The Effect of Shrubs on Community Structure of Annual Plants in a Sandy Desert Ecosystem

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Synopsis

Results from a variety of ecosystems suggest that biologically- induced patchiness caused by the presence of shrubs may be important in structuring communities of desert annual plants. The study described here was designed to evaluate the role of shrubs in determining local-scale patterns of variation in the distribution and abundance of annual plants in a sandy desert ecosystem near Nizzana in the western Negev Desert of Israel. Twenty-seven annual species were recorded, of which five species were found only under the canopies of shrubs and four species occured only in the open areas between shrubs. However, all of these species were very rare and were found in less than 10% of the overall quadrats. Most of the dominating annual species were significantly more abundant in the shrub habitat and only one species, *Ifloga spicata,* showed significantly higher densities in the open areas. Yet, species showing higher densities under shrub canopies differed from each other significantly in the magnitude of their between- habitat differences in density. An ordination analysis of the whole quadrat x species data set revealed a statistically significant separation between quadrats of the two habitat types. The overall results are consistent with previous studies emphasizing the role of shrubs as a source for patchiness in the distribution of annual plants.

Annual plants, community structure, demography, desert, habitat heterogeneity, shrubs.

Einjährige Pflanzen, Gesellschaftsstruktur, Demographie, Wüste, Habitat-Heterogenität, Sträucher.

Introduction

A variety of theoretical studies have emphasized the importance of investigating demographic responses of natural populations to local-scale environmental heterogeneity. Mathematical models have pointed to the impact of small scale habitat patchiness on ecological processes like the long-term persistence of populations (PULLIAM 1988), the coexistence of competing species (SHMIDA & ELLNER 1984, CHESSON 1985, PACALA 1987) and the stability of plant communities (LEVIN 1976, WIENS 1976). In arid and semi-arid environments, local-scale gradients in habitat conditions are often produced by the presence of perennial shrubs and results from a variety of ecosystems indicate that such biologically induced patterns of local heterogeneity may play an important role in structuring communities of annual species (SHREVE 1931, WENT 1942, MULLER 1953, KEELEY & JOHNSON 1977, SHMIDA & WHITTAKER 1981, SORIANO & SALA 1986, GUTIERREZ & WHITFORD 1987). In this contribution we represent the results of a study that was designed to investigate the role of shrubs in structuring communities of annual plants in a sandy desert ecosystem in the western Negev Desert of Israel.

Methods

Description of the study site

The study was conducted during 1993/94 at the Nizzana research station, an area representing the eastern margin of the Sinai continental fields (TSOAR & MØLLER 1986). Average annual rainfall is 78 mm (TSOAR & MØLLER 1986) but during the 1993/94 season was much below average with a total of 49 mm. The landscape consists of linear dunes trending from west to east. Dune ridges are 15–25 m high and 50–150 m apart from each other. A typical dune ridge is characterized by a highly mobile crest, dominated by the perennials *Stipagrostis scoparia* and *Heliotropium digynum* and less mobile slopes (dune 'plinths') are dominated by *Moltkiopsis ciliata.* The stable interdune areas are characterized by variety of perennial species like *Cornulaca monacantha, Echiochilon fruticosum, Retama raetam, Stipagrostis plumosa, Thymelaea hirsuta* and *Anabasis articulata* (TIELBÖRGER 1993).

Observational design

An area of about 500 x 50 m along the gentle north facing slope (plinth) of a dune was selected for the study. Within this area, four permanent plots of approx. 50 x 50 m were marked for subsequent measurements and each plot was subdivided into two habitats: shrubs and

* Dedicated to Prof. Dr. Reinhard Bornkamm on the occasion of his 65th birthday.

openings. The 'shrub' habitat was defined as the zone beneath canopies of perennial plants and the remaining area was defined as 'openings'. The dominating perennial species in all of the plots were *Molkiopsis ciliata* (70% relative cover), *Heliotropium digynum* (20%) and *Stipagrostis scoparia* (10%).

