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COMMUNITY NICHE, AN EFFECTIVE CONCEPT TO MEASURE DIVERSITY OF GRADIENTS AND HYPERSPACES

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Abstract: An appropriate index has been proposed to measure beta-diversity taking into account both richness and equitability. Existing niche overlap indices have been examined and extended to include community niche concept. Niche hypervolumes and percentages of overlap between communities have been determined using data from southeastern Ethiopia.

Introduction

The term niche has been used in a wide variety of ways. The idea has gradually been strongly linked with the concept of competitive exclusion in that ecologically similar species can seldom coexist and species living together must each have their own niche (Gause 1934, May 1974). Some ecologists (*e.g.* McArthur 1972, Schoener 1974, May 1975, Pianka 1975, Pianka 1981) identify the term with resource utilization spectra while others (*e.g.* Hutchinson 1957) consider the realized niche as a portion of the n-dimensional hyperspace defined by the total factors to which a species must be adapted and under which species populations live and reproduce themselves. Hutchison's view can be extended to communities. Several niche overlap indices have so far been proposed (Hurlbert 1978). These indices are, however, used in connection with utilization of resource states by species. Extending the niche concept to community (community niche) can have an important role in measuring diversity along gradients and in ecological hyperspaces. Diversity is here understood as a measure of richness and equitability of communities along a gradient, equitability being the proportional extension of each community along the gradient (Feoli 1984). Moreover community overlap is considered as a basic concept to measure the predictive value of environmental factors (simple or complex) on the distribution of communities along gradients. The purpose of this paper is therefore:

1. to evaluate the degree of overlap of vegetation types (communities) along single gradients (environmental factors) and give a relative measure of the predictive value of each environmental factor for the communities,
2. to measure the relative niche hypervolume of each community and the diversity of the hyperspace,
3. to analyse the degree of overlap of the hypervolumes and/or the distances between them.

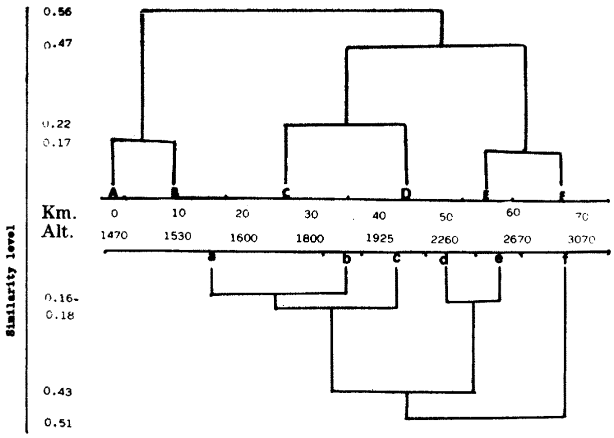

Fig. 1. Dendrogram of communities in tree-shrub (A-F) and herb layer (a-f) after Zerihun *et al.* (1988).

Data and Methods

The data set used in this paper is obtained from Zerihun, Feoli and Lissanework (1988). It regards 12 vegetation types for two layers (three-shrub and herb) of a forest and 11 environmental factors from southeastern part of Ethiopia. Figure 1 shows the dendrogram of the cluster analysis of the forest communities of both layers (see Zerihun *et al.* 1988). The ranges of the environmental factors are given in Table 1 and 2. To measure the degree of overlap along a single gradient we applied mutual information on the square matrix of overlap of communities in an environmental factor relativized:

$$RI = \sum\sum\left[r_{ij} \ln \frac{r_{ij}\, T}{r_{i} . r_{.j}} \right] / \left[T \ln N \right] ; \quad i, j = 1, \ldots, N.$$

If $i = j$ r_{ij} is the range of the ith community. If $i \neq j$ rij is the overlap of the ith and the jth communities. T is the grand total of the symmetric matrix of the ranges and overlaps and $r_{i.}$ and $r_{.j}$ are the marginal totals. N is the number of communities. RI (Relative Intersection) becomes 0 when the communities are completely overlapping and tends to 1 when the overlapping por-

Tab. 1. Range of environmental factors in tree-shrub layer communities (A to F).

