

# Role of host identity in effects of phytogenic mounds on plant assemblages and species richness on coastal arid dunes

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## Abstract

**Question:** Phytogenic mounds (nebkhas) – the natural accumulation of wind-blown sediments within or around the canopies of plants – have been proposed as important structures for locally maintaining high species richness in coastal and arid ecosystems. Nebkhas are assumed to increase habitat heterogeneity, but what is the importance of the nebkha host species relative to other nebkha characteristics in determining the associated plant assemblages? Are some host species more effective in creating diversity hotspots, or does a single species-area relationship apply to all nebkhas, regardless of host species? Can the influence of the host be ascribed to its indirect effects on abiotic attributes of the nebkha complex?

**Methods and location:** We investigated plant species richness and composition on nebkhas around six psammophytic species on Mediterranean coastal dunes of the Sinai Peninsula.

**Results:** Plant species richness was significantly related to nebkha size by the single power function according to the general prediction of island biogeography theory, but this relationship was modified – though to a limited degree – by nebkha host species identity. Canonical Correspondence Analysis revealed that nebkha host species identity and nebkha environmental and non-environmental factors significantly explained species composition on the nebkhas, but host species identity did so to a greater extent. The latter might reflect differences in seed trapping ability or free space for colonization between host species.

**Conclusion:** Differences in community composition and richness among nebkhas formed by different host species represent a key factor in the maintenance of plant diversity on arid coastal dunes.

**Keywords:** Arid ecosystem; Facilitation; Island biogeography; Nebkha; Phytogenic hillock; Psammophytic species; Sinai Peninsula.

**Nomenclature:** Täckholm (1974); Boulos (1995).

**Abbreviations:** EC = Soil electrical conductivity; IBT = Island biogeography theory; PAR = Photosynthetically active radiation.

## Introduction

Understanding the causes and consequences of spatial heterogeneity has become one of the central aims of modern ecology (Levin 1992). Small-scale heterogeneity may be particularly important in determining plant community structure because the strength of biotic interactions depends on the spatial setting of plants (Reynolds et al. 1997). Conversely, habitat heterogeneity is, itself, generated by biological activity, which can create, modify or maintain habitats.

For example, in many arid and semi-arid regions throughout the world, the patchy pattern of perennial vegetation (Tielbörger 1997; Schlesinger et al. 1990) leads to spatial heterogeneity of soil properties because the infiltration of rainfall to the soil profile can be modified below the plant canopy. The factors involved could be reduced run-off relative to the surrounding barren spaces, which would increase water availability, canopy interception and evaporation which would decrease availability, and stemflow which could spatially concentrate the water. The barren inter-plant spaces, on the other hand, generate soil erosion by wind and nutrient losses from the landscape (Hennessy et al. 1985; Langford 2000; Parsons et al. 2003). Under these conditions plant canopies can act as natural barriers reducing wind velocity, leading to wind blown sand deposition and formation of sand mounds within or around the canopy. These phytogenic mounds or ‘nebkhas’ often contain much greater numbers of species than their surroundings and seem to play an important role in structuring the annual plant community (Brown & Porembski 1997, 2000; El-Bana et al. 2003).

Nebkhas are an interesting model on which to test ecological theory about interspecific interactions. The balance between negative interactions, e.g. competition or allelopathy, and positive interactions or facilitation is not

stable but is known to shift with environmental conditions (Holzapfel & Mahall 1999; Callaway et al. 2002). Under favourable conditions competition would prevail and in harsh conditions facilitation would dominate (Bertness & Callaway 1994). However, in desert shrubs, Tielbörger & Kadmon (2000) found increasingly positive effects on fitness of associated annuals in years with high rainfall. They attributed this to shrubs intercepting rainfall above-ground (negative effect, alleviated in wet years), whilst improving nutrient availability below-ground (positive effect). The role of 'host' plants in shrub-annual interactions in deserts, seems more complex than assumed. The question arises as to whether the effects of host plants observed so far are species specific, or are the expression of a more general pattern? The fact that positive interactions are generally species-specific (Callaway 1998), would point to the former possibility. Most nebkha studies to date were limited to a single, or only a few, host species (e.g. Tielbörger & Kadmon 1997; Holzapfel & Mahall 1999; El-Bana et al. 2003) so data are needed on the associated species of multiple host plants with diverging characteristics.

Nebkha systems are highly suitable for this, given the variation in growth habits, life forms and rooting habits of nebkha building plants (Batanouny & Batanouny 1968; Bornkamm et al. 1999; Dougill & Thomas 2002). This variation apparently also gives rise to a range of nebkha sizes and shapes. By separating these size effects from the identity effects of the nebkha host, the analysis of plant-plant interaction on nebkhas can be extended to the principles of island biogeography (IBT) of MacArthur & Wilson (1967), since nebkhas typically appear as isolated patches within a 'sea' of sand dunes. IBT has been successfully applied before in arid regions, for example on shrub dwelling arthropods across a desert shrubland-grassland ecotone (Sanchez & Parmenter 2002).

The species specific traits of nebkha host plants may affect the structure of the associated community in at least five ways. 1. The interception of rainfall (which is one of the major determinants of plant productivity in sandy environments) by different plant architectures create differences in stemflow volumes, causing nebkhas to differ in moisture content (Navar & Bryan 1990; Martinez-Meza & Whitford 1996). 2. The differences among nebkha host plants in leaf litter production and ability to fix atmospheric nitrogen may induce variation in nebkha fertility (Jackson & Caldwell 1993; Dougill & Thomas 2002). 3. Differences in canopy structure between nebkha hosts may yield a range in microclimatic variables on nebkhas, e.g. in soil temperature, wind velocity and solar radiation (Hesp & McLachlan 2000; El-Bana et al. 2003). 4. Nebkha host plants may differ in their ability to absorb water through roots from deeper soil horizons by hydraulic lift (Richards & Caldwell 1987; Caldwell et al.

1998), thus contributing to differences in the water budget of nebkhas. 5. The ability to trap seeds and propagules from nearby areas, creating safe sites for the establishment of seedlings on nebkhas, may vary (Brown 2001). In spite of this variety of possible pathways through which nebkha hosts can induce ecological consequences, we have little evidence about which of these effects govern the pattern of associated plant species composition, and whether these influences are general across host species or species specific (Batanouny & Batanouny 1968; Tielbörger & Kadmon 1997; Batanouny 2001). The relative importance of the various changes induced by the nebkha host plant is not clear and also requires investigation.

Given the observation that nebkhas of different host plants vary strongly in the quantity of accumulated soil, we first hypothesize that the number of plant species on nebkhas relates to nebkha size as predicted by IBT, but that this relationship is modified by nebkha host identity for the reasons outlined above. We also hypothesize that the host effect on the associated community can be broken down into an environmental component, a non-environmental component and nebkha host identity. The environmental component consists of soil and microclimatic variables which previous studies have shown to be modified by the nebkha host, i.e. they represent the indirect effect of the host on the associated community through abiotic changes. The non-environmental component consists of mostly biotic variables directly related to the host plant, such as canopy size. By also allowing for a third component 'nebkha host identity', yet unidentified effects of the host plant can be detected which do not fall in the other two categories. To test these hypotheses, we studied the pattern of plant species richness and composition on nebkhas formed by six coastal dune species along the Mediterranean coastal dunes of the Sinai Peninsula, which represent a range of morphologies and life forms. Specifically, we (1) compared the attributes of nebkhas formed by the six selected species, (2) evaluated the relationships between nebkha size (area) and the number of associated plant species, (3) determined whether different nebkha host species have different influences in terms of species richness and composition of beneficiary plants and (4) evaluated the relative importance of nebkha environmental characteristics, nebkha non-environmental characteristics, and a possible remaining influence of host species identity, on nebkha species composition.

## Methods

### Field site and species

The study was carried out in the Zaranik nature protection area in the eastern part of Lake Bardawil (31°03' N, 33°30' E), on the Mediterranean coast of the Sinai Peninsula. This landscape is broken by huge sand dunes and salt marshes. The Lake Bardawil climate is arid, with an Emberger's degree of aridity of ca. 13.6 (Shaheen 1998). Precipitation amounts to 82 mm.yr<sup>-1</sup> but is highly variable, and usually extends from October to May (Zahran & Willis 1992). Monthly mean relative humidity varies between 68% and 74% with an annual mean of 72%. The common psammophytic vegetation includes *Stipagrostis scoparia*, *Artemisia monosperma*, *Moltkiopsis ciliata*, *Panicum turgidum*, *Calligonum polygonoides* and *Retama raetam*. Other species in the area include *Asparagus stipularis*, *Echium angustifolium*, *Lycium shawii*, *Pancratium sickenpergeri* and *Thymelaea hirsuta*. A detailed description of the vegetation is available from El-Bana et al. (2002a).

The first six species of the above list were selected for this study, not only because of their predominance at the field site, but also because of their differences in life form and other morphological characteristics that can be relevant to the formation of nebkhas. In addition, they are representative of different successional stages on the coastal desert dunes. Succession on these dunes typically proceeds from chamaephytic grass (*Stipagrostis scoparia*), small shrubs and grass (*Artemisia monosperma*, *Moltkiopsis ciliata* and *Panicum turgidum*) to colonization by late successional, large shrubs including *Calligonum polygonoides* and *Retama raetam* (Danin 1983; Tielbörger 1997; Bornkamm et al. 1999; El-Bana et al. 2002a). These three life forms characterize the mobile, partially stabilized and stabilized dunes, respectively. *S. scoparia* is a perennial grass, widely distributed on mobile desert sand dunes of Asia and Africa (Danin 1983). It forms spaced or diffuse canopies which decrease wind velocity inside the tuft sufficiently to act as a sand trap for building nebkhas. *A. monosperma* is an important *Asteraceae* shrub of both mobile and partly stabilized sands of the study area (El-Bana et al. 2002a) and is sometimes used as a sand binder in the Middle East (Koller et al. 1964). It forms nebkhas through sand deposition around its main lignified stems (Danin 1996). *P. turgidum* is a perennial tufted bunch grass up to 1.5 m in height, with glabrous and indurated stems. Its tufts are able to sprout and expand when sand engulfs and surrounds the plants, creating nebkhas up to 0.4 m high. *M. ciliata* is a perennial *Boraginaceae* semi-shrub with a dense canopy which produces root-borne vertical shoots when covered with sand. *C. polygonoides* is

a perennial *Polygonaceae* woody shrub up to 2 m tall and 4 m wide. When the plant is engulfed with sand, it is able to produce both shoot-borne roots and rootborne shoots, creating dense nebkhas up to 4 m in diameter. *R. raetam* is a leguminous leafless, woody shrub with vertical roots that can reach depths of 20 m (Zohary & Fahn 1952). These roots usually form bacterial nodules that are tolerant to elevated salinity (Sarig et al. 1999). The plant can survive consecutive cycles of sand accumulation and deflation, and often forms a nebkha up to 8 m in diameter when covered by sand (El-Bana et al. 2003).

### Sampling procedures

A field survey was carried out during April and May 2004 at five 1-ha experimental sites on dune slopes characterized by intermediate sand stability. The five sites were located on north-facing slopes, with similar soil types and slope aspects. Within each site, we located all nebkhas of the six selected host species. This yielded a data set consisting of 132 nebkhas: 27 from *S. scoparia*, 22 from *A. monosperma*, 18 from *M. ciliata*, 16 from *P. turgidum*, 24 from *C. polygonoides* and 25 from *R. raetam*. In 15 nebkhas per host species (randomly selected), we delineated the mound by an array of fine iron erosion pins (300 cm high and 0.5 cm diameter) that were inserted at 10 cm intervals in two lines along two perpendicular axes (length and width) from the nebkha top to the inter-nebkha space. Nebkha height was calculated as the mean height of these pins above the zero levelled reference in the surrounding inter-nebkha space. Nebkha area was estimated from its length and width with the formula of an ellipse. The projected area of the host plant canopy was calculated with the same procedure, allowing for different perpendicular axes than the nebkha if necessary. In addition to the measurements on 15 nebkhas per host species, the associated plant species were identified on all nebkhas, yielding nebkha species richness.

Within ten (randomly selected) nebkhas of each of the six selected host species, we measured the following environmental factors: photosynthetically active radiation (PAR), soil temperature and moisture, soil texture, total soil nitrogen, soil electrical conductivity (EC) and soil organic matter. Incident PAR was recorded 30 cm above the ground with a gallium arsenide PAR sensor (JYP-1000, SDEC, France) and soil temperature at a depth of 30 cm using a thermistor probe (4 × 10K, EC-95 thermistors in line, Rhopoint Components Ltd., Oxted, UK), both measurements were taken at the nebkha centre. All sensors were interfaced to portable data loggers (DL2, Delta-T Devices, Burwell, UK), taking readings between 11:00 and 14:00 on a single day without clouds or wind (15 May 2004). Three soil samples were collected

and mixed from the top 30 cm of each nebkha, each at a distance of 10–15 cm from the centre of the host plant. These soil samples were taken during April and May, together with the vegetation survey, at the end of the rainy season when soil decomposer activity is greatest. Gravimetric soil moisture content was calculated from the mass difference before and after drying at 105 °C for 48 h. Soil texture was determined with the hydrometer method, providing percentage sand and fine fractions (silt and clay). Organic matter was estimated by drying and subsequent ignition at 600 °C for 3 h. EC was determined in an aqueous solution (20 g soil dissolved in 40 ml distilled water, manually shaken for 2 h) using a digital conductivity meter (YSI Inc., OH, US.). Total soil nitrogen (N) was determined using the micro-Kjeldahl method.

### Data analysis

According to IBT, species richness ( $S$ ) on individual nebkhas would be related to the area ( $A$ ) of these nebkhas by the single power function  $S = cA^z$ . Regression analysis was performed to determine this relationship for each species, and slopes and intercepts were compared ( $F$ -test, SYSTAT 7.0). In addition, we compared both nebkha area and species richness among different host species using ANOVA followed by Tukey's studentized test of unequal means (Wilkinson 1997) and species richness among different host species using ANCOVA with nebkha area as covariate. These analyses were performed with SPSS 10.0 (SPSS Inc., Chicago, US.).

The species composition of the nebkhas of the six host species was compared using three techniques. 1. Jaccard similarity indices (Colwell 1997) were calculated for all pair-wise comparisons of species based on the relative incidence of the associated species. To correct for non-normality of proportional data, the Jaccard index was arcsine transformed, with the significance being corrected for multiple comparisons using Bonferroni. 2. Detrended Correspondence Analysis (DCA) ordination based on species presence-absence data for each nebkha was performed to examine patterns in species composition among nebkhas of different host species. DCA is a

robust technique based on reciprocal averaging (Peet et al. 1998) which, although useful for describing and displaying trends in species composition, is primarily used as exploratory technique. 3. We therefore also performed a Canonical Correspondence Analysis (CCA) (ter Braak & Prentice 1988) to evaluate the relative importance of host species identity, nebkha environmental characteristics and nebkha non-environmental characteristics, as determinants of associated species occurrence. In these analyses, the matrix of plant species richness (binary variable) constituted the response matrix. The species identity matrix was formed by six variables defining the identity of the host species forming the nebkha. The nebkha environmental characteristics matrix included PAR, soil temperature and moisture, soil texture, soil total nitrogen, EC and soil organic matter. The nebkha non-environmental characteristics matrix was formed by the area of the host-plant, the area of the nebkha and the number of species present on it. To quantify the amount of variation that could be explained by the three constraining matrices, the sum of all canonical eigenvalues for each analysis was divided by the sum of all eigenvalues for the three analyses (Borcard et al. 1992). A Monte Carlo test was performed to assess the significance of the CCA matrices (ter Braak & Prentice 1988). CANOCO for Windows (ter Braak & Šmilauer 1998) was used for all ordinations.

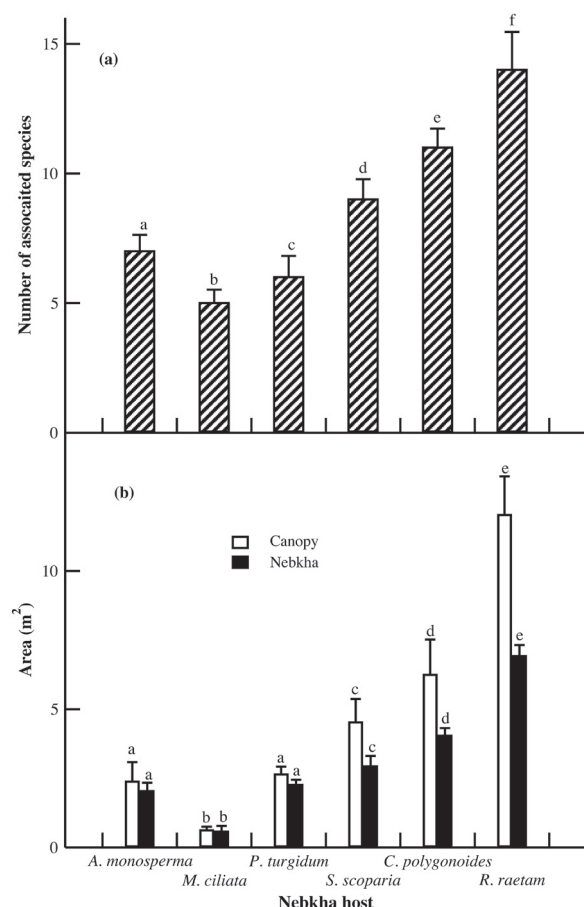
### Results

Nebkhas varied in area and species richness according to the identity of the host plant species ( $P < 0.01$ , Fig. 1a, b). This variability seems to be associated with host canopy area (Fig. 1b). Nebkhas formed by *R. raetam* (large woody shrub) were the largest and richest in species, while those of *M. ciliata* (semi-shrub) were the smallest and poorest in species (Fig. 1a, b).

For each of the evaluated host species, the associated plant species richness was related to nebkha area by the power function (Fig. 2). The equations of these (log-log) species-area relationships showed coincidental slopes ( $F = 3.12$ ,  $P = 0.15$ , Table 1). However, after accounting for

**Table 1.** Linear regression of number of associated species on nebkha area (both log-transformed) for different host species.

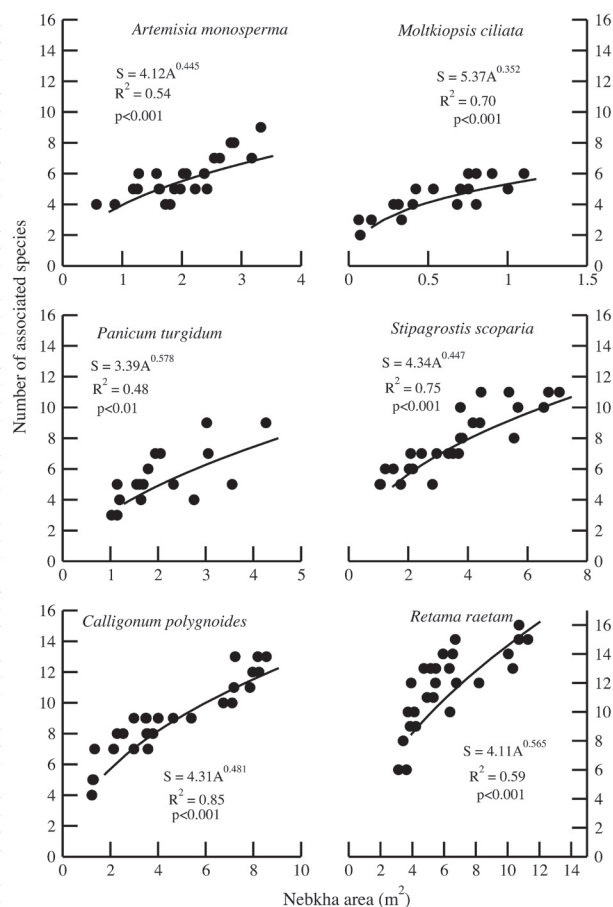
Host species	Slope	Intercept	$R^2$	ANOVA	
				F	P
<i>Artemisia monosperma</i>	0.446	0.615	0.547	25.32	< 0.001
<i>Moltkiopsis ciliata</i>	0.354	0.573	0.672	42.06	< 0.001
<i>Panicum turgidum</i>	0.402	0.350	0.484	14.06	0.002
<i>Stipagrostis scoparia</i>	0.454	0.457	0.774	82.01	< 0.001
<i>Calligonum polygonoides</i>	0.352	0.517	0.424	20.16	< 0.001
<i>Retama raetam</i>	0.578	0.740	0.530	9.37	0.005
All species	0.402	0.680	0.726	362.54	< 0.001



**Fig. 1.** (a) Number of plant species growing on the nebkhas of the six evaluated host species and (b) areas of canopy and nebkha. Bars are means  $\pm$  1 SE of 15 replicates; different letters indicate significant differences at  $P < 0.05$  (Tukey's studentized range test).

the effect of nebkha size, nebkha species richness still differed to some extent among the different host species (ANCOVA,  $P < 0.001$ ), indicating effects of the host plant beyond the species-area relationship.

Ordination of the nebkha plots revealed that the major gradients in species composition were primarily related to nebkha host species identity (Fig. 3). Nebkhas of the early successional species (*S. scoparia*) were located at the lower end of the first axis, whereas the late succes-



**Fig. 2.** Relationships between nebkha area and number of associated species (by host species). Readings of individual nebkhas and fitted power functions. Note the differences in x-axis scale between species.

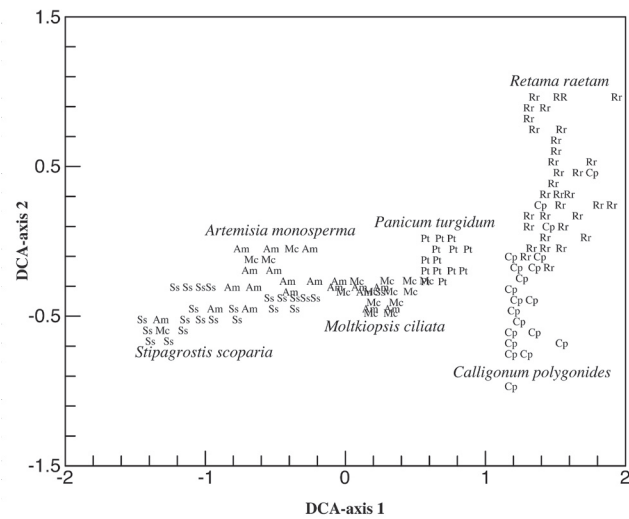
sional species (*C. polygonoides* and *R. raetam*) nebkha plots scored higher on this axis. These differences in community composition were reflected in significant differences in similarity between host species (Table 2). Comparisons between early and late successional host species yielded extremely low levels of similarity, confirming the low degrees of species overlap.

The relative locations of the nebkha plots of *A. monosperma*, *M. ciliata* and *P. turgidum* in ordination

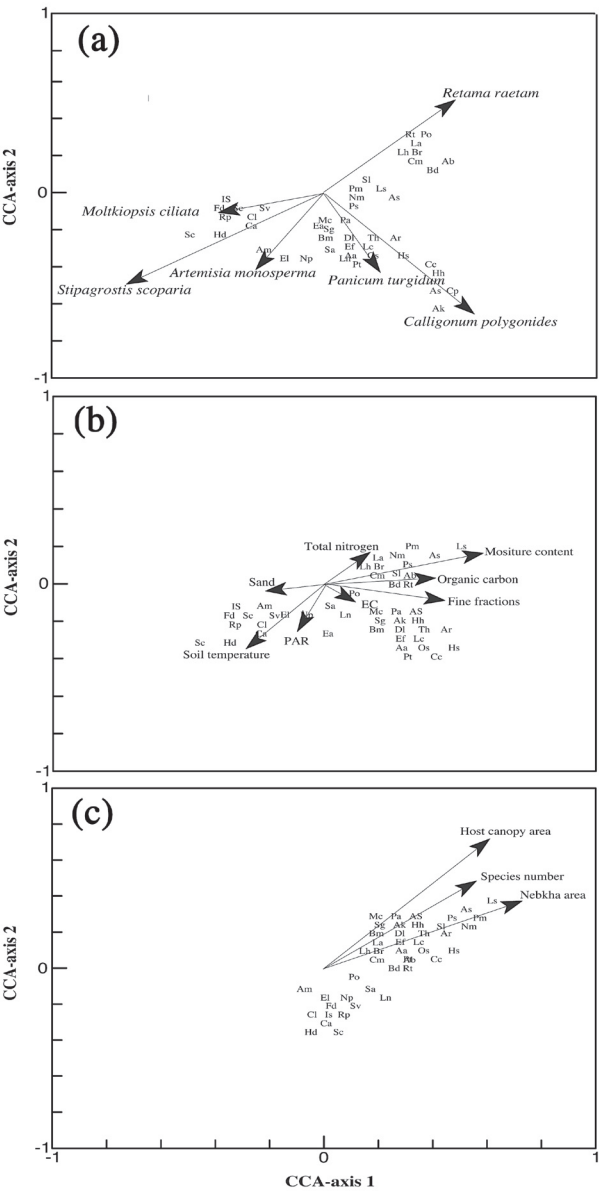
**Table 2.** Jaccard similarity index for pairwise comparison of species composition on nebkhas of different host species. Values with asterisks indicate significant difference at  $P < 0.05$  using a Bonferroni test for multiple comparisons.

Nebkha host species		Jaccard similarity index			
	<i>Artemisia monosperma</i>				
<i>Calligonum polygonoides</i>	0.21	<i>Calligonum polygonoides</i>			
<i>Moltkiopsis ciliata</i>	0.56*				
<i>Panicum turgidum</i>	0.40*				
<i>Retama raetam</i>	0.18				
<i>Stipagrostis scoparia</i>	0.48*				
		<i>Moltkiopsis ciliata</i>			
		<i>Panicum turgidum</i>			
		<i>Retama raetam</i>			





**Fig. 3.** Overlay plot of the six nebkha host species on the first two axes of the DCA vegetation nebkhas ( $n = 90$ ) ordination.



**Fig. 4.** CCA ordination diagrams based on (a) nebkha-host species identity; (b) environmental characteristics and (c) non-environmental characteristics. For species abbreviations, see App. 1.

**Table 3.** Summary of CCA models using presence/absence of associated nebkha species as the main matrix and data sets of nebkha host species identity, nebkha environmental and nebkha non-environmental factors as constrained matrices. X1, X2 and X3 are the eigenvalues for the first three axes; SumX = the sum of all constrained axes; TVE = total variation explained; Axis 1 = *F*-ratio statistic (*P*-value) computed using the first canonical axis as reference (999 randomizations); All axes = *F*-ratio statistic (*P*-value) computed using the trace or sum of all canonical axes as reference (999 randomizations).

Constraining matrix	X1	X2	X3	SumX	TVE (%)	Axis 1	All axes
Nebkha host species identity (6 variables)	0.531	0.323	0.185	1.249	18.72	13.58 (0.001)	7.24 (0.001)
Nebkha non-environmental factors (3 variables)	0.463	0.241	0.146	0.963	12.41	9.79 (0.001)	5.41 (0.001)
Nebkha environmental factors (8 variables)	0.242	0.152	0.114	0.710	8.33	4.86 (0.001)	4.06 (0.001)

space (Fig. 3) suggests that composition did not vary consistently among these three species. Hence, we performed a CCA to assess the effects of nebkha host species identity, nebkha environmental characteristics and nebkha non-environmental characteristics, as dummy explanatory variables for species occurrence. A Monte Carlo test revealed that these three variables all had significant effects on species composition (Table 3), but the amount of variation of the species richness matrix that was explained by nebkha host species identity was greatest.

In the CCA biplot with the nebkha host species identity matrix, *S. scoparia*, *A. monosperma* and *M. ciliata* were negatively related with both the first and second axis, while *R. raetam* was positively related with these axes (Fig. 4a). *P. turgidum* and *C. polygonoides*, on the other hand, were positively related with the first axis, but negatively with the second. In the CCA biplot with the nebkha environmental variables, soil moisture content and soil fertility (fine fractions, organic carbon and total nitrogen) were positively related with the first axis of the ordination (Fig. 4b). It is also clear that the occurrence of geophytes such as *Asparagus stipularis*, *Lycium shawii* and *Pancratium maritimum* coincided with these variables. The three variables defining the nebkha non-environmental characteristics (nebkha host canopy area, nebkha area and number of associated species) were positively related with both the first and the second axis of the ordination (Fig. 4c). The occurrence of species such as *Aegilops kotschyi*, *Avena sativa* and *Lobularia arabica* increased with increasing number of associated species. Species such as *Asparagus stipularis*, *Echiochilon fruticosum*, *Lycium shawii*, *Noaea mucronata* and *Stipagrostis plumosa*, on the other hand, were positively correlated with nebkha area.

## Discussion

Our results indicate that nebkhas formed by different psammophytes greatly contribute to the variation in community structure in arid and semi-arid regions, owing in part to differences in canopy size of the nebkha building plants (Fig. 1). Size, shape and architecture of the host species canopy have been suggested as a key determinant of nebkha size in several arid and semi-arid regions (Tengberg & Chen 1998; Hesp & McLachlan 2000; Dougill & Thomas 2002). In agreement with this, we found that nebkhas formed under the semi and small shrubs (*M. ciliata* and *A. monosperma*) were smaller than those of grasses (*S. scoparia* and *P. turgidum*) and large shrubs (*C. polygonoides* and *R. raetam*). Very large nebkhas occur under *C. polygonoides* and *R. raetam* due to the height of the canopy and the area of these shrubs (Fig. 1).

The observed species-area relationships indicate that the richness of the associated species is directly related to nebkha size (which itself is related to the size of the host plant, Figs. 1, 4c). This suggests a time and/or a size dependence in that more species are found on older and/or larger nebkhas. Larger nebkhas have a larger seed bank (Brown & Porembski 2000) and are spatially more heterogeneous in microclimate and soil nutrients (Hesp & McLachlan 2000; El-Bana et al. 2002b). The simultaneous presence of these abiotic and biotic resources creates niche differentiation, and promotes the recruitment of species with different life and growth forms on the nebkhas (Bornkamm et al. 1999). Moreover, the species-area relationships for different nebkha host species were consistent with the prediction of IBT, lending further support to the island like nature of nebkhas within sand-deflated, sand-depleted and oil polluted areas in coastal and desert dunes (Brown & Porembski 2000; El-Bana et al. 2000b, 2003). Although this support should be considered with caution because no data were collected from the inter-nebkha spaces, several previous studies (e.g. Tielbörger & Kadmon 1995; Brown & Porembski 1997; Brown 2001) have found that number of species, as well as plant density and biomass, are much higher

on nebkhas than in the inter-nebkha space, even in very disturbed sites (El-Bana et al. 2003). Therefore, substantial differences between the species-area relationships of nebkha and inter-nebkha areas are likely to exist, and we expect the increase in number of species with increasing area to be much smaller in the inter-nebkha.

Our results showed that the relationship between nebkha area and species richness was modified by the identity of the host species building the nebkha. Apart from plant size, such modification may arise from the differences in species specific traits of host species such as atmospheric nitrogen fixation, water use and rainfall interception. For example, woody, nitrogen fixing legumes such as *R. raetam* may enhance soil nutrient content and improve soil structure by adding nitrogen rich organic matter to the soil through litterfall and root turnover, owing to their symbiotic associations with both rhizobial bacteria and mycorrhizal fungi (Sarig & Steinberg 1994; Sarig et al. 1999). In agreement with this, *R. raetam* had the highest intercept in Table 1.

The difference in community structure and richness between the nebkhas of early and late successional host species suggests a mode of succession in which the recruitment of species on nebkhas results in a general increase in diversity over time. It seems that the order in which species associate to a specific nebkha host is not random, with few species, predominantly annuals and dwarf species, associating to the early successional nebkhas and a large subset of species, mostly perennial herbs and geophytes, recruiting in large and diverse late successional nebkhas (Figs. 1 and 3, App. 1), with the exception of *S. scoparia* nebkhas, which had intermediate richness. These results are similar to changes in perennial plant richness that became more pronounced with increasing soil development during primary succession on coastal and desert dunes (Bornkamm et al. 1999; Stallins 2003; Malkinson et al. 2003).

The dominance of nebkha host species identity over the other two matrices (nebkha environmental and non-environmental characteristics) (Table 3) as a determinant of observed species occurrences, could be attributed to the role that shape and/or architecture of the host plant play in trapping seeds and establishing seedlings in arid and semi-arid areas (Halvorson & Patten 1975; De Soyza et al. 1997; Raffaele & Veblen 1998). Although seed banks were not investigated in this study, we found evidence suggesting that several low frequency species (such as geophytes, *Asparagus stipularis* and *Lycium shawii*) are mostly restricted to the highly diverse, large nebkhas built mainly by the two late successional host species *C. polygonoides* and *R. raetam* (App. 1, Fig. 4 c). On the other hand, the early successional host species such as *S. scoparia* and *M. ciliata* form tight cushions which could limit the growth of some species, especially those that

require free space (e.g. geophytes or woody species).

Despite the prevalence of nebkha host identity, the nebkha environmental characteristics and non-environmental characteristics (Table 3) accounted for significant fractions of the variation in species occurrence on nebkha patches. This indicates the importance of considering multiple factors when examining the role of patchiness in structuring plant communities of xeric environments (Kellman & Kading 1992; Belsky 1994; Greenlee & Callaway 1996; Tielbörger & Kadmon 2000). Concerning the environmental characteristics, our simultaneous study on multiple host species demonstrates that not all the benefits of nebkha formation that were previously identified in research on single nebkha hosts, can be generalized across many species. For example, soil moisture and fertility (Hesp & McLachlan 2000; Dougill & Thomas 2002; El-Bana et al. 2002b, 2003) were more important for species composition than microclimate (Fig. 4b); effects of the latter may therefore be species specific. Locally increased nutrient concentrations arise *inter alia* from nebkha building plants trapping their own litter and intercepting other windblown litter (Dougill & Thomas 2002). The modifications in soil microclimate could, in spite of their lesser importance, still play a role in seedling establishment and survival, as mortality is often highest in the early life stage of desert plants due to desiccation and heat stress (Gutterman 1993).

In conclusion, this study has demonstrated floristic differentiation among nebkhas of different host species, in addition to different abilities to build nebkha mounds, and different potentials to generate locally high plant diversity. Apart from nebkha features such as mound size and biogeochemistry, more subtle features such as canopy shape and architecture, may be at the basis of these influences of nebkha identity. The variety of nebkha host species must therefore be considered a key element in the maintenance of biodiversity in coastal and desert dunes.

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## References

- Batanouny, K.H. 2001. *Plants in the deserts of the Middle East*. Springer-Verlag, Heidelberg, DE.
- Batanouny, K.H. & Batanouny, H.M. 1968. Formation of phytogenic hillocks. I. Plants forming phytogenic hillocks. *Acta Bot. Acad. Scient. Hung.* 14: 243-252.
- Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922-932.
- Bertness, M.D. & Callaway, R. 1994. Positive interactions in communities. *Trends Ecol. Evol.* 9: 191-193.
- Borcard, D., Legendre, P. & Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology* 73: 1045-1055.
- Bornkamm, R., Darius, F. & Prasse, R. 1999. On the life cycle of *Stipagrostis scoparia* hillocks. *J. Arid Environ.* 42: 177-186.
- Boulos, L. 1995. *Flora of Egypt, a checklist*. Al Hadara, Cairo, EG.
- Brown, G. 2001. Factors maintaining plant diversity in degraded areas of northern Kuwait. *J. Arid Environ.* 54: 183-194.
- Brown, G. & Porembski, S. 1997. The maintenance of species diversity by miniature dunes in a sand-depleted *Haloxylon salicornicum* community in Kuwait. *J. Arid Environ.* 37: 461-473.
- Brown, G. & Porembski, S. 2000. Phytogenic hillocks and blow-outs as 'safe sites' for plants in an oil-contaminated area of northern Kuwait. *Environ. Conserv.* 27: 242-249.
- Caldwell, M.M., Dawson, T.E. & Richards, J.H. 1998. Hydraulic lift: consequences of water efflux for the roots of plants. *Oecologia* 113: 151-161.
- Callaway, R.M. 1998. Are positive interactions species-specific? *Oikos* 82: 202-206.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschhoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417: 844-888.
- Colwell, R.K. 1997. *EstimateS: statistical estimation of species richness and shared species from samples*. Version 5. URL: <http://viceroy.eeb.uconn.edu/estimates>.
- Danin, A. 1983. *Desert vegetation of Israel and Sinai*. Cana, Jerusalem, IS.
- Danin, A. 1996. *Plants of desert dunes*. Springer-Verlag, Heidelberg, DE.
- De Soyza, A.G., Whitford, W.G., Martinez, M.E. & Van Zee, J.W. 1997. Variation in creosote bush (*Larrea tridentata*) canopy morphology in relation to habitat, soil fertility and associated annual plant communities. *Am. Midl. Nat.* 137: 13-26.
- Dougill, A.J. & Thomas, A.D. 2002. Nebkha dunes in the Molopo Basin, South Africa and Botswana: formation controls and their validity as indicators of soil degradation. *J. Arid Environ.* 50: 413-428.
- El-Bana, M.I., Khedr, A.A., Van Hecke, P. & Bogaert, J. 2002 a. Vegetation composition of a threatened hypersaline Lake (Lake Bardawil), North Sinai. *Plant Ecol.* 163: 63-75.
- El-Bana, M.I., Nijs, I. & Kockelbergh, F. 2002 b. Micro-environmental and vegetational heterogeneity induced by phytogenic nebkhas in an arid coastal ecosystem. *Plant Soil* 247: 283-293.
- El-Bana, M.I., Nijs, I. & Khedr, A.A. 2003. The importance of phytogenic mounds (Nebkhas) for restoration of arid degraded rangelands in Northern Sinai. *Restor. Ecol.* 11: 317-324.
- Greenlee, J.T. & Callaway, R.M. 1996. Abiotic stress and the relative importance of interference and facilitation in Montane bunch-grass communities in Western Montana. *Am. Nat.* 148: 386-396.
- Gutterman, Y. 1993. *Seed germination in desert plants*. Springer-Verlag, Heidelberg, DE.
- Halvorson, W. & Patten, D. 1975. Productivity and flowering of winter ephemerals in relation to Sonoran desert shrubs. *Am. Midl. Nat.* 93: 311-319.
- Hennessy, J.T., Gibbens, R.P., Tromble, J.M. & Cardenas, M. 1985. Mesquite (*Prosopis glandulosa* Torr.) dunes and interdunes in southern New Mexico: a study of soil properties and soil water relations. *J. Arid Environ.* 9: 27-38.
- Hesp, P. & McLachlan, A. 2000. Morphology, dynamics, ecology and fauna of *Arctotheca populifolia* and *Gazania rigens* nabkha dunes. *J. Arid Environ.* 44: 155-172.
- Holzapfel, C. & Mahall, B.E. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave desert. *Ecology* 80: 1747-1761.
- Kellman, M. & Kading, M. 1992. Facilitation of tree seedling establishment in a sand dune succession. *J. Veg. Sci.* 3: 3679-3688.
- Koller, D., Sachs, M. & Negbi, M. 1964. Germination regulating mechanisms in some desert seeds. VIII. *Artemisia monosperma*. *Plant Cell Physiol.* 5: 85-100.
- Jackson, R.B. & Caldwell, M.M. 1993. Geostatistical pattern of soil heterogeneity around individual perennial plants. *J. Ecol.* 81: 683-692.
- Langford, R.P. 2000. Nabkha (coppice dune) fields of south-central New Mexico, U.S.A. *J. Arid Environ.* 46: 25-41.
- Levin, S.A. 1992. The problem of pattern and scale in Ecology. *Ecology* 73: 1943-1967.
- MacArthur, R. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ, US.
- Malkinson, D., Kadmon, R. & Cohen, D. 2003. Pattern analysis in successional communities – An approach for studying shifts in ecological interactions. *J. Veg. Sci.* 14: 213-222.
- Martinez-Meza, E. & Whitford, W.G. 1996. Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs. *J. Arid Environ.* 32: 271-287.
- Navar, J. & Bryan, R.B. 1990. Interception loss and rainfall redistribution by three semi-arid growing shrubs in north-eastern New Mexico. *J. Hydrol.* 115: 51-63.
- Parsons, A.J., Wainwright, J., Schlesinger, W.H. & Abrahams, A.D. 2003. The role of overland flow in sediment and nitrogen budgets of mesquite dunefields, southern New Mexico. *J. Arid Environ.* 53: 61-71.
- Peet, R.K., Knox, R.G., Case, J.S. & Allen, R.B. 1998. Putting things in order: the advantages of detrended correspondence analysis. *Am. Nat.* 131: 924-934.
- Raffaele, E. & Veblen, T.T. 1998. Facilitation by nurse shrubs of resprouting behaviour in a post-fire shrubland in northern

- Patagonia, Argentina. *J. Veg. Sci.* 9: 693-698.
- Reynolds, H.L., Hungate, B.A., Chapin, F.S. & D'Antonio, C.M. 1997. Soil heterogeneity and plant competition in an annual grassland. *Ecology* 78: 2076-2090.
- Richards, J.H. & Caldwell, M.M. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73: 486-489.
- Sanchez, B.C. & Parmenter, R.R. 2002. Patterns of shrub-dwelling arthropod diversity across a desert shrubland-grassland ecotone: a test of island biogeographic theory. *J. Arid Environ.* 50: 247-265.
- Sarig, S. & Steinberger, Y. 1994. Microbial biomass response to seasonal fluctuation in soil salinity under the canopy of desert halophytes. *Soil Biol. & Bioch.* 26: 1405-1408.
- Sarig, S., Fliessbach, A. & Steinberger, Y. 1999. Soil microbial biomass under the canopy of coastal sand dune shrubs. *Arid Soil Res. Rehab.* 13: 75-80.
- Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrel, W.M., Virginia, R.A. & Whitford, W.G. 1990. Biological feedbacks in global desertification. *Science* 247: 1043-1048.
- Shaheen, S.E. 1998. *Geoenvironmental studies on El-Bardawil lagoon and its surroundings, North Sinai, Egypt*. Ph.D. Thesis, Mansoura University, Mansoura, EG.
- Stallins, J.A. 2003. Dune plant species diversity and function in two barrier island biogeomorphic systems. *Plant Ecol.* 165: 183-196.
- Täckholm, V. 1974. *Students flora of Egypt*. Cairo University Press, Cairo, EG.
- Tengberg, A. & Chen, D.L. 1998. A comparative analysis of nebkhas in central Tunisia and northern Burkina Faso. *Geomorphology* 22:181-192.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- ter Braak, C.J.F. & Prentice, I.C. 1988. Theory of gradient analysis. *Adv. Ecol. Res.* 18: 271-317.
- ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination*. Version 4. Microcomputer Power, Ithaca, NY, US.
- Tielbörger, K. 1997. The vegetation of linear desert dunes in the north-western Negev, Israel. *Flora* 192: 261-278.
- Tielbörger, K. & Kadmon, R. 1995. The effect of shrubs on the emergence, survival and fecundity of four coexisting annual species in a sandy desert ecosystem. *Ecoscience* 2: 141-147.
- Tielbörger, K. & Kadmon, R. 1997. Relationships between shrubs and annual communities in a sandy desert ecosystem: a three-year study. *Plant Ecol.* 130: 191-201.
- Tielbörger, K. & Kadmon, R. 2000. Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* 81: 1544-1553.
- Wilkinson, L. 1997. *SYSTAT: The System Analysis for Statistics*. SPSS Inc. Chicago, IL.
- Zahran, M., & Willis, A.J. 1992. *The vegetation of Egypt*. Chapman & Hall, London, UK.
- Zohary, M. & Fahn, A. 1952. Ecological studies on East Mediterranean dune plants. *Bull. Res. Counc. Isr. Sect.* 1: 38-53.

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