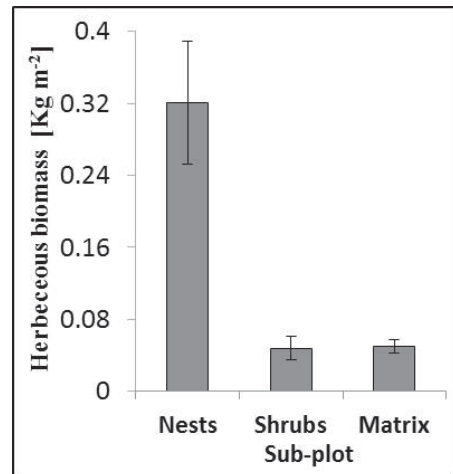


Fig. 2. The mean of herbaceous biomass in the different sub-plots, in the moderately grazed plot at spring 2010.

Thin lines above and below columns represent +/- Standard errors.

* - Statistical confidence (α) = 0.05

and 'perennial herbs' sub-plots, the nests are as were characterized mainly by Gramineae species (*Stipa capensis*, *Aegilops crass* and *A. Kotschy*), while at the other sub-plots these species were only around 25% of the total annuals. These higher rates of cereals could indicate combined predation and dispersion scheme of a non-myrmecorous plant species [Retana et al. 2004]. Additionally, plants from the same species were more productive in the nests than in the other patches. Analysis of the total herbaceous biomass demonstrated significantly six fold difference between the nests and shrub sub-plots, or the matrix in favor of the nests (Fig. 2). As noted earlier, the analysis was done on active nests, yet, similar effects were found also in case of the abandoned ones [Farji-Brener 2005].

The soil quality parameters of the different sub-plots

The soil quality parameters were divided into fertility and hydrological ones (Fig. 3 and 4, respectively)

From Fig. 3 it could be noticed that with regard to all measured nutrients parameters, higher values were found in the nests than in the matrix soil. In the case of Potassium, even higher results were observed when compared to the 'shrubs' patches (Fig. 3C).

The highest field capacity values were measured at the 'shrubs' patches soil, middle values were found in the nests, and the lowest ones were in the Matrix. Regarding the water balance parameters, the high water capacity

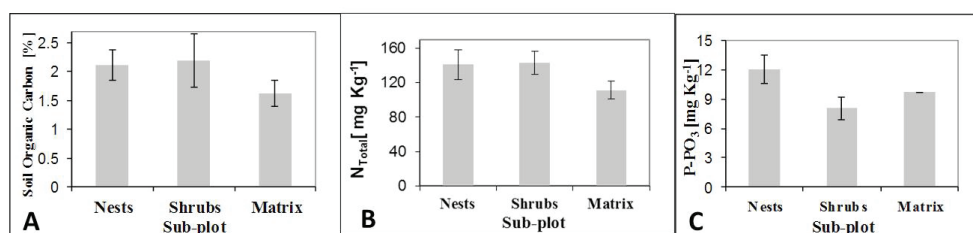


Fig. 3. Soil nutrients concentrations in the different micro-topographic groups moderately grazed plot at spring 2009.

A- Organic carbon; B- Nitrogen (total); C- Potassium.

Thin lines above and below columns represent \pm Standard errors.

* Measured in patches with stand-alone 'examined group'

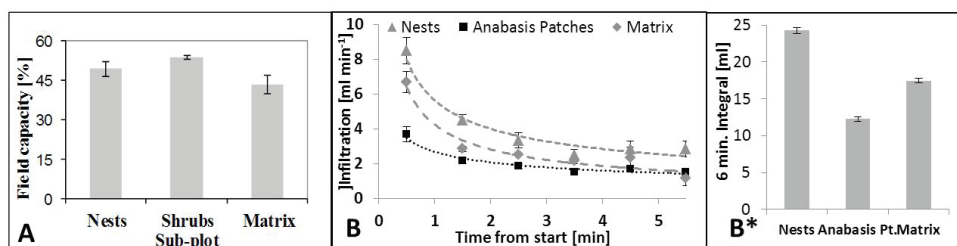


Fig. 4. The impact of the different groups on soil water balance.

A- Field capacity, moderately grazed shrubland at spring 2009; B- Infiltration in the soil of nests, shrub patch and matrix micro-topographic groups at wadi Atir area, summer 2014. Thin lines above and below columns represent \pm Standard errors

was found at the nest soil as compared to the bare soil (Fig. 4A). The infiltration rates were higher in the nests for the whole duration of the study as compared to the matrix, and even when compared to the *Anabasis setifera* shrub patches (Fig. 4B). These findings are adding new aspects to ones of Dostal et al. [2005] on *Lasius flavus*.