	Depth	No.	A	B	C	D	E	F
pH	10 cm	1	4.90	5.40	4.70	4.20	3.90	3.80
			5.30	6.60	7.40	5.40	4.20	4.60
	50 cm	2	3.80	3.70	3.90	3.70	3.90	3.80
			4.10	5.80	6.00	5.10	4.50	4.60
OM	10 cm	3	4.80	6.40	8.60	5.60	10.40	8.40
			6.00	12.00	11.20	13.80	15.20	15.80
	10 cm	4	0.80	0.80	2.00	1.50	1.50	2.60
			2.40	3.40	6.80	6.80	7.00	6.90
SAND	10 cm	5	20.20	27.60	29.00	23.60	26.20	31.40
			28.20	38.90	49.80	41.90	36.30	44.50
	50 cm	6	18.20	9.40	17.60	17.60	22.30	21.30
			22.20	19.20	33.00	37.80	34.30	34.70
CLAY	10 cm	7	57.00	44.00	33.00	18.00	16.00	11.00
			75.00	57.00	56.00	38.00	32.00	38.00
	50 cm	8	67.00	39.00	39.00	21.00	31.00	30.00
			77.00	78.00	69.00	60.00	56.00	47.00
K	10 cm	9	0.33	0.47	0.36	0.62	0.30	0.34
			0.43	1.54	2.23	2.04	0.81	1.81
	50 cm	10	0.06	0.08	0.06	0.09	0.26	0.30
			0.09	0.08	1.97	0.78	1.49	0.86
Na	10 cm	11	0.24	0.21	0.23	0.18	0.17	0.18
			0.42	0.35	0.38	0.31	0.20	0.34
	50 cm	12	0.27	0.11	0.21	0.15	0.14	0.19
			0.28	0.28	0.28	0.30	0.24	0.37
Ca	10 cm	13	13.30	21.40	28.80	0.00	0.00	3.30
			22.80	37.00	46.00	21.40	3.30	19.60
	50 cm	14	3.30	3.00	0.00	1.00	0.00	0.00
			6.59	19.70	32.80	36.50	0.00	13.30
Mg	10 cm	15	5.10	5.10	5.10	1.10	0.50	1.10
			5.30	8.60	11.60	11.30	2.20	5.70
	50 cm	16	3.20	1.10	0.50	4.50	0.00	1.10
			3.40	5.40	8.90	7.10	4.10	3.30
Slop	-- --	17	2.00	0.00	0.00	1.00	4.00	4.00
	-- --		9.00	9.00	8.00	23.00	25.00	30.00
Aspect	-- --	18	0.00	1.00	1.00	0.00	0.00	0.00
	-- --		1.50	3.50	3.50	4.00	3.50	3.00
Alt.	-- --	19	1470	1600	1980	2130	2390	2810
	-- --		1510	1950	2130	2390	2800	3300

Tab. 2. Range of environmental factors in herb layer communities (a to f).

	Depth	No.	a	b	c	d	e	f
pH	10 cm	1	3.80	5.40	5.00	4.20	3.90	3.80
			7.40	5.80	5.40	5.50	4.20	4.80
	50 cm	2	4.70	4.90	3.70	4.30	4.00	3.90
			6.10	5.40	4.70	5.10	4.50	4.60
OM	10 cm	3	6.00	8.80	9.10	5.60	10.40	8.40
			12.00	9.90	12.00	13.80	15.20	15.80
	50 cm	4	0.80	1.50	3.60	3.80	1.50	2.60
			6.80	2.80	4.60	6.80	7.00	6.90
SAND	10 cm	5	0.20	29.10	23.60	29.80	26.20	31.60
			49.60	52.70	41.30	35.60	36.30	44.90
	50 cm	6	9.60	19.40	17.60	22.20	22.20	21.80
			25.50	33.00	37.80	27.80	34.30	34.70
CLAY	10 cm	7	36.00	25.00	21.00	19.00	16.00	14.00
			75.00	48.00	60.00	34.00	32.00	48.00
	50 cm	8	65.00	38.00	24.00	23.00	39.00	31.00
			78.00	64.00	62.00	56.00	57.00	47.00
K	10 cm	9	0.30	0.36	0.41	0.30	0.26	0.30
			2.72	2.34	1.05	2.04	1.49	1.81
	50 cm	10	0.06	0.09	0.09	0.23	0.17	0.26
			1.97	0.72	0.76	0.76	0.24	0.86
Na	10 cm	11	0.21	0.23	0.19	0.18	0.17	0.17
			0.42	0.34	0.31	0.28	0.20	0.34
	50 cm	12	0.11	0.28	0.23	0.15	0.14	0.17
			0.28	0.34	0.28	0.28	0.24	0.37
Ca	10 cm	13	13.30	22.80	3.30	3.3.	0.00	3.30
			46.00	27.80	28.00	39.00	3.30	19.60
	50 cm	14	0.00	10.00	0.00	16.00	0.00	0.00
			24.20	32.80	21.40	21.40	0.00	13.30
Mg	10 cm	15	4.90	5.70	1.10	1.10	1.10	1.10
			11.00	9.90	8.90	11.20	2.20	6.10
	50 cm	16	0.50	0.50	6.00	5.20	0.00	0.50
			6.40	8.90	7.10	5.60	4.10	3.30
SLOP.	-- --	17	0.00	2.00	1.00	4.00	4.00	4.00
	-- --		8.00	20.00	25.00	25.00	25.00	30.00
Aspect	-- --	18	0.00	0.00	0.00	0.00	0.00	0.00
	-- --		3.50	4.00	4.00	4.00	2.00	3.00
Alt.	-- --	19	1470	1490	1600	1800	2380	2800
	-- --		1510	1600	1950	2350	2780	3000

