

Paola Ganis

PROGRAMS FOR NICHE BREADTH, OVERLAP AND HYPERVOLUMES.

Quaderni del
Gruppo Elaborazione Automatica Dati
Ecologia Quantitativa

Dipartimento di Biologia
Universita' di Trieste

GEAD-EQ n.9

Trieste 1989

This work has been supported by CNR within the project "Oceanografia e Tecnologia Marina".
I wish to thank prof. E. Feoli for reading and commenting the manuscript and dr. Jo Hughes for linguistic corrections.

Introduction

The concept of niche involves two complementary aspects, one related to the hypervolume occupied by a species or a community in the ecological space (e.g. Hutchinson 1957, 1978; Feoli, Ganis and Woldu 1988) and the other related to the pattern of resources exploitation and competition (e.g. May 1975a, 1975b, Hulbert 1978, 1981; Pianka 1981; Maurer, 1982; Smith 1982; Giller 1984; Holt, 1987). Many niche overlap indices have been proposed and used by ecologists: some of them are frequently equated with the competition coefficient, others can be classified as distance measure (Levins 1968), association indices (Cody 1974), correlation coefficient (Pianka 1973), information measures (Horn 1966). The actual relationship between niche overlap and competition is not clear. Abrams (1980) specifies that mere overlap in resource use does not necessarily lead to competition and viceversa the intensity of competition cannot be related to the degree of niche overlap. He suggested that "niche overlap can be used to determine the relative amounts of inter- and intraspecific competition, but, before estimating this, it is necessary to have a model of the consumer- resource interaction, and some knowledge of the parameters in the model".

If the competition arises from the common utilization of resources it is important to consider the resource availability to understand better the relationship between niche- overlap and competition. Hurlbert (1978) is one among the few authors who have incorporated the availability of resource states in the overlap and competition measures. The resource state is used in a broad sense and it can be variously expressed e.g. food resources consumed, a set of natural sampling units, a set of prey species and so forth.

In the present paper a set of computer programs is presented to measure niche breadth and overlap and examples of applications are given with simple data sets. The formulas used in the programs are several, for some of them (Petraitis (1979) there are already computer programs available (Ludwig and Reynolds 1988). However not all those proposed in the literature are considered (e.g. Sugihara 1986).

The aim of this paper is not to discuss about niche theory but only to give tools to work on it.

Programs

Five programs are presented:

- HYPERV computes the hypervolumes of the niches and their overlap on the basis of the species or community ranges on single environmental factors. Notwithstanding other suggestions e.g. Burgman (1988), the hypervolumes are computed according to the product of the ranges, the overlap is computed as the common hypervolume of two niches or as distance between the hypervolumes.

In this case the overlap does not include the intensity of the interaction between the species in terms of competition for space or resources.

- OVNICHE computes several coefficients of niche breadth and overlap on the basis of the intensity of resource use. The basic formula is the scalar product weighted in several ways.

- OVERLAP computes diversity along single gradients both for species or communities. This may be used to measure predictivity of single ecological factors and/or linear and non linear combinations of them.

- POSTDU prepares the input for HYPERV and OVERLAP if the computations are required for community niches.

- SPRANG prepares the input for HYPERV and OVERLAP for species niches.

The programs presented in this manual are written in FORTRAN 77 and run on any personal computer with MS-DOS system. In each program the output printing lines are of 132 characters. To have a good printing, it is necessary, if possible, to adapt the parameters of the printer related to the printing characters. The diskette containing the program is available on request free of charge. One empty diskette is to be send to the author:

Paola Ganis
Dipartimento di Biologia
Sezione Elaborazione Dati ed Ecologia Quantitativa
v. Valerio 30
34100 TRIESTE
ITALY

Program **HYPERV**

This program reads the minimum and the maximum values of each environmental variable of a data set stored into two matrices: these are the output of POSTDU for computing niche hypervolume and overlap of communities, or of SPRANG for computing niche hypervolume and overlap of species or their characteristics (taxonomic, structural, textural etc. see Feoli 1984). The program calculates:

1. The niche hypervolumes for the species or communities according to

$$1) \quad HV = \prod_i (\max - \min)_i$$

where \prod is the product of the ranges over all environmental factors and i is the i th environmental factor (see also May, 1975a, 1975b).

