

THE RELATIONSHIPS AMONGST DOMINANCE, DIVERSITY AND COMMUNITY MATURITY IN A DESERT VEGETATION.

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Abstract

Relationships among dominance, diversity and its components and community maturity were statistically evaluated. Dominance and diversity were found to be inversely related. The two components of diversity – richness and equitability were found to be intimately associated with general diversity, and were equally important in governing the overall diversity. Community maturity was negatively correlated with general diversity and its components but was not significantly associated with dominance. The relationships among the expressions of community organization are discussed.

Introduction

Among the attributes of community organization, dominance, diversity and maturity are of paramount importance. Although, natural communities are usually composed of a number of species, generally a relatively few species, i.e., dominants in a community exert a powerful influence on the overall community structure, function, dynamics and the physical environment. Various indices of dominance have been proposed to ascertain the structural organization of communities (Simson, 1949; McNaughton, 1968; Berger & Parker, 1971).

Braun (1950) demonstrated that the number of species in eastern deciduous forests of N. America were inversely related to community dominance, and a similar relationship has been reported for annual grasslands of California by McNaughton (1968). Fager (1968) related the dominance and species diversity in the invertebrate community of decaying oak logs in Wythan woods, England, and found a slight tendency for dominance to be low when diversity was high, though such a relationship was not a very close one. The relationship of dominance with the various components of diversity, however, has been ignored in the past. Odum *et al.* (1971), Hill (1973), Heip & Decraemer (1974) and Peet (1974) have clearly illustrated the desirability of separating the species richness and relative abundance (equitability) components of species diversity. Consequently, it would be interesting to know the behaviour of the various components of diversity with respect to community dominance.

Maturity is a dynamic concept related to structural complexity and organization (Margalef, 1968). Its relationship with dominance and diversity has been incompletely

explored by some workers (Monk & McGinnis, 1966; Loucks, 1970; Reiners *et al.*, 1971) though completely overlooked by others. Pichi – Sermoli (1948) suggested an index for the estimation of maturity in plant communities that works on the principle that the greater the frequency per cent of each species and lesser the number of sporadic species, the more mature is the community.

This investigation determines the relationships among dominance, diversity and its components, and community maturity for the vegetation of a desert terrain in Southern Sind.

Description of the area

Gadap, a small village, is situated in Southern Sind, at latitude $25^{\circ} 9'N$ and longitude $67^{\circ} 13'E$. Samples were selected from an area of approximately 200 square miles around the village. The bioclimate of the area falls in the category of 'tropical desert bush formation' (Holdridge, 1947). The details of climatic conditions, vegetational composition and edaphic features are described by Shaukat *et al.* (1976).

Material and Methods

a) Field Methods:

A reconnaissance survey preceded the vegetational sampling. Twenty-two stands were subjectively selected and sampled by the point-centered quarter method described by Cottam & Curtis (1956). Criteria for the selection of a stand were adequate size (5 acres or more) of the sample area, visual homogeneity of vegetation and physiography, and as far as possible lack of disturbance. The stands were located to include a range of topographic situations such as sandy plains, sand dunes and dry stream beds. Procedure and the criteria of sample selection are described by Shaukat *et al.* (1976).

b) Vegetational analysis and statistical procedures:

The relative frequency, relative density and relative dominance were computed and combined by summation into a single importance value index (I.V.I) following Curtis & McIntosh (1951). The importance value expresses the massiveness, conspicuousness, activity or interest of a given species in the community (Whittaker, 1967).

