

SPECIES COMPOSITION, SPATIAL HETEROGENEITY, INTERSPECIFIC ASSOCIATION AND DIVERSITY OF AN EARLY SUCCESSIONAL PLANT COMMUNITY: A COMPARISON OF SOME SPECIES ASSOCIATION INDICES

S. Shahid Shaukat¹, Faisal Hussain², Hina Zafar³, Toqeer A. Rao³, Khalid Mahmood¹ and Abid Raza⁴

¹ Institute of Environmental Studies, University of Karachi, Karachi-75270, Pakistan

² Department of Agriculture & Agribusiness Management, University of Karachi, Karachi-75270, Pakistan

³ Department of Botany, Federal Urdu University of Arts, Science and Technology, Gulshan-e-Iqbal, Karachi, Pakistan

⁴ Department of Environmental Science, Federal Urdu University of Arts Science and Technology, Gulshan-e-Iqbal, Karachi, Pakistan

ABSTRACT

The investigation focuses on species composition, spatial heterogeneity, diversity and interspecific associations in an early successional plant community. A total of twenty species were recorded of which five were grasses while the rest were undershrubs or perennial herbs. Out of 11 species investigated for spatial pattern using variance/ mean ratio and Morisita's index, ten exhibited aggregated distribution pattern which was presumably caused by topographic-edaphic heterogeneity or by limited seed dispersal. Test for species richness pattern within the community showed variability in species richness which can be attributed to environmental heterogeneity. Species diversity (H') was moderate ($H' = 2.442$), equitability was also moderate ($J' = 0.815$) while species richness (d) was 0.575. Dominance-diversity curve approached geometric distribution. Dominance (D) was low. Ten different species association coefficients (or similarity indices) were tested and compared of which three including those proposed by Jaccard, Soenksen & Dice and Ochiai provided consistent results in terms of disclosing the degree of interspecific association. These three measures are recommended for application in ecology.

Key-words: Diversity, species composition, heterogeneity, plant community, species association indices.

INTRODUCTION

The studies on spatial patterns of individual populations and communities abound in literature and currently a subject of focus of many workers because of their great ecological significance and also because they can be approached in varied manner and for different purposes. The distribution pattern of plants in space as a consequence of diverse regulatory mechanisms involved within the community has received considerable attention from numerous investigators (Greig-Smith, 1983; Dale, 1999). Identifying and characterizing spatial pattern of plant populations is often necessary as various ecological processes may be explained with reference to the current spatial patterns (Greig-Smith, 1983; Legendre and Fortin, 1989; Batista and Maguire, 1998; Shaukat *et al.*, 2012; 2014). Pattern inherent in a population may be defined as a quantitative description of the horizontal distribution individuals of a population in space. (Ludwig and Reynolds, 1988). Spatial patterns of plants reflect multifold ecological processes, including competition, predation, dispersal, herbivory, allelopathy, disturbance, plant-microbe interactions and responses to edaphic-microtopographic variation (Whittaker and Levin, 1977; Potts, 2003; Woods, 2004). While most investigations conducted on vegetation ecology / phytosociology in the Indo-Pak sub-continent ignore within community spatial patterns, exceptions being Khan *et al.* (1987); Khan *et al.* (2014) and Shaukat *et al.* (2014), the present study emphasizes the small scale spatial patterns of the major plant populations of the assemblage. Such patterns are often of critical ecological significance as they shed light on many interesting processes operating at community level and provide explanation of not only within-community patterns but also vegetation processes such as dynamics, stability, structuring and functioning of communities and species diversity (Monzeglio, 2007; Legendre and Fortin, 1989; Harte *et al.*, 2005; Warrens, 2008). Regardless of their immense importance only a few investigations have directed their attention on these processes (Kareiva and Wennegren, 1995; Tilman and Kareiva, 1997; Bolker *et al.*, 2003; Herben *et al.*, 2006; Maestre, 2006; Schmitz, 2010). For the quantitative assessment of the spatial structures, several approaches have been proposed. One simplest test of spatial patterning or heterogeneity in population distribution pattern is the variance / mean ratio (Greig-Smith, 1983). Another popular and a robust test of spatial pattern is Morisita's index (Morisita, 1971). The species richness within a large area is generally not constant but varies which is regarded as within community heterogeneity. This is

generally attributable to changes in topographic and edaphic factors. The loss of biodiversity has become an issue of great public attention and understanding of local diversities and their causal factors is crucial for the maintenance of diversity and stability of communities from the standpoint of conservation. Although environmental heterogeneity is known to be an important determinant of biodiversity, this has rarely been tested using field data (but see Palmer, 1987). We propose and provide evidence for the simple hypothesis that local species diversity is related to spatial environmental heterogeneity. The spatial configuration of habitats affects the rates of ecological processes, such as dispersal or competition.

Even if the area is largely spatially homogeneous and relatively least interactions occur among species (species distributed independently of each other), we expect at least some variation in species richness due to stochastic factors. The variance test originally developed for testing association between species (McCulluch, 1985) can be directly employed to test variability in species richness within an area of interest (Palmer, 1987). High variability in the species richness is generally the product of competition and the resulting competitive exclusion rates and the small-scale environmental heterogeneity.

Species interactions are of prime importance during the successional sequence. With the onward march of succession, species interactions, such as facilitation and inhibition (Connell and Slatyer, 1977; Walker *et al.*, 2007) play a major role in determining the species sequence. In addition to food webs, the structure of the community is built on other types of interactions. Species not only eat one another; they compete for resources, forging a variety of interspecific interactions. Many species also interact cooperatively to search for food or avoid predators. Interspecific interactions and the organization of communities arise between populations of different species form the interactive web of communities. These interactions range from antagonistic to cooperative and have either positive, negative, or neutral effects on the species involved. In antagonistic relationships the interaction is detrimental to individuals of either one or both species. These and other nontrophic relationships between species are as important as food chains.

Facilitation allows establishment of a species by another species in its vicinity by modifying the immediate environment making it more favourable for the other species thus playing a role in the change in species composition for the next sequential stage (Walker and del Moral, 2003). Inhibition model is generally more important in the early successional community.

Association coefficients are not only used for the detection of association between species but are valuable in many other facets of data analysis including multivariate analysis (Janson and Vegelius, 1981). Association indices were originally developed to describe the co-occurrence of plant species within communities or habitats but zoologists have adopted these methods to measure the degree of association between individuals (Bejder *et al.*, 1996). Considerable literature is available concerning association coefficients for 2×2 tables (Janson and Vegelius, 1981; Gower and Legendre, 1986; Krippendorff, 1987; Baulieu, 1989; 1997; Kenkel and Booth, 1992; Albatineh *et al.*, 2006). Traditionally, Cole's (1949) coefficient (C_7) has been most popular but other coefficients such as phi (ϕ) coefficient, Cohen's kappa, or the observed proportion of agreement, also known as the simple matching coefficient are also employed. Association coefficients for 2×2 tables are extensively used, e.g., in ecology for measuring the degree of coexistence between two species in various areas (cf. Sneath and Sokal, 1973), in psychology or biometrics for a 2×2 reliability study where two observers classify a sample of individuals using a dichotomous response or in cluster analysis for comparing two partitions of a set of objects derived from different clustering algorithms (Albatineh *et al.*, 2006; Steinley, 2006; Popping, 1983; Hubert, 1985).