The computation of the hypervolume in this way is realistic only if the variables are independent each from the other; if there is correlation between them, it would be better to orthogonalize the variables or to compute the principal components. If an environmental factor has constant values for a species (or community), it is not considered in the hypervolume computation in order to avoid the product becoming zero; the same variable has to be excluded also for the other niches otherwise the hypervolumes, not having the same dimensions, are not comparable.

2. The symmetric matrix for the niche overlaps in terms of hypervolume or percentage of hypervolume. If required, the high triangular matrix with diagonal is saved.

Each value of the matrix is a measure of the hypervolume (HV(a,b)) representing the intersection between two niches according to the formula:

$$2) \quad HV(a,b) = \prod_i (\min \text{ of } \max \text{ values} - \max \text{ of } \min \text{ values})_i$$

where a and b are two species or communities. \prod is the product of intersections along all environmental axes and i is the i th environmental factor. The hypervolumes of overlaps can be changed

to a relative measure ($HV_r(a,b)$) according to the following formulas:

$$3) \quad HV_r(a,b) = HV(a,b)/[HV(a) * HV(b)]^{1/2}$$

$$4) \quad HV_r(a,b) = (HV(a,b)/HV(a) + HV(a,b)/HV(b)) / 2$$

where $HV(a)$ and $HV(b)$ are respectively the hypervolumes of niche a and b.

In this matrix the zero values represent both contiguity on one or more dimensions and distances between two niches. The positive values indicate overlap.

3. The symmetric matrix for distances (D) between the niches . These distances are measured inside hypervolumes of two different kinds: hypervolumes of overlapping (intersections) and hypervolumes separating two niches. They represent the diagonals inside the hypervolumes. In this case the hypervolumes are computed only by the axes on which there is no overlap. It follows that the distance between two niches having e.g. ten dimensions can be computed just on one axis if the niches don't overlap only for that. Fig. 1 helps to make clear the computation visualizing graphically the niche areas, the overlaps and the considered distance.

In the symmetric matrix the elements in the diagonals are the breadths of the niche measured by the lenght of the diagonal of the corresponding hypervolume.

Two different formulas for computing the distance inside the hypervolumes are proposed:

$$5) \quad D(a,b) = (\sum_i [\min \text{ of max values} - \max \text{ of min values}]_i^2)^{1/2}$$

In the formula Σ is the summation of the overlapped or intervalled range in the different environmental axes and i is the i th factor.

$$6) \quad D(a,b) = HV(a,b)_i^{1/N} * N^{1/2}$$

In formula (6) for dimension $N > 3$, the hypervolumes take the shape of a hypercube.

