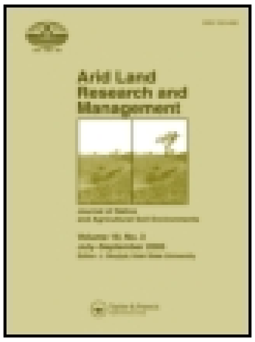

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Assessing the effects of shrubs on ecosystem functions in arid sand dune ecosystems

Azam Khosravi Mashizi and Mohsen Sharafatmandrad

Department of Natural Resources, University of Jiroft, Jiroft, Kerman Province, Iran

ABSTRACT

Shrub species play an important role in providing ecosystem functions and these functions may vary based on dominant shrubs and their facilitation roles in the arid ecosystems. This study was done to assess the potential of three shrubs (*Tamarix macatensis*, *Calligonum polygonoides*, and *Haloxylon ammodendron*) for providing three functions i.e. soil fertility, soil stability, and habitat provision in sand dune ecosystems of Iran. Two ecological indicators were selected to measure each function (soil organic matter content and litter mass for soil fertility; mound height and clay content for soil stability; understory plants and macrofauna diversity for habitat provision). As well, some shrub traits were measured for each shrub to assess their relationships with ecological indicators. Results showed that shrubs can significantly change ecological indicators ($p < 0.05$), except *H. ammodendron* which had no significant effect on habitat provision ($p < 0.05$). There were some relationships between shrub traits and provision of ecosystem functions. Stem density and litter production were the most important functional traits affecting regulating and habitat functions. Also, there was a significant positive relationship between soil fertility, soil stability and habitat provision ($p < 0.05$). It can be recommended that planting spherical shrubs with high potential for litter production will enhance functions and can sustainably maintain sand dunes in arid ecosystems.

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Ecological value; ecosystem function; facilitation; sand dunes

Introduction

Arid lands have a unique vegetation pattern. In these areas, vegetation patterns comprise of mosaics of fertile patches with dense cover interspersed within the low cover or bare soil components known as inter-patch (Saco, Willgoose, and Hancock 2006; Moreno-de las Heras et al. 2011). The services provided by arid and semi-arid ecosystems is widely influenced by the structural components, processes, feedbacks, and interactions between them (Noy-Meir 1973; Wilcox, Breshears, and Allen 2003). As an obvious feature of arid and semi-arid ecosystems, vegetation structure consists of "high plant-cover patches in a low-cover matrix" (Aguiar and Sala 1999).

Shrubs are considered as the spots with high productivity and diversity due to intercepting water and trapping sediments, nutrients, and seeds (Li et al. 2007; Schlesinger

CONTACT Azam Khosravi Mashizi Aazam.khosravi@yahoo.com, Azam.khosravi@ujiroft.ac.ir Department of Natural Resources, University of Jiroft, km 8 Bandarabbas Road, Jiroft, Kerman Province, Iran.
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et al. 1996; Shachak and Lovett 1998; Shachak et al. 1999). The concentration of different resources in the shrub patches increases their productivity which causes increased seedlings establishment, germination rate and reduced mortality rate of plants in these patches (Wilcox, Breshears, and Allen 2003).

Ecosystem functions related to soil properties, such as organic carbon content, had the most considerable effects on ecosystem sustainability (Zuo et al. 2009). Shrubs can improve the nutrient cycle by creating islands of enhanced fertility (Zhao et al. 2007). Formation of the fertile island is a biophysical process during which nutrient materials accumulate from a wide area to patches (islands) and into plant biomass (Facelli and Temby 2002).

Shrubs can enhance biodiversity in arid ecosystems through acting as nurse plants for understory plants and animals (Maestre and Cortina 2005). Shrubs shield the understory plants and animals from high solar radiations and wind disturbances (Berg and Steinberger 2012). Species diversity is commonly used as a functional indicator of ecosystem health (Pinto, de Jonge, and Marques 2014).

Various functions of shrubs in ecosystems are derivative of their morphological characteristics (Quetire et al. 2007; Kohler et al. 2017). The size, shape and spatial distribution of the shrubs are effective on the function of this productivity because it can control how resources are concentrated in space along a gradient, from patches to inter-patches (Bracis et al. 2015). Therefore, different shrubs have different effects on arid ecosystem function and characteristics such as plant facilitation, biodiversity and functional properties, including nutrient cycling, and soil stability. Knowing of shrub function can reveal the ecological value of individual species to sustain the ecosystem and services provided by them (De Groot, Wilson, and Boumans 2002).