tions are decreasing provided the communities have the same evenness. This index may more appropriately be used to measure beta diversity than the one proposed by Whittaker (1972) since it takes into consideration the two components of diversity, namely richness (number of communities) and equitability (proprotional extension) while Whittaker's beta diversity is based only on half change which is just a measure of heterogeneity.

The intersection between two communities niches (A, B) along one environmental axis is here obtained by the following simple formula:

$$I(A, B) = (\text{lesser of max values} - \text{greater of min values}).$$

The intersection in many dimensions is obtained by:

$$I(A, B) = \Pi\ (\text{lesser of max values} - \text{greater of min values})\ i$$

where A and B are two communities, Π is the product of the intersections over all environmental factors and i is the ith environmental factor. A complete separation between two communities on at least one axis would result in two non-overlapping hypervolumes. This is analogous to what May (1974, 1975) proposed for the determination of the resource utilization coefficient of competing species. An environmental factor without a range should be discarded during the computation of the hypervolumes to prevent the product from being zero. In our particular case potassium and calcium both in the lower horizon of the soil were discarded.

The niche hypervolume is simply the product of the ranges in the diferent dimensions (see also May 1974, 1975):

$$V = \Pi\ (\text{max-min})\ i$$

This formula which admittedly assumes the shape of niche to be hyperparallelepiped could result in over-estimation if in natural situation the shapes appear to have smooth surfaces. The higher the number of dimensions the lower should be the over-estimation.

The diversity of the hypervolumes is computed using the Shannon-Weaver entropy. The euclidean distances between two hypervolumes is computed by:

$$D(A, B) = (\text{Sum}\ d(A, B)\ i^{2})^{1/2}$$

where d (A, B) i is the distance between communities A and B on the ith environmental factor. We also computed euclidean distance between the centroids of the hypervolumes and correlation between the two distances for the communities in each layer of the forest. The correlation coefficient gives a clue about the shape and direction of the hypervolumes. Before computations the environmental variables must be normalized or standardized. It should be stressed that the hypervolumes have only a relative value and valid only in the context of the data set under study.

Results and discussion

The degree of overlap of communities along single environmental factors is given in Table 3. Altitude shows the least overlap and highest RI-diversity (0.90, 0.65) in both layers. This is mainly because altitude is a complex gradient affecting more than one factor at a time such as moisture, average temperature, minimum and maximum temperature directly, and some edaphic factors indirectly. RI is very low for most of the soil physical and chemical factors except pH, sand and sodium in the tree-shrub communities. This could also be attributed to the nature of the parent material of the soil and the higher variation of altitude in the communities (see also Zerihun *et al.* 1988).

Tab. 3. RI values (Beta diversity) of environmental factors in the tree-shrub and herb layer communities.