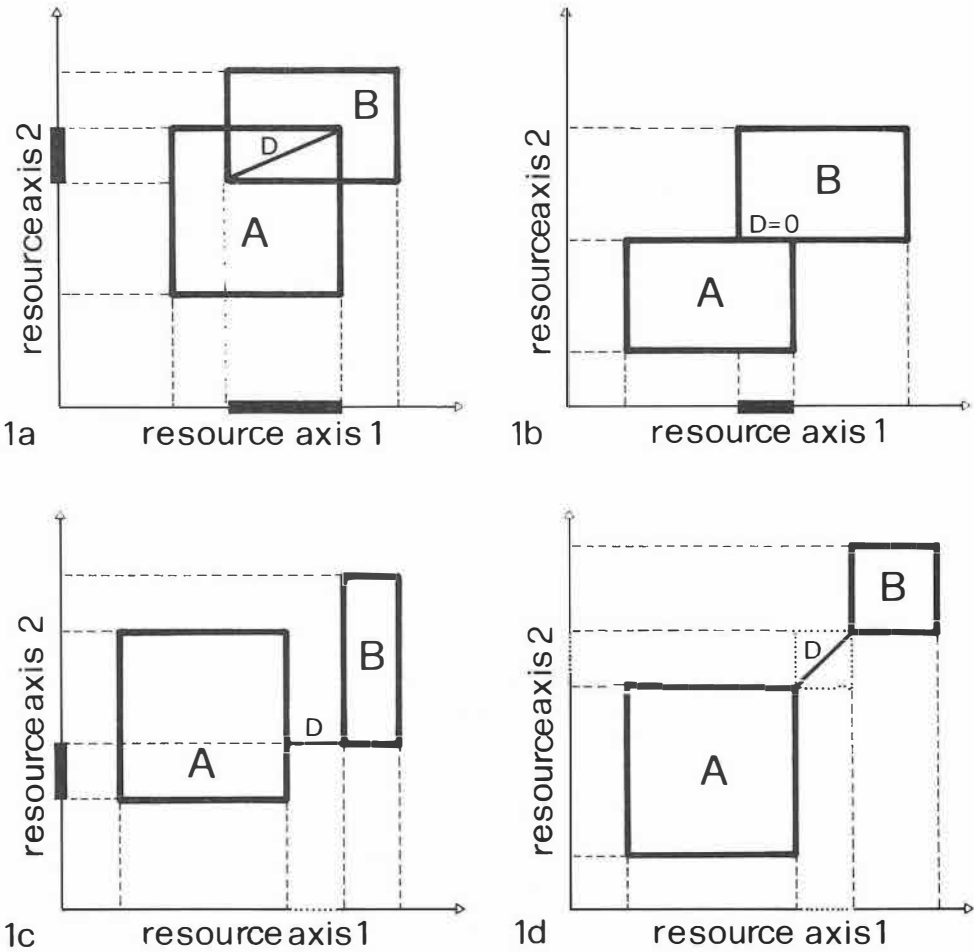


Fig. 1 - Position of two hypothetical species or community niches (A and B) in a bi-dimensional resource space for four possible cases. 1a) the overlap between niches is due by the overlap between the two niches along each axis; 1b) the two niches are contiguous along the second axis; 1c) niche A and B are separated on the resource axis 1; 1d) there is no overlap on both axes. D represents the distance calculated by program HYPERV: 1a) D is the diagonal of the common area between A and B niches; 1b) $D = 0$, there is no distance and no overlap; 1c) D is simply the distance between the two niche ranges along the first axes; 1d) D is the diagonal of the minimum area interposed between the two niches areas. In this example the niches are represented by area because two dimensions are considered. Niches will be represented by volumes and hypervolumes if the calculation will involve respectively three or more axes.

The distances can be relativized (D_r) according to:

$$8) D_r(a,b) = D(a,b)/[D(a) * D(b)]^{1/2}$$

$$9) D_r(a,b) = [D(a,b)/D(a) + D(a,b)/D(b)] / 2$$

where $D(a)$ and $D(b)$ are the diagonals of the niches a and b .

The negative values in the matrix indicate overlap, the positive values distance and zeros contiguity.

The high triangular matrix with diagonal is optionally saved: in this case the values are transformed to have all positive values according to :

$$10) \quad x_i = X_i - X_{\min}$$

INPUT

Program HYPERV requires as input:

- a) - input file name of the matrix of minimum ecological values for each community or for each species (program POSTDU or SPRANG creates this)
- b) - input file name of the matrix of maximum values (program POSTDU or SPRANG creates this)
- c) - output file name for hypervolumes of each niche: they are saved in ascendent order; if blank they are not saved
- d) - output file name for matrix of overlaps (in terms of hypervolumes); if blank it is not saved
- e) - output file name for matrix of overlaps (in terms of distance) between niches; if blank it is not saved
- f) - number of rows and number of columns of the matrices of minimum and maximum values
- g) - option related to the variables normalization: 'Y' for the normalization; it is necessary to normalize when the environmental factors have different measures. In the program all the variables values are multiplied by 10 after normalization to avoid hypervolumes values being too small or too big.

