

The effect of microhabitats on vegetation and its relationships with seedlings and soil seed bank in a Mediterranean coastal sand dune community

S. Yu^{a,b,*}, D. Bell^c, M. Sternberg^d, P. Kutiel^e

^a State Key Laboratory of Vegetation and Environmental Changes, Institute of Botany, the Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China

^b Department of Geography, Bar-Ilan University, Ramat Gan 52900, Israel

^c Botany, School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

^d Department of Plant Sciences, Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv, Israel

^e Department of Geography and Environmental Development, Ben-Gurion University of the Negev, Be'er Sheva 84105, Israel

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ABSTRACT

We examined species composition and diversity of vegetation and soil seed bank associated with different microhabitats in Mediterranean semiarid sand dune community, to identify which functional groups or species benefit from trampling, and to provide a basis for management. In this community microhabitats were found to significantly influence species abundance and biomass of dominant functional groups and dominant species. The open patches generally have the greatest species richness, diversity and productivity. The highest value of similarity occurred during June to September and the lowest value occurred in April when seedling emergence stopped but before new seeds dispersed. Shrubs did not benefit their understorey plant functional groups except for perennial forbs and Apiaceae due to their denser canopy and larger litter amount. Tramplng decreased the species diversity of vegetation and did not facilitate the establishment of herbaceous plants, but was beneficial for some functional groups such as Apiaceae and Brassicaceae as well as some species such as *Polycarpon succulentum*. A positive relationship was found between productivity and diversity in this community and on the trail, but the relationship in the open area and shrub understorey was not significant. This work can provide a deeper understanding of small-scale vegetation processes and mosaic patterns of distribution.

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1. Introduction

Recruitment and seed bank development in microhabitats is intrinsically linked to differences in physical conditions, such as soil temperature, moisture and light, and different biotic conditions, such as abundances of seed predators, herbivores, and pathogens (Alpert and Mooney, 1996). In semiarid ecosystems, there are significant micro-climatic differences between the shrub understoreys and exposed open areas among shrubs, even among different positions in the shrub understorey (Moro et al., 1997). Shrubs may facilitate the development of understorey vegetation by ameliorating

* Corresponding author at: State Key Laboratory of Vegetation and Environmental Changes, Institute of Botany, the Chinese Academy of Sciences, 20 Nanxincun, Xiangshan, Beijing 100093, China. Tel.: +86 10 62836506; fax: +86 10 62590835.

E-mail address: shunliyu@ibcas.ac.cn (S. Yu).

a variety of physical conditions as a result of reduced evaporation (Moro et al., 1997; Tielbörger and Kadmon, 1995) and by providing richer nutrient supply, compared to nearby open areas (Pugnaire et al., 1996). Recent studies on spatial patterns of seedling emergence in holly woodland recruitment showed that the emergence in gaps was lower than under shrub canopies (Arrieta and Suarez, 2005).

Soil seed banks may also exhibit high microhabitat heterogeneity. For example, in desert ecosystems, the seed density under shrubs is much higher than in open areas (Crawford and Young, 1998; Guo et al., 1998; Kemp, 1989; Pake and Venables, 1996). However, in semiarid ecosystems such as Mediterranean sand dunes, the seed density under shrubs is much lower than in open areas (Yu et al., 2003).

Similarity between soil seed banks and aboveground vegetation has been compared in many communities and two results have been documented: high similarity (Kirkham and Kent, 1997; Levassor and Ortega, 1990; Marone et al., 1998; Peco et al., 1998) or little correspondence (Demel and Granström, 1995; Egan and Ungar, 2000). However, in these studies little attention has been paid to changes in similarity due to the temporal dynamics of soil seed banks.

Community attributes such as diversity and productivity may also differ among microhabitats. Both experimental and investigative sampling have generally demonstrated that diversity has a positive relationship with productivity because of niche complementarity (Dimitrakopoulos and Schmid, 2004; Pfisterer et al., 2004; Tilman et al., 2001). Models of multi-species competition predict that the greater the diversity, the greater the increase in community productivity (Lehman and Tilman, 2000). Whether these observed relationships exist in natural ecosystems at microhabitats scales requires investigation.

Mediterranean eastern coastal sand dune communities in Israel are ideal systems for studying microhabitats differences since the vegetation is composed of a spatially heterogeneous matrix of two microhabitat types: shrubs (*Retama raetam*) and open stabilized patches (among the shrubs) dominated by herbaceous plants. In addition, the whole area is crisscrossed by pedestrian trails, thus providing a third microhabitat for an exploration of the impacts of human activity. Outdoor recreation activities on public lands can cause ecological damage especially on high impact areas such as paths (Lance et al., 1985). Earlier research has mainly focused on the effects of trampling on species richness and diversity (Gómez-Limón and Lucio, 1995; Liddle, 1997), the response of plant communities to disturbance (Cole, 1995) and vegetation recovery and succession after exclusion of recreation (Roovers et al., 2005), but few studies have investigated the response of different functional groups to trampling. Recreation effects such as trampling often lead to the loss of species diversity (Gómez-Limón and Lucio, 1995). Thus an awareness of the effects of visitor pressure on the structure and composition of species-rich sand dune communities is of considerable interest.

Investigating distribution patterns of plant functional groups in vegetation communities, and exploring discrepancy of the pattern among microhabitats is meaningful for understanding small-scale vegetation processes in the dune field. In this article, we have examined the changes in species composition and diversity of vegetation, seedlings and soil seed banks of a Mediterranean sand dune community, and have identified which functional groups or species benefited from trampling, thus providing a basis for management choice. This work also contributes to a more detailed understanding of patchy regeneration strategies of vegetation and its mosaic pattern of distribution.

The main questions in this study are as follows: (1) Do different microhabitats show significant differences in patterns of species composition, diversity and biomass? (2) Are there significant similarities between soil seed banks and vegetation in microhabitats and do these exhibit seasonal dynamics? (3) Are shrubs beneficial to their understorey plants? (4) Do plants in disturbed habitats possess more persistent seeds than plants in undisturbed habitat, in other words, do short-lived plants possess more persistent seeds?

2. Material and methods

2.1. Study site

This investigation was carried out in a Mediterranean coastal sand dune at the Poleg Nature Reserve (34°45'N, 30°32'E, 5–15 m elevation), Israel, located near the border of Netanea city, 50 miles from Tel Aviv. The climate is a typical Mediterranean climate, with a mean annual rainfall of 500 mm. The growing season extends from October to May. Rainfall occurs mainly in autumn and winter. Mean maximum temperature is 32 °C in July and the mean minimum is 5 °C in January. The soil is developed on a siliceous substrate.