	No.	Depth	Tree-shrub	Herb
pH	1	10 cm	0.30	0.11
	2	50 cm	0.01	0.26
OM	3	10 cm	0.05	0.03
	4	50 cm	0.04	0.03
Clay	5	10 cm	0.06	0.02
	6	50 cm	0.09	0.02
Sand	7	10 cm	0.34	0.07
	8	50 cm	0.07	0.07
K	9	10 cm	0.03	0.00
	10	50 cm	0.21	0.02
Ca	11	10 cm	0.04	0.03
	12	50 cm	0.03	0.08
Na	13	10 cm	0.37	0.06
	14	50 cm	0.01	0.05
Mg	15	10 cm	0.10	0.05
	16	50 cm	0.07	0.05
Slop	17	-- --	0.04	0.00
Aspect	18	-- --	0.01	0.00
Alt.	19	-- --	0.90	0.65

The total number of non-overlaps of communities in each environmental factor in shown in Figure 2 a and b. The factor that shows the highest number of non-overlaps in both layers is altitude (max = 15). Spearman's rank correlation of the number of non overlaps in each environmental factor between the two layers is not significant when altitude is excluded.

The niche hypervolumes are given in Table 4. The descending order of the hypervolumes in the tree-shrub layer communities is D, C, F, B, E, A, whereas that of the herb layer communities is a, f, d, c, b, e. Communities D and a occupy 84% and 95% of the total niche hypervolumes in their respective layer. The diversity of the niche hypervolumes of the tree-shrub layer communities is higher than those of the herb layer communities (Shannon-Weaver entropy = 0.566 and 0.237 respectively). Five of the six communities in the tree-shrub layer (B, C, D, E, F) have greater hypervolumes than their corresponding counterparts (b, c, d, e, f). This also agrees with the extension of the communities along the transect in the forest as shown in Fig. 1. It can be seen that community D is associated with three herb layer communities b, c, d and community a with three tree-shrub layer communities A, B, C.

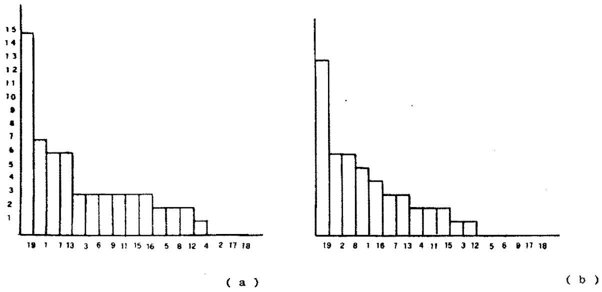

Fig. 2. The total number of non-overlaps of communities in each environmental factor (a) tree-shrub and (b) herb layer communities (the numbers on the horizontal axis are those of the environmental factors in Tab. 1 and 2).

Tab. 4 Relative Niche hypervolumes of the tree-shrub and herb layer communities (Veg. type) and total number of species (n).

Veg. type	n	Hypervolume of niche	Veg. type	n	Hypervolume of niche
A	32	.616390E-26	a	48	.133028E-14
B	50	.156816E-16	b	37	.162030E-18
C	52	.139878E-15	c	40	.271725E-17
D	39	.122379E-13	d	30	.100235E-16
E	31	.394996E-19	e	43	.207905E-19
F	20	.708080E-16	f	52	.614299E-16

The hypervolumes of the communities in the same forest layer do not overlap but are rather well separated. The distances between the centroids of the clusters and the distances between the hypervolumes are more correlated in the herb layer than the tree-shrub layer (r = 0.86 and r = 0.57 respectively). This suggests that the shape of the hypervolumes in the herb layer are more isodiametric or hyperspherical than those of the tree-shrub layer. Fig. 3 a and b show two-dimensional reconstructions of the positions and shapes of the hypervolumes based on the eigenvectors of matrices (D algorithm, Orlóci 1978). The Spearman's rank correlation between number of species and the volumes (Table 4) is not significant suggesting that species richness is not related to the community niche hypervolume.