The dominance was ascertained by the index proposed by Simpson (1949) as follows:

$$c = \sum_{i=1}^s \left(\frac{ni}{N} \right)^2 \quad \text{where } c \text{ is Simpson's index, } \frac{ni}{N} \text{ is the proportion of individuals}$$

belonging to the i th species to the total number of individuals in the sample. The general species diversity incorporates two components of diversity: (1) the richness component which is variously expressed in the form of ratios between number of species and total

number of individuals. (ii) equitability or evenness, is the measure of allocation of individuals among the constituent species (Lloyd & Ghelardi, 1964; Peet, 1974). The general species diversity was determined by the information theory function $H = - \sum_{i=1}^S p_i \log_2 p_i$ where p_i is the proportion of total I.V.I. belonging to the i th species Margalef (1957). Equitability was expressed as $J' = H / H_{\max}$ where $H_{\max} = \log_2 S$, the logarithm of the number of species (S) in the sample (Pielou, 1969) Whittaker (1975) points out that scaling evenness in the form H / H_{\max} or $H - H_{\max}$ increases their fluctuation with sample size. However, in this study sample size was kept constant, hence equitability function used is entirely unexceptionable. The species richness was calculated as $d = \frac{S}{\sqrt{N}}$ (Menhinick, 1964) where d is species richness and S and N are total number of species and total number of individuals respectively. The community maturity was established using the index suggested by Pichi - Sermoli (1948) as follows:

Community maturity (C.M.) = $\frac{\sum_{i=1}^S F_3}{S}$, where F_3 equals the percentage frequency of a species, and S equals the number of species in the sample.

The relationships among the various attributes of community organization were accomplished by computing product - moment correlation coefficients and regression equations, and by analysing variance of regressions using the procedures outlined in Steel & Torrie (1976).

It may be argued (R.P. McIntosh, *private communication*) that the maturity index is circular as it depends on the assumption that maturity is related to diversity. The percentage frequency that the index utilizes is a function of density in part, though the relationship between them is logarithmic and not linear (Greig-Smith, 1964). However,

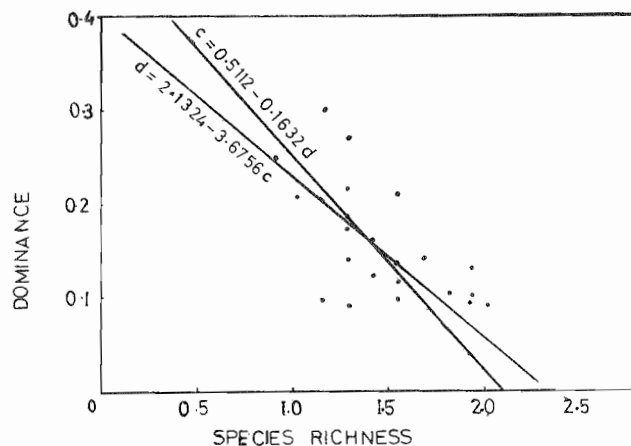


Fig. 1. The relationship between species richness and dominance.

TABLE 1. Analysis of variance of regression between attributes of community organization, and other sample statistics of the correlation and regression data.

Attributes of community organization	Source of variation	Degree of freedom	Mean Square	F	b and r
Dominance & Species richness	Due to regression	1	0.0555	29.98***	b=-0.163
	Due to error	20	0.0018		r=-0.7745
Dominance & Equitability	Due to regression	1	0.0502	23.68***	b=-1.4043
	Due to error	20	0.0021		r=-0.7363
Dominance & General diversity	Due to regression	1	0.0515	25.05***	b= 0.2070
	Due to error	20	0.0021		r=-0.7457
Species richness & General diversity	Due to regression	1	0.6961	786.69***	b= 1.688
	Due to error	20	0.0008		r= 0.9875
Species richness & Equitability	Due to regression	1	0.0244	466.02***	b= 8.8541
	Due to error	20	0.0005		r= 0.9722
General diversity & Equitability	Due to regression	1	0.6340	158.82***	b= 4.9863
	Due to error	20	0.0099		r= 0.9424
Community maturity & Species richness	Due to regression	1	1.0530	20.30***	b=-0.0.26
	Due to error	20	0.0516		r=-0.7104
Community maturity & Equitability	Due to regression	1	0.0111	15.53***	b=-0.0029
	Due to error	20	0.0007		r=-0.6611
Community maturity & General diversity	Due to regression	1	0.3363	17.14***	b=-0.0161
	Due to error	20	0.0188		r=-0.6863
Community maturity & Dominance	Due to regression	1	0.0045	1.13ns.	b= 0.0018
	Due to error	20	0.0044		r= 0.2224