The vegetation of the coastal sand dune consists of a matrix of shrubs (*R. raetam*) with open stabilized patches dominated by herbaceous plants. In this area *R. raetam* is the most abundant shrub in terms of cover and shrub thickets of *R. raetam* are about 80–120 cm high. Annual plants are dominant in the open areas among the shrubs and wind has an important impact on the dynamics of vegetation (Kutiel et al., 1979). The whole area is crisscrossed by pedestrian and off-road (occasional) vehicle trails and the upper soil layer on these trails has been destroyed, leaving loose sand. The field study was conducted from October 2000 to June 2001.

2.2. Investigation of vegetation and biomass

Four different areas, which experience very similar broad scale environmental conditions, were chosen in the study site. In each area, three different microhabitats were selected: (1) open patches among shrub (*R. raetam*) in stabilized sand

dunes, (2) shrub (*R. raetam*) understorey in stabilized sand dunes, and (3) trails disturbed by visitors, passers-by and occasional vehicles. Within each microhabitat, four quadrats of 25 cm × 25 cm were randomly set up (giving a total of 48 quadrats). At the peak of the herbaceous flowering season (April) in each quadrat, presence/absence data for all species in the vegetation was recorded. Above- and belowground biomass of the herbaceous vegetation was sampled by harvesting whole plants. After harvesting, the plants were brought back to the laboratory, classified by species and individuals of each species counted. Vegetation samples were then dried in an oven at 80 °C for 3 days. Dried samples were weighed at room temperature on an electronic balance to the nearest 0.01 g.

2.3. Investigation of seedling emergence

Seedling emergence was monitored within each microhabitat type using forty 25 × 25 cm² quadrats, randomly distributed and fixed in place with a steel peg in each corner of the quadrat. Seedling emergence was examined on four occasions: mid-November 2000, mid-December 2000, early January 2001, and early March 2001. Emerging seedlings in each quadrat were identified, counted and removed at each sampling event until no new seedlings emerged.

2.4. Plant functional groups

Plant species were classified into eight functional groups on the basis of dominance, taxonomic status, morphology and intrinsic physiology, since these influence differences in resource requirements, seasonality of growth, and life history (Tilman et al., 1997a,b). These groups were: (1) annual grasses, (2) perennial grasses, (3) legumes, (4) the species in the family Asteraceae, (5) Brassicaceae, (6) Apiaceae, (7) other annual forbs, and (8) perennial forbs (all other dicots). Legumes, Asteraceae, and Apiaceae were recorded separately because of their great abundance in the community. Legumes have hard seeds that need more time to break the testa (Peco et al., 1998). Nearly all legumes (except *R. raetam*, which contributed a very small proportion of total seedlings), were annual plants, therefore we did not consider annual legumes and perennial legumes as separate functional groups. For similar reasons, we regarded annual Apiaceae (or Asteraceae) and perennial Apiaceae (or Asteraceae) within the same functional family groups. Asteraceae and Apiaceae were regarded as separate functional groups, respectively, since Asteraceae often produce more seeds and Apiaceae are dominant in semiarid regions and also produce copious seeds. The Brassicaceae were recorded separately because of their dominance in the vegetation of trails. Owing to their abundance, annuals and perennial grasses and forbs were each divided into two groups. Annual (or perennial) forbs included species other than legumes, Asteraceae, Apiaceae and Brassicaceae.

2.5. Soil seed banks

The persistent seed bank was measured by sampling the upper 5 cm of soil and litter in May at the end of the rainfall season and before seed dispersal. Composition and size of the soil seed bank was estimated by natural germination (germinated from seeds) combined with the physical separation method. One hundred and twenty permanent quadrats were set up randomly and soil samples (25 × 25 × 5 cm) were collected from within them. The persistent seed bank was measured by separating, identifying, and counting seeds. For details of the investigation method, see Yu et al. (2007). Seasonal variation in the seed bank was estimated by investigating seedlings (mid-November 2000, mid-December 2000, early January 2001, and early March 2001) and the persistent soil seed bank.

2.6. Seed longevity index

Seed longevity indices of different microhabitats were calculated according to Thompson's formula (1998), which takes any value from 0 (no persistent records) to 1 (all records persistent).

2.7. Data analysis

Analysis of variance (ANOVA) techniques were used to analyze the differences in densities of species and functional groups among microhabitats (Sokal and Rohlf, 1995). We also analyzed the differences in the total biomass, the biomass of each functional group and dominant species in the three microhabitats by use of ANOVA. Species diversity and the species evenness index of Pielou were compared among the microhabitats using ANOVA. Regression analyses were performed to determine the correlation between individual abundance, species richness and diversity and biomass in the whole community and in each of three microhabitats (Ludwig and Reynolds, 1988).

Species diversity was measured using the Shannon–Wiener index:

$$H' = - \sum_{i=1}^s P_i \ln p_i,$$

where H' is the value of the Shannon–Wiener diversity index, P_i the proportion of the i th species, and S is the number of species in the community. The evenness index of Pielou (J) was estimated as follows: $J = H' / \ln S$, where S is species richness and H' is the Shannon–Wiener diversity index.

Motyka's similarity index (Mueller-Dombois and Ellenberg, 1974) was used to make comparisons between species composition of vegetation, seedling bank and seed bank in each microhabitat: similarity index (%) = $2c/(a+b) \times 100\%$, where c is the number of species common to the both samples, a and b are the number of all species in sample A and all species in sample B, respectively.

3. Results

3.1. Some physical conditions comparison of three microhabitats

Differences in physical conditions occurred among the three microhabitats (Table 1). The greatest litter weight occurred under shrubs. The degree of soil compaction was highest on the trail.

3.2. The effect of microhabitat on species richness, abundances, species diversity, and composition

Fifty-four plant species were found in the whole community. The open area had the most species (47 species) and the highest species richness (12.25 ± 0.99 species/quadrat), followed by shrub understorey (27 species and 6.5 ± 0.47 species/quadrat, respectively) and the trail (23 species and 5.0 ± 0.95 species/quadrat, respectively).

Microhabitats significantly affected the patterns of individual abundances and species diversity in the vegetation ($p < 0.0001$). Among the three microhabitats, the open area had the greatest species density (1913 ± 287 individuals/m²) (Fig. 1a) and diversity (H') (1.85 ± 0.11), followed by the trail (829 ± 140 and 1.29 ± 0.10 , respectively) and shrub understorey (256 ± 62 and 0.96 ± 0.17 , respectively). Microhabitats did not significantly affect patterns of evenness indices ($F = 0.46$, $p > 0.05$). In the open area, evenness indices were 0.76 ± 0.019 , under shrub 0.68 ± 0.13 , in the trail 0.71 ± 0.025 .

The similarity in species composition between the open and the shrub understorey was 65.9%, between the open and trail 72.4%, and between shrub understorey and trail 53.6% (Table 2).

3.3. The effect of microhabitats on functional groups patterns

Microhabitats significantly influenced the distribution patterns of most functional groups (Fig. 1). The greatest density of every functional group except Apiaceae occurred in the open area (Fig. 1).

The percentages of functional groups overall were: 36.2% annual forbs, 20.7% annual grasses, 19.3% Asteraceae, 16.1% legumes, 5.4% perennial forbs, 1.9% Apiaceae, 0.5% Brassicaceae, and 0% perennial grasses.

3.4. The effect of microhabitats on patterns of biomass in functional groups and dominant species

The open area had the highest biomass (216 ± 18.86 g/m²), followed by the shrub understorey (55.36 ± 16.32 g/m²) and trail (59.06 ± 7.74 g/m²). Microhabitats significantly influenced the distribution patterns of total biomass ($p < 0.0001$) (Fig. 2). Microhabitats also significantly influenced the distribution patterns of biomass of the legumes, annual forbs, and perennial forbs. However, no significant differences were found in the distribution patterns of biomass of other functional groups such as annual grasses, perennial grasses, Brassicaceae, Apiaceae, and Asteraceae (Fig. 2).

Microhabitats significantly affected the biomass patterns of some species such as *Anthemis leucanthemifolia* var. *leucanthemifolia*, *Plantago sacrophylla*, *Anagalis arvensis*, *Bromus rigidus*, *Trifolium palaestinum*, *Polycarpon succulentum* (Fig. 5). The biomass of *P. succulentum* on the trail was significantly higher than that in other two microhabitats. The open areas had the highest biomasses of *A. leucanthemifolia* var. *leucanthemifolia*, *P. sacrophylla*, *A. arvensis*, *B. rigidus* and *T. palaestinum* among the three microhabitats.

Table 1

A comparison of some micro-environmental characteristics among three microhabitats in a Mediterranean coastal sand dune community

Microhabitats	The trail area	The open area	Shrub understorey
Litter weight (g/m ²)	51.52 ± 20.17	356.2 ± 33.31	1693.7 ± 86.8
Litter coverage (%)	2–5	45–55	90–100
Micro-topography	Concave	Flat	Convex
Soil compaction (cm)	3.1 ± 0.3 (harder)	3.3 ± 0.5 (harder)	5.5 ± 0.2 (softer)

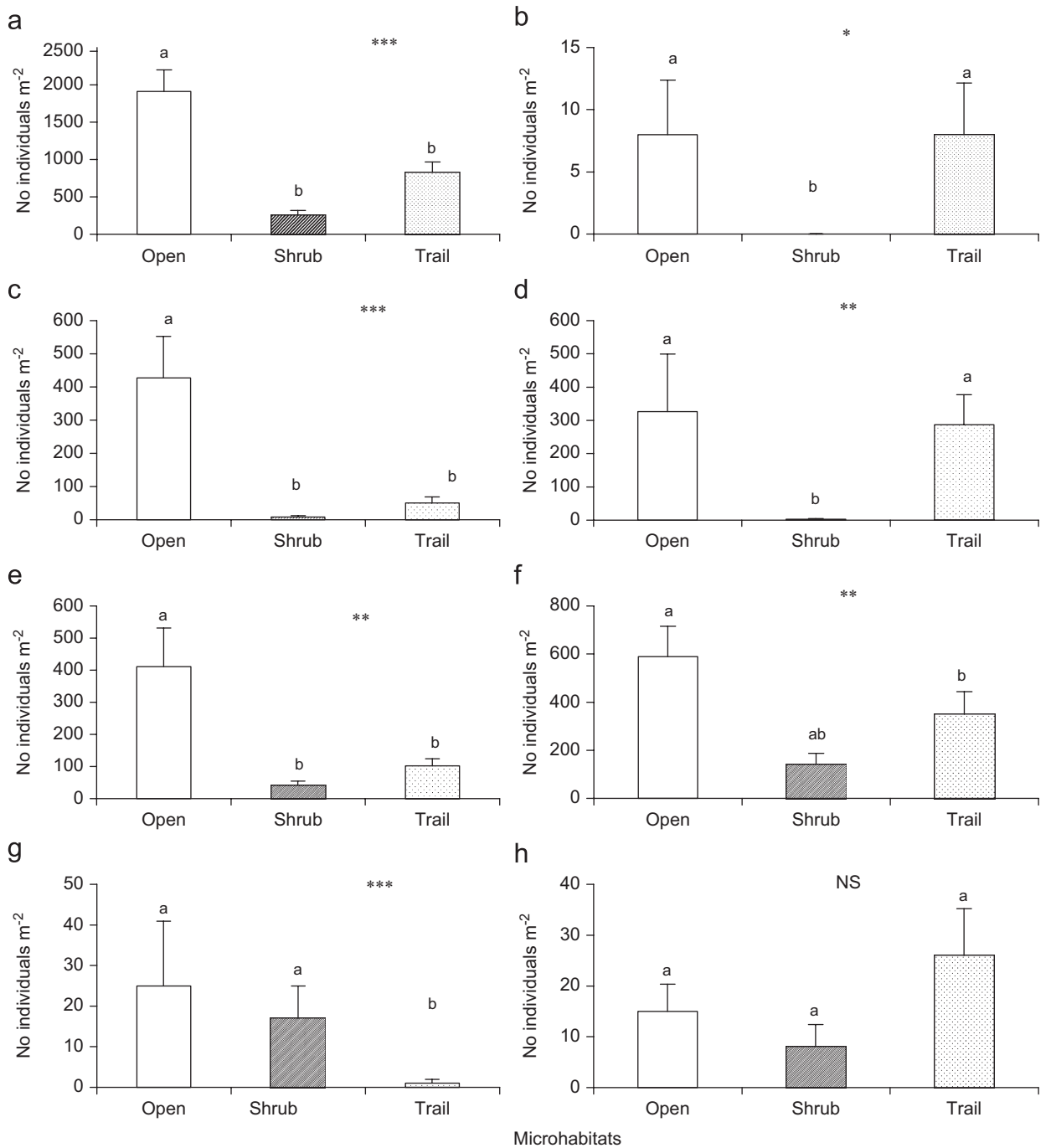


Fig. 1. Effects of microhabitats on individual densities of functional groups in a Mediterranean coastal sand dune community. Total (all functional groups) density (a), Brassicaceae (b), legumes (c), annual grasses (d), Asteraceae (e), annual forbs (f), perennial forbs (g), Apiaceae (h). Significance: NS, no significance; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Treatments bearing the same letter are not significantly different at $p < 0.05$.

3.5. The effect of microhabitats on relationships between abundance, richness, diversity, and biomass

In the community as a whole, a positive correlation was found between individual abundance and biomass ($F = 26.6$, $p < 0.0001$). However, no significant relationships between these measures were found in the open area ($F = 1.19$, $p = 0.29$), the shrub understorey ($F = 2.54$, $p = 0.13$) and the trail ($F = 0.30$, $p = 0.59$).

Table 2

Percent similarity (Motyka's similarity index) between the vegetation, seedling bank and persistent soil seed bank in three microhabitats and the whole community in a Mediterranean coastal sand dune community

Types	Microhabitats			All
	Open	Shrub	Trail	
Vegetation × seedling bank (%)	59.7	52.0	51.9	70.0
Vegetation × soil seed bank (%)	44.0	36.1	36.7	52.4
Seedling bank × soil seed bank (%)	30.0	45.0	48.5	44.1

The index was based on comparisons of presence/absence of species.

In the whole community and in the shrub understorey, a positive correlation was found between species richness and biomass ($F = 46.6$, $p < 0.0001$; $F = 5.58$, $p = 0.03$). However, no significant relationship was found in the open area ($F = 1.26$, $p = 0.28$) and on the trail ($F = 2.85$, $p = 0.11$) (Fig. 3).

In the whole community and in the trail, a positive correlation was found between species diversity and biomass ($F = 26.05$, $p < 0.0001$; $F = 4.62$, $p = 0.0497$). However, no significant relationships were found between these values in the open area ($F = 0.99$, $p = 0.33$) and shrub understorey ($F = 3.74$, $p = 0.07$) (Fig. 4).

3.6. Seasonal dynamics of soil seed banks and the similarity between soil seed banks, seedling bank and vegetation

The soil seed banks in a Mediterranean coastal sand dune showed seasonal variation. The maximum density of seeds in soil seed banks occurred at about the end of May and the beginning of June, when seeds were released from plants. The minimum density of seeds in soil seed banks occurred at the end of April, when germination from the seed bank had occurred and when new season seeds had not been dispersed. In Mediterranean grasslands, the greatest density of the seed bank occurs in summer, following pasture maturity, and then declines to a minimum in spring (Ortega et al., 1997). Losses of seeds during summer were mainly due to germination, but some seeds are eaten by fauna in soil or died owing to fungi invasion.

Correspondingly, the similarity between soil seed bank, vegetation and seedling bank displayed seasonal dynamics. The percentage similarity between the vegetation, seedling bank and seed bank varied for each microhabitat in this Mediterranean coastal sand dune community (Table 2). A high similarity, about 70%, occurred between vegetation and seedling bank in the Mediterranean coastal sand dune community (Table 2), whereas both vegetation and seedling bank had low similarity with soil seed bank (52.4% and 44.1%, respectively) (Table 2). However, the highest value (about 80%) of similarity between vegetation and soil seed bank occurred at the time when seedlings had not emerged but after ripe seeds had dispersed (about in September and October). The lowest value (about 44%) occurred at the time when germination of seedlings ended (about from April and July).

3.7. Species composition of persistent soil seed banks

In the total persistent soil seed bank, the percentage of seeds of annual plants (74.9%) was greater than that of seeds of perennial plants (25.1%). Twenty-seven plant species were found to have persistent soil seed banks, while another 23 plant species did not.

3.8. The longevity indices of three microhabitats

Twenty species in the trails, 22 species in the open area, and 22 species in the shrub understorey had persistent soil seed banks. The disturbed microhabitat (trails) did not possess more species, proportionally, with persistent seeds than did undisturbed microhabitats. For the soil seed banks as a whole, there were 43 species in the trails, 48 species in the open area, and 54 species in the shrub understorey. The highly disturbed trail microhabitat had a higher longevity index (46.5%) than the open (45.8%) and the shrub understorey (40.7%).

4. Discussion

4.1. Density, richness and diversity of plant species and functional groups

Species composition differed among the three microhabitats (Appendix) thus illustrating different ecological amplitudes of plants in this community driven in part by the heterogeneous physical conditions that occur here. Seeds may germinate under a wide range of environmental conditions, but successful establishment of seedlings depends on the nature of the microenvironment. Environmental variation among microhabitats has been measured in this system and referenced from other studies (Alpert and Mooney, 1996; El-Bana et al., 2002).

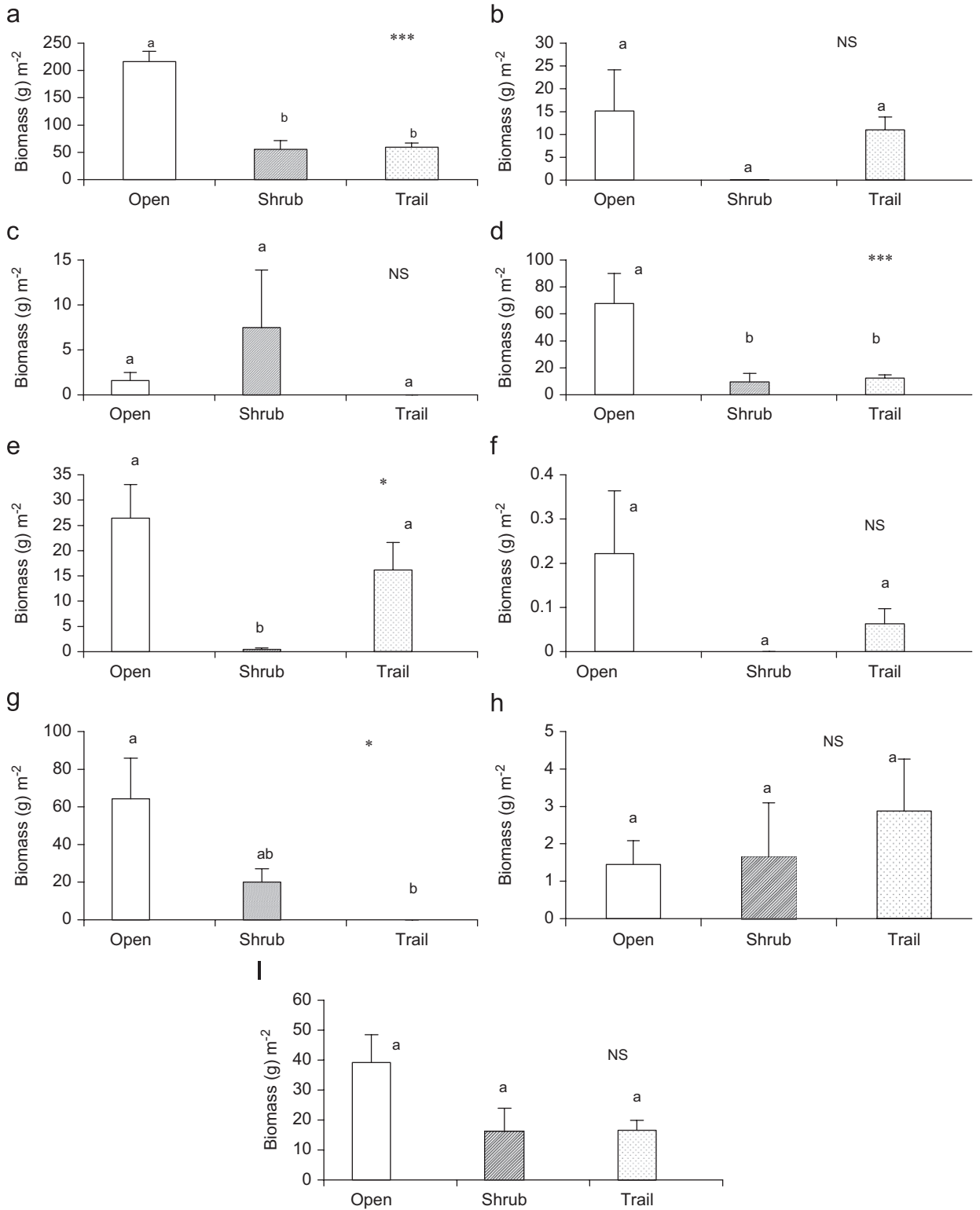


Fig. 2. Biomass of plant species in functional groups in three different microhabitats in a Mediterranean coastal sand dune by several functional groups. Total biomass (a), annual grasses (b), perennial grasses (c), annual forbs (d), legumes (e), Brassicaceae (f), perennial forbs (g), Apiaceae (h), Asteraceae (i). Significance keys as for Fig. 1.

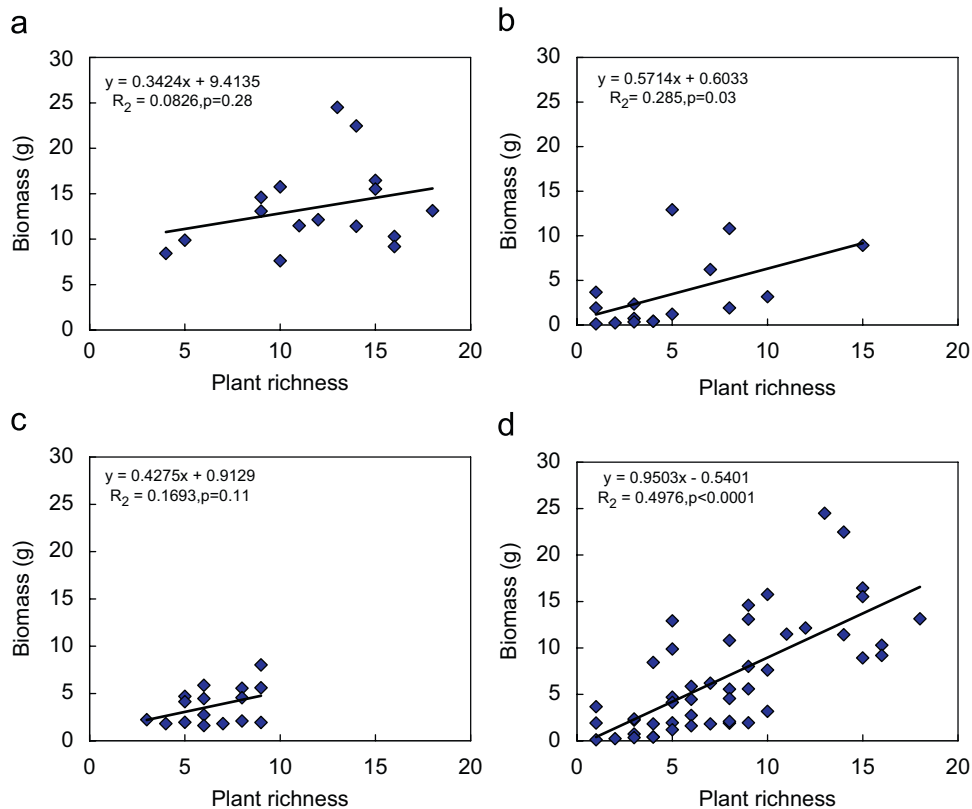


Fig. 3. Relationships between species richness and vegetation biomass per quadrat in three microhabitats in Mediterranean coastal sand dune community. Open (a), shrub understorey (b), trail (c), whole community (d).

Vegetation distribution patterns are related to the initial framework created by the patterns of seed arrival (Schupp and Fuentes, 1995), especially for a plant community dominated by annual plants. Floristic differences between microhabitats have been related to: (1) stochastic dispersal events and dispersal barriers, (2) recruitment limitation (e.g. Cornell and Lawton, 1992), and (3) structural heterogeneity of microhabitats (El-Bana et al., 2002). In this sand dune community, there were significant differences among the three microhabitats in the distribution patterns of total soil seed banks and seed banks for functional groups and species (Yu et al., 2003). Microhabitats can be distinguished by different abiotic factors such as soil moisture, light intensity and nutrient supply. For example, the microhabitats under shrubs are moister and have lower temperatures (Shumway, 2000). Light flux can decrease up to 80% at 35 cm near the ground inside shrub canopies (Alpert and Mooney, 1996). Biological factors such as competition and prey may also differ in different microhabitats. Other environmental factors such as soil water, light, and light period can impact upon the germination and survival of seeds of many species (Baskin and Baskin, 1998; Guterman, 1993).

Significant differences were found in species richness and diversity between microhabitats. The open area has the highest species densities, richness, and diversity. Reasons may be as follows. First, the soil in the open area had the richest species composition of seeds and highest densities of seed in the seed bank (Yu et al., 2003). Second, the open area may have more suitable conditions, for example, enough light, high soil nutrients, and moderate soil moisture for germination and plant growth.

For some functional groups, a significant difference in distribution patterns occurred in different microhabitats (Fig. 1). Species in the same functional group are assumed to share the same collection of attributes. These attributes together allow the group to function in a different way to other functional groups, even if the latter happen to share some (but not all) of the same individual attributes. Therefore, variation in aboveground vegetation structure is thought to influence patterns of seed deposition and the likelihood of subsequent seed movements (Aguiar and Saa, 1997). Microhabitat structure not only directly influences the quality of the microhabitat for dispersed seed, but can also influence how many seeds arrive and how many stay in that microhabitat. Thus density-dependent processes, such as herbivory, predation, and competition, can then indirectly influence the quality of a microhabitat. In addition, recruitment processes are affected by the conditions of the microhabitat, even in sites with similar patterns of seed-fall densities.

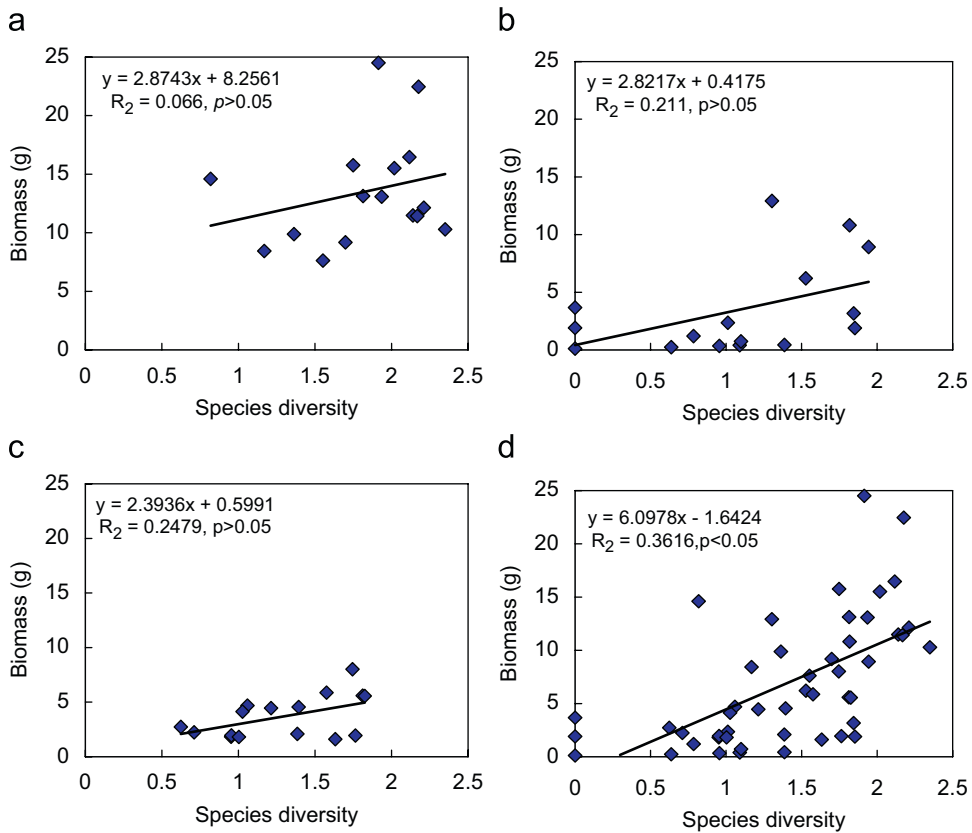


Fig. 4. Relationships between species diversity and biomass of vegetation per quadrat in three microhabitats in a Mediterranean coastal sand dune community. Open (a), shrub understorey (b), trail (c), whole community (d).

4.2. The effect of shrubs on their understorey functional groups and dominant species

The shrub canopy was generally unfavorable to understorey vegetation (Fig. 1a) including most functional groups (such as species in Brassicaceae, legumes, annual grasses, Asteraceae and annual forbs) (Fig. 1) and dominant species such as *A. leucanthemifolia* var. *leucanthemifolia*, *P. sacrophylla*, *A. arvensis*, *B. rigidus*, *T. palaestinum* and *P. succulentum* (Fig. 5). However, perennials and Apiaceae showed no significant response to shrub canopies, neither did functional groups and species appear to benefit from shrub canopies. Apart from the light-shielding effect of a thick canopy, another reason why shrub understoreys do not facilitate species may be due to the large amount of litter beneath the canopy. The presence of deep litter has been shown to play a negative role in seedling regeneration and survival (Xiong and Nilsson, 1999).

Numerous studies have recognized the facilitation effect of shrubs on their understorey species (e.g. Castro et al., 2002; Pugnaire et al., 1996; Shumway, 2000). In contrast, a negative effect of shrubs on their understorey functional groups and species were found in this study. This effect was reflected in the lowest abundance, richness, and diversity under shrubs. Recent studies have showed that the balance between species negative and positive interactions should shift along an environmental gradient (Pugnaire and Luque, 2001; Tiélbrger and Kadmon, 2000). The interaction between the shrubs and their associated species was positive in a water-stressed, but negative in a more fertile habitat (Pugnaire and Luque, 2001). A leguminous shrub, *Retama sphaerocarpa*, facilitated the establishment of other species in the south-eastern Spain, where the annual average rainfall is 218 mm (Pugnaire et al., 1996). However, the less stressful climate in a Mediterranean coastal sand dune, where the annual precipitation is about 500 mm, may account for the negative effect in this study. Rodríguez-Echeverría and Pérez-Fernández (2003) found shrubs facilitate their understorey herbs, but species abundance, richness and diversity were reduced in the presence of a dense canopy of *R. sphaerocarpa*. On the basis of our observations, we suggest that the negative effects of shrubs on plant fitness were mainly due to the denser litter layer of the shrub understorey and the dense canopy (decreasing light and temperature). This result supports the hypothesis that negative interactions should prevail under benign conditions, while positive correlation should increase with increasing abiotic stress (Brooker and Callaghan, 1998).

4.3. The effect of trails on its functional groups and dominant species in vegetation

In comparison with the open area, the trail had lower density, species richness and species diversity in the vegetation. Trampling was unfavorable for total plant abundance (Fig. 1), but different functional groups showed a variable response to trampling. The annual forbs, perennial forbs, legumes, and Asteraceae were vulnerable to trampling (Fig. 1), but annual grasses, Apiaceae, and Brassicaceae appeared to be more tolerant. This tolerance results from mechanisms of both resistance and resilience to the disturbance. The densities of annual plants were higher in the trail than in other microhabitats, presumably because the trail had been disturbed continuously in the past (1 year ago), leading to the death of many perennial plants and an accumulation of seeds of annual plants in the seed bank (Kutiel et al., 2000).

As is the case of this community, it appears that the tolerance of different species to trampling varies and these variations can sometimes be very large. Some species, for example, *A. leucanthemifolia* var. *leucanthemifolia*, *P. sacrophylla*, *A. arvensis* and *T. palaestinum*, appear to be very sensitive to trampling. Other species such as *B. rigidus* are very tolerant of trampling. Other species again could actually benefit from trampling, as in the case of *P. succulentum*. In such microhabitats where the irradiance is high because of low litter cover and exposed soil, *P. succulentum*, a plant with high light tolerance, is likely to be found preferentially in this microhabitat.

Undue trampling can lead to a significant loss in species diversity and the disappearance of a species. The conservation value and interest of this community in the Poleg Nature Reserve lies in its species richness, diversity and its “wildness”, rather than in any especially emblematic and distinctive species. Therefore, it is necessary to set up some measurable parameters such as the frequency of indicator species, densities of key species, and richness of species in order to select appropriate management measures.

4.4. Similarity between seed bank, seedling and vegetation

A high similarity between seedling and vegetation is probably explained by the fact that the seedling bank is essentially an early stage of the extant or mature vegetation. After seedlings establish, many to most of them survive and become a part of the extant vegetation. However, some species or individuals disappear following predation, a short life history, and for other reasons such as pathogen attack or susceptibility to drought. In this coastal sand dune community a low similarity was found between the soil seed bank and the vegetation. These discrepancies are explained by: (1) sampling time and (2) seed attributes in early-successional vegetation. At the beginning of May, most seeds from the previous season germinated and new season seeds had not begun to disperse. So at this sampling time only persistent seeds, with persistence of more than 1 year, were detected in soil. The species composition and size of the soil seed bank displayed seasonal dynamics because seeds of some species do not survive long in soil and thus are present in the seed bank for only a short time following dispersal (Ortega et al., 1997). Therefore, similarity showed a seasonal change. Thus for soil seed bank investigations, an informed choice of sampling time is vital. Long-lived seeds of some species from early-successional vegetation slowly accumulate in the seed bank over many years but may not be present in the mature extant vegetation. For example, the seedlings and mature individuals of the pioneer *Osyris alba*, whose seeds were found only in persistent soil seed bank, were not observed in seedlings and vegetation.