Conclusion

The forest in Harena National Park shows a number of features which indicate the high level of its complexity. There is a clear zonation in the forest with each community restricted to an ecological space with narrow range of environmental factors few of which show clear trend of variation. In general it appears that the tree-shrub layer communities show less overlap than the herb layer communities in many of the environmental factors, suggesting that the tree-shrub layer is more directly related to the environmental factors measured. The communities in each forest layer do not

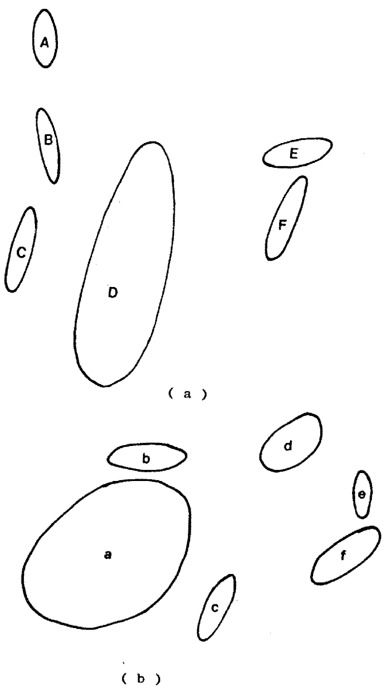

Fig. 3. Relative shape and direction of the hypervolumes of the tree-shrub and herb layer communities.

overlap in ecological space notwithstanding similarity between the communities in species occurrence.

The large extent of community D can be accounted for by the fact that it occupies a transition zone between the closed forest communities A, B, C and the shrubby and relatively more open communities E and F and contains species which are not highly adapted to conditions on either side (see Zerihun *et al.* 1988). Community a occurs under tree-shrub communities where the relatively uniform moisture and temperature can have overriding influences and mask the effect of the other environmental factors. Another possible explanation for the spread of this community in large hypervolume and physical space could be the effect of cattle grazing which would compensate for the environmental variation.

The number of species in each community is not proportional to the size of the niche hypervolumes. This shows that there is more species packing (more complexity) in the communities with small niche hypervolume, a condition which can make them less stable (see May 1974). Although closer species packing tends to give better fit to the resource spectrum and a more efficient use of the available environmental resource (May 1974), the highly specialized communities in the small hypervolumes would be more fragile and face local extinction when confronted with disturbances beyond their normal experience.

The information on the forest collected through this study can be used to issue remarks of significance to management. The problem of managing biological resources so as to maximize social benefits differs from all other resource managements, among other things, in their complexity inherent in the biology. Biological resources often involve characteristic difficulties centered largely around conflicts of interest. Logging in the interior of the forest is a threat to the continued survival of these fragile communities as they are not renewable resources in the sense that recovery may hardly be possible at least in the human lifespan. Disturbance may result in the loss of the yet unexploited gene pool of the wild coffee which occurs mainly in community B which has one of the smallest hypervolumes (see Zerihun *et al.* 1988). We therefore strongly suggest that logging and grazing in the forest should be prohibited, and stronger protective measures should be implemented.

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REFERENCES

Feoli, E. 1984. Some aspects of classification and ordination of vegetation data in perspective. Studia geobotanica 4: 7-23.

Gause, G.F. 1934. *The struggle for existence*. Williams and Wilkins, Baltimore.

Hurlbert, T.S. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67-77.

Hutchinson, G.E. 1957. Concluding remarks. Cold Spring Harbor. Quant. Biol. 22: 415-427.

May, R.M. 1974. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton, New Yersey.

May, R.M. 1975. Some notes of estimating the competition matrix. Ecology 56: 737-741.

McArthur, R.H. 1972. *Geographical Ecology*. New York, Harper and Row.

Orloci, L. 1978. *Multivariate Analysis in Vegetation Research* 2nd ed. Dr. W. Junk b.v: Publishers, The Hague.

Pianka, E.R. 1975. Niche relations of desert lizards. In: M. Cody and J. Diamond (eds.), *Ecology and Evaluation of communities*. pp. 291-314. Harvard University Press. cambridge Mass.

Pianka, E.R. 1981. *Competition and niche theory*. In R.M. May (ed.), *Theoretical Ecology* Principles and Applications. pp. 167-196. Blachwell Publications, London.

Schoener, T.W. 1975. Resource partitioning in ecological communities. Science 185: 7-39.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

Zerihun Woldu, E. Feoli and Lissanework Nigatu. 1988. Partitioning a complex gradient, an example from southeast Ethiopia. Vegetatio (in press).