Drylands cover about 85% of Iran's surface (Le Houérou 1992). Desert regions and sandy lands comprise 34 million hectares of the country and 5 million hectares of them are considered as active dunes (Amiraslani and Dragovich 2011). In arid lands, shrubs can be used as stabilizing agents in active sand dune systems (Li et al. 2007). The shrub growth-form is a widespread category of woody plants, which differ in shape, size, branching pattern, etc. (Götmark, Götmark, and Jensen 2016), so different shrubs have different potentials in stabilizing sand dunes. Therefore, knowledge of the key shrub traits associated with ecosystem functioning is of potentially great benefit to practitioners and policymakers involved in ecosystem restoration (Laughlin 2014). Here, we assess the potential of three dominant shrubs in ecosystem functioning in sand dunes.

The aim of this study was to examine the potential of three shrubs (*Tamarix macatensis*, *Calligonum polygonoides*, and *Haloxylon ammodendron*) for providing three ecosystem functions i.e. soil fertility, soil stability and habitat provision in arid sand dune ecosystems of Iran. Each function was assessed through six selected ecological indicators (soil organic matter content and litter mass for soil fertility; mound height and clay content for soil stability; understory plants and macrofauna diversity for habitat provision). We hypothesized that the differences between shrubs in ecological indicators are related to their functional traits. Therefore, the relationships between shrub traits and ecological indicators were assessed to know how shrub traits can predict their potential in ecosystem functioning, in order to select them for future restoration schemes. Thus, the main objectives of this study were: (1) to assess the potential of shrubs for improving six ecological indicators (soil organic matter (SOM), mound height, clay%, litter mass, soil macrofauna and plant diversity), (2) to investigate relationships between shrub traits and ecological indicators, and (3) to determine the relationship between ecological indicators in sand dune ecosystem.

Materials and methods

Research site

The study was conducted at the Negar plain (56° 38′–56° 53′ E and 29° 35′–29° 53′ N) with 295.6 km^2 area, located in Kerman province, southeastern Iran (Figure 1). The mean annual rainfall is about 120 mm, occurring mostly between October and December. The prevailing winds blow usually from the southwest in the winter and northeast in the spring with 7 ms^{-1} average velocity. The region's soils are sandy Entisol, with loose aggregates which are very susceptible to wind erosion. Rangelands cover ~77% of Negar plain which are grazed mainly by goats (the main domestic livestock species in the region). The dominant shrub species are *Tamarix macatensis* Bunge., *Calligonum polygonoides* L., and *Haloxylon ammodendron* (C.A.Mey.) Bunge., which have different traits (Table 1). The main rangeland types are *Tamarix macatensis*

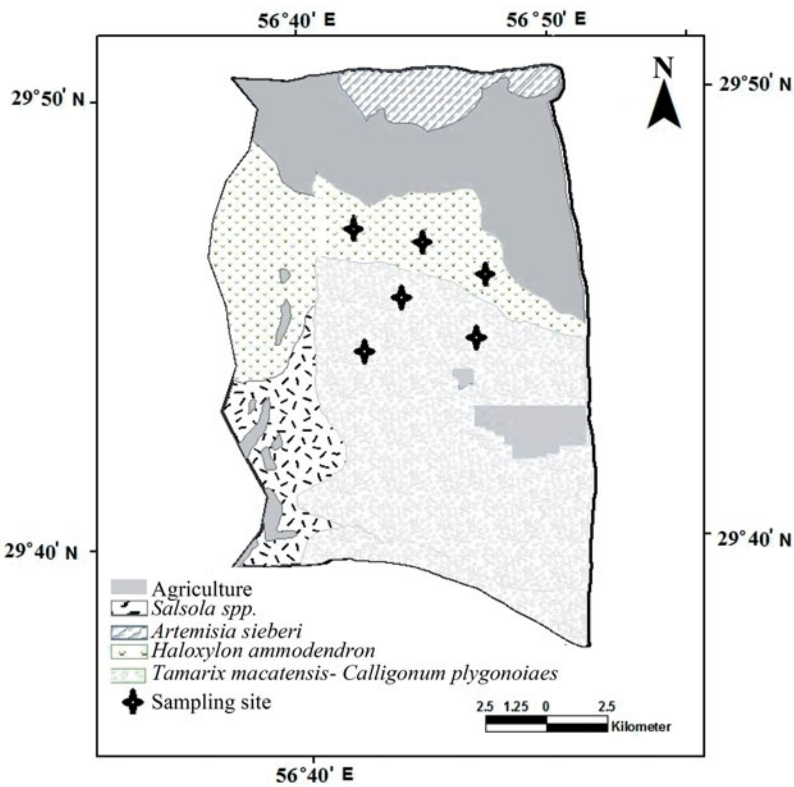

Figure 1. Land cover map of the study area. For rangelands, the name of vegetation types is presented.

Table 1. The dominant shrub species in Negar plain and their main traits.

	Trait				
Shrub species	Life form	Height (m)	Leaf lifespan	Palatability for goat	Shape
Tamarix macatensis	Phanerophytes	1.79	Evergreen	Medium	Hemispherical
Calligonum polygonoides	Phanerophytes	0.88	Deciduous	Medium	Hemispherical
Haloxylon ammodendron	Phanerophytes	1.67	Evergreen	Medium	Y-shaped

Bunge.-*Calligonum polygonoides L.* (57%), and *Haloxylon ammodendron* (C.A.Mey.) *Bunge* (25%). Agricultural lands cover 23% of all Negar plain area.

Sampling design

Two adjacent sites were selected for data collection during May 2018. The first site is dominated by *T. macatensis* and *C. polygonoides* with 47% canopy cover and the second one is dominated by *H. ammodendron* with 46% canopy cover. In each site, three $30 \times 30\,m^2$ plots were selected for sampling. For each shrub species, 15 individuals, with different sizes (large, medium, and small) were selected for sampling. If a sufficient number of shrubs were not encountered within the plots, more plots were sampled.

Ecosystem functions and their ecological indicators

In order to assess the facilitative performance of *T. macatensis*, *C. polygonoides*, and *H. ammodendron*, three ecosystem functions including soil fertility, soil stability, and habitat provision were evaluated under the canopy of shrubs and the interspace between them. Sometimes a single ecosystem function is the product of two or more indicators. Two ecological indicators were selected to measure each function (Table 2).

Ecological indicators, SOM content, mound height, clay content, litter mass, soil macrofauna, and plant diversity were selected to measure shrub potential to fix sand dunes in Negar plain due to the following reasons: shrubs enhance soil fertility by adding litter to soil surface and promoting SOM (Yang et al. 2014; Gang et al. 2012). Providing habitat for understory plants or animals and maintaining biological diversity are the main shrub functions to support ecosystem health (Millennium Ecosystem Assessment 2005). Soil fauna has an important role in decomposing organic matter and facilitating the nutrition cycle in ecosystems (Coleman and Wall 2014). Macrofauna refers to soil fauna having more than 2 mm body size, that spends more time of its life in the soil (Smith, Potts, and Eggleton 2008; Barrios 2007). Mound development under shrubs reduces wind velocity and sand transport rate (Constantine et al. 2012). Clay content is thought to increase mound stability (Jouquet, Tessier, and Lepage 2004).

Field measurements

Litter was sampled using $1 \times 1\,m^2$ plots established under the canopy of each shrub and in the interspace between the shrubs (Salunkhe et al. 2014). Mound height was measured relative to the surrounding terrain level. Soil samples were taken from 0–25 cm depths under the canopy of shrubs and from the interspace between them. Particle size distribution (sand, silt and clay contents) of each soil sample was determined using the

Table 2. Ecological indicators considered for each ecosystem function.

Functions	Ecological indicators	Sources
Soil fertility	SOM and litter mass	Yang et al. (2014), Gang et al. (2012)
Soil stability	Mound height and clay content	Constantine et al. (2012), Jouquet, Tessier, and Lepage (2003)
Habitat provision	Diversity of understory plants and macrofauna	Millennium Ecosystem Assessment (2005)

hydrometer method (Soil Survey Staff 1994). The Walkley–Black method was used for estimating SOM content (Nelson and Sommers 1982).

In order to measure macrofauna diversity, $25 \times 25 \times 25\,cm^3$ soil samples were taken under the canopy of each shrub and from the interspace between the shrubs (Sandhu, Wratten, and Cullen 2010; Ghaley, Vesterdal, and Porter 2014). Samples were emptied onto polythene sheets and macrofauna were extracted by hand and immediately killed by dipping into 70% alcohol solution. The macrofauna were identified at the level of family (Table A1).

In order to measure plant diversity at the species level, $50 \times 50\,cm^2$ plots were established under the canopy of each shrub and in the interspace between them (Bueno et al. 2016). All plant species encountered in each plot were listed (Table A2).

Shannon diversity index (H) for understory plants and macrofauna was calculated as follows:

$$H = -\sum_{i=1}^{S} p_i \log_2 p_i \tag{1}$$

Where p_i is the relative number of species i in each plot.

Shrub trait measurements

We hypothesized that variation in shrub traits i.e. canopy, height, and stem density could influence shrubs' potential to enhance ecosystem services (Figure 2). For each shrub, 15 adult individuals with different sizes (small, medium and large) were randomly selected based on the shortest and tallest shrubs in the region (Table 3). So the longest and perpendicular diameters of canopy, height and stem density of three shrubs were measured.

Plant height was defined as the shortest distance between the upper foliage boundary of shrub and center of their basal point of attachment (Cornelissen et al. 2003). Stem density was determined by counting shrub stems per plant.

Data analyses

ANOVA followed by the least significant difference (LSD) test was used to compare different shrubs in terms of measured traits. Student's t-test was applied to compare ecological indicators under the canopy of shrubs with the interspace between them.

For each ecological indicator (clay content, mound height, litter mass, SOM content, plant, and macrofauna diversity), a standardized value was calculated between 0 and

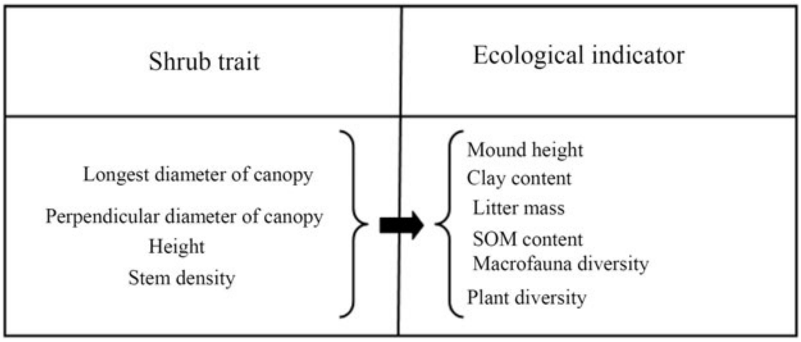

Figure 2. The relationship between shrub traits and ecological indicators.

Table 3. Shrubs height classes based on the shortest and tallest individuals in the region.

	Height classes (m)		
Shrub species	Small	Medium	Large
T. macatensis	>1.30	1.30–2	2<
C. polygonoides	>0.5	0.5–1	1<
H. ammodendron	>1.30	1.30–2	2<

100. Standardized values were calculated as follow:

$$\text{Standardized } EI_i = (EI_{imean} - EI_{imin})/(EI_{imax} - EI_{imin}) \times 100 \quad (2)$$

Where, EI_{imean}, EI_{imin}, and EI_{imax} are the mean, minimum and maximum of ecological indicator i respectively for each shrub, then standardized *EI*s of three shrubs were represented in a spider plot.

The data were first analyzed by Detrended Correspondence Analysis (DCA) to confirm RDA as an appropriate approach for further analysis (length of gradient <3 for ecological indicators). Then, Redundancy analysis (RDA) was applied to assess the relationship between ecological indicators and shrub traits. Pearson correlation coefficient was used to quantify the relationship between ecological indicators.

Results

Tamarix macatensis and *Calligonum polygonoides* had the highest and lowest major axes, minor axes and plant height respectively (Table 4). *Tamarix macatensis* also had the highest stem density. *Haloxylon ammodendron* had the lowest stem density. Cover area of mid-*T. macatensis* didn't significantly differ from large-*H. ammondendron*. Small-*T. macatensis* and large-*C. polygonoides* were not significantly different in terms of cover area, height, and stem density (Table 4).

There were significant differences between the three sizes of *T. macatensis* and the interspace between the shrubs in terms of ecological indicators (Table 5). In comparison to the interspace between the shrubs, *T. macatensis* significantly increased clay content, silt content, SOM content, litter mass, mound height, macrofauna, and plant diversity

Table 4. Differences in traits between shrubs with different sizes (large, medium, and small).

	T. macatensis						*C. polygonoides*						*H. ammodendron*					
	Large		Medium		Small		Large		Medium		Small		Large		Medium		Small	
Trait	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Longest diameter of canopy (m)	3.57a	0.34	2.82b	0.06	2.1c	0.28	2.3c	0.15	1.7d	0.12	1.24e	0.11	2.72b	0.19	2.01c	0.18	1.1e	0.13
Perpendicular diameter of canopy (m)	3.41a	0.3	2.47b	0.34	1.82cd	0.23	2.06c	0.08	1.54d	0.08	0.98e	0.16	2.38b	0.21	1.72d	0.31	0.78e	0.13
Height (m)	2.92a	0.43	1.60cd	0.23	1.28d	0.14	1.34d	0.11	0.88e	0.18	0.40f	0.07	2.48b	0.28	1.66c	0.11	0.78e	0.13
Stem density (stem number /individual)	89.8a	8.16	68.2b	5.36	59.7b	2.9	64.8b	1.48	42.6c	2.7	35.2d	1.64	17.4e	1.8	12.8ef	0.83	9.2f	1.3

Significant differences obtained by the post hoc test are shown by the superscripts a, b, c, d, e, and f, the same letter indicates no significant difference.

Table 5. Differences in ecological indicators between shrubs with different sizes (large, medium, and small).

	T. macatensis								*C. polygonoides*								*H. ammodendron*							
	Large		Medium		Small		Open		Large		Medium		Small		Open		Large		Medium		Small		Open	
Ecological indicator	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*	Mean	*SD*
Clay content	21.8b	1.8	21.6b	1.1	22.2b	2.1	10.3a	1.1	13.6a	2.1	15.4a	1.1	16.1b	0.5	14.1a	1.1	7.6a	0.5	10.6a	0.5	11.6b	0.5	7.3a	0.5
Silt content	31b	1.3	32.8b	2.1	35.1b	1.4	20.8a	2.1	19a	0.7	19a	0.4	19.1a	0.8	17a	2.1	11.8a	0.8	14.2a	0.8	12.6a	0.4	14.1a	0.1
Sand content	47.2b	1.2	45.6b	1.1	45.7b	0.8	68.9a	1.1	67.4b	0.7	65.6a	0.8	64.8a	0.5	68.9a	1.1	80.6a	0.8	75.2a	1.3	75.8a	0.5	78.6a	0.4
SOM content	1.33b	0.4	1.08b	0.1	1.01b	0.2	0.32a	0.1	0.48b	0.8	0.44b	0.2	0.42b	0.2	0.25a	0.2	0.30a	0.1	0.28a	0.2	0.25a	0.1	0.21a	0.1
Macrofauna diversity	0.87b	0.23	0.79b	0.05	0.66b	0.08	0.44a	0.1	0.67b	0.08	0.57b	0.21	0.53b	0.01	0.42b	0.2	0.25a	0.1	0.43a	0.1	0.43a	0.09	0.43a	0.05
Plant diversity	1.03b	0.01	0.95b	0.05	0.82b	0.03	0.59a	0.08	0.81b	0.08	0.73b	0.02	0.68b	0.01	0.57a	0.02	0.61a	0.04	0.61a	0.08	0.59a	0.06	0.57a	0.07
Litter mass (g/m^2)	1340 b	207	726b	94	610b	74	50a	9	528b	142	342b	23	212b	55	54a	10	95b	13	797b	7	52a	19	407a	17
Mound height (m)	1.74b	0.25	1.38b	0.34	0.92b	0.2	0.10a	0.08	1.34b	0.56	1.06	0.44	0.86b	0.35	0.11a	0.05	0.87b	0.13	0.83b	0.11	0.72b	0.06	0.10a	0.5

Significant differences obtained by the post hoc test are shown by the superscripts a, b, c, d, e, and f, the same letter indicates no significant difference.

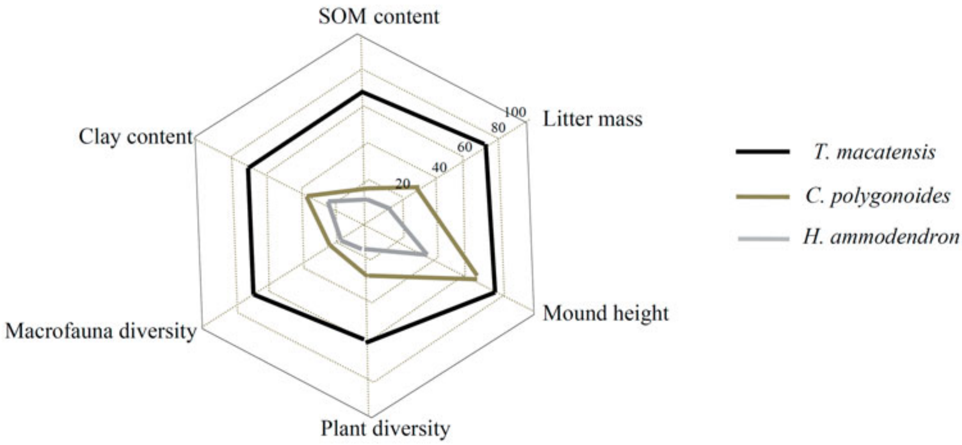

Figure 3. Redundancy discriminant analysis (RDA) biplot showing the relationship between ecological indicators (clay content, mound height, litter mass, SOM content, plant, and macrofauna diversity) and shrub traits (the longest diameter and perpendicular diameter of canopy cover, height, and stem density).

but decreased sand percent ($p < 0.05$). Ecological indicators were increased with raising shrub size of *T. macatensis*. *Calligonum polygonoides* significantly increased SOM, litter mass, mound height, macrofauna, and plant diversity compared to the interspace between the shrubs, but it did not have a significant effect on soil particles ($p < 0.05$). There was no significant difference between indicator values under the canopy of *H. ammodendron* and the interspace between the shrubs in soil particle fractions, SOM, litter mass, mound height, macrofauna and plant diversity ($p > 0.05$). *Haloxylon ammodendron* significantly increased litter and mound height compared to the interspace between the shrubs ($p < 0.05$).

Spider plot showed that *T. macatensis* enhanced ecological indicators more than 65%. *Calligonum polygonoides* and *Haloxylon ammodendron* were more successful in providing mound height. *Calligonum polygonoides* increased other indicators about 30% and *H. ammodendron* increased all ecological indicators less than 20% (Figure 3).

RDA showed that stem density had the highest correlation with ecological indicators (SOM, litter, clay content, mound height, plant, and macrofauna diversity) (Figure 4). Pearson correlation analysis revealed a significant relationship between clay content, litter mass, SOM content, plant and macrofauna diversity ($R^2 > 0.507$, $p < 0.01$). There was a non-significant relationship between mound height and clay content ($R^2 = 0.349$, $p > 0.05$), mound height also had the lowest correlation coefficient with other ecological indicators (Table 6).

Discussion

Generally, shrubs are expected to have positive impacts on functions in arid land ecosystems (Li et al. 2007). We compared functions provided by three shrubs through assessing their ecological indicators.

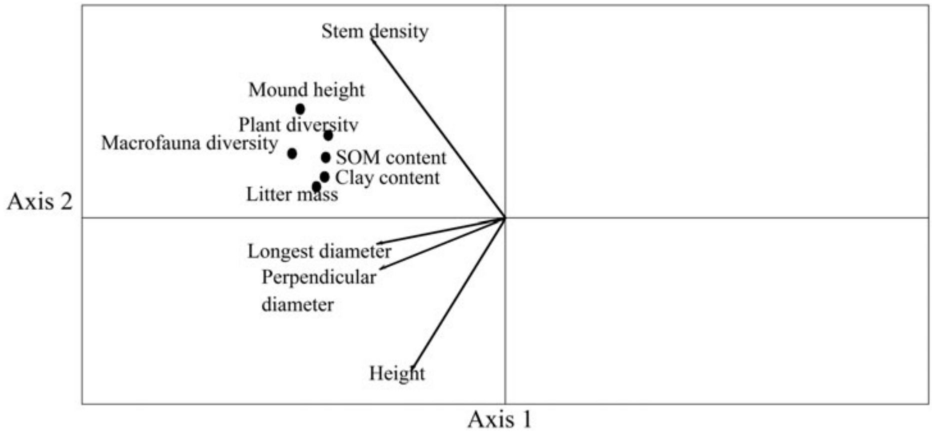

Figure 4. Spider diagram comparing three studied shrubs based on ecological indicators (clay content, mound height, litter mass, SOM content, plant, and macrofauna diversity) represented as rectangular shapes.

Table 6. Pearson correlation coefficient between ecological indicators (clay content, mound height, litter mass, SOM content, plant, and macrofauna diversity) provided by shrubs.

	Mound height	Clay content	Litter mass	SOM content	Plant diversity	Macrofauna diversity
Mound height	1	0.349^{ns}	0.775**	0.507*	0.754**	0.734**
Clay content		1	0.987**	0.901**	0.929**	0.924**
Litter mass			1	0.973**	0.987**	0.984**
SOM content				1	0.894**	0.892**
Plant diversity					1	0.923**
Macrofauna diversity						1

*Significant at $p < 0.01$; **Significant at $p < 0.05$; ^{ns}Not significant.

Soil fertility

All three shrubs had increased SOM in comparison to the interspace between the shrubs but the differences for *H. ammodendron* were not significant. Generally, litter accumulation under the canopy of shrubs was higher than in the interspace between them. *Tamarix macatensis* and *Calligonum polygonoides* had significantly higher litter mass than the interspace between the shrubs, and litter accumulation was increased with shrub size. *Haloxylon ammodendron* (large and medium sizes) had significantly lower litter mass than the interspace between the shrubs, but the shrubs in medium size had significantly higher litter mass under their canopy. Therefore, it can be concluded that *T. macatensis* and *C. polygonoides* are successful in enhancing soil fertility. Although mounds are particularly affected by shrubs in the study region, Li et al. (2007) also reported that *H. ammodendron* were less capable of maintaining litter and providing fertile islands in comparison with *Tamarix* spp. in the desert ecosystem.

Soil organic matter was increased under the canopy of shrubs. These results are in accord with other researches which suggest an increase in soil organic matter by increasing the *Haloxylon* spp. cover (Farzaneh 2014; Jafari, Niko, and Sadeghi Pour 2007). As the plant canopy expands, the amount of litter production increases, leading to an increase in soil organic matter (Jafari, Niko, and Sadeghi Pour 2007). This is the case for soil moisture too. The higher canopy cover of shrubs in the arid ecosystems results in more shading areas which, together with higher levels of litter mass and SOM, cause the soil to have lower temperature and more moisture content and that results in better conditions for biological activities and increases biological diversity (Berg and Steinberger 2010; Kidron 2009; Habekost et al. 2008).

Soil stability

Shrubs had significantly increased mound height and all three shrubs exhibited the same pattern. Mount heights were found to be significantly different between the three shrubs. Mound height was increased with shrub size, although the differences between different sizes were not significant.

Shrubs can play an important role in improving soil texture of sandy soils in arid lands. Many studies showed the positive impacts of *Haloxylon* spp. on the increasing clay content of sandy soils (Haghian and Sharafatmandrad 2016; Farzaneh 2014; Jafari, Niko, and Sadeghi Pour 2007). However, our study showed that shrubs are not highly influential on clay content. Significant increase of clay content was only observed under the canopy of *T. macatensis*.

Habitat provision

All shrubs played a crucial role in the provision of habitat for plant species and macrofauna in the studied ecosystems. Shrubs had increased biological diversity in studied arid ecosystems. *Tamarix macatensis* and *Calligonum polygonoides* had significantly higher plant and macrofauna diversity than the interspace between them. The three shrub sizes differed in their ability to provide habitat for plant species and macrofauna, and Shannon diversity index was greater with the increase of shrub size. Some researches emphasized the role of vegetation cover in enhancing biological activity through providing organic matter and a physical barrier, both contributing to the formation of fertile islands (Berg and Steinberger 2010; Dornbush 2007; Kidron 2009; Habekost et al. 2008). Shelef and Groner (2011) found that beetles spend more time under the canopy of *Haloxylon scoparium*, because its open-branching structure could provide a good place for basking beetle in arid highlands. However, this result contrasts with the recent findings of by Boscutti et al. (2018), which expressed that greater shrub cover had a negative effect on species richness, also affecting species composition.

Haloxylon ammodendron was not significantly able to facilitate plant and macrofauna species, probably due to its structure. Some reports indicate the adverse effects of introducing non-native plant species on soil and vegetation in the region. In the areas where *Haloxylon* had been planted, soil alkalinity and salinity have increased, which will have negative effects on the flora and soil macrofauna of the region in the long run. The increase in acidity and electrical conductivity in the areas planted with *Haloxylon* has been attributed to the transfer of solutes from the deep soil to the surface by these plants.

Shrubs had greater biological diversity under their canopy than the interspace between them. These results are in accord with other reports (Holzapfel and Mahall 1999; Berg and Steinberger 2010; Howard, Eldridge, and Soliveres 2012; Koch et al. 2015). The positive effect of *Haloxylon* on diversity is probably due to the formation of microclimate resulting from their shading effect on soil and their physical effects on wind speed reduction and consequently evapotranspiration, which increase moisture availability enabling organisms to cope with the harsh environment (Mohammadi, Naseri, and Heshmati 2014; Berg and Steinberger 2010).

It was assumed that different shrubs differently impact on ecosystem functions. Our findings showed that the three studied species i.e. *T. macatensis*, *C. polygonoides*, and *H. ammodendron* differently affect ecosystem functions in sand dune ecosystems. *Tamarix macatensis* could enhance ecological indicators two times more than *C. polygonoides* and three times more than *H. ammodendron* (Figure 2). The differences in different shrubs in improving ecosystem functions can be related to their structural traits (Sasaki et al. 2010; Liu et al. 2011).

RDA was used to assess the relationships between shrub traits and all measured parameters and their relative contribution to the ecosystem functions in sand dune ecosystem. RDA results showed that the shrub traits were correlated with ecological indicators. Stem density, as the most important shrub trait, was significantly correlated with ecological indicators. Canopy cover and plant height had no significant facilitative effects on ecosystem. Based on Table 3, the small shrubs with dense branches can considerably enhance ecological indicators rather than the larger ones with open-branches. We introduced stem density as a key shrub trait to drive the desired restoration goals in sand dunes. Shrubs with multi-stemmed hemispherical crowns such as *T. macatensis* and *C. polygonoides* are favorable for capturing and maintaining litter and soil under their canopy compared to shrubs with Y-shaped crown such as *H. ammodendron*. Our results are in accord with some previous studies (May 1979; Sasaki et al. 2010; Liu et al. 2011, Gang et al. 2012). In contrast, Zhao et al. (2017) and Yapp, Walker, and Thackway (2010) suggested plant height and cover as appropriate plant traits impacting ecological indicators.

The results of Pearson correlation coefficients showed that SOM content, litter mass, clay content, plant and macrofauna diversity are positively associated in sand dune ecosystems (Table 4). SOM not only promotes soil structure but also enhances soil biota community (Weller et al. 2002). In addition, soil biota density is significantly correlated with litter mass as a food resource under the canopy of shrubs (Peterson et al. 2001). The diversity of animals in the soil subsequently has positive effects on physical soil structure (Ettema and Wardle 2002) and can improve SOM and soil fertility through accelerating the decomposition process and humus formation in soil (Sileshi and Mafongoya 2006; Liu et al. 2011). Our results also indicated that mound height had the lowest positive effect on ecological indicators and there was no significant relationship between expanding mound and increasing clay content. For both *C. polygonoides* and *H. ammodendron*, mound expansion coincided with sand content increase and clay content decrease under the canopy of shrubs, and subsequently SOM was not considerable under their canopy. Previous researches showed that mound expansion leads to a reduction in the ability of soil to conserve nutrients and SOM (Itoh et al. 2003; Gajic, Dugalic, and Djurovic 2006; Sasaki et al. 2010).

Our results showed that the size of shrubs was not correlated with ecological indicators and stem density was the most effective plant trait to drive shrub functions in stabilizing sand dunes. Although all shrubs were successful in soil retention and mound expansion more than 1 m, *T. macatensis* and *C. polygonoides* patches were enriched with more litter mass and SOM, which provide better shelter for growing understory plants and macrofauna compared to *H. ammodendron*.

There were also synergies between different ecological indicators. However, mound expanion had the lowest positive effect on enhancing ecological indicators through increasing sand content as a negative factor under the canopy of shrubs.

Conclusion

The results obtained in the present study show that the selection of a shrub to restore an arid ecosystem is not as simple as we might think. There are many interacting ecological indicators which are correlated with plant traits. Therefore, these results will help managers to select appropriate plant species with higher ecological values for biological restoration of degraded arid lands. Shrub impacts on ecosystem functioning usually are ignored in restoration programs and ecosystem managers focus commonly on choosing long-living xerophytic shrubs with high tolerance to water scarcity and high potential for sand-fixation such as *Haloxylon* spp. However, *Haloxylon* has been widely planted to restore sand dunes over 50 years of anti-desertification activities in Iran. Our findings showed that the role of *H. ammodendron* in improving ecosystem functions is not as important as that of *T. macatensis* and *C. polygonoides*. Due to the highest ecological value of *T. macatensis* in improving ecosystem functions, this species can be a good suggestion to restore sand dune ecosystems in Iran and other arid zones of the world. It can be recommended that planting shrubs with multi-stemmed hemispherical crowns such as *T. macatensis* will enhance ecosystem functions and can sustainably maintain sand dunes in arid ecosystems. These findings have important implications for sustainability appraisal of remediation alternatives and sand dune management.

ORCID

Mohsen Sharafatmandrad http://orcid.org/0000-0003-4890-1839

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Appendix

Table A1. Macrofauna family observed under the shrub canopy and the interspace between shrubs.

Macrofauna family	*T. macatensis*	Interspace	*C. polygonoides*	Interspace	*H. ammodendron*	Interspace
Silphidae	*		*			
Carabidae			*			
Formicidae			*	*		
Lumbricidae	*	*			*	*
Scarabaeidae	*					
Silphidae	*	*	*	*	*	*
Tenebrionidae	*					
Curcurionidae	*		*			
Sarcophagidae					*	

Table A2. Plant species observed under the shrubs canopy and the interspace between shrubs.

Plant species	*T. macatensis*	Interspace	*C. polygonoides*	Interspace	*H. ammodendron*	Interspace
Peganum harmala L.	*		*			
Cousinia umbrosa Bunge.	*	*		*		*
Boissiera danthoniae (Trin.) A. Braun.			*			
Eremurus persicus J.et. Sp.	*			*		
Salsola kali L.			*		*	
Salsola brachiata Pall.	*				*	*
Bromus tectorum L.			*		*	
Alhagi camelorum (Fisch).	*	*				*
Aelleni subaohylla (C.A.M.) Botsch.	*	*		*	*	
Aristida pennata Trin.	*		*			