DISCUSSION

The study findings are an indication of the beneficial effects of ants' nests on the surrounding ecosystem much beyond being bio-indicators of the soil fertility [de Bruyn, 1999]. Quantification of the spatial-ecological impact was achieved using measurements on the number and sizes of the nests in the over- and moderately grazed sites by making an assumption that the spatial difference among these sites could indicate the ants' dynamic contribution during the transition from over grazing into moderately grazing regime. The comparison between the years hint on the climate dependency of this dynamics, whereas the comparison to the shrub patches gives attribution points to this dynamics. It is easily observed that at the over-grazed sites the number of nests was equal to the shrub patches, but after decreasing the grazing intensity, a massive propagation of the nest has occurred, which in turn contributed to the herbaceous growth at the nest boundaries. The *Messor* sp. resistance to drought stress in arid areas is exemplified by dolichoderine ants [Bestelmeyer 1997] and is evident from the study by Pihlgren et al. [2010] on hilly topography and grazing in Europe. It is also evident from the preservation of the nests' numbers and sizes in the drought year (2009 compared to 2008, Fig. 1B), as only a small decrease of them was observed at the moderately grazed site (Fig. 1C). It has to be stressed that the nests sizes were estimated based on the ants' external soil disturbances (entrance holes, dumps, etc.), and not the total area of the nests rooms and channels, so the whole impact was assumed by us to be higher than the calculated one in the paper of Tschinkel [2004].

The documented correlations between the nests and the number of *Thymelaea hirsutae*

shrubs, the nests and *Thymelaea hirsutae* canopy sizes, the nests and other species such as *Anchusa strigosa* at the site of the study provided additional evidence for the beneficial impact of nests on the perennials, and not only on the annuals (mainly cereals as stressed earlier [Brown and Human, 1997]). Nevertheless, in case of several species such as *Pituranthos triradiatus*, the ants' activity was not observed under the shrub canopies. Such lack of association could be explained by the higher alkaloids concentrations of this plant that opposes nests' establishment [Hamada et al. 2004]. The ants positive impact on the arid ecosystem is also evident from the higher ratio of the nests in the complex patches, which indicate their better 'hospitality' rate with compare to the shrubs (Fig. 1 D) and the 'perennial herbs' group (data not shown) [Mor-Musser et al. 2013]. One of the most limiting factors for the functioning of arid ecosystem is the water holding capacity, which is crucial in resisting the inconsistency patterns of the precipitation (with regard to their amounts, spreading and intensity) [Le'onard and Rajot 2001; Ward et al. 2000].

The presence of ants positively contributed to water holding of the soil since the infiltration rates and the field capacity were higher compared to the matrix. It has to be stressed, as opposed to the findings of the most former studies, which claim that the shrub patches reduce the runoff and increase the soil' water holding capacity [Ludwig et al. 2005], the measured infiltration rates of *Anabasis setifera* patch were lower than those of the matrix plots. Such a discrepancy could be explained by the dependence of the infiltration rates on the shrubs' root system which is tightly correlated to the local conditions [Mitchell et al. 1995]. Thus, the area which acts as water reservoir in arid areas has been increased in the presence of ants [Le'onard and Rajot 2001].

Our findings, concerning the higher nutrients concentrations in the nests, together with the increase in the water holding capacity are similar to those of Ludwig and Tongway [1995] on shrub patches. Their Sink-Source theory view on the impact of the shrub patches on the ecosystem fertility could be

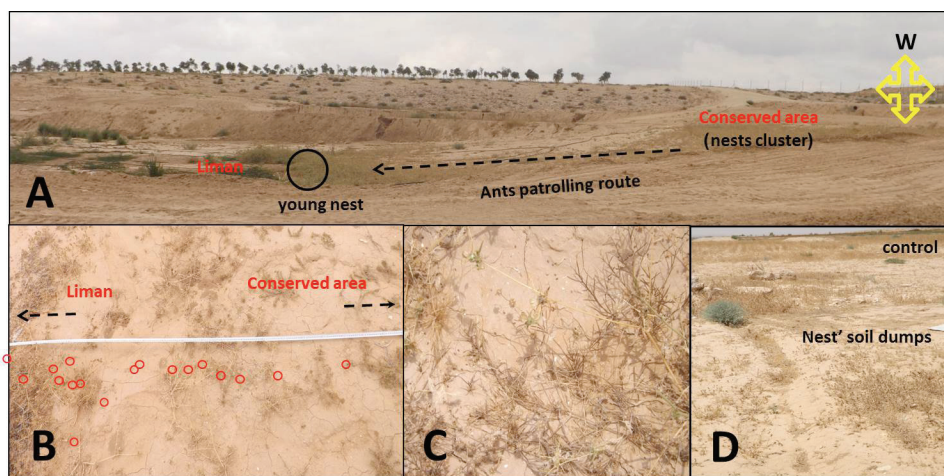


Fig. 5. The spatial effect of *Messor* sp. ants on area under conservation process (1 year from establishment), wadi Atir area, summer 2014.

A- Far view of the ants patrolling route from undisturbed plot to area after massive soil design (Limán); B- Close-up of the young nest inside the liman (The nest' entrance holes have 'X' shape, each edge as 1.9 m with soil dumps inside); C- Close up of the ants patrolling route (length 3.5m); D- Soil dumps from nest located in conserved area (one of the Byzantine farms)

also valid in case of the nests. In accordance to their theory, the nutrients that have been collected during the rain period from the surrounding sources to the nests, have gradually defused underground laterally from the nest areas to the surroundings after that. Thus, the nests were able to add 0.55 ton herbaceous biomass per hectare to the bare soil value, compared to addition of only 0.23 ton ha⁻¹ herbaceous biomass in case of the shrub patches. Importantly, the bare soil is assumed to contain 0.8 ton ha⁻¹ of herbaceous biomass. Additionally, the nests added to the bare soil values around 8.4 Kg ha⁻¹ of nitrogen and 1.9 Kg ha⁻¹ of organic carbon. The calculated values of nitrogen and organic carbon for bare soil in relation to root zone depth were 0.3 and 45.3 Kg ha⁻¹, respectively. Remarkably, similar results were obtained by the authors (unpublished data) on abandoned nests, which could hint to the long term effects of the *Messor* sp. nests, as documented on patches with dead shrubs [Jouquet et al. 2007]. Importantly, the samplings of the soil for the nutrient analyses were taken in the spring, so the results could be different in other seasons, due to the different dynamics of the nests and shrub patches [Zaady 2005].

Additional impact pattern of the nests on their surrounding ecosystem was observed after the heavy rain event in January 2013 (the rain amounts between the 8 and 10 of January in the site of study were 65mm, data from the farm owner) as soil dumps flooding from the nests to their sloped surrounding areas were observed. Specifically, in wadi Atir we found organic matter concentration of 14.4% in the soil dumps from nest in conserved area, compared to only 2.2% in adjacent conserved location (Fig. 6D). These results are in support of Cerda and Jurgensen [2008] findings, and add new aspect to the study of Wagner and Jones [2006] on the ants' impact on ecosystem fertility.

Observations from wadi Atir site at 2014 demonstrated the role of harvester ants' colonies spreading as the first step of degraded areas rehabilitation. This is achieved by the very presence of dense patrolling routes between source nests located at conserved plots and the daughter nests located at the degraded areas [Gordon 1987]. Fig. 5A-C presents patrolling route between the conserved and the degraded plots (created after massive groundwork). It has to be stressed that at the edges of the daughter

nest we noticed in 2015 evidence of massive seedlings germination and annuals growth, much higher than at the surrounding area. These observations strengthen the findings from the main research site at Yatir farm about the dynamic of ants in area which was previously disturbed by over-grazing and which is now under conservation.

Based on the all former findings one can summarize the beneficial impact of ants on the arid ecosystem in the scheme of Fig. 6 which could be divided into several stages as follows:

Stage 1. Ants from the source nests settle in the young nests (Fig. 6A-C) [Gordon 1987; Schultheiss et al. 2010].

Stage 2. While the young nests in the areas exposed to over-grazing are minimally developed (Fig. 1C), in the moderately grazed areas the ants' activity creates patches enriched with nutrients (Fig. 4 A-C) and increased water holding capacity (Fig. 5).

Stage 3. The high nutrients concentrations together with the high water holding capacity encourage the primary production of annuals biomass which is an intermediate

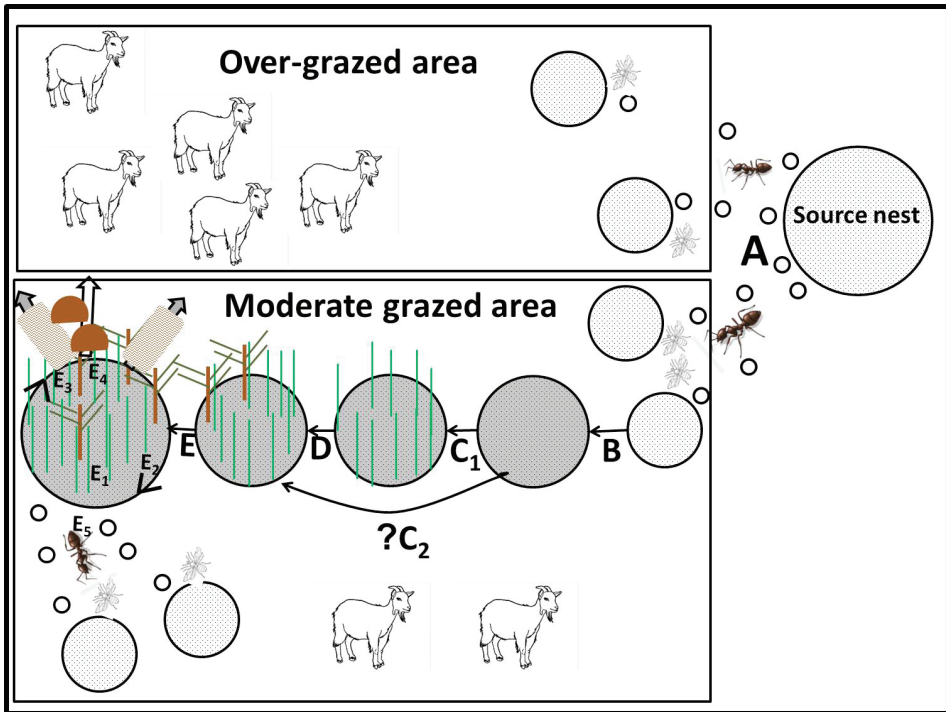


Fig. 6. The schematic representation of interactions between annuals, shrubs and nests in arid land.

A- Patrolling from the source nest and their establishments in new areas; B- In the moderately grazed area the nest absorb nutrients and water which cause its subsequent size enlargement (less common state in the overgrazed area); C1- The nest size enlargement and the higher nutrients concentrations encourage annuals establishment (mainly herbaceous species); C2- Based on Davidson and Morton [1984] findings there is higher germination and growth of several perennial species inside nests, even without the former settlement of the annuals, which may settle later on; D- The annuals growth encourages perennial germination and growth; E- Due to the ants activity and flora growth the patch' soil fertility has been increased (E1) and its size has been enlarged (E2), the surrounded ecosystem has been fertilized based on Ludwig and Tongway [1995] theory (E3) and based on the soil dumps spreading (E4), other ants are emissaries for patrolling (E5) (occur only in active nests).

step before perennials settlement (Fig. 2 and 3) [Farji-Brener and Ghermandi 2004].

Stage 4. Shrubs establishment.

Stage 5. Due to the shrubs establishment and their canopy enlargement, the ants' activity also increases in a positive feedback loop (Fig. 1B and 1E), along with the increase in the patch fertility (Fig. 1D). This leads to the rise in the fertility of the surrounding ecosystem according to the Source-Sink theory of Ludwig and Tongway [1995] and spreading of the nests' soil dumps (Fig. 6D). Parallel to these stages, ants continue to establish new young nests [Mailleux et al. 2003].

Optional stage related to several perennial species could be also defined. At this stage, the increase in the nutrients, moisture and the other nests dependent characteristics could encourage the germination and growth of perennials, even without the primary stage of annuals establishment and growth as demonstrated by Davidson and Morton [1984] on *Acacia* species.

It has to be stressed that these effects on the ecosystem are pronounced even in

case of abandoned nests as found by our observations and based on Bieber et al. [2011] findings on leaf cutting ants' nests, which indicate the long-term effects of the nests on the ecosystem.

CONCLUSION

This paper indicates the positive impact of ants belonging to *Messor sp.* on arid ecosystem. This influence increased and spatially enlarged along the years, even in cases whereas the nests have been abandoned. These paper findings are emphasizing the need to avoid restricting the ants' activity, due to its tight correlation to the arid ecosystem functioning.

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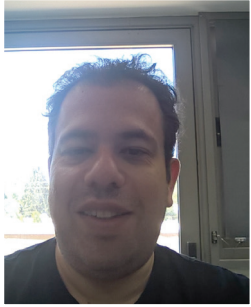
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