*** p < 0.001

frequency is not only dependent on the density of the individuals but also on several other factors of which the predominant one is the pattern which in turn is largely governed by inter-specific competition. Moreover, competition is a function of community maturity. In view of these facts the use of Pichi-Sermoli's index as a measure of community maturity appears to be justified. However, the stability of communities (related to maturity) was also independently evaluated by the extension of the Community Quality Index concept proposed by Vasek *et al* (1975). This concept is related to stability through life span considerations which is believed to be particularly appropriate for desert communities (Johnson *et al*, 1975). Accordingly stability is here judged on the basis of the proportion of the vegetation made up of long-lived perennials. Leading dominant groups (Brown & Curtis, 1952) were established and the arithmetic mean of species richness, equitability, general diversity and of the proportion of very long-lived (V.L.L.), long-lived (L.L.) and short-lived (S.L.) species were calculated for the stands belonging to each group.

Results

The relationships among the various attributes of Fig. 1–10 and the analysis of variance of these relationships appear in Table 1. In general, the various parameters of community structure function and dynamics were intimately related to each other as indicated by highly significant values of correlation and regression coefficients (Table 1.). The details of these relationships are as follows:

a) Relationships between dominance and diversity measures:

Species richness and dominance had a highly significant negative relationship ($r = 0.7745$, $p < 0.001$; Fig. 1). Dominance and equitability were also highly negatively correlated but the value of correlation coefficient (r) was lower ($r = -0.6611$, $p < 0.001$;

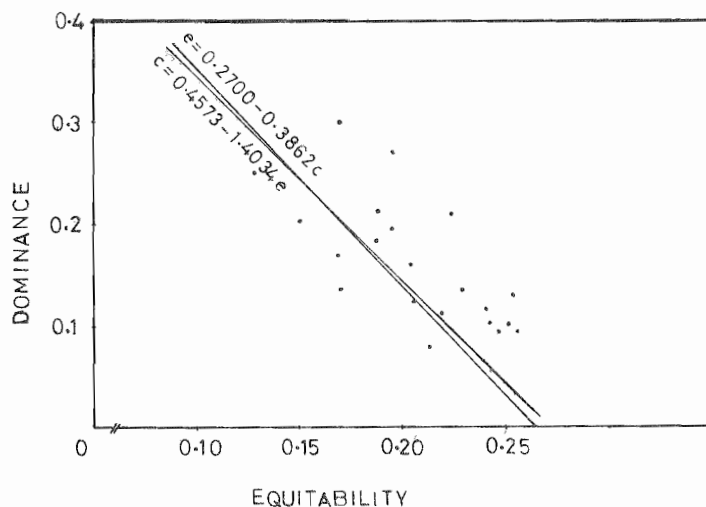


Fig. 2. The relationship between equitability and dominance.

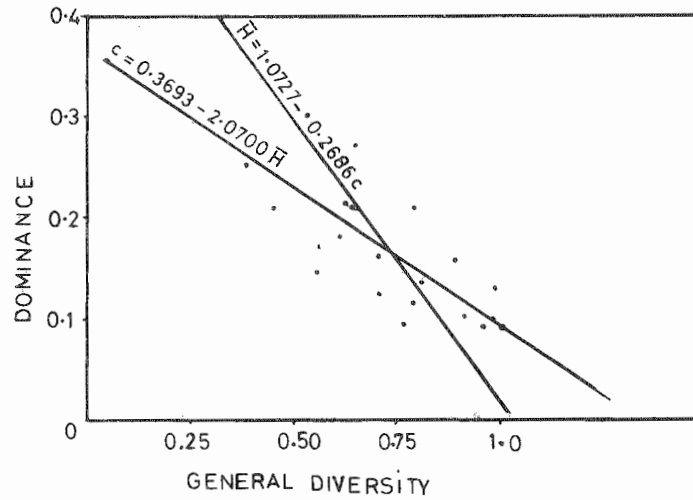


Fig. 3. The relationship between general diversity and dominance.