- h) - indication of the position of the variables: 'Y' or blank, on the columns: 'N' on the rows; in this case the matrix is transposed by the program
- i) - option for distance measure inside the hypervolume:
 - 1) diagonal according to formula (5)
 - 2) diagonal according to formula (6)
- l) - input format of the input matrices; if blank they are read as if they were in free format
- m) - option for selecting overlap index:
 - 1 - in the overlap matrix the overlap between two niches is given by the common hypervolume (HV(a,b)) representing the intersection between them (see formula (2)); in the distance matrix the values are computed by formulas (5) or (6) according to i).
 - 2 - the overlap and distance measures are expressed in percentages according to formulas (3) and (8).
 - 3 - the overlap and the distance measures are expressed by averaging the percentages according to formulas (4) and (9)

Before computing the total overlap between niches, the program calculates for each pair the overlap on each variable; this output is printed only if the niches are not more 10, otherwise it is saved on file PAIR.OVP in order to avoid a too long printout. The distances between the niche ranges for each variable are printed with negative values.

EXAMPLE

An example of input is shown below, with the results of the calculation. The input matrices had been obtained by POSTDU program and are reported in Tab. 1 and in Tab. 2; these tables have been prepared by program POSTDU using Tab. 7.

C:\PAOLA\type min.e							
1.760	3.720	2.220	2.900	2.810	2.980	4.020	2.600
1.960	3.200	2.320	3.070	3.170	2.820	3.770	2.830
2.340	3.100	2.450	3.260	3.320	2.650	3.730	2.650
2.650	3.320	2.640	3.320	3.450	2.350	3.500	2.600
2.030	3.560	2.190	2.990	2.830	2.860	3.580	3.090

Tab. 1

C:\PAOLA\type max.e							
2.070	3.910	2.550	3.100	3.120	3.160	4.710	3.250
2.450	3.680	2.540	3.280	3.540	3.050	4.290	2.950
2.690	3.600	2.690	3.390	3.630	2.830	3.870	3.040
2.920	3.500	3.010	3.460	3.680	2.720	3.800	2.940
2.400	3.680	2.530	3.210	3.250	3.170	3.710	3.240

Tab. 2

```

C:\PAOLA\hyperv
MINIMUM VALUES FILE NAME
min.e
MAXIMUM VALUES FILE NAME
max.e
HYPERVOLUMES FILE NAME (IF BLANK, NOT SAVED)

OVERLAP MATRIX NAME (10G10.3)(IF BLANK, NOT SAVED)

DISTANCE MATRIX NAME (10G10.3)(IF BLANK, NOT SAVED)
dov.e
N. OF ROWS, N. OF COLUMNS
5,8
ARE THE VARIABLES ON THE COLUMNS ? (Y/N)
y
ARE THE VARIABLES TO BE NORMALIZE ? (Y/N)
n
INPUT FORMAT (IF BLANK FREE FORMAT)

OPTION FOR DISTANCE INSIDE THE HYPERVOLUME :
  1 DIAGONAL (SQRT (I range**2))
  2 DIAGONAL (SQRT(HV(a,b) ^ SQRT(N))
1
OPTION FOR OVERLAP (a) AND DISTANCE (b) INDICES :

  1 a) OVERLAPPED HYPERVOLUME   (HVab)
    b) HYPERVOLUME DIAGONAL     (Dab)
  2 a) HVab/SQRT(HVa*HVb)       b) Dab/SQRT(Da*Db)
  3 a) (HVab/HVa+HVab/HVb)/2   b) (Dab/Da+Dab/Db)/2
3

```

LIST OF CONSIDERED VARIABLES (number = 8)

1 2 3 4 5 6 7 8

		SORTED	
		HYPERVOLUMES	DIAGONAL
1	5	.843202E-05	.791960
2	3	.166349E-04	.864407
3	4	.218523E-04	.810679
4	2	.577024E-04	1.01863
5	1	.972872E-04	1.14377

OVERLAP OF EACH VARIABLE FOR EACH OBJECT

I II

	1	2	3	4	5	6	7	8
1 1	.310	.190	.330	.200	.310	.180	.690	.650
1 2	.110	-.400E-01	.220	.300E-01	-.500E-01	.700E-01	.270	.120
2 2	.490	.480	.220	.210	.370	.230	.520	.120
1 3	-.270	-.120	.100E+00	-.160	-.200	-.150	-.150	.390
2 3	.110	.400	.900E-01	.200E-01	.220	.100E-01	.100E+00	.120
3 3	.350	.500	.240	.130	.310	.180	.140	.390
1 4	-.580	-.220	-.900E-01	-.220	-.330	-.260	-.220	.340
2 4	-.200	.180	-.100	-.400E-01	.900E-01	-.100E+00	.300E-01	.110
3 4	.400E-01	.180	.500E-01	.700E-01	.180	.700E-01	.700E-01	.290
4 4	.270	.180	.370	.140	.230	.370	.300	.340
1 5	.400E-01	-.400E-01	.310	.110	.290	.180	-.310	.150
2 5	.370	.120	.210	.140	.800E-01	.190	-.600E-01	-.140
3 5	.600E-01	.400E-01	.800E-01	-.500E-01	-.700E-01	-.300E-01	-.200E-01	-.500E-01
4 5	-.250	-.600E-01	-.110	-.110	-.200	-.140	.130	-.150
5 5	.370	.120	.340	.220	.420	.310	.130	.150

OVERLAP HYPERVOLUMES MATRIX ACCORDING TO FORMULA : (HVab/HVa + HVab/HVb)/2
zeros indicate contiguity or distance

	1	2	3	4	5
1	1.00				
2	.000	1.00			
3	.000	.810E-04	1.00		
4	.000	.000	.341E-03	1.00	
5	.000	.000	.000	.000	1.00

DISTANCE MATRIX ACCORDING TO FORMULA: (Dab/Da + Dab/Db)/2
negative values indicate overlap
zeros indicate contiguity on one or more dimensions

	1	2	3	4	5
1	-1.00				
2	.594E-01	-1.00			
3	.452	-.538	-1.00		
4	.860	.275	-.489	-1.00	
5	.334	.171	.128	.518	-1.00

This matrix is saved on file

```
C:\PAOLA)type dov.e
.000 1.06 1.45 1.86 1.33
.000 .462 1.27 1.17
.000 .511 1.13
.000 1.52
.000
```

Program OVERLAP

The program OVERLAP reads the minimum and maximum values for each environmental variable of a data set stored into two matrices as in the program HYPERV. These values may be related to communities (output of POSTDU) or to species or to the characteristics (output of SPRANG) ; considering a variable at a time it calculates the ranges in which each community or species exists and the overlaps between them along the single environmental factor and gives a graphic representation of the overlaps. The matrices of overlap for each factor are optionally printed; on them the mutual information (MI) and the following index (RI=Relative Intersection, see Feoli et al., 1988) are computed as an overall overlap and diversity measure:

$$10) \quad RI = 1 - MI / \log N * T$$

where N is the number of communities or species and T is the grand total of the matrix of overlaps. This index has the property of taking into account both the overlap of the ranges and their equitability; it also depends on the richness (number of communities or species). An index equal to 1 indicates complete overlap between all the communities or species, an index equal to 0 is for equal and not overlapped ranges .

INPUT

Program OVERLAP requires as input:

- a) - input file name of the table of minimum ecological values for each community or for each species (program POSTDU or SPRANG prepares this)
- b) - input file name of the table of maximum ecological values.
- c) - number of rows and number of columns of table.
- d) - indication of the position of the ecological variables; 'Y' or blank for columns, 'N' for rows.
- e) - input format of the input tables; if blank they are read in free format . If the tables are outputs of POSTDU or SPRANG the format is (10F10.3).
- f) - option for printing of the overlap matrices: 'Y' for printing.
- g) - input file name of the labels (max 40 chars.) of the ecological variables; if blank, they are not read.

h) - input file name of the labels (max 20 chars.) of communities or species; if blank, they are not read.

EXAMPLE

An example of input data and the resulting output is given below; the input matrices are the same as in program HYPERV (Tab. 1 and Tab. 2) obtained by program POSTDU.

```
C:\PAOLA\overlap
MINIMUM VALUES FILE NAME
min.e
MAXIMUM VALUES FILE NAME
max.e
N. OF ROWS, N. OF COLUMNS
5,
8
ARE THE ECOLOGICAL VