

A MULTIVARIATE ANALYSIS OF THE NICHES AND GUILD STRUCTURE OF PLANT POPULATIONS IN A DESERT LANDSCAPE

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Abstract

The first three components (explaining 71.75% of the total variance) derived from principal component analysis were used to define the ecological niches of the plant populations in a desert landscape. The paper examines the niche parameters of breadth and overlap and investigates the guild structure within the assemblage. On the basis of overall (product) niche width three species *Blepharis sindica*, *Commiphora wightii* and *Prosopis cineraria* were shown to be generalists while five species - *Prosopis juliflora*, *Cordia gharaf*, *Senna holosericea*, *Rhazya stricta* and *Grewia tenax* appeared to be specialists. Average importance value of species was weakly positively correlated with the niche width.

Pairwise niche overlaps varied considerably, ranging from 0.0886 to 0.9958 but the average overlap was high on all three niche axes. Although the niche dimensions were theoretically independent from each other, pairwise overlaps, along the axes were correlated. The extent of diffuse overlap for different species varied with the niche axes. In the three dimensional niche space, *Senna holosericea* experiences the least overlap while *Zizyphus nummularia* faces the most. Analytical study of niche packing disclosed that species were packed more closely along niche dimensions than is predicted by competition theory. The problem of interpreting overlap measures as indices of competition intensity are discussed. Analysis of guild structure revealed two major guilds each comprising of two subguilds. Coexistence of species in the face of high niche overlap is explained.

Introduction

Multivariate analytical techniques have been primarily used by ecologists for the purpose of trend seeking and summarization of ecological data sets. However, recently some authors have focused on multivariate niche models, in the context of animal communities which permit estimation of niche width and overlap (Green, 1971, 1974; Shugart & Patten, 1972; Dueser & Shugart, 1978; Anderson & Shugart, 1974; Rotenberry & Weins, 1980; Carnes & Slade, 1982; van Horne & Ford, 1982). Despite the frequent use of such models in zoological studies, there has been paucity of work on multivariate statistical analogies to the niche in plants; the exceptions being Johnson (1977a,b) and Mann & Shugart (1983).

Hutchinson (1958) formalized the niche as an n-dimensional hypervolume whose axes are critical physical and environmental factors that determine the existence space of an organism. In contrast to the earlier subjective and vague definitions of niche (cf. MacArthur, 1968; Ayala, 1970), Hutchinson's model provides an explicit objective concept of greater potential utility and encourages ecologists to test and develop hypotheses about the structure of communities.

Root (1967) coined the term 'guild' to describe a group of species that exploit the same class of environmental resources in a similar manner without regard to their taxonomic affinities. Thus, the community structure can be conceptualized as being organized into clusters of species that overlap significantly in their niche requirements. The concept of guild has begun to attract increasing attention (Feinsinger, 1976; Inger & Colwell, 1977; Pianka, 1980) though little has been done with regard to guild structure existing within plant communities.

Levins (1968) hypothesized that dominant species have broad niche widths. McNaughton & Wolf (1970) provided evidence indicating that dominants have broader niches than the subordinate species. Positive correlation between niche or ecotope width and abundance or dominance has also been demonstrated by Parrish & Bazzaz (1976) and Johnson (1977). Adams & Anderson (1982), however, obtained an inverse relationship between habitat breadth and dominance.

The present study uses principal component analysis to define ecological niches of the plant populations in a desert terrain in southern Sind. Secondly, it tests the relationship between dominance and niche width in the context of the desert environment and lastly it exposes the guild structure within the assemblage.

Methods

Sampling: Twentytwo stands were sampled using pointcentered quarter method in Gadap area, southern Sind. Soil samples collected from each stand were analysed physically and chemically. Details of the study area sampling strategy and soil analysis procedures have appeared in Shaukat *et al.* (1980). For the description of the vegetation and edaphic relations the reader is referred to Shaukat *et al.* (1980).

For the analyses of niche structure, shrub or tree species that occurred in at least 5 stands were retained.

Niche breadth and overlap: Niche breadth (B_i) measures the position and degree of performance of a species population along its niche dimension. Usually a variance equation of some form is regarded as adequate. Several measures of niche breadth have been proposed (Levins, 1968; McNaughton & Wolf, 1970; Colwell & Futuyama, 1971; Dueser & Shugart, 1979; van Horne & Ford, 1982). In the present study, the expression developed by McNaughton & Wolf (1970) was preferred because it not only measures variance along the dimension but also weights the positions. The niche breadth (B_i) expression is:

$$B_i = \left[\frac{\sum (y_p \cdot p^2) - \sum (y_p \cdot p)^2 / \sum y}{\sum y} \right]^{1/2}$$

where p is the position of a study site along the gradient, Y_p is the species Importance Value Index (IVI) at that site, E^y is the sum of a species' IVI for all occurrences. The IVI is a measure of relative success of a species at a given point along the gradient and is the sum of relative density, coverage and frequency of occurrence.

Data for niche breadth computation were prepared in the following manner. A principal component ordination was performed on the data of 11 soil physical and chemical characteristics (Orloci & Kenkel, 1985). Each of the first three principal components (that together explained 71.75% of the total variance) were divided into 8 equally spaced segments numbered from 1 at the far positive end to 8 at the, far negative side. The IVI of the *i*th species in each segment were summed and divided by the number of stands falling in the segment. Niche overlap which quantifies the degree of similarity in resource use on one unique resource dimension, can be measured by several niche overlap measures (Hurlbert, 1978; Abrams, 1980; Ganis, 1989; Neet, 1989). Pianka's (1973) symmetrical index which is related to the "competition coefficients" of the Lotka-Volterra equations was used to measure niche overlap, as follows:

$$O_{ij} = \frac{\sum_{h=1}^{NS} P_{ih} p_{jh}}{\left[\sum_{h=1}^{NS} p_{ih}^2 \cdot \sum_{h=1}^{NS} p_{jh}^2 \right]^{1/2}}$$

where *p_{ih}* is the proportion of the IVI of the *i*th species in *h*th segment of the environmental gradient represented by the principal component and NS equals the number of segments. The advantages of the use of a symmetrical overlap measure are discussed by May (1975). It must be noted that the niche overlap does not necessarily imply simultaneous use of the same resources in a competitive relationship and that niche overlap is not sufficient to infer competition (Holt, 1987).

Average overlap is the mean overlap among all species pairs while diffuse overlap is the average overlap experienced by one species from the rest of species in the assemblage (Pianka's, 1974 'diffuse competition').

Average (*O_{ij}*) and diffuse overlap (*O_d_i*) were calculated as follows:

$$\bar{O}_{ij} = \bar{O}_{ji} = \frac{\sum_{i=1}^{S-1} \sum_{j=i+1}^S O_{ij}}{\{S(S-1)/2\}}$$

$$O_i^d = \sum_j^{S-1} O_{ij} / (S-1) \quad i \neq j$$

where S equals the number of species.,

Total overlap combines values from resource/niche dimensions into one inclusive measure of the overall similarity in between two species and is determined either as summation overlap or product overlap:

$$\text{Summation overlap} = \sum O_{ij} = \sum_{r=1}^n O_{ijr} / n$$

$$\text{Product overlap} = \prod O_{ij} = \prod_{r=1}^n O_{ijr} \quad \text{Where } n = \text{number of dimensions.}$$

Summation overlap represents the upper bound on the true multidimensional overlap whereas product overlap usually, but not always sets the lower bound (May, 1975).

Guild structure in the assemblage was determined in accordance with Pianka (1980). Two methods were used (i) nearness rank of neighbours in niche space, and (ii) cluster analysis. The first technique, which depicts some of the community's "connectedness", involves ranking each species' neighbours in niche space from the nearest to the mostdistant (Inger & Colwell, 1977) and plotting overlap or mean overlap and their standard deviation against neighbour's rank in niche space. Cluster analysis is used to objectively define guild structure. Average linkage clustering strategy (Orloci & Kenkel, 1985) was employed as this, provides a spherical group (guild) structure inherent in the niche space.

Results and Discussion

The principal component analysis (PCA) of the soil data revealed that the first three components accounted for 71.75% of the total variation with the first, second and third components explaining 37.51, 18.64 and 16.60% of the total variability respectively. The first component was primarily a function of soil pH, exchangeable K^+ , $CaCO_3$ and water holding capacity of soil. The second component was principally governed by water holding capacity and the clay percentage of soil while the third component was heavily weighted on soil pH and coarse and fine sand percentages. Thus the first component represents the soil chemical gradient, the second component, a moisture regime gradient and the third component an admixture of the two gradients.

Niche breadth: The niche breadth magnitudes on the three components (axes) of PCA ordination and the overall niche breadths are, presented in (Table 1). The overall niche breadth can be taken to indicate a species' performance on several niche dimensions combined. Because the axes described here are by definition orthogonal and therefore independent, overall niche breadth is represented by the product of niche width of species along each of the axes (May, 1975; Pianka, 1975). Although, it must be noted that the niche widths of species along the three axes are themselves correlated (widths on axes I & II, $r = 0.6497$; axes I & III, $r = 0.3204$; axes II & III, $r = 0.5304$). *Commiphora wightii*, *Senna holosericea*, *Zizyphus nummularia* and *Prosopis cineraria* showed wide niche widths on the first component while *Prosopis juliflora*, *Cordia gharaf* and *Rhazya stricta* exhibited narrow widths. On the second component, *Blepharis sindica*, *Lycium edgeworthii* and *Prosopis cineraria* had wide niches whilst *Prosopis juliflora* and *Cordia gharaf* narrow niche widths. With respect to third component, *Blepharis sindica* and *Indigofera oblongifolia* showed greater widths while *Senna holosericea*, *Grewia tenax* and *Rhazya stricta* exhibited narrow niche widths. On the basis of overall niche width *Blepharis sindica*, *Commiphora wightii* and *Prosopis cineraria* were generalists while *Prosopis juliflora*, *Cordia gharaf*, *Senna holosericea*, *Rhazya stricta* and *Grewia tenax* were specialists to a greater or lesser degree.

Table 1. Niche breadths of shrubs and undershrubs on three niche axes (components of PCA) and the overall (product) breadth.

Species	Symbol	Niche breadths			
		Compo- nent-I	Compo- nent-II	Compo- nent-III	Overall (product)
<i>Pteropyrum oliveri</i>	Pto	1.0025	1.4297	1.4159	2.0294
<i>Leptadenia pyrotechnica</i>	Lp	1.3258	1.3789	1.2698	2.3214
<i>Senna italica</i>	Si	1.3897	1.4462	1.3504	2.7140
<i>Prosopis cineraria</i>	Pc	1.4246	1.5660	1.5005	3.3475
<i>Rhazya stricta</i>	Rs	0.8463	1.1677	0.7897	0.7804
<i>Zizyphus nummularia</i>	Zn	1.4504	1.4326	1.3836	2.8749
<i>Indigofera oblongifolia</i>	Io	1.3422	1.3609	1.5812	2.8882
<i>Blepharis sindica</i>	Bs	1.3058	1.7063	1.5910	3.5449
<i>Fagonia arabica</i>	Fa	1.0027	1.1736	1.3924	1.6385
<i>Senna holosericea</i>	Sh	1.4669	0.7248	0.6244	0.6638
<i>Prosopis juliflora</i>	Pj	0.4414	0.3823	1.1037	0.1862
<i>Commiphora wightii</i>	Cw	1.7785	1.3210	1.4900	3.5006
<i>Cordia gharaf</i>	Cg	0.6408	0.5930	1.3177	0.5007
<i>Capparis decidua</i>	Cd	0.9644	1.0925	1.3705	1.4439
<i>Lycium edgeworthii</i>	Le	1.2687	1.5093	1.3741	2.6312
<i>Gymnosporia senegalensis</i>	Gs	1.0180	1.1515	0.8639	1.0127
<i>Grewia tenax</i>	Gt	0.9216	1.1252	0.7558	0.7837

Levins (1968) contented that dominant species have broad niche widths. This relationship was tested and it was found, that there was a weak correlation ($r = 0.4323$, $p < 0.10$) between overall niche breadth and the average IVI of species. Logarithmic transformation of the average IVI slightly improved this relationship ($r = 0.4911$, $p < 0.05$). The result, to some extent, corroborates the findings of McNaughton & Wolf (1970), Parrish & Buzzaz (1976), Johnson (1977b) and Dueser & Shugart (1979). The niche breadths along individual niche axes were, however, poorly correlated with the average IVI ($r = 0.3136$, 0.3859 and 0.3907 between average IVI and niche breadths on axis I, II and III respectively). It seems that the high niche breadths are not merely the consequence of the dominance as the generalist species like *Blepharis sindica* and *Commiphora wightii* are neither ubiquitous species in the sample nor are they numerically abundant. While subordinate species tended to have narrow niche widths as measured here, the opposite was not always true.

Niche overlap: The niche overlaps between species on first three principal components (representing gradients) and the overall (product) overlaps are presented in (Tables 2 and 3). Overlaps based on the manner of computation are of course confounded by the spatial cooccurrence of species within the stands; such aspects of

Table 2. Niche overlaps between species pairs on niche axis I (above the diagonal) and axis II (below the diagonal). For key to species symbols see Table 1.

	Pto	Lp	Si	Pc	Rs	Zn	Io	Bs	Fa	Sh	Pj	Cw	Cg	Cd	Le	Gs	Gt
Pto	-	0.7470	0.5358	0.6332	0.6626	0.7216	0.5489	0.8598	0.7942	0.2563	0.8453	0.9166	0.8443	0.8892	0.4924	0.8288	0.5889
Lp	0.9274	-	0.6057	0.6924	0.8110	0.7008	0.6256	0.9132	0.7015	0.2637	0.5133	0.8868	0.5182	0.6225	0.7012	0.8609	0.9020
Si	0.9364	0.9060	-	0.9908	0.6188	0.9567	0.9958	0.5216	0.7089	0.8824	0.3324	0.6373	0.3840	0.4796	0.9723	0.6256	0.5858
Pc	0.9505	0.9234	0.9647	-	0.6711	0.9821	0.9876	0.6297	0.7680	0.8308	0.4303	0.7331	0.4784	0.5756	0.9670	0.6984	0.6468
Rs	0.3410	0.4983	0.5676	0.4465	-	0.6642	0.6721	0.6279	0.8324	0.2151	0.2028	0.7698	0.2365	0.3852	0.6936	0.9667	0.9544
Zn	0.8926	0.9044	0.9761	0.9438	0.7034	-	0.9471	0.7057	0.8411	0.7632	0.5589	0.8134	0.6131	0.7047	0.9060	0.7187	0.6329
Io	0.7299	0.7637	0.9171	0.8147	0.8069	0.9386	-	0.5153	0.7214	0.8603	0.3004	0.6416	0.3488	0.4512	0.9795	0.6720	0.6279
Bs	0.9037	0.8673	0.8699	0.9618	0.2169	0.8197	0.6500	-	0.7274	0.2063	0.7983	0.9529	0.8071	0.8703	0.5421	0.7544	0.7107
Fa	0.6490	0.6362	0.8362	0.7087	0.8575	0.8867	0.9575	0.4493	-	0.3313	0.5301	0.8975	0.5999	0.7215	0.6618	0.8647	0.7622
Sh	0.7641	0.5259	0.7574	0.6771	0.3498	0.7191	0.6613	0.5461	0.7485	-	0.2048	0.2750	0.2334	0.2642	0.8253	0.2352	0.1749
Pj	0.5243	0.2890	0.4664	0.4406	0.3150	0.5091	0.3880	0.3076	0.5760	0.8596	-	0.7520	0.9922	0.9646	0.2325	0.4289	0.1956
Cw	0.9651	0.8773	0.9643	0.9160	0.4918	0.9322	0.8390	0.8074	0.8034	0.8639	0.6113	-	0.7834	0.8736	0.6287	0.8718	0.7803
Cg	0.7074	0.4702	0.6463	0.5741	0.3193	0.6333	0.5357	0.4331	0.6656	0.9688	0.9284	0.8001	-	0.9850	0.2734	0.4481	0.2277
Le	0.8336	0.8843	0.9584	0.9334	0.7190	0.9832	0.9516	0.8248	0.8679	0.6130	0.3764	0.8675	0.4962	0.6802	-	0.6740	0.6988
Gs	0.4861	0.6110	0.6955	0.5501	0.9705	0.7898	0.8933	0.3185	0.9185	0.4776	0.3373	0.6399	0.4271	0.6035	0.7918	-	0.9093
Gt	0.2823	0.4859	0.5181	0.3913	0.9870	0.6503	0.7741	0.1706	0.7962	0.2314	0.1670	0.4251	0.1950	0.4099	0.6822	0.9600	-

Table 3. Niche overlaps between species pairs on niche axis III (above the diagonal) and the overall (product) overlaps (below the diagonal). For key to species symbols see Table 1.

Pro	Lp	Si	Pc	Rs	Zn	Io	Bs	Fa	Sh	Fj	Cw	Cg	Cd	Lc	Gs	Gt	
Pro	-	0.8973	0.9538	0.9827	0.6089	0.9963	0.9526	0.8780	0.8864	0.7066	0.8628	0.8356	0.8544	0.9689	0.9762	0.7633	0.6626
Lp	0.6216	-	0.9363	0.8930	0.5009	0.8751	0.7920	0.9056	0.6244	0.4442	0.6698	0.5358	0.5718	0.8068	0.9301	0.7710	0.6021
Si	0.4784	0.5138	-	0.9556	0.4387	0.9384	0.8729	0.8856	0.7650	0.7248	0.7919	0.6822	0.7031	0.8966	0.9398	0.6531	0.5053
Pc	0.5915	0.5709	0.9133	-	0.5232	0.9647	0.9759	0.9334	0.8426	0.7251	0.7715	0.8148	0.7853	0.9302	0.9636	0.6744	0.5667
Rs	0.1375	0.2024	0.1540	0.1567	-	0.6415	0.5723	0.3355	0.7491	0.1064	0.7038	0.4785	0.6166	0.5396	0.6953	0.9019	0.9798
Zn	0.6417	0.5546	0.8763	0.8941	0.2997	-	0.9375	0.8362	0.9089	0.7080	0.8999	0.8486	0.8861	0.9776	0.9679	0.7840	0.6935
Io	0.3816	0.3784	0.7971	0.7852	0.3103	0.8334	-	0.8890	0.8857	0.7227	0.7485	0.8792	0.8234	0.9094	0.9281	0.6470	0.5868
Bs	0.6822	0.7172	0.4018	0.5652	0.0456	0.4837	0.2977	-	0.6054	0.5475	0.5185	0.6642	0.5766	0.8016	0.8738	0.5692	0.4138
Fa	0.4569	0.2786	0.4534	0.4586	0.5346	0.6785	0.6117	0.2198	-	0.7334	0.9265	0.8752	0.9242	0.8835	0.8566	0.7100	0.7256
Sh	0.1383	0.0616	0.4844	0.4078	0.0080	0.3885	0.4111	0.0616	0.1818	-	0.6941	0.7742	0.7276	0.7597	0.5848	0.1503	0.0886
Fj	0.3831	0.0989	0.1228	0.1462	0.0449	0.2560	0.0872	0.1273	0.2828	0.1221	-	0.7690	0.9035	0.8880	0.8235	0.7568	0.7255
Cw	0.7391	0.4168	0.4192	0.5471	0.1811	0.6434	0.4732	0.5110	0.6310	0.1839	0.3535	-	0.9560	0.9106	0.7272	0.5138	0.4946
Cg	0.5103	0.1393	0.1745	0.2156	0.0465	0.3439	0.1538	0.2015	0.3687	0.1644	0.8322	0.5992	-	0.9344	0.7614	0.6573	0.6428
Cd	0.7037	0.3432	0.3309	0.3856	0.1074	0.5509	0.2751	0.3939	0.4861	0.1821	0.7515	0.7031	0.8682	-	0.8971	0.7011	0.6043
Lc	0.4008	0.5767	0.8757	0.8697	0.3467	0.8621	0.7732	0.3906	0.4920	0.2958	0.0720	0.3966	0.1033	0.2343	-	0.8316	0.7403
Gs	0.3075	0.4055	0.2841	0.2590	0.8461	0.4450	0.3883	0.1367	0.5639	0.0168	0.1094	0.2866	0.1257	0.2418	0.4438	-	0.9651
Gt	0.1102	0.2638	0.1527	0.1434	0.9229	0.2854	0.2852	0.0501	0.4404	0.0035	0.0236	0.1745	0.0285	0.0938	0.3529	0.8425	-

local and geographic distributions, however, may be at least partially unrelated to the relationships of species across the environmental gradients derived here. For example, inter-species overlaps on the first component were found significantly correlated ($r = 0.86$, $p < 0.001$) with the overlaps derived from species cooccurrence alone.

The overlaps on the first niche axis (component I) ranged from 0.1749 between *Senna holosericea* and *Grewia tenax* to 0.9958 between *Senna italica* and *Indigofera oblongifolia* with a mean overlap of 0.6545, $SD = 0.2258$ (Table 2). Niche overlaps on the second axis (component II) ranged from 0.1670 for *Prosopis juliflora* and *Grewia tenax* to 0.987 between *Rhazya stricta* and *Grewia tenax* with an average of 0.69061, $SD = 0.21983$ (Table 2). The mean overlap on the third axis (0.7562, $SD = 0.1795$) was significantly higher than that on first axis ($p < 0.05$) and second axis ($p < 0.01$), ranging between 0.0886 for *Senna holosericea* and *Grewia tenax* to 0.9963 between *Pteropyrum oliveri* and *Zizyphus nummularia* (Table 3).

Conventional niche theory predicts that species pairs that occupy a similar position along one niche dimension tend to differ along another (complementary) dimension in order to permit coexistence (Cody, 1974; Schoener, 1974). However, in the present data pairwise niche overlaps on the different axes were correlated to varying extent (see below). Twelve pairwise overlaps were greater than or equal to 0.9 on all three axes, 24 overlaps were ≥ 0.8 , 43 overlaps were ≥ 0.7 , and 68 were ≥ 0.6 on all three niche axes.

Of perhaps greater utility is not just the overlap between two species on a single niche dimension but their overlap when several niche dimensions are considered concurrently. Multidimensional overlaps were computed as the summation overlap and product overlap. The former measure provides an upper bound on the multidimensional overlap and is an appropriate choice when the niche axes are interdependent (May, 1975). The latter measure (product overlap) sets the lower bound and is appropriate when the niche dimensions are truly independent (May, 1975; Pianka, 1975). As the niche axes here are orthogonal by definition the product overlaps are relevant and are presented in Table 3. Correlation between summation and product overlap values, however, was high (Spearman's rank correlation $r_s = 0.9961$, $p < 0.001$). However, although the niche dimensions are theoretically independent from each other, pairwise overlaps along the axes were correlated as follows: component I component II, rank correlation $r_s = 0.4835$, $p < 0.001$; component I component III, $r = 0.3263$, $p < 0.001$; component II component III, $r = 0.6602$, $p < 0.001$. These data suggest that there is some form of complex interaction among the niche dimensions and that the species distributions along the different niche dimensions is not independent. The mechanism(s) that could generate this form of nonrandomness can not be detected with the data at hand.

Analysis of diffuse overlap along the first niche axis (soil chemical gradient) experienced by one species with the rest of the species showed that *Senna holosericea* was least similar with all other species responses to soil chemical gradient whilst *Zizyphus nummularia* and *C. wightii* most similar in this respect (Table 4). *C. wightii* is known to have a wide ecological amplitude (Baig, 1966). Diffuse overlap along second niche axis (moisture regime gradient) was lowest for *Prosopis juliflora*

and highest for *Senna italica*. The overall (product) diffuse overlaps were considerably decreased over the diffuse overlap along single niche dimensions. It seems that in the 3-dimensional niche space *Senna holosericea* experiences the least diffuse overlap while *Zizyphus nummularia* faces the most (Table 4).

Often in literature the niche overlap measures are subjected to misinterpretation (Brown & Lieberman, 1973; Hulbert, 1978; Abrams, 1980). Because of the mathematical derivation of many overlap indices from the Lotka-Volterra equations (cf. Hutchinson, 1978) workers frequently equate values of overlaps with the competition coefficients. Estimates of overlaps in the field do not reflect the intensity of competition, except perhaps under special, circumstances but rather they measure the degree to which two species share a particular set of resources (Hurlbert, 1978; Lawlor, 1980). In fact, it is more realistic to expect the field measures of overlap to vary inversely with the intensity of interspecific competition (Colwell & Futuyma, 1971; Pianka, 1975). The use of overlap indices for assessing the role of competition leading to structuring of plant communities is also questionable (Abrams, 1980). The basic assumption of these indices is that effects are averaged over all individuals within a population. This assumption is usually satisfied by populations of mobile animals. However, in case of communities composed of sessile plants, such population wide averaging effect is unlikely to

Table 4. Diffuse overlaps of the 17 species on three niche axes and the overall (product) diffuse overlaps.

Species	Component-I	Component-II	Component-III	Overall diffuse overlap
<i>Pteropyrum oliveri</i>	0.6978	0.7320	0.8617	0.4553
<i>Leptadenia pyrotechnica</i>	0.6916	0.7034	0.7348	0.3839
<i>Senna italica</i>	0.6771	0.7969	0.7901	0.4645
<i>Prosopis cineraria</i>	0.7322	0.7448	0.8315	0.4944
<i>Rhazya stricta</i>	0.6240	0.5692	0.5871	0.2715
<i>Zizyphus nummularia</i>	0.7645	0.8176	0.8665	0.5648
<i>Indigofera oblongifolia</i>	0.6810	0.7683	0.8202	0.4526
<i>Blepharis sindica</i>	0.6965	0.6101	0.7022	0.3304
<i>Fagonia arabica</i>	0.7166	0.7606	0.8064	0.4462
<i>Senna holosericea</i>	0.4264	0.6670	0.5749	0.1945
<i>Prosopis juliflora</i>	0.5177	0.4984	0.7784	0.2384
<i>Commiphora wightii</i>	0.7634	0.7930	0.7350	0.4537
<i>Cordia gharaf</i>	0.5484	0.6090	0.7703	0.3047
<i>Capparis decidua</i>	0.6326	0.7257	0.8381	0.4157
<i>Lycium edgeworthii</i>	0.6646	0.7790	0.8436	0.4679
<i>Gymnosporia senegalensis</i>	0.6956	0.6544	0.6906	0.3565
<i>Grewia tenax</i>	0.6111	0.5079	0.6247	0.2609

take place. Competition among plants appears to be purely a neighbourhood phenomenon (Mack & Harper, 1977; Turkington *et al.*, 1977; Turkington & Harper, 1979) and interactions occur only among sufficiently closely located individuals (Silander & Pacala, 1985; Ford & Sorrensen, 1992).

Despite the limitation of overlap measure, one of the motivation of analysing niche structure in the assemblage is to determine whether or not competitive interactions are important. Thus, additional analysis was undertaken to explore the question of the importance of competition in structuring the community. For this purpose the analytical model developed by May & MacArthur (1972) was used. The model, states that a limiting distance (d) must separate the centres of species' distributions along critical resource axes. The simplest version of the model assumes that the standard deviation in the distribution of the species along relevant resource axes (w) is equal for all species in the assemblage. The ratio d/w of <1 indicates substantial overlap of niches while >1 segregation of niches. The d/w ratios for the first, second and third axes were found to be 0.10165, 0.0330 and 0.1058 respectively while the corresponding overlap function (average of consecutive species' pairs along the niche axes) were 0.7776, 0.684 and 0.8999 respectively. All values of d/w are <1 , indicating that species packing along the three niche dimensions was much tight than would be predicted by competition theory. The tighter packing could also be due to non-Gaussian distribution along the niche axes.

Guild structure: Product overlap and its standard deviation is plotted against nearness rank in the 3-dimensional niche space (Fig. 1). The presence of guilds generates two humps indicating the existence of two major guilds. Greater details of guild structure are depicted in the dendrogram resulting from average linkage clustering (ALC) using the matrix of product overlap values as the interspecies similarity matrix (Fig.2). Like the nearness rank/overlap analysis the dendrogram, shows two major guilds. The species included in guild 1 are generally those that abound the sandy plains. The subguild 1a includes species that generally exploit the sites with impoverished moisture and nutrient regimes while those that form the subguild 1b generally exploit sites with relatively better moisture and nutrient status. Members of guild 2 are either the dominant species on sand dunes or dry stream beds. The six species making up subguild 2a generally exploit the sand dune habitat where the soil depth, pH and exchangeable Na and K are high. On the other hand, the three species included in subguild 2b generally exploit the dry stream bed habitats where the soil is shallow with low water retaining capacity but high in exchangeable K. Thus in the desert landscape there seems to exist guilds (or subguilds) of edaphic and topographic specialists.

Once the guild structure is described and quantified several intriguing questions can be raised about guilds though yet definitive answers can not be supplied. One fundamental question is: Are the guilds merely the result of builtin design constraints and/or gaps in resource space, or can guild structure evolve even when resources are continuously distributed? (Pianka, 1981). The theoretical knowledge of community design is not yet strong enough to provide definitive answers to these questions.

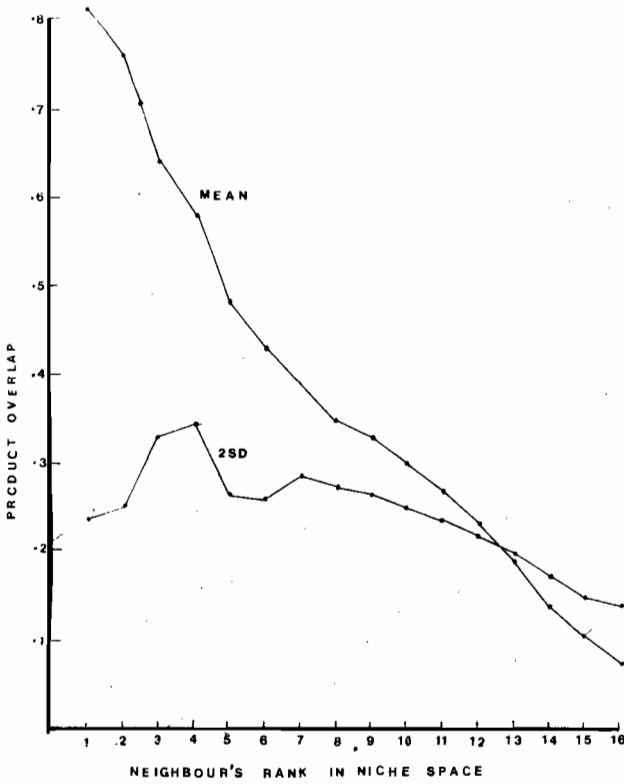


Fig. 1. Mean and standard deviation (SD) of product overlap as a function of nearness rank in niche space.

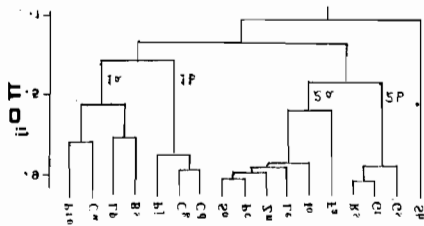


Fig. 2. Dendrogram derived from average linkage clustering, based on product overlaps, showing guild structure.

For key to symbols see Table.1.

CONCLUDING REMARKS

The analysis of niche widths disclosed that species with wide niches generally had greater abundance. It is conceivable that in such species interaction among the individuals of the population is greater than the interaction between the individuals of other species populations. The between individual interaction in a species population is expected to cause 'internal' divergence of the individual's niches which would lead to widening of the population's niche (Johnson, 1977b). Severity and unpredictability of the environment (characteristic features of desert ecosystems) also forces populations to have wider niches which allow fewer species to be packed in the niche space (Slobodkin & Sanders, 1969; Pielou, 1975).

From the analysis of niche overlap it was learned that many species had high niche overlap on all three niche axes. Thus it is apparently difficult to conceive how such species manage to coexist. A number of arguments may be given to explain the coexistence of plant species. One obvious argument is that other niche dimensions are involved. Though the requirements of plants are essentially similar, subtle differences in their requirements permit coexistence in the face of apparently large overlap. Tilman (1982) has shown that theoretically a number of plant species can coexist if they differ in ratio of limiting nutrients required rather than their absolute amounts. An alternative mechanism that contributes to reduced competition is the use of many different growth and regenerative strategies which consequently permit coexistence (Grime, 1979; Grubb, 1986). Similar to the situation in Sonaran desert (cf. Whittaker, 1975) a gradient of leaf persistence and the height at which plant species bear the greater portion of their foliage as well as differentiation in the depth of rooting and differences in the primary life history strategy contribute towards reduced competition and thereby coexistence. A number of studies (Lorimer, 1977; Slack, 1977; Connell, 1978; Watson, 1981; Walker & Peet, 1983) suggest that plant communities often do not attain equilibrium and that perturbations of various sort create conditions that allow coexistence without the need to invoke niche differentiation. In such non-equilibrium situations, species interactions are of limited significance. Instead, crucial factors include dispersal abilities, establishment order, availability of safe microsites, predation pressure, density independent mortality and population persistence (Caswell, 1978; Huston, 1979; Pickett, 1980; Pickett & White, 1985; Silvertown & Law, 1987). Aggregation is also an important factor facilitating coexistence as it leads to increased intraspecific and reduced interspecific competition. Field observations as well as results from a previous study (Shaukat *et al.*, 1983) have disclosed the contagious (aggregated) pattern for most of the species in the assemblage. The scale and the intensity of pattern could be explained on the basis of limited seed dispersal, vegetative reproduction and environmental heterogeneity. Aggregated distribution provides one of the fundamental basis for coexistence (Shimida & Ellner, 1984).

Fluctuations in the recruitment rates may also provide a mechanism for non-equilibrium coexistence of plant populations provided that 'good recruitment years' and 'bad recruitment years' differ for the different species in the assemblage (Warner & Chesson, 1985). Cohorts established in the available gaps in 'good years'

allow persistence through the 'bad years' by the 'storage effect'. This mechanism is attributed for coexistence in Australian eucalyptus communities by Comins & Noble (1985) and for chalk grassland communities by Grubb (1986).

In conclusion, evidence in support of the critical role of competition in the structuring of the desert community along the synthetic environmental gradients (niche axes) is weak while the community seems to conform to most of the assumptions of non-equilibrium hypothesis.

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