Fig. 2). Likewise, general diversity also possessed a very high inverse relationship with dominance, yielding an intermediate value of r between the former two values of correlation coefficient ($r = 0.7457$, $p < 0.001$; Fig. 3).

b) Relationships among the diversity measures:

The diversity measures were highly positively correlated with each other (Fig. 4-6). The closest relationship was revealed between species richness and general diversity ($r = 0.9875$, $p < 0.001$; Fig. 5). Species richness and equitability were also very closely related ($r = 0.9792$, $p < 0.001$; Fig. 4). Though the computation of correlation coeffi-

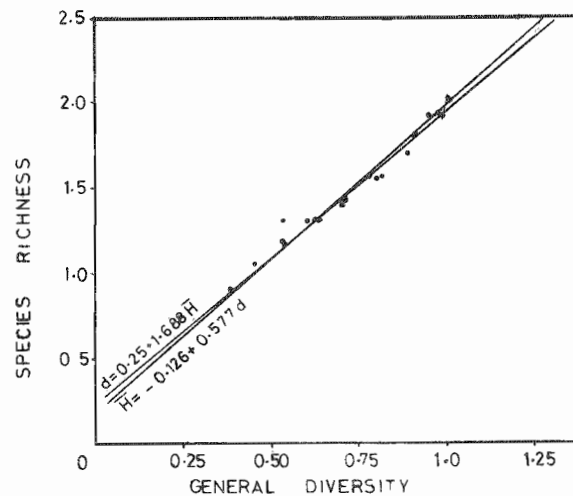


Fig. 4. The relationship between general diversity and species richness.

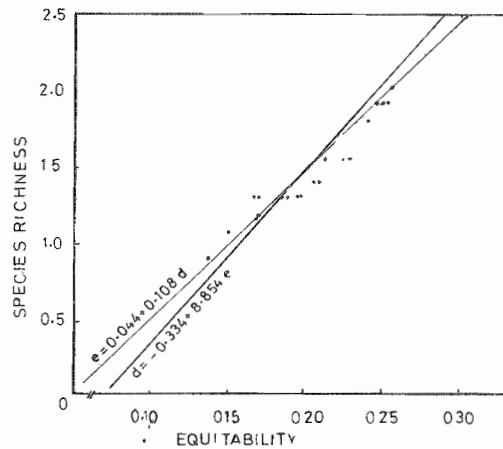


Fig. 5. The relationship between equitability and species richness.

cient between equitability and general diversity yielded a relatively lesser value, nonetheless it was also highly significant ($r = 0.9424$, $p < 0.001$; Fig. 6).

c) Relationships of community maturity with the diversity measures and dominance:

Community maturity displayed the tightest inverse relationship with species richness ($r = 0.7104$, $p < 0.001$; Fig. 7). Compared to its relation with other diversity functions. Equitability was also found to be highly negatively related to community maturity ($r = 0.6611$, $p < 0.001$; Fig. 8) but general diversity was slightly more closely related to community maturity ($r = -0.6864$, $p < 0.001$; Fig. 9). However, community maturity was found to be uncorrelated with the measure of dominance ($r = 0.2224$ n.s; Fig. 10).

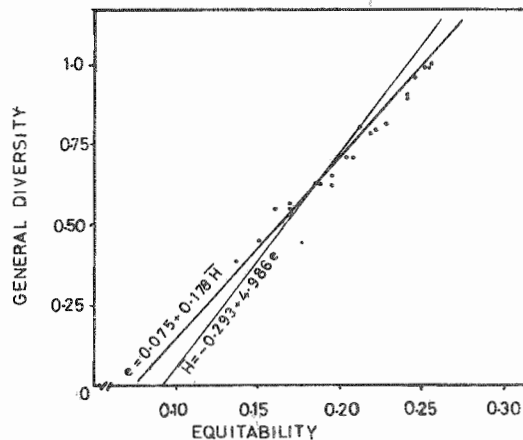


Fig. 6. The relationship between equitability and general diversity.