Within each plot, 16 quadrats of 25 x 25 cm were established in the open areas and additional 16 quadrats were located under randomly selected shrubs. Thus, a total of 128 quadrats (two habitats x 16 repetitions per plot x four plots) was established. Seedlings emerging in these quadrats were counted every 2 – 3 weeks, beginning after the first rainfall (November 1993).

Statistical analysis

Two sets of analyses were performed, one focusing on patterns represented by individual species and the other analyzing whole-community patterns.

Individual species patterns
To test the effect of habitat type (shrubs vs. openings) on the distribution of individual species, two measures of abundance were quantified for each species in each of the two habitats; (1) average density per quadrat, and (2) the percentage of quadrats in which the species occured. Differences in densities between the two habitats were tested using Student's t-tests and corresponding differences in the frequency of occurrence were tested with chi^2-tests. The hypothesis that coexisting species respond differentially to differences in habitat conditions was tested using two-way ANOVAs with habitat type and annual species as fixed effects. In these analyses, mean seedling density per plot and mean occurrence were treated as the dependent variables, and among plot variation was the error term. The density data was log(x+1)-transformed to improve the linearity of the models.

Community patterns
Patterns of variation in the overall annual community composition were analyzed with principal component analysis as an ordination method (GAUCH 1982). Two ordinations were performed, one on the quadrats and the other on the species. Species that occured in less than 10% of the quadrats and quadrats with no detected germination were excluded from these analyses. A sample of 40 quadrats in each of the habitats was chosen for the ordination of quadrats.

The effect of habitat type on the whole community composition was tested using two different approaches, one based on the position of quadrats along the PCA axes and the other based on the position of species. In the first analysis, quadrats were categorized according to their habitat type and differences between the mean PCA-scores of quadrats belonging to the two habitat types were tested using t-tests. In the second analysis, species were categorized into three groups according to their observed distribution pattern: species that were significantly more abundant in the shrub habitat, species that were significantly more abundant in the openings and species showing no significant differences in abundance between habitats. Differences between PCA scores of species belonging to the three groups were tested using one-way ANOVAs and the corresponding pairwise differences were tested using Duncan range tests.

Results

Individual species patterns

A total of 27 annual species was recorded during the study. Of these, five species (*Crucianella membranacea, Ctenopsis pectinella, Eremobium aegyptiacum, Linaria haelava, Plantago cylindrica)* could only be detected in the openings, whereas four species (*Hordeum marinum, Launaea tenuiloba, Leontodon laciniatus, Reichardia tingitana)* were found only in the shrub habitat (Table 1). However, all of these species were very rare and occured in less than 11% of the quadrats. The rest of the species occured in both types of habitats. Eight species (*Rumex pictus, Erodium laciniatum, Bromus fasciculatus, Carduus getulus, Cutandia memphitica, Launaea tenuiloba, Leontodon laciniatus* and *Picris asplenioides*) showed significantly higher frequency of occurrence in the shrub habitat, and only one species (*Eremobium aegyptiacum*) occured significantly more often in quadrats of the open areas (Table 1). The results of the two-way ANOVA indicated that the separate effects of habitat type and species, as well as their interaction were highly significant (Table 2).

Allover densities were higher in the shrub habitat than in the openings (4.15±0.47 vs 2.94±0.52), but these differences were not statistically significant ($t = 1.73$, $p = 0.083$). For ten species (*Senecio glaucus, Rumex pictus, Erodium laciniatum, Bromus fasciculatus, Centaurea pallescens, Carduus getulus, Cutandia memphitica, Launaea tenuiloba, Leontodon laciniatus* and *Picris asplenioides*) densities were significantly higher in the shrub habitat, whereas only one species (*Ifloga spicata*) showed an opposite pattern being significantly more abundant in the openings (Table 1).

The results of the two-way ANOVA constructed to test the effect of annual species and habitat type on emergence density indicated, that both effects as well as their interaction were highly significant (Table 2).

Tab. 1
Differences between the shrubs and the openings in density (#/625cm²) and percentage of occurrence of annual species in the Nizzana sand field.

Species	Density			Occurrence		
	Shrubs	Openings	t	Shrubs	Openings	$\chi 2$
Senecio glaucus	53.7±6.7	10.6±1.7	6.1***	100.0	95.1	3.1
Ifloga spicata	29.0±6.8	70.4±12.5	-2.3**	83.9	91.8	1.8
Rumex pictus	7.7±1.5	0.8±0.2	4.6***	82.3	39.3	23.8***
Erodium laciniatum	1.8±0.4	0.3±0.2	3.6***	51.6	8.2	27.6***
Bassia muricata	0.1±0.05	0.1±0.05	0.5	4.8	3.3	0.2
Brassica tournefortii	0.03±0.02	0.02±0.02	0.5	3.2	1.6	0.3
Bromus fasciculatus	2.8±0.7	0.3±0.1	3.9***	48.4	14.8	16.1***
Carduus getulus	0.6±0.2	0.03±0.02	3.0***	25.8	3.3	12.5***
Centaurea pallescens	0.5±0.2	0.05±0.02	2.1*	14.5	4.9	3.2
Crucianella membranacea	0.0±0.0	0.02±0.02	-1.0	0.0	1.6	1.0
Ctenopsis pectinella	0.0±0.0	0.05±0.04	-1.4	0.0	3.3	2.1
Cutandia memphitica	18.8±5.3	1.6±0.4	3.2**	79.0	44.3	15.8***
Eremobium aegyptiacum	0.0±0.0	0.1±0.04	-1.9	0.0	6.6	4.2*
Hippocrepis areolata	0.2±0.06	0.2±0.1	- 0.3	14.5	9.8	0.6
Hordeum marinum	0.1±0.07	0.0±0.0	1.2	3.2	0.0	2.0
Launaea tenuiloba	0.4±0.1	0.0±0.0	3.3**	21.0	0.0	14.3***
Leontodon laciniatus	0.2±0.06	0.0±0.0	2.4*	9.7	0.0	6.2*
Linaria haelava	0.0±0.0	0.1±0.07	-1.2	0.0	3.3	2.1
Lotus halophilus	0.4±0.2	0.2±0.06	1.3	17.7	14.8	0.2
Ononis serrata	0.2±0.1	0.2±0.06	0.3	11.3	11.5	0.0
Picris asplenioides	1.2±0.3	0.2±0.1	3.1**	33.9	11.5	8.8**
Plantago cylindrica	0.0±0.0	0.05±0.03	-1.8	0.0	4.9	3.1
Polycarpon succulentum	0.6±0.2	0.9±0.2	- 0.6	21.0	32.8	2.2
Reichardia tingitana	0.02±0.02	0.0±0.0	1.0	1.6	0.0	1.0
Schismus arabicus	0.3±0.1	0.3±0.1	- 0.1	14.5	18.0	0.3
Silene villosa	0.1±0.05	0.3±0.1	1.6	4.8	13.1	2.6
Trisetaria linearis	0.2±0.1	0.5±0.3	1.3	11.3	23.0	3.0

*** P < 0.001; ** P < 0.01; * P < 0.05

Source of variation (df)	Density		Occurrence	
	SS	F	SS	F
Habitat (1)	0.8	60.8 ***	0.4	29.4***
Annual species (26)	34.5	105.7 ***	13.3	42.9***
Habitat x Annual species (26)	3.5	10.8 ***	1.3	4.2***
Error	2.0		1.9	
Total	40.9		16.8	

*** p < 0.001

Tab. 2
Analysis of variance for the effect of habitat type (shrubs vs. openings) on densities and percentage of occurrence of annual species in the Nizzana sand field.

Community patterns

The quadrat ordination using principal component analysis revealed a clear separation between the two habitat types (Fig. 1). The differences between mean scores of quadrats belonging to the two habitats on both PCA axes were significantly different (Axis I: $t = 8.62$, $p < 0.001$; Axis II: $t = 9.51$, $p < 0.001$).

The scattering of species in the species ordination (Fig. 2) was related to their differential abundance in the two habitats. The results of the oneway ANOVA constructed to test for differences in PCA scores among subgroups of species showing different distribution patterns revealed statistically significant results for both PCA axes (Axis I: $F = 15.3$, $p = 0.0005$; Axis II: $F = 5.5$, $p = 0.0205$). The results of the Duncan range tests indicated a significant ($p < 0.05$) difference between the group of species that were significantly more abundant in the shrub habitat and the two other subgroups (notice that the subgroup of species showing higher frequencies of ocurrence in the openings contained only one species).

Discussion

The overall results of this study indicate that shrubs have a considerable effect on the distribution and abundance of annual plant species in the Nizzana sand field. This finding is consistent with results from other ecosystems (SHREVE 1931, WENT 1942, MULLER 1953, KEELEY & JOHNSON 1977, SHMIDA & WHITTAKER 1981, SORIANO & SALA 1986, GUTIERREZ & WHITFORD 1987, CARLSSON & CALLAGHAN 1991).

In general, shrubs had an enhancing effect on both densities and occurrence of species (Table 1) a result that is consistent with most previous studies on the impact of shrubs on understory annual populations in desert environments (SHREVE 1931, WENT 1942, KEELEY & JOHNSON 1977, SHMIDA & WHITTAKER 1981, GUTIERREZ & WHITFORD 1987). Most of the species that responded significantly to the differences in habitat conditions showed either higher densities or higher percentage of occurrence or both in the shrub habitat. Exept for one species, the dwarf plant *Ifloga spicata*, seven out of the eight most common species in the area had significantly higher densities in the shrubs (Table 1). SHMIDA & WHITTAKER (1981) found similar results for a desert shrubland in Southern California with dwarf plants being more abundant in the open areas between shrubs.

TIELBÖRGER & KADMON (1995) investigated the demography of four dominant annual species in the Nizzana research site and found that three of the species (*Senecio glaucus*, *Rumex pictus*, *Erodium laciniatum*) exhibited higher seed production under the canopy of shrubs, while one species (*Ifloga spicata*) showed an opposite pattern with higher seed production in open areas. These demographic responses were in the same direction like the patterns of distribution, suggesting that fecundity responses are im-

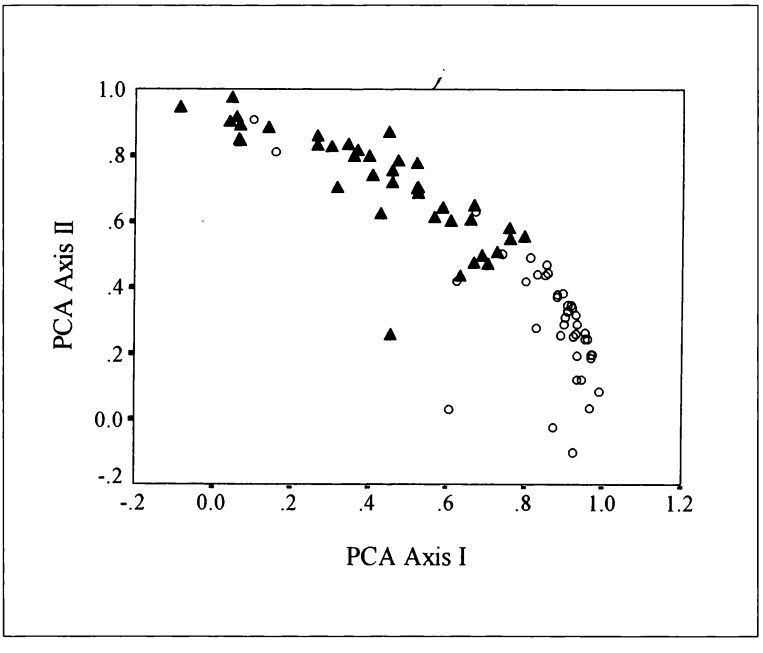

Fig. 1
PCA results of quadrat ordination based on species densities. Circles – quadrats in shrub habitat; triangles – quadrats in openings.

portant in determining differences in the abundance of annual plants between the two habitat types.

The data we have do not allow us to determine the mechanisms by which the presence of shrubs affects the demography of the studied populations. However, results from previous studies conducted at the Nizzana research site do allow us to suggest some hypotheses. For example, it has been previously found (KADMON & LESCHNER 1995) that surface stability is one of the main factors determining the abundance of annual plants in the studied system, Shrubs reduce wind velocity (PARMENTER & MCMAHON 1983, CARLSSON & CALLAGHAN 1991) and thus may represent patches of low surface dynamics, and therefore more favorable conditions for most plants, than the surrounding open areas. Also, by decreasing wind velocity and forming rough surface, shrubs may function as seed traps and increase the density of seeds available for germination below their canopies. Recent experiments manipulating the roughness of the sand (Prasse, unpublished data) have indicated that manipulated surfaces with higher roughness had higher densities of annual plants than undisturbed surfaces, a result consistent with this hypothesis.

It is interesting to compare the results of this study with those of a previous study conducted by KADMON & LESCHNER (1995) in the same area. In their study, KADMON & LESCHNER distinguished between two main types of habitats in the Nizzana area – stable interdune corridors and relatively unstable slopes ('plinths'). These two habitat types were found to differ considerably from each other in their annual plant communities. In the present study we focused on the 'plinth' habitat and found, that in terms of the annual plant communities, it can be subdivided into two subhabitats – shrubs and openings. Nearly all species (except *Ononis serrata*) that were not sensitive to differences in habitat conditions in the study of KADMON & LESCHNER (1995) were here found to be sensitive to the presence of shrubs and were more abundant in the shrub habitat. Moreover, TIELBÖRGER & KADMON (1995) found that emergence densities of plants growing under the canopies of shrubs were influenced by the identity and morphological properties of the canopy species. These results indicate that even the 'shrub' habitat is not uniform, and that different species of shrubs my provide different microsite conditions for annual plants.

The allover results suggest, that small scale environmental patchiness caused by the presence of shrubs may have considerable effects on the spatial patterns of accompanying desert annual plant communities.

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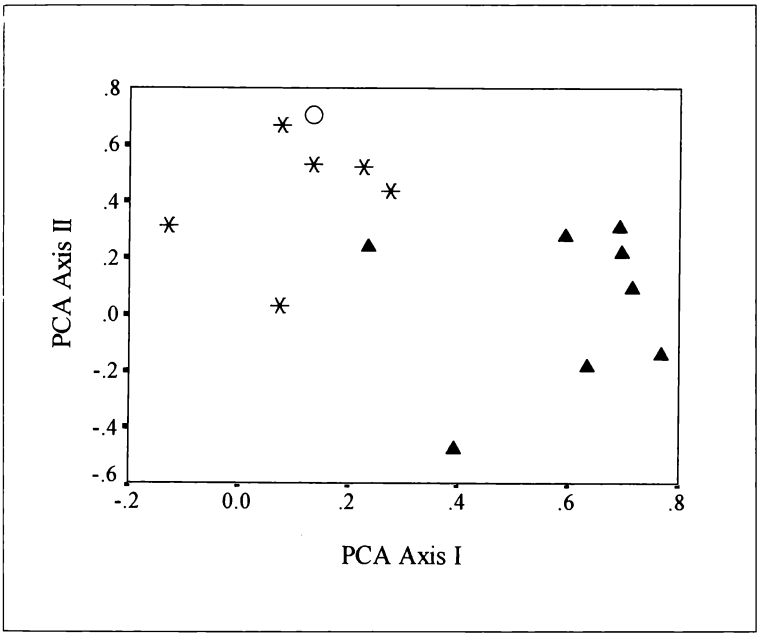

Fig. 2
PCA results of species ordination based on species densities. Circles - species whose densities were significantly higher in the shrub habitat; triangles – species whose densities were significantly higher in the openings; asterisks – species showing no significant differences in densities between the two habitats.

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