4.5. Bet-hedging hypothesis, seed persistence hypothesis and adult longevity in the sand dune ecosystem on the Mediterranean eastern coast

Seed persistence for more than 1 year was considered to be a bet-hedging adaptation to environmental uncertainty in annuals (Kemp, 1989). The investigation in this study demonstrated this adaptation for 25 species (Table 1). The percentage of species with persistent banks was relatively lower (54%) in comparison to other findings for dry Mediterranean grass and scrublands (Peco et al., 2003). Previous results have often suggested that desert annuals had persistent seed banks (Pake and Venables, 1996). In this Mediterranean coastal sand dune semiarid ecosystem, not only annuals but also perennials and shrubs had persistent soil seed banks, and this showed an evolutionary adaptation to an unpredictable environment for plants. Adult longevity was considered to be negatively correlated with seed persistence (Rees, 1993). In our results, annual plants had more persistent seeds than related perennials. This result was similar to the study of north-west European flora (Thompson et al., 1998) and verified the hypothesis that seeds of short-lived species are more persistent in soil than those of long-lived ones.

In the north-western European flora, long-lived seeds were the characteristics of species living in disturbed habitats such as arable fields (Thompson et al., 1998). In this Mediterranean coastal sand dune community, the trail, the highly disturbed microhabitat, had a higher longevity index than did undisturbed microhabitats (shrub understorey and the open), but the variation was not large in comparison to the open area. The number of species with long-lived seeds in soil was not higher in the trail than in the other two microhabitats, so we were not able to conclude that disturbed microhabitats always have more species with persistent soil seed banks.

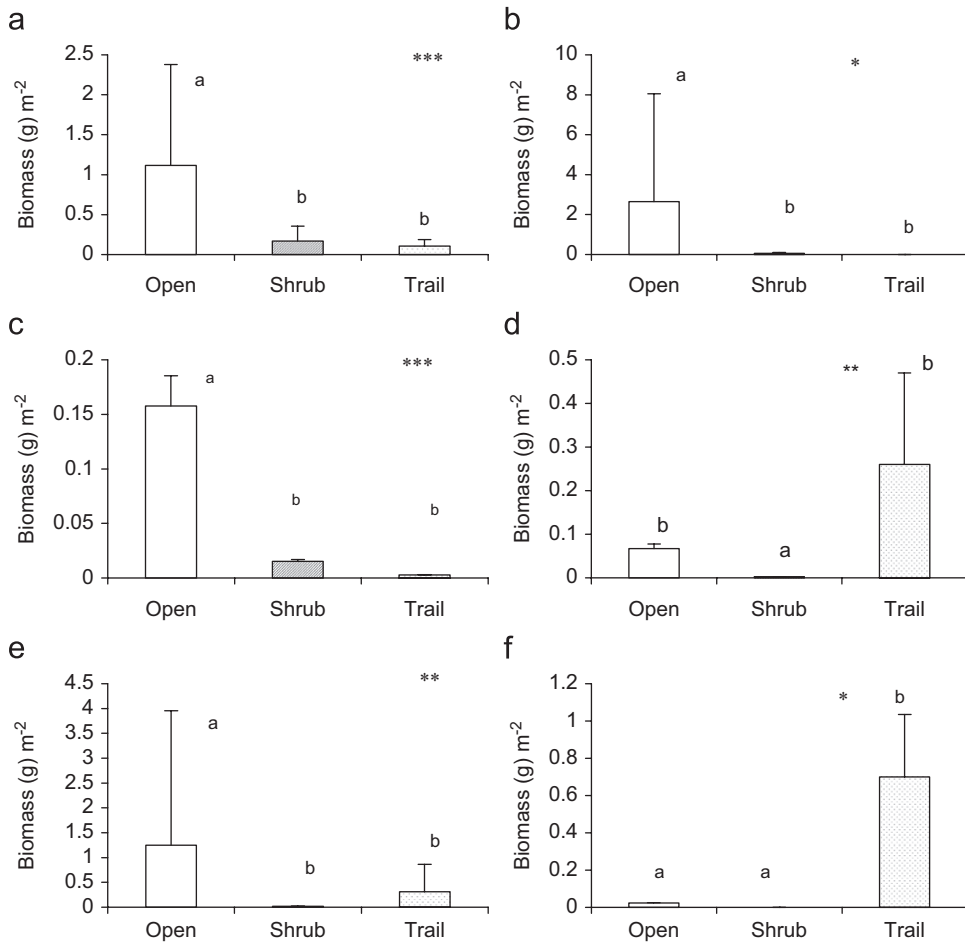


Fig. 5. Relationships between species diversity and biomass of vegetation per quadrat in three microhabitats in a Mediterranean coastal sand dune community. *Anthemis leucanthemifolia* var. *leucanthemifolia* (a), *Plantago sacrophylla* (b), *Anagallis arvensis* (c), *Bromus rigidus* (d), *Trifolium palaestinum* (e), *Polycarpon succulentum* (f). Significance keys as for Fig. 1.

4.6. Diversity–productivity relationships at smaller scale

In this coastal sand dune system, species abundance, richness, and diversity were found to relate significantly and positively to biomass. However, these significant relationships do not occur in all three microhabitats (Figs. 3 and 4). Thus the scale of a study can alter the relationship between diversity and productivity and more importantly indicates that scale is a very important factor in the relationship between diversity and productivity. Previous studies have repeatedly found that productivity has a positive relationship with species diversity since a great number of species can provide better “coverage” of the varying temperature conditions (Hooper et al., 2005; Lehman and Tilman, 2000). Ecologists have known that ecosystem process depends on species composition. Moreover, recent theory has shown that the effects of species diversity should depend on the magnitude of inter-specific differences in such traits as resource use efficiency or productivity (Tilman, 1997). Nutrient use would then increase with diversity (Tilman, 1997). Higher species diversity makes full use of environmental resources such as light since different species use different light intensities.

5. Conclusions

In a Mediterranean coastal sand dune community, species abundance, richness, diversity, and biomass in the vegetation showed heterogeneous distribution patterns in three microhabitats. The open patches generally had the greatest species richness, diversity, and productivity. In the whole community and on the trail, species diversity was related positively to biomass, however, no significant relationships were found for the open area and shrub understory. Shrubs did not benefit their understory plant functional groups except in the case of perennial forbs and Apiaceae. This result supports the hypothesis that negative interactions should prevail under benign conditions, while positive correlations should increase with increasing abiotic stress. Trampling decreased the species diversity of vegetation and did not facilitate the

establishment of herbaceous plants, but was beneficial for some functional groups such as Apiaceae and Brassicaceae as well as some species such as *P. succulentum*. The similarity between the aboveground vegetation and the soil seed bank were found to be seasonally dynamic with highest similarity value occurring during May to September and the lowest value at about the end of April when no new seedlings were emerging. Annual plants had far more persistent soil seed banks than perennial plants, but seed longevity indices and the abundance of persistent seeds in the disturbed microhabitats (trail) were similar to those of the open area and shrub understoreys.

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Appendix. Species list with abundances in vegetation of three microhabitats in a Mediterranean coastal sand dune community

Species list in Poleg Nature	Vegetation			Seedling bank			Persistent seed bank		
	Open	Shrub	Trail	Open	Shrub	Trail	Open	Shrub	Trail
<i>Maresia pulchella</i>	+	+	++	+	–	+	–	–	–
<i>Lathyrus maromorus</i>	–	+	+	–	–	–	+	+	+
<i>Vicia tetrasperma</i>	+	–	–	–	–	+	+	–	–
<i>Retama raetum</i>		+	+	+	+	+	+	+++	+
<i>Trifolium palestenum</i>	+++	+	+	+++	+	+	++	+	+
<i>Trifolium campestre</i>	+	–	–	–	–	–	–	–	–
<i>Medicago constricta</i>	–	+	–	+	–	+	+++	+	++
<i>Coronilla scorpioides</i>	–	++	+	–	–	–	–	–	–
<i>Hippocrepis unisiliquosa</i>	+	+	–	–	–	–	++	–	+
<i>Trigonella cylindrea</i>	–	+	+	–	+++	–	+++	–	+
<i>Lotus halophilus</i> var. <i>halophilus</i>	–	+	–	–	+++	–	+	–	–
<i>Ononis viscosa</i>	–	+	+	+	+	+	–	–	–
<i>Nigella arvensis</i> var. <i>palaestina</i>	+	–	–	–	–	–	–	–	–
<i>Fumaria judaica</i>	+	+	+	+	–	+	–	–	–
<i>Plantago sacrophylla</i>	+	+	–	+	–	+	–	–	–
<i>Plantago albicans</i>	++	++	+	+++	+	+	–	–	–
<i>Bilacunaria boissieri</i>	+	+	+	+	++	–	–	–	–
<i>Papaver humile</i>	++	+	+	–	+	–	–	–	–
<i>Mercuriales annua</i>			+	–	+++	–	–	–	–
<i>Euphorbia peplus</i>	+	+	+	–	+	–	–	–	–
<i>Rumex bucephalophorus</i>	+	+	+	+++	+	+	+	+++	++
<i>Pseudolaya pumila</i>	+	+	–	+	+	+	++	++	+
<i>Ainsworthia cordata</i>	–	–	+	–	–	–	–	–	–
<i>Ainsworthia trachycarpa</i>	–	–	+	–	–	–	–	–	–
<i>Echium angustifolium</i>	+	–	–	+	+	–	–	–	–
<i>Lapula spinocarpus</i>	+	–	–	–	+	–	+	+	+
<i>Lycium schweinfurthii</i>	–	–	+	–	–	–	–	–	–
<i>Solanum luteum</i>	–	–	+	–	–	–	–	–	–
<i>Valantia hispida</i>	+++	++	–	–	–	–	+	++	–
<i>Galium philistaeum</i>	+	+	+	+	+	+	–	+	–
<i>Anagallis arvensis</i>	++	+	+	+	++	+	–	+	+
<i>Arenaria leptocladus</i>	++	+	+	+	–	–	–	–	–
<i>Stellaria media</i>	+	+	+	–	–	–	–	–	–
<i>Silene colorata</i>	+	–	–	–	–	–	–	++	–
<i>Paronychia argentea</i>	++	+	+	+	–	+	+	–	–
<i>Polycarpon succulentum</i>	++	+	+++	++	+	+++	–	+	–
<i>Polycarpon tetraphyllum</i>	+	+	–	–	+	–	–	–	–
<i>Chrysanthemum corotarium</i>	+	–	–	–	–	–	–	–	–
<i>Phagnalon rupestre</i>	+	–	+	+	++	–	–	–	–
<i>Centaurea speciosa</i>	+	–	+	–	–	–	–	–	–
<i>Senecio vernalis</i>	+	+	–	–	+++	–	+	–	–
<i>Senecio joppoensis</i>	–	+	+	+++	–	–	–	–	–
<i>Anthemis leucanthemifolia</i> var. <i>leucanthemifolia</i>	+++	+	+	–	–	–	–	–	+++
<i>Chrysanthemum segetum</i>	+	–	–	–	–	–	–	–	–
<i>Crepis aculeate</i>	++	+	+++	+++	–	–	–	–	+
<i>Ifloga spicata</i>	+	+	–	–	–	–	–	–	–
<i>Sonchus oleraceas</i>	+	–	–	–	+	+	–	–	+
<i>Asparagus stipularis</i>	–	+	+	+	–	–	–	–	–
<i>Tulipa agensis</i>	+	–	–	–	–	–	–	+	–
<i>Cyclamen persicum</i>	+	–	+	–	–	–	–	–	–

<i>Iris haynei</i>	+	++	–	++	–	–	–	–	–
<i>Allium curtum</i> subsp. <i>curtum</i>	+	–	–	–	–	–	–	–	–
<i>Sporobolus pungens</i>	+	–	+	+	–	++	–	–	–
<i>Cutandia philistacea</i>	+++	+	+++	–	–	–	–	–	–
<i>Avena barbata</i>	+	–	–	–	–	–	–	–	–
<i>Lagarus ovatus</i>	+	–	–	–	–	–	–	–	–
<i>Bromus rigidus</i>	+	+	+	–	+	+	–	–	–
<i>Cyperus conglomeratus</i>	+	–	–	++	+	–	–	–	–
<i>Cyperus capitatus</i>	+	+	+	+	+	+++	++	+	+
<i>Ammochloa palaestina</i>	+	–	–	–	–	–	–	–	–
<i>Erodium alnifolium</i>	+	–	–	+	–	–	–	–	–
<i>Adonis cupaniana</i>	–	–	–	+	–	–	–	–	–
<i>Hymenocarpus circinnatus</i>	–	–	–	+	–	–	–	–	–
<i>Galium verrucosum</i>	–	–	–	+	–	–	–	–	–
<i>Fumana arabica</i>	–	–	–	+	+++	–	–	–	–
<i>Bellevallia macrobotrys</i>	–	–	–	+	–	–	–	–	–
<i>Lupinus luteus</i>	–	–	–	–	+	–	–	–	–
Total number of species	46	36	35	32	26	19	15	14	14

+: Low ($n < 3 \text{ m}^{-2}$); ++: medium ($3 \text{ m}^{-2} \leq n < 10 \text{ m}^{-2}$); and +++: high ($n \leq 10 \text{ m}^{-2}$) abundance; –: absent.

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