Cole (1949) proposed a coefficient of ecological association that measures the degree to which the observed proportion of joint occurrences of two species exceeds or falls short of the proportion of joint occurrences expected due to chance factor alone. The measure, denoted by C_7 (Hurlbert, 1969), can be expressed as

$$\begin{array}{ll} \text{(i) } C_7 = \frac{ad - bc}{(a+b)(b+d)} & \text{if } ad \geq bc \text{ and } c < b, \\ \text{ii) } C_7 = \frac{ad - bc}{(a+b)(a+c)} & \text{if } ad < bc \text{ and } a > d \\ \text{iii) } C_7 = \frac{ad - bc}{(a+c)(c+d)} & \text{if } ad \geq bc \text{ and } c \geq b \\ \text{(iv) } C_7 = \frac{ad - bc}{(b+d)(c+d)} & \text{if } ad < bc, a > d. \end{array}$$

Coefficient C_7 is equivalent to Loevinger's (1948) H as both are linear transformations of the observed proportion of agreement given the marginal probabilities. It can be verified that the formulas given above and C_7 expression given below are equivalent:

$$C_7 = \frac{ad - bc}{|ad - bc|} \left| \frac{[\text{Obs } \chi^2]}{[\text{Max } \chi^2]} \right|^{\frac{1}{2}}$$

They are often employed by biologists in cluster analysis procedures to recognize species assemblages and biogeographic patterns (Everitt, 1979; Jackson *et al.*, 1989; Legendre and Legendre, 2012). Hurlbert (1969) showed that Cole's index was biased and suggested a correct measure C_8 which was further improved by Ratliff (1982). The first term on the left in both C_7 and C_8 determines the sign.

$$C_8 = \frac{ad - bc}{|ad - bc|} \left| \left[\frac{\text{Obs } \chi^2 - \text{Min } \chi^2}{\text{Max } \chi^2 - \text{Min } \chi^2} \right]^{\frac{1}{2}} \right|$$

Likewise, ordination techniques including principal coordinate analysis (PCoA) and nonparametric multidimensional scaling (NMDS) also make use of such coefficients (Kenkel and Booth, 1987; 1992) though their use is somewhat limited (Gower and Legendre, 1986; Jackson *et al.*, 1992).

The first step (transformation) in ordination or clustering is the computation of a resemblance matrix of elements which are similarities (or distances) between samples or species that are referred to as Q or R-mode of analysis respectively (Orloci and Kenkel, 1985; Shaikat and Siddiqui, 2005). This transformation is implicit in the popular ordination methods such as principal component analysis and correspondence analysis. Nonetheless, a wide choice is available regarding qualitative coefficients (Hubalek, 1982) in case of cluster analysis, non-parametric multidimensional scaling (NMDS) ordination and principal co-ordinate analysis (PCoA) (Jackson *et al.*, 1989). Another reason for greater use of qualitative coefficients in community and biogeographic studies is that the quantitative sampling on a large scale is prohibitively expensive therefore workers are often restricted to employ qualitative coefficients (Lamont and Grant, 1979).

The qualitative coefficients can be categorized into two types (Hubalek, 1982; Clifford and Stephenson, 1975). The first group includes those measures that range between 0 and 1. Their numerator consists of a or $a + d$. The second group comprises of coefficients that range between -1.0 to 1.0. Their numerator is usually $ad - bc$ where a , b , c and d are the usual symbols of 2 X 2 contingency table and the sum of these $a + b + c + d = N$, the total number of samples or total frequency (see below)

		Species B	
		+	-
Species A	+	a	b
	-	c	d

Many comparative studies of qualitative coefficients have been conducted (e.g., Cheetham and Hazel, 1969; Baroni-Urbani and Buser, 1976; Hubalek, 1982; Gower and Legendre, 1986; Kenkel and Booth, 1987; Bejder *et al.*, 1996) but the conclusions of these studies were controversial and the workers generally agree that the results are data-dependent (Janowitz, 1979, 1980). Most of these comparative studies have been conducted in temperate areas and no such study has been undertaken in species poor desert areas. It is therefore interesting to know that how far similar results and conclusions can be drawn on the basis of various qualitative association coefficients. In this regard, it has been emphasized by Gower and Legendre (1986) and Orloci and Kenkel (1985) that the consequences of selecting a particular coefficient in a specific study (particular vegetation type) a greater understanding can be achieved through such comparative studies.

The present study examines the implications of the choice of different qualitative coefficients by comparing their resemblance matrices with one another and with a PCA ordination of species (Orloci and Kenkel, 1985). Secondly, the study explores the within-community spatial pattern of species using two different methods. Thirdly we attempt to investigate the species richness pattern within the area. Lastly, we quantify species diversity and the relative abundance pattern.

MATERIAL AND METHODS

Sampling and data collection

A vacant lot situated within the campus of Federal Urdu University was selected for the study. The total area of the plot was about 1.5 acre. The vegetation of the entire area that comprised of low shrubs, perennial herbs and annuals was completely removed by the development authorities in 2011. However, no development work since then has been initiated and new vegetation has emerged that comprises of perennials as well as annuals that are characteristic species of pioneer stage of secondary succession. The area was sampled by one-hundred and fifty randomly placed 1.m² quadrats in October 2013. The density of species was recorded in each quadrat. Percentage frequency, relative frequency, absolute density and relative density were calculated.

Spatial pattern (heterogeneity)

Spatial pattern of individual species was detected using two different methods of pattern detection employing the data of 150 quadrats. Morisita's index (Morisita, 1971) which is unaffected by random thinning was used as one of the quadrat based method, as follows:

$$I_{\delta} = \frac{Q \sum X_i(X_i - 1)}{N(N - 1)}$$

where $N = \sum X_i$, Q equals the number of quadrats and X_i are the number of individuals in each quadrat. The jackknife method of robust estimation was employed to obtain the variance of each estimate of I_{δ} (Shaukat and Siddiqui, 2005; Chernick, 2011; Staudte and Sheather, 2011). The significance of I_{δ} was checked using an F-distribution (Greig-Smith, 1983):

$$F = \frac{(I_{\delta}(N - 1) + Q - N)}{(Q - 1)}$$

which is tested against $v_1 = Q$ and $v_2 = \infty$. Based on the quadrat data, the popular variance/mean ratio was also computed (Greig-Smith, 1983). The variance/mean ratio (s^2/m) of 1 corresponds to complete spatial randomness (CSR), a ratio > 1 indicates aggregation, while a ratio < 1 implies regular distribution. The significance of the ratio is usually determined using a t-test where the expected value is 1 (for CSR) and the standard error (SE) of the ratio is

$$SE = \left[\frac{2}{(N - 1)} \right]^{1/2}$$

Where n equals the number of quadrats. Alternatively, the significance of s^2/m ratio can be tested using a chi-squared (χ^2) test (Greig-Smith, 1983) as follows:

$$\chi^2 = \frac{(N - 1)s^2}{m}$$

with $n-1$ degrees of freedom (Hurlbert, 1990). Despite some criticism regarding a ratio of 1 for random (Poisson distribution), the index is reliable for large and significant values of the ratio.

Simulation studies have shown that the methods used here for detection of spatial pattern are adequately powerful against both aggregate and regular alternatives (Shaukat, 2001). In addition to the above mentioned tests of significance developed for different pattern detection methods, 500 Monte Carlo simulations were performed using uniform random distributions in a sampling window A with the given plant density incorporating the edge effect (Shaukat, 2001; Shaukat and Siddiqui, 2005). A principal component analysis (PCA) ordination of the 11 species was performed to assess the consistency of the results of qualitative association coefficients (Orloci and Kenkel, 1985).

Association coefficients:

Ten qualitative coefficients were evaluated: Jaccard, Sorensen-Dice, Russell and Rao, simple matching, Rogers-Tanimoto, Ochiai, Yule, Phi, Cole C_7 and Hurlbert's C_8 (Table 1).

Some indices were developed by two different workers independently such as that of Sorensen (1948) and Dice (1945), henceforth the index is referred to as Sorensen-Dice index. Resemblance matrices for various coefficients were constructed and compared using Pearson's correlation coefficient to evaluate the similarity between the resemblance matrices. Thus, correlation coefficient is used as an empirical similarity measure rather than as a parametric test. A PCA ordination of species was also developed to compare the results of the qualitative coefficients with the ordination to seek consistency.

Variability in species richness

The test of species association proposed by (Schluter, 1984) as adapted by Palmer (1987) can be employed to test whether species richness varies within an area than expected under the null model of the absence of interactions among species. The proposed test statistic is:

$$V = \frac{S_o^2}{S_E^2}$$

Where S_o^2 is the observed variance in number of species per quadrat while S_E^2 equals the expected variance. If we assume that each species is independently distributed of the rest of the species then

$$S_E^2 = \sum_{i=1}^M p_i (p_i - 1)$$

Where p_i is the proportion of quadrats that contain species I and M equals the total number of species in the area. The statistic V (ratio of observed to expected variance) when multiplied by the number of quadrats N , is approximately distributed as Chi-square with N degrees of freedom (Palmer, 1987).

Table1. The qualitative coefficients compared in the present study.

Coefficient	Algorithm	Reference
Jaccard	$\frac{a}{a + b + c}$	Jaccard (1912)
Sorensen-Dice	$\frac{2a}{2a + b + c}$	Dice (1945)
Russell & Rao	$\frac{a}{a + b + c + d}$	Russell & Rao (1940)
Simple matching	$\frac{a + d}{a + b + c + d}$	Sokal & Mitchner (1958)
Rogers-Tanimoto	$\frac{a + d}{a + 2b + 2c + d}$	Rogers & Tanimoto (1960)
Ochiai	$\frac{a}{[(a + b)(a + c)]^{\frac{1}{2}}}$	Ochiai (1957)
Phi	$\phi = \frac{ad - bc}{\sqrt{(a + b)(a + c)(b + d)(c + d)}}$	Yule (1912)
Yule	$\frac{ad - bc}{ad + bc}$	Yule (1900)
Cole's C_7	See above	Cole (1949)
Hurlbert's C_8	See above	Hurlbert (1969)

Measurement of Species Diversity

A host of diversity indices have been proposed to measure species diversity (Magurran, 2004). Indices of diversity provide a useful means for quantifying community diversity and have been instrumental in revealing the species diversity associated with various types of communities (Shaukat *et al.*, 1981; Shaukat & Siddiqui, 2005; Ahmed & Shaukat, 2012). A wide variety of diversity indices have been employed to compare diversity at different sites and in various communities (Shaukat *et al.*, 1981; Magurran, 2004). The different diversity measures estimate different aspect of community structure (see Shaukat *et al.*, 1981; Magurran, 2004). The general species diversity of the fungal communities was measured by the popular Shannon–Wiener information theory function:

$$H' = - \sum_{i=1}^S P_i \log P_i$$

Where H' is the general species diversity and P_i the proportion of total number of individuals of the i th species and S equals the total number of species in the assemblage (Shannon and Weaver, 1963). The variance of general diversity $\text{Var}(H')$ was calculated in accordance with Magurran (2004), as follows:

$$\text{Var}(H') = \sum_{i=1}^S [P_i \log(P_i)]^2 - \left(\sum_{i=1}^S P_i \log P_i \right)^2 / N + (S - 1/2N^2)$$

The general diversity incorporates two components of diversity: species richness, which expresses the number of species S as a function (ratio) of the total number of individuals N ; and equitability that measures the evenness of

allotment of individuals among the species (Shaukat *et al.*, 1981; Magurran, 2004). The equitability component of diversity and its variance were measured in accordance with Pielou (1975):

$$J' = \frac{H'}{H'_{max}} = \frac{H'}{\log S}$$

The equitability index J' is the ratio between observed H' and maximal diversity H'_{max} . Variance of equitability was estimated as:

$$\text{Var}(J') = \frac{H'}{(\log S)^2}$$

Another approach to examine diversity is the graphic representation of the relative abundances of species by means of dominance-diversity curve (Whittaker, 1965). The dominance-diversity curve for the community at hand was drawn on EXCEL. The computer programs for all the computations of pattern analysis, qualitative coefficients, the test of variation in species richness, and species diversity indices were written by the senior author S. Shahid Shaukat in C++ and are available at a nominal cost.

RESULTS AND DISCUSSION

Vegetation composition

In all 20 species were recorded. Relative density (%), absolute density (or density sq m^{-1}), frequency percent and relative frequency (%) for the 20 constituent species are given in Table 2, *Tragus roxburghii* showed highest density, followed by *Euphorbia hirta* and *Salsola imbricata*. Whereas, frequency and relative frequency were highest for *Indigofera cordifolia*, followed by *Tragus roxburghii* and *Launaea procumbens*. Absolute density (or density per m^2) was generally low for all species. The presence of *Parkinsonia aculeata* (seedlings), which is a tree species, is not surprising as there were a number of trees of this species at the periphery of the field.

Table 2. Analytical attributes of the species recorded at the sampling site in the Federal Urdu University, Karachi.

Species	Relative Density (%)	Density sq.m^{-1}	Frequency (%)	Relative Frequency (%)
<i>Amaranthus viridis</i> Linn.	0.91	0.073	5.33	2.15
<i>Cenchrus biflorus</i> Roxb.	9.02	0.72	21.33	8.60
<i>Chloris barbata</i> Swartz.	4.14	0.33	12.66	5.11
<i>Convolvulus prostratus</i> Forssk.	0.33	0.026	1.33	0.13
<i>Cyperus rotundus</i> Linn. .	7.05	0.046	2.66	0.80
<i>Dactyloctenium aegyptium</i> (L.) Willd.	7.36	0.59	18.00	7.25
<i>Euphorbia hirta</i> Linn.	12.58	1.01	24.66	9.94
<i>Heliotropium currasavicum</i> (E.May ex DC).DC	0.08	0.006	1.33	0.53
<i>Heliotropium ohloglossum</i> Clarke.	0.24	0.02	2.66	1.06
<i>Heliotropium strigosum</i> Willd.	0.16	0.013	1.33	0.53
<i>Indigofera cordifolia</i> Linn..	9.27	0.74	28.66	11.56
<i>Launaea procumbens</i> (Roxb.) Ramayya & Rajagopal	9.51	0.76	26.66	10.57
<i>Ochradenus baccatus</i> Delile	0.08	0.006	0.66	0.27
<i>Parkinsonia aculeata</i> Linn. *	0.58	0.046	1.33	0.53
<i>Phyllanthus fraternus</i> Web.	3.89	0.31	10.00	4.03
<i>Portulaca oleracea</i> Linn..	4.38	0.35	14.66	5.9
<i>Rhynchosia minima</i> (L.) DC	0.24	0.02	1.33	0.53
<i>Salsola imbricata</i> Forssk.	12.34	0.99	22.66	9.14
<i>Tephrosia subtriflora</i> Baker	8.60	0.69	24.66	9.94
<i>Tragus roxburghii</i> Panigrahi	15.64	1.26	27.5	10.75

* seedlings

Pattern detection

With the exception of *Euphorbia hirta*, the other 10 species *Launaea procumbens*, *Salsola imbricata*, *Dactyloctenium aegyptium*, *Portulaca oleracea*, *Cenchrus biflorus*, *Tephrosia subtriflora*, *Indigofera cordifolia*,

Tragus roxburghii, *Phyllanthus fraternus* and *Chloris barbata* exhibited aggregated pattern as measured by variance / mean ratio and Morisita's index (Table 3). Lloyd's mean crowding and patchiness also showed high magnitude for the above mentioned species. A number of workers have obtained aggregated distribution of shrubs and under-shrubs (Shaukat *et al.*, 2012; 2014).

Table 3. Variance / mean ratio (V/M ratio), Lloyd, Morisita and Patchiness indices for 11 species. A number of workers have obtained aggregated distribution of shrubs and undershrubs (Morisita index was test by F-ratio).

Plant Species	Variance	V/M ratio	t-value	Lloyd	Morisita	Patchiness
<i>Launaea procumbens</i>	2.193	2.861	16.06***	2.608	3.43***	3.402
<i>Euphorbia hirta</i>	0.108	1.182	1.16 n.s.	0.345	1.23n.s..	7.438
<i>Salsola imbricata</i>	1.373	4.291	28.41***	3.583	11.43***	11.197
<i>Dactyloctenium aegyptium</i>	4.436	4.406	29.40***	4.384	4.38***.	4.355
<i>Portulaca oleracea</i>	2.793	4.707	32.00***	4.269	7.27***	7.196
<i>Cenchrus biflorus</i>	1.035	2.938	16.66***	2.264	6.53***	6.407
<i>Tephrosia subtriflora</i>	2.241	2.802	15.55***	2.583	3.25**	3.229
<i>Indigofera cordifolia</i>	1.917	2.904	16.44***	2.545	3.89***	3.856
<i>Tragus roxburghii</i>	2.603	3.455	21.19***	3.185	4.26***	4.228
<i>Phyllanthus fraternus</i>	6.18	5.01	34.61***	5.21	4.24***	4.224
<i>Chloris barbata</i>	7.721	7.284	54.24***	7.295	6.92***	6.882

Significance *** p<0.001, ** p<0.01

The results of variance / mean ratio and that of Morisita's index were essentially the same, both disclosed aggregated distribution of 10 out of 11 species. However, the magnitude of the indices varied somewhat for different species showing low or high degree of aggregation where it was significant. Similar results were reported by Shaukat *et al.* (2014). It is noteworthy that Monte Carlo tests for both the indices of pattern detection essentially gave the same results as the conventional statistical tests thereby confirming the results of the classical tests (results are not shown for the sake of brevity). Liang and Dong (2004) while studying the pattern of various mangrove populations using Morisita index found both random and aggregated patterns. Although the community studied was an early successional community (about 3 years old) but most of the abundant species, that were either perennial herbs or undershrubs, showed aggregated pattern. Usually the pioneer species show complete spatial randomness (CSR). Therefore, it appears that none of the constituent species of the vegetation was truly a pioneer species.

Species richness variability and heterogeneity

To test whether species richness shows a significant variability than is expected under the assumption of the null model of no interactions among the species, Palmer's variance ratio test was employed. The observed and expected variance in species richness were found to be 1.352 and 1.137. Therefore, the ratio $V=1.189$ was found to be significant ($p<0.01$). Evidently, a significant variability exists with respect to species richness within the habitat. The change in species richness within the habitat can be due to small scale habitat heterogeneity, i.e., variation in soil characteristics or microtopography. These factors were not measured but merely observed in the habitat and exhibited some variation in soil colour and microtopography. Palmer (1987) investigated variation in species richness in Minnesota old field. Species richness was more variable than expected by chance alone in some fields and less variable in other fields. He also examined the effect of quadrat size and demonstrated that the result of the variance test depends to some extent on quadrat size. Therefore, the result found in this study based on one quadrat size should be treated with caution though the quadrat size chosen was of medium size compared to plant size and was possibly suitable for this particular analysis as only excessively large or very small quadrats may provide erroneous results. With respect to sampling, it must be noted that even in the case of random sampling the quadrats may not be independent samples as the variation in species richness in the field may influence the quadrats (that may be species poor or species rich accordingly) situated in the vicinity of each other in species poor or species rich sections (Cliff and Ord, 1981; Fingleton, 1986).

Comparison of qualitative coefficients

The matrices derived from the 11 measures of qualitative similarity indices are given in Figs. 1-5. Using Jaccard or Sorensen's indices *Indigofera cordifolia* and *Phyllanthus fraternus* showed highest similarity. *Tephrosia subtriflora* and *Indigofera cordifolia* were also found to be highly positively associated. *Salsola imbricata* did not

co-occur in any quadrat together with *Dactyloctenium aegyptium*, *Tragus roxburghii* and *Portulaca oleracea*, therefore, showed zero or low similarity. In other words, they are negatively associated (see Yule's index and Phi coefficient). *Indigofera cordifolia* and *Tephrosia subtriflora* were found associated. Likewise, *Launaea procumbens* and *Euphorbia hirta* generally showed high similarity (Fig.1). Cole's C₇ showed high degree of similarity between *Euphorbia hirta* and *Launaea procumbens* (Fig.2). The indices of Sokal and Michner (1958) and Ochiai (1957) showed high similarity between *Salsola imbricata* and *Chloris barbata* (Fig.3,4). High values of similarities were shown between *Tephrosia subtriflora* with *Tragus roxburghii* and *Indigofera oblongifolia* and *Tragus roxburghii* by Ochiai's coefficient (Fig4). Phi coefficient showed high association between *Euphorbia hirta* and *Launaea procumbens*. Likewise phi coefficient showed association between *Salsola imbricata* and *Chloris barbata* (Fig. 5). Yule's index also exhibited greater similarity between the above mentioned species (Fig. 5).

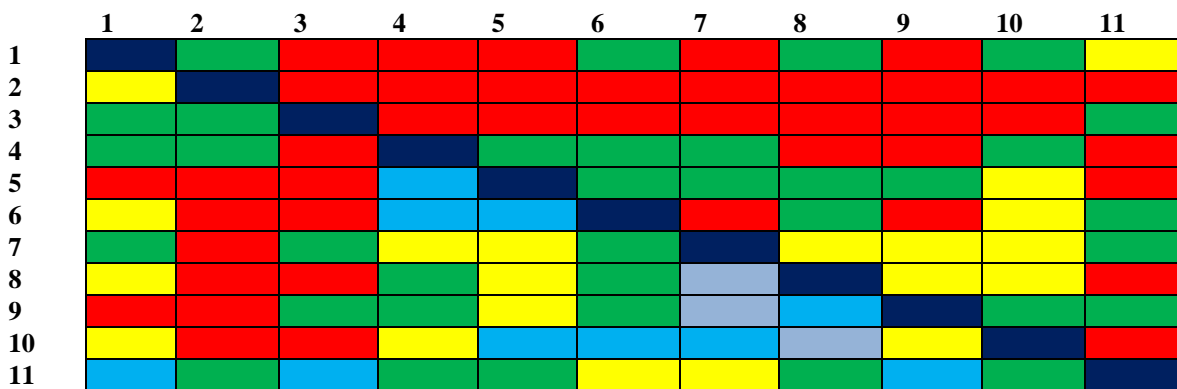


Fig. 1. The triangular matrices of Jaccard index and Sorensen-Dice index for the selected 11 species. The species chosen were: 1 *Launaea procumbens*, 2 *Euphorbia hirta*, 3 *Salsola imbricata*, 4 *Dactyloctenium aegyptium*, 5 *Portulaca oleracea*, 6 *Cenchrus biflorus*, 7 *Tephrosia subtriflora*, 8 *Indigofera cordifolia*, 9 *Tragus roxburghii*, 10 *Phyllanthus fraternus*, 11 *Chloris barbata*.

Key to the values of the indices

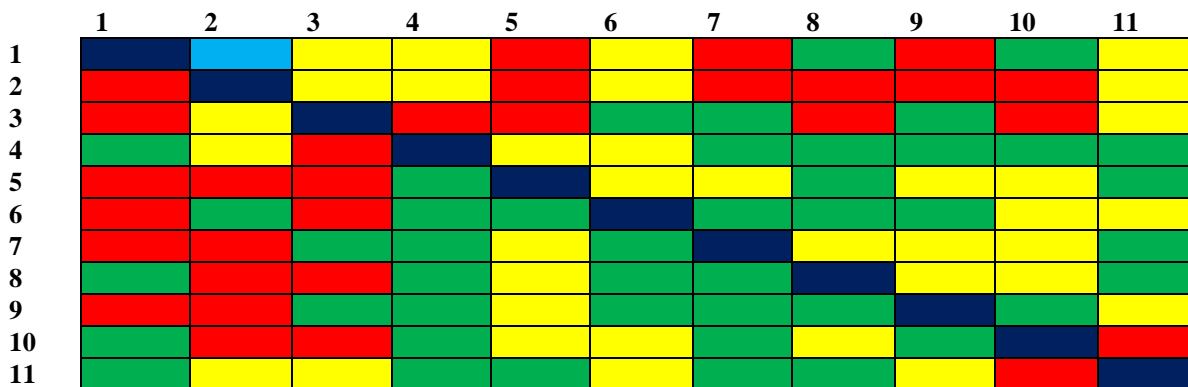
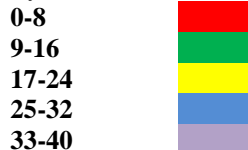


Fig.2. The triangular matrices of Cole's C₇ and Hurlbert's C₈ indices for the selected 11 species. The species chosen were : 1 *Launaea procumbens*, 2 *Euphorbia hirta*, 3 *Salsola imbricata*, 4 *Dactyloctenium aegyptium*, 5 *Portulaca oleracea*, 6 *Cenchrus biflorus*, 7 *Tephrosia subtriflora*, 8 *Indigofera cordifolia*, 9 *Tragus roxburghii*, 10 *Phyllanthus fraternus*, 11 *Chloris barbata*.

Key to the values of the indices



A perusal of PCA ordination of species (Fig.6) reveals that the relationships shown between the species conforms closely to the results of similarity matrices. For instance *Tragus roxburghii* has low similarity (negatively associated) with *Phyllanthus fraternus* as indicated by most of the association coefficients tested and this conforms to PCA ordination result where the two species are located apart. Similarly, *Salsola imbricata* and *Tragus roxburghii* are distantly located in the ordination (Fig.6) and this pair of species shows low similarity or negative association. Those species which have high similarity (as indicated by association coefficients) are situated as a group in the centre of the ordination configuration. Investigating spatial pattern and interspecific association of plant species yield valuable insights into processes and mechanisms that lead to coexistence of certain species.

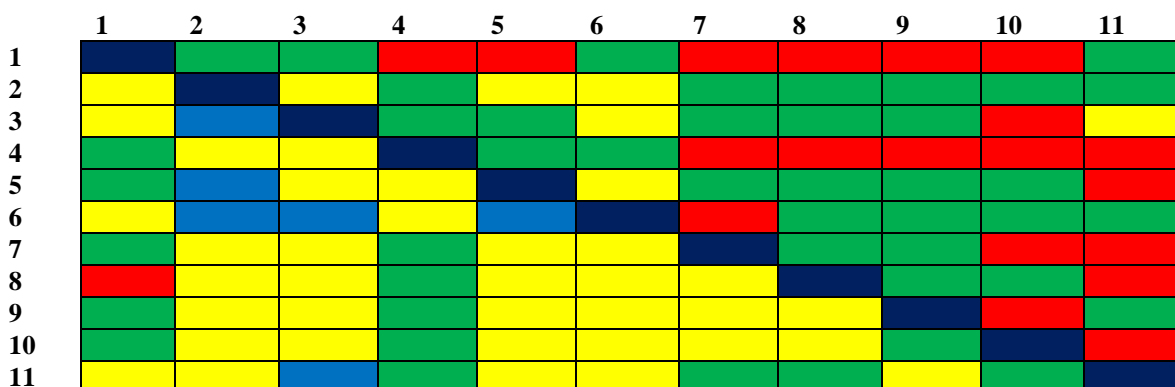


Fig. 3. Triangular matrices of Rogers & Tanimoto and Sokal & Michner for the selected 11 species. Species corresponding to numbers are given in the legend of Fig.1.

Key to the values of the indices

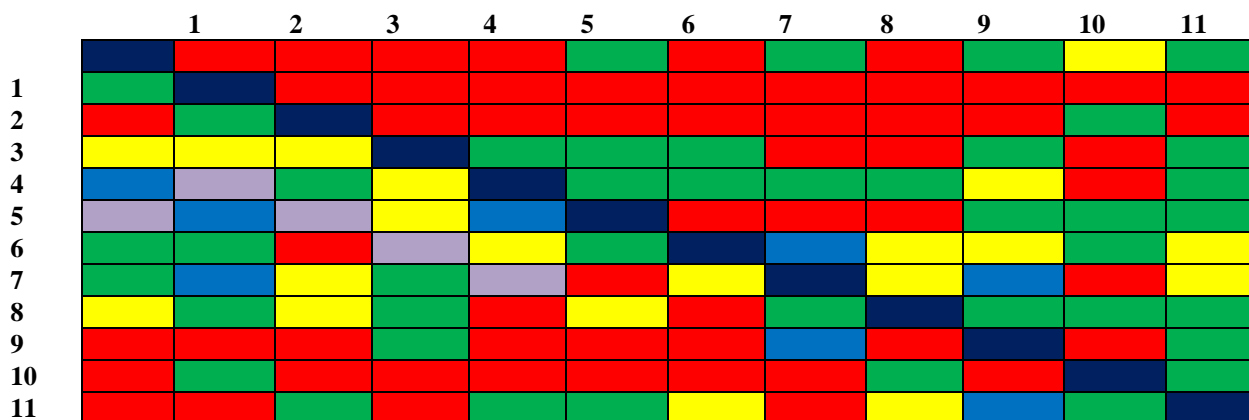
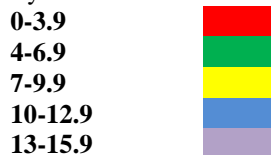


Fig. 4 Triangular matrices if the coefficients of Russell & Rao and that of Ochiai for selected 11 species. Species corresponding to numbers are given in the legend of Fig. 1.

Key to the values of the indices



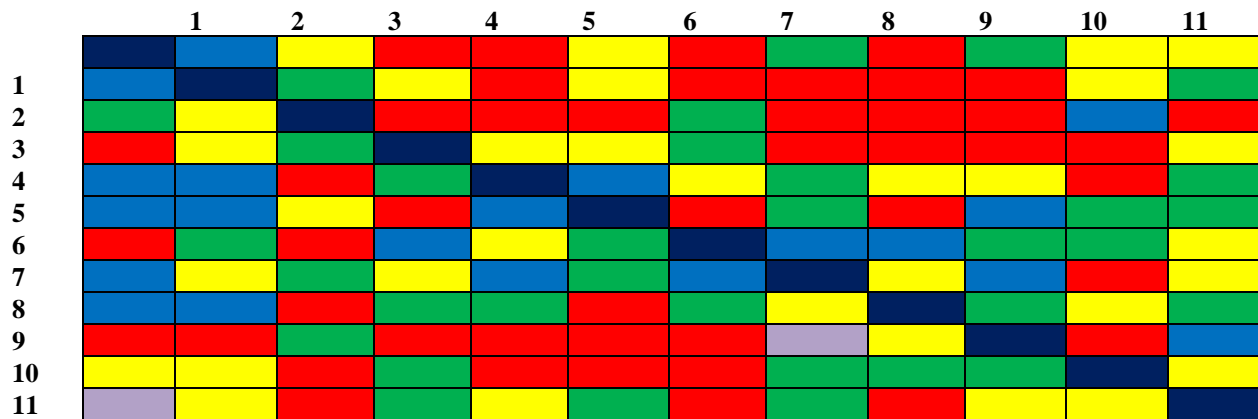


Fig. 5 Triangular matrices of phi and Yule coefficients of 11 selected species. The species corresponding to numbers are given in the legend of Fig. 1.

Key to the values of the indices

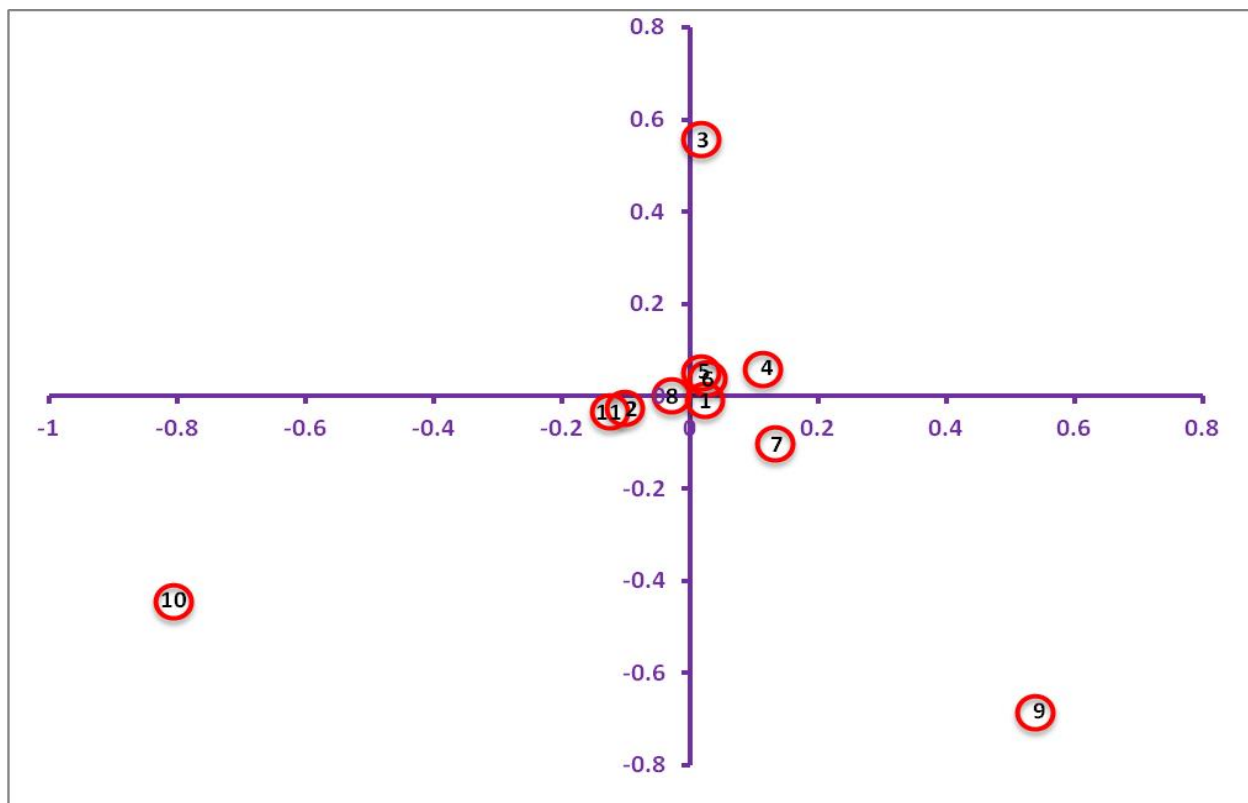
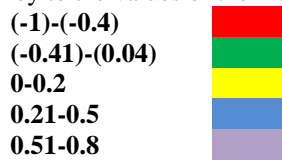


Fig.6. PCA ordination of the selected 11 species; the first component explained 56% of the total variance while second explained 28% of the variance. See legend of Fig. 1 for species 1-11.

Table 4. Correlation matrix of 10 different qualitative association indices. Abbreviations using authority are used for most indices that are in the same order as given in Tables 1-5.

	Jaccd.	Soren.	C7	C8	R&T	S&M	R&R	Och	Phi	Yule
Jaccd.	X									
Soren.	0.998	X								
C7	0.841	0.858	X							
C8	0.683	0.705	0.833	X						
R&T	0.969	0.02	0.273	0.158	X					
S&M	0.008	0.006	0.281	0.157	0.997	X				
R&R	0.969	0.966	0.735	0.624	-0.192	-0.174	X			
Och.	0.936	0.934	0.738	0.750	-0.147	-0.129	0.954	X		
Phi	0.829	0.826	0.909	0.654	0.474	0.492	0.688	0.684	X	
Yule	0.85	0.870	0.993	0.806	0.314	0.323	0.739	0.741	0.941	X

Jaccard and Sorensen's indices are most highly correlated Table 4. Incidentally, these are the two indices that are most extensively used in ecology (Ludwig and Reynolds, 1988). Sorensen's index gives relatively greater similarity compared to Jaccard's index because of 2a in the numerator which implies that it gives twice weight to joint presences. Indices of both Jaccard and Sorensen-Dice are also highly correlated with that of Ochiai which is in agreement with Hubalek (1982). Jaccard's index also shows a high correlation with that of Russell & Rao (1940) because of closely similar formulation and the same numerator in both the indices. The association coefficient of Jaccard (1912) also exhibited a strong correlation with the index developed by Rogers and Tanimoto (1960), the two essentially have similar formulation but the latter gives double weight to b (+,-) and c (-,+). Not surprisingly Cole's C7 and Yule's index showed a very high correlation. Cole's C7 and its corrected version C8 (Hurlbert, 1969), as expected also showed high positive correlation. Theoretical considerations of these indices are given in Hubalek (1982). On the basis of comparison of 43 coefficients of similarity, Hubalek (1982) concluded that a set of association (community) coefficients that generally work well (at least in the interspecific association) includes Jaccard's, Sorensen-Dice and Ochiai's coefficients. Our results also show consistency in these three measures. It is interesting to note that Baroni-Urbani and Buser (1976), Austin *et al.* (1977), Janowitz (1980) and Ludwig and Reynolds (1988) also obtained consistency in the results of the three measures mentioned above. These three similarity measures are most popular and are recommended for use in ecology by Ludwig and Reynolds (1988). One desirable property of a similarity index is that it increases linearly with some fixed minimum to some finite maximum. The three indices mentioned above possess this important property (Wolda, 1981). It must be understood that changes in interspecific association are related to quadrat size, position on a gradient of vegetation and abundance (or presence/absence) measure used in calculating indices (Byer, 1970). In the current study, attention was focused on qualitative data (presence/absence) as we compared qualitative association coefficients. While some authors have concluded that the results of association coefficients are data dependent, our study clearly demonstrates consistency of Jaccard, Sorensen-Dice and Ochiai coefficients. In conclusion, there is considerable evidence for the presence of positive as well as negative interactions among the constituent species.

Species diversity

Species diversity of the community was measured by the commonly used indices. In all there were 20 species in the assemblage. The general diversity of the community was high $H' = 2.442$ with a variance of $\text{Var}(H') = 0.003$. Equitability component (J') was moderate 0.815 with a variance $\text{Var}(J') = 0.00004$. Species richness as measured by Menhenick's index was also moderate 0.575. Dominance concentration was low 0.0987. In addition, a dominance-diversity curve was also plotted in accordance with Whittaker (1965) (Fig.4). The rank-abundance curve was more or less intermediate between geometric and MacArthur's broken stick model (MacArthur, 1957). Such curves are generally the result of physically controlled rugged environments such hot desert conditions that usually represent low diversity. MacArthur's model shows the influence of species with intermediate abundances that confer slight flatness in the curve in the middle portion. This type of curve is followed by taxonomically homogeneous group of species. It is noteworthy here that there were a number of grass species in the community which can be designated as a grass-undershrub community. However, the curve was more like that of geometric distribution which is more or less linear. The soil moisture regime prevailing in the community was in general low.

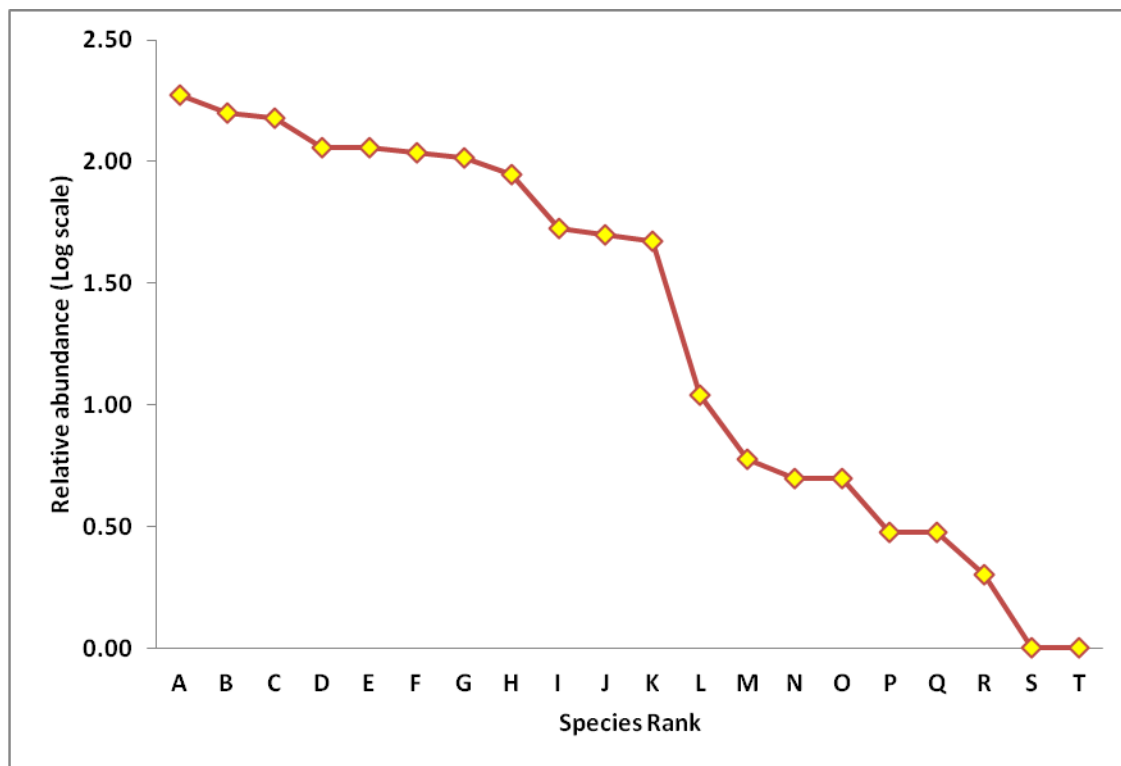


Fig. 7. Dominance-diversity curve for the assemblage.

In essence, the community under study is an early successional organized community (*sensu* Sugihara, 1980; Anderson and Calmay, 2004; Ferreira and Petrere, 2008; Meyer and Leveau, 2012) with a low number of species. Species richness as evaluated by the test proposed by Palmer (1987) showed variability within the different sections (or patches) of the community. However, it does not distinguish the mechanism e.g., competition, environmental heterogeneity, etc causing variability in species richness. Nonetheless, field observations suggested topographic-edaphic variability as the major factor contributing to spatial variability in species richness.. Besides, inter-specific or intra-specific competition (as evidenced by aggregated pattern of most dominant species) could also play a vital role in species richness variability in the field. Ten out of eleven species examined for spatial pattern showed aggregated pattern which could be explained by heterogeneity in topographic-edaphic factors or due to limited seed dispersal. The diversity of the community (H') was moderate- to- low though equitability component. (J') was moderate. The relative abundance pattern was found to be close to geometric model which can readily be associated with the rugged and xeric environment of the community. Particular attention was focused on the qualitative association coefficients (similarity indices) where ten such coefficients were empirically compared.. Species were not distributed independently as many species showed positive or negative interactions. The association indices developed by Jaccard, Sorensen-Dice and Ochiai performed consistently yielding closely similar results and these are strongly recommended for application in ecological studies.

REFERENCES

- Ahmed, M. and S.S. Shaukat (2012). *A Textbook of Vegetation Ecology*. Abrar Sons Publ., Karachi. 396p.
- Albatineh, A.N., M. Niewia-Domska-Bugaj and D. Mihalko (2006). On similarity indices and correction for chance agreement. *J. Classification*, 23: 301-313.
- Anderson, I.C. and J.W. G. Calmay (2004). Diversity and ecology of soil fungal communities: increased understanding through the application of molecular techniques. *Environ. Microbiol.*, 8: 769-779.
- Austin, B., D.A. Allen, A.L. Mills and R.R. Colwell (1977). Numerical taxonomy of heavy metal tolerant bacteria

- from estuary. *Can J. Microbiol.*, 23: 1433-1447.
- Baroni-Urbani, C. and M.W. Buser (1976), Similarity of binary data. *Syst. Zool.*, 25: 251-259.
- Batista, J.L.F. and D.A. Maguire (1998). Modelling the spatial structure of tropical forests. *Ecol. Monogr.*, 110: 293-314.
- Baulieu, F.B. (1989). A classification of presence/absence based dissimilarity coefficients. *J. Classification*, 6: 233–246.
- Baulieu, F.B. (1997). Two variant axiom systems for presence/absence based dissimilarity coefficients. *J. Classification*, 14: 159–170.
- Bejder, L., D. Fletcher and S. Brager (1996). A method for testing association patterns of social animals. *Anim Behav.*, 56: 719–725.
- Bolker, B.M., S.W. Pacala and C. Neuhauser (2003). Spatial dynamics in model plant communities. What do we really know. *Amer. Natur.*, 162: 135-138.
- Byer, M.D. (1970). Interspecific plant associations as influenced by three variables. *Ecology*, 51: 103-112.
- Cheetham, A.H. and J.E. Hazel (1969). Binary (presence-absence) similarity coefficients. *J. Paleontol.*, 43: 1130-1136.
- Chernick, M.R. (2011). The jackknife: a resampling method with connections to the bootstrap. *Comput. Stat.*, 4: 224-226.
- Cliff, A.D. and J.K. Ord (1981). *Spatial Processes: Model and Applications*. Pion, London.
- Clifford, H.T. and W. Stephenson (1975). *An Introduction to Numerical Classification*. Academic Press, New York. 229p.
- Cole, L.C. (1949). The measurement of interspecific association. *Ecology*, 30: 411-424.
- Connell, J.H. and R.O. Slatyer (1977). Mechanisms of succession in natural communities and their role in community stability and organization. *Amer. Natur.*, 11: 1119-1144.
- Dale, M.R.T. (1999). *Spatial Pattern Analysis in Ecology*. Cambridge University Press, Cambridge.
- Dice, L.R. (1945). Measures of the amount of ecologic association between species. *Ecology*, 26: 297-302.
- Everitt, B.S. (1979). Unresolved problems in cluster analysis. *Biometrics*, 35: 169-181.
- Ferreira, F.C. and P. Petreire (2008). Comments about some species abundance patterns: classic, neutral, and niche partitioning models. *Braz. J. Biol. (Suppl.)*, 68: 1003-1012.
- Fingleton, B. (1986). Analyzing cross-classified data with spatial dependence. *Geogr. Anal.*, 18: 48-81.
- Gower, J.C. and P. Legendre (1986). Metric and Euclidean properties of dissimilarity coefficients. *J. Classification*, 3: 5-48.
- Greig-Smith, P. (1983). *Quantitative Plant Ecology*. Cambridge University Press, Cambridge.
- Harte, J., E. Conlisk, A. Ostling, J.L. Green and A.B. Smith (2005). A theory of spatial structure in ecological communities at multiple spatial scales. *Ecol. Monogr.*, 75: 179-197.
- Herben, T., Z. Munzbergova, M. Milden, J. Ehrlen, S.A.A. Cousins and O. Eriksson (2006). Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape : linking dynamical modeling with historical maps. *J. Ecol.*, 94: 131-143.
- Hubalek, Z. (1982). Coefficients of association and similarity, based on binary (presence-absence) data: an evaluation. *Biol. Rev. Camb. Philos. Soc.*, 57: 669-689.
- Hubert, L.J., and P. Arabie (1985), Comparing partitions. *J. Classification*, 2: 193–218.
- Hurlbert, S.H. (1969). A coefficient of interspecific association. *Ecology*, 50: 1–9.
- Hurlbert, S.H. (1990). Spatial distribution of the montane unicorn. *Oikos*, 58: 257-271.
- Jaccard, P. (1912). The distribution of the flora in the Alpine zone. *The New Phytol.*, 11: 37–50.
- Jackson, D.A., K.M. Somers and H.H. Harvey (1989). Similarity coefficients: Measures of co-occurrence and association or simply measures of occurrence. *Amer. Natur.*, 133: 436-453.
- Jackson, D.A., K.M. Somers and H.H. Harvey (1992). Null models and fish communities: evidence of nonrandom patterns. *Amer. Natur.*, 139: 930-951.
- Janowitz, M.F. (1979). A note on phenetic and phylogenetic classification. *Syst. Zool.*, 28: 197-199.
- Janowitz, M.F. (1980). Similarity measures on binary data. *Syst. Zool.*, 29: 342-359.
- Janson, S. and J. Vegelius (1981), Measures of ecological association. *Oecologia*, 49: 371-276.
- Kareiva, P. and U. Wennergren (1995). Connecting landscape patterns to ecosystem and population processes. *Nature*, 373: 299-302
- Kenkel, N.C. and T. Booth (1987). A comparison of presence/absence resemblance coefficients for use in biogeographical studies. *Coenoses*, 2: 25-30.

- Kenkel, N.C. and T. Booth (1992). Multivariate analysis in fungal ecology. In: C.C. Carrol and D.T. Wicklow (Eds.). *The Fungal Community: Its Organization and Role in Ecosystem*, pp 209-227. 2nd edn. Dekker, New York, USA.
- Khan, D., S.S. Shaukat and S. Ismail (1987). Structure and composition of *Achyranthes aspera* L. dominated rural vegetation in the suburbs of Karachi. *Pak. J. Bot.*, 19: 157-174.
- Khan, D., S.S. Shaukat and M. J. Zaki (2014). Structure, composition and pattern in *Peristrophe paniculata* (Forssk.) Brumitt. dominated ruderal vegetation emerging after summer rains in Karachi. *Int. J. Biol. Biotech.*, 11 (2-3): 421-434.
- Krippendorff, K. (1987). Association, agreement and equity. *Quality and Quantity*, 21: 109-123.
- Lamont, B.B. and K.J. Grant (1979). A comparison of twenty-one measures of site dissimilarity. In: L. Orloci, C.R. Rao and W.M. Stiteler (Eds.). *Multivariate Methods in Ecological Work*, pp101-126. International Cooperative Publ. House, Bethesda, Maryland, USA.
- Legendre, F. and M. Fortin (1989). Spatial pattern and ecological analysis. *Vegetatio*, 80: 108-137.
- Legendre, P. and L.F.O. Legendre (2012). *Numerical Ecology*. 3rd Ed. Elsevier, The Netherland.
- Liang, S.C. and M. Dong (2004). Spatial heterogeneity of population structure of the mangrove *Bruguiera gymnorhiza* at Yingluo Bay, South-China Coast. *Acta Bot. Sin.*, 46: 1015–1024.
- Loevinger, J.A. (1948). A technique of homogeneous tests compared with some aspects of scale analysis and factor analysis. *Psychol. Bull.*, 45: 507-530.
- Ludwig, J.A. and J.F. Reynolds (1988). *Statistical Ecology*. Wiley, New York. 436p.
- MacArthur, R.H. (1957). On the relative abundance of bird species. *Proc. Nat. Acad. Sci., U.S.A.*, 43: 203-295.
- Maestre, E.T. (2006). Linking the spatial pattern of organisms and abiotic factors to ecosystem function and management: insights from semi-arid environments. *Web. Ecol.*, 6: 75-87.
- Magurran, A.I. (2004). *Measuring Biological Diversity*. Blackwell Scientific, Oxford. 254p.
- McCulloch, C.E. (1985). Variance test for species association. *Ecology*, 66: 1676-1681.
- Meyer, K.M. and J.H.J. Leveau (2012). Microbiology of the phylloplane: A playground for testing ecological concept. *Oecologia*, 168: 621-629.
- Monzeglio, U. (2007). *Small-scale patterns and dynamics of experimental plant communities*. Ph.D. thesis, University of Basel, Switzerland.
- Morisita, M. (1971). Composition of I_{δ} index. *Res Popul.Ecol.*, 13: 1-7.
- Ochiai, A. (1957). Zoogeographic studies on the soleoid fishes found in Japan and its neighbouring regions. *Bull. Jap. Soc. Sci. Fish.*, 22: 526-530.
- Orloci, L. and N.C. Kenkel (1985), *Introduction to Data Analysis*. International Cooperative Publ. House, Fairland, Maryland, USA.276p.
- Palmer, M.W. (1987). Variability in species richness within Minnesota old fields: a use of the variance test. *Vegetatio*, 70: 61-64.
- Pielou, E.C. (1975). *Ecological Diversity*. Wiley-Interscience, New York, USA. 165p.
- Popping, R. (1983), *Overeentemingsmalen Veer Nominale Data*. Ph.D. thesis, Groningen University, The Netherlands.
- Potts, M. D. (2003). Drought in a Bornean everwet rain forest. *J. Ecol.*, 91: 467–474.
- Ratcliff, R.D. (1982). A Correction of Coles's C_7 and Hurlbert's C_8 Coefficients of Interspecific Association. *Ecology*, 63: 1605–1606.
- Rogers, J.S. and T.T. Tanimoto (1960), A computer program for classifying plants. *Science*, 132: 1116-1118.
- Russell, P.F. and T.R. Rao (1940). On habitat and association of species of anapholinae larvae in south-eastern Madras. *J. Mataria Inst. India*, 3: 153-178.
- Schluter, D. (1984). Variance test for species association with some applications. *Ecology*, 65: 998-1005.
- Schmitz, O.J. (2010). Spatial dynamics and ecosystem functioning. *PLoS Biol.*, 8: 1-3.
- Shannon, C.E. and W. Weaver (1963). *The Mathematical Theory of Communication*. Urbana University of Illinois Press, Illinois, USA. 367p.
- Shaukat, S.S., A. Khairi, D. Khan and M. Afzal. (1981). On the applicability of McIntosh's diversity measures. *Tropical Ecol.*, 22: 54-81.
- Shaukat, S.S. (2001). Spatial point processes and the detection of non-randomness using distance methods. *Proc. Fifth Statistics Conf., Karachi*, 7: 56-62.
- Shaukat, S.S. and I.A. Siddiqui (2005). *Essentials of Mathematical Ecology: (Computer Programs in BASIC, FORTRAN and C++)*. Farquan Publisher, University of Karachi Publication, Karachi.
- Shaukat, S.S., M.A. Khan, M. Mett and M.F. Siddiqui (2014). Structure, composition and diversity of the vegetation of Hub dam catchment area, Pakistan. *Pak. J. Bot.*, 46: 65- 80.

- Shaukat, S.S., S. Aziz, W. Ahmed and A. Shahzad (2012). Population structure, spatial pattern and reproductive capacity of two semi-desert undershrubs *Senna holosericea* and *Fagonia indica* in Southern Sindh. *Pak. J. Bot.*, 44: 1-9.
- Sneath, P.H.A. and R.R. Sokal (1973). *Numerical Taxonomy*. W.H. Freeman, San Francisco, CA.
- Sokal, R.R. and C.D. Michner (1958). A statistical method for evaluating systematic relationships. *Univ. Kansas Sci. Bull.*, 38: 1409-1438.
- Sorensen, T. (1948). A method for establishing groups of equal amplitude in plant sociology based on similarity of species content. *Det Kong Danske Vidensk. Selak Biol. Skr. (Copenhagen)*, 5: 1-34.
- Staudte, R.G. and S.J. Sheather (2011), *Robust estimation and Testing*. Wiley, New York. 189p.
- Steinley, D. (2006). K-means clustering: a half century synthesis. *Br. J. Math. Statist. Psychol.*, 59: 1-34.
- Sugihara, G. (1980). Minimal community structure: An explanation of species abundance patterns. *Amer. Natur.*, 116: 770-787.
- Tillman, D. and P. Kareiva. (Eds.). (1997). *Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interaction*. Princeton University Press, Princeton, New Jersey. 327p.
- Walker, L.R. and R. del Moral (2003). *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge. 245p.
- Walker, L.R., J. Walker and R.J. Hobbs (Eds.). (2007), *Linking Restoration and Ecological Succession*. Springer, New York. 274p.
- Warrens, M.J. (2008). On association coefficients for 2 X 2 tables and properties that do not depend on marginal distributions. *Psychometrika*, 73: 777-789.
- Whittaker, R.H. (1965). Dominance and diversity in land plant communities. *Science*, 147: 250-260.
- Wolda, H. (1981). Similarity indices, sample size and diversity. *Oecologia*, 50: 296-302.
- Whittaker, R.H. and S. A. Levin (1977). The role of mosaic phenomenon in natural communities. *Theor. Popul. Ecol.*, 12: 117-139.
- Woods, K.D. (2004). Intermediate disturbance in a late-successional hemlock-northern- hardwood forest. *J. Ecol.*, 92: 464-467.
- Yule, G.U. (1900). On the association of attributes in statistics. *Philos. Trans. Royl Soc. A*, 194: 257-319.
- Yule, G.U. (1912). On the methods of measuring association between two attributes. *J. Royl. Stat. Soc.*, 75: 579-642.

(Accepted for publication September 2014)