TABLE 2. Mean species richness, equitability, general diversity and the proportion of I.V.L. in terms of species longevity as a measure of stability of the leading dominant groups.

Leading dominant group	Species richness (d)	Equitability (J)	General diversity (\bar{H})	Proportion of V.L.L.*	Proportion of L.L.	Proportion of V.L.L. + L.L.	Proportion of S.L.
<i>Preropyrum olivieri</i>	1.463	0.219	0.746	0.535	0.357	0.892	0.108
<i>Cordia gharaf</i>	1.291	0.168	0.662	0.848	0.142	0.990	0.010
<i>Prosopis cineraria</i>	1.419	0.200	0.734	0.552	0.218	0.770	0.230
<i>Capparis decidua</i>	1.549	0.212	0.755	0.690	0.189	0.879	0.121
<i>Euphorbia caducifolia</i>	2.000	0.886	1.007	0.637	0.105	0.742	0.258

* V.L.L. = very long-lived, L.L. long-lived, S.L. = short-lived.

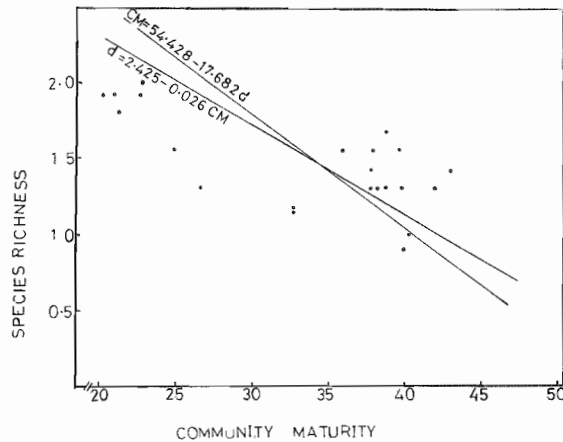


Fig. 7. The relationship between community maturity and species richness.

d) *Relationship between stability and diversity:*

The perennials were classified as to whether they were short, long- or very long-lived, the relative contribution of each to the total I.V.I. was calculated and averaged for the five leading dominant groups (Table 2). The higher the values in the V.L.L., L.L. or V.L.L. + L.L. column, the more stable are the communities. When the averages of longevity values are compared with the means of various diversity measures for the leading dominant groups (that form abstract communities) in Table 2, it becomes apparent that there exists an inverse relationship between diversity and stability. *Euphorbia caducifolia* group that is most diverse shows the least proportion of V.L.L. + L.L. and the reverse is true for the *Cordia gharaf* group. The type of stability analysis performed here can be refined greatly by determining the average life span of each species instead of subjective estimation of longevity, but so far no attempt has been made to gather this sort of information on the local species.

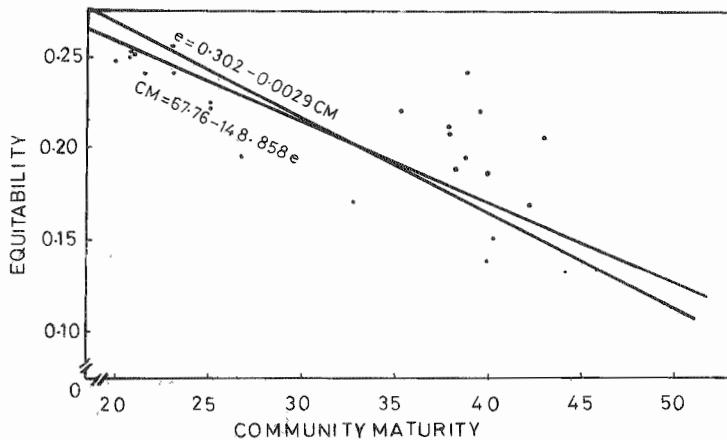


Fig. 8. The relationship between community maturity and equitability.

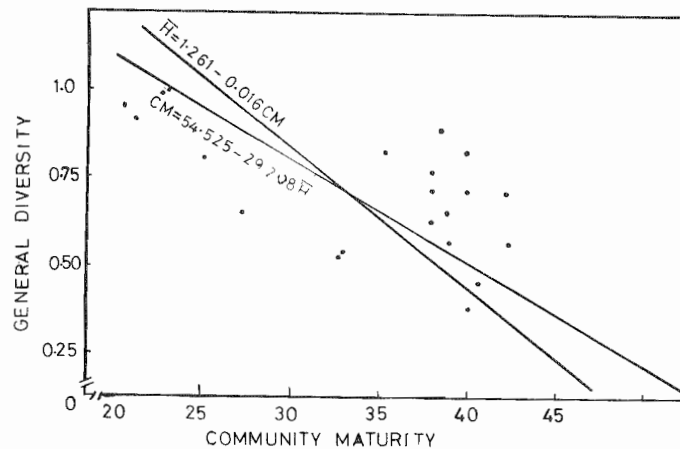


Fig. 9. The relationship between community maturity and general diversity

Discussion

Diversity is a measure of the complexity of form and function within a community. Its precise measurement leads to understanding the processes involved in the development, change and organization of communities. On the other hand, dominance expresses the importance or the success of one or a few species. Unlike diversity, its focus is the species rather than the community *per se*. Whittaker (1965) viewed the natural community as an admixture of unequally successful species. The successful species or dominants not only influence the structure and function of subordinate species but also determine the structure and diversity of communities. The vegetation of most of the stands analysed was simple in its organization, as indicated by high values of dominance, presumably due to scarcity of moisture and the consequent scanty plant cover of the phytocenoses.

A substantially strong inverse relationship was found between species richness and dominance. Similarly, Berger & Parker (1970) obtained a well-marked negative correlation between dominance (p_{max}) and diversity using the complement of Simpson's (1949) index. Certain other workers like Braun (1950), Austin & Greig-Smith (1968), Fager (1968), McNaughton (1968), and Glenn-Lewin (1975) also demonstrated dominance to be inversely related to the number of species (the simplest measure of richness). The relationship between equitability component and dominance was also found to be a negative one. This is in agreement with the findings of Whittaker (1965) who observed that the dominance concentration corresponds inversely with the evenness of allotment of individuals among the species. The general species diversity (information theory function) was also negatively correlated with dominance and yielded an intermediate value of correlation coefficient ($r = -0.7457$) between the degree of association in the two preceding cases. This is ascribable to the fact that the information function expresses the interaction between the two diversity components (Odum, 1971), and consequently shows an intermediate response

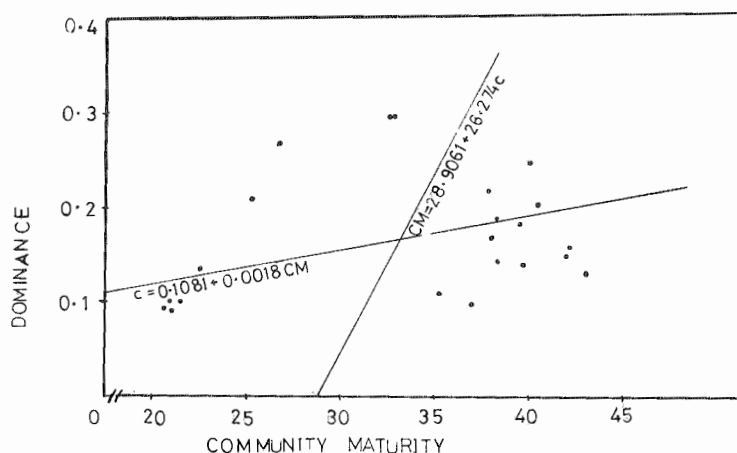


Fig. 10. The relationship between community maturity and dominance.

The relationship among the three measures of diversity employed in this study was highly significant. This accords with the findings of Auclair & Goff (1971), Hurlbert (1971) and Robichaud (1971). The results indicate that the two components of diversity i.e. richness and equitability were equally important in determining the overall diversity of communities. Tramer (1969) suggested that communities from rigorous environment (e.g. adverse environmental conditions) will vary in diversity according to their relative abundance component, while diversity in nonrigorous (biologically controlled environment) will be a function of species richness. The environment of communities under consideration was presumably neither excessively harsh and rugged nor extremely favourable but it was of an intermediate nature; consequently the two components of diversity assumed more or less equal significance towards regulating the overall diversity of form and function.

The concept of maturity is central to the ideas about ecosystem proposed by Margalef (1963 a, 1968). Maturity is a dynamic concept related to structural complexity and organization (Odum, 1969). Unfortunately the subject of diversity trends in succession has become a confused and a controversial issue. Margalef (1963 a, 1969), Monk (1967) and Monk & McGinnis (1966) demonstrated that progression leads in the direction of high species diversity. In another article, Margalef (1963 b) hypothesized that following the initial increase in diversity along succession, diversity tends to become stabilized or to decrease slightly as a result of competitive exclusion and other community changes. Paine's (1966) experiments with starfish-bivalve food subwebs, on the other hand, show that the removal of top predators from the system results in decreased species diversity along a successional (or temperal) gradient. For the present study, maturity was found to be negatively correlated with diversity. Similarly, Loucks (1970) found that species diversity in Wisconsin forests decreased after 100 years of forest succession. Whittaker (1965) comments that so far as the data can be interpreted in relation to community development or succession they suggest that diversities may both increase during succession and decrease during parts of succession. The interpretation of

the present result is not straight forward but certain hypothetical possibilities can be raised: a) Greater degree of adaptability of a few species (dominants) to the prevailing habitat conditions and capability of the terminal species to monopolize the environmental resources would have resulted in lesser diversity in relatively mature or stable communities. b) Environmental stress due to disturbance factors e.g. fire, grazing or erosion might be involved in abating species diversity of communities in advanced stages of progression.

The results presented here lead to the conclusion that the various attributes of community organization are closely integrated with each other and their mutual relationships in a desert terrain may differ considerably from other ecological situations. The concept of diversity is of great theoretical interest because it can be related to other measurable community parameters. However, for a detailed and comprehensive understanding of community organization, the approach outlined above should be broadened to include the powerful technique of system analysis.

Acknowledgement

We wish to express our gratitudes to Dr. S.I. Ali, Professor of Botany, University of Karachi, for a critical review of the manuscript.

References

- Auclair, A. N. and F.G. Goff. 1971. Diversity relations of upland forests in the western Great Lakes area. *Am. Natur.*, **105** : 499-528.
- Austin, M.P. and P. Greig Smith. 1968. The application of quantitative methods to vegetation survey. II. Some methodological problems of data from rain forest. *J. Ecol.*, **56** : 827-844.
- Berger, W.H. and F. L. Parker. 1979. Diversity of planktonic foraminifera in deep-sea sediments. *Science, N.Y.*, **168**: 1345-1347
- Braun, E.L. 1950. Deciduous forests of eastern North America. Hafner, New York. 596 pp.
- Brown, R.T. and J.T. Curtis. 1952. The upland conifer hardwood forests of northern Wisconsin. *Ecol. Monog.*, **22** : 217-234.
- Cottam, G. and J.T. Curtis. 1956. The use of distance measure in phytosociological sampling. *Ecology*, **37** : 451-460.
- Curtis, J.T. and R.P. McIntosh. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. *Ecology*, **32** : 476-496.
- Fager, E.W. 1968. The community of invertebrates in decaying oak wood. *J. Anim. Ecol.*, **37** : 121-142.
- Glenn-Leiwn, D.C. 1975. Plant species diversity in ravines of the southern Finger Lakes region. New York. *Can. J. Bot.*, **53** : 1465-1472.
- Greig-Smith, P. 1964. Quantitative plant ecology. 2nd ed. Butterworths, London. 256 pp.

- Heip, C. and W. Decremer. 1974. The diversity of nematode communities in the southern North Sea. *J. mar. biol. Ass. U.K.*, 54 : 251-255.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54 : 427-432.
- Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science*, N.Y., 105 : 367-368.
- Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology*, 52 : 577-586.
- Johnson, H.B., F.C. Vasek and T. Yonkers. 1975. Productivity, diversity and stability relationships in Mojave desert roadside vegetation. *Bull. Torrey Bot. Club*, 102: 106-285.
- Lloyd, M. and R.J. Ghelardi. 1964. A table for calculating the "equitability" component of species diversity. *J. Anim. Ecol.*, 33 : 217-225.
- Loucks, O.L. 1970. Evolution of diversity, efficiency, and community stability. *Amer. Zool.*, 10 : 17-25.
- Margalef, D.R. 1957. La teori de la informacion en ecologia. *Mems. R. Acad. Cienc. Artes Barcelona*, 32 : 373-449.
- Margalef, D.R. 1963a. On certain unifying principles in Ecology. *Am. Natur.*, 97 : 357-374.
- Margalef, D.R. 1963b. Succession in marine populations. *Adv. Front. Pl. Sci.*, 2 : 137-188.
- Margalef, D.R. 1968. Perspectives in ecological theory. Univ. Chicago Press, Chicago, 111 pp.
- Margalef, D.R. 1969. Diversity and stability: a practical proposal and a model of interdependence. *Brookhaven Symp. Biol.*, 22 : 25-37.
- McNaughton, S.J. 1968. Structure and function in California grasslands. *Ecology*, 49 : 962-972.
- Menhinick, E.F. 1964. A comparison of some species-individuals diversity indices applied to samples of field insects. *Ecology*, 45 : 859-861.
- Monk, C.D. 1967. Tree species diversity in the eastern deciduous forests with particular reference to north central Florida. *Am. Natur.*, 101 : 173-187.
- Monk, C.D. and J. T. McGinnis. 1966. Tree species diversity in six forest types in north central Florida. *J. Ecol.*, 54 : 341-344.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science*, N.Y., 164 : 262-270.
- Odum, E.P. 1971. Fundamentals of ecology. 3rd. ed. W.B. Saunders Co., Philadelphia., 574 pp.
- Odum, E.P., G. Barrett and R. Pulliam. 1971. *In* : Odum, E.P. 1971. Fundamentals of ecology (Chap. 6, p. 153). W.B. Saunders Co., Philadelphia. 574 pp.
- Paine, R.T. 1966. Food web diversity and species diversity. *Am. Natur.*, 100 : 65-75.
- Peet, R.K. 1974. The measurement of species diversity. *A. Rev. Ecol. Syst.*, 5 : 285-307.

- Pielou, E.C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York. 286 pp
- Pichi-Sermoli, R. 1948. An index for establishing the degree of maturity in plant communities. *J. Ecol.*, **36**: 85-90.
- Reiners, W.A., I.A. Worley and D.B. Lawrence. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska, *Ecology*, **52** : 55-69.
- Ribichaud, B. 1971. Diversity in vegetation of New Jersey. Ph.D. Dissertation, Rutgers University.
- Shaukat, S.S., A. Khairi and R. Ahmed. 1976. A phytosociological study of Gadap area. Pak. *J. Bot.*, **8** : 133-149.
- Simpson, eE. H. 1949. Measurement of diversity. *Nature, Lond.*, **163** : 688.
- Steel, R.G.D. and J. H. Torrie. 1976. Introduction to statistics. McGraw-Hill, New York. 416 pp.
- Tramer, E.J. 1969. Bird species diversity; components of Shannon's formula. *Ecology*, **50** : 927-929.
- Vasek, F.C., H.B. Johnson and D.H.Eslinger. 1975. Effects of pipeline construction on creosote bush scrub vegetation of Mojave desert. *Madrono*, **23** : 1-13.
- Whittaker, R.H. 1965. Dominance and diversity in land plant communities. *Science, N.Y.*, **147** ; 250-260.
- Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biol. Rev.*, **42** : 207-264.
- Whittaker, R.H. 1975. *Communities and ecosystems*. 2nd. ed. Macmillan Pub. Co., New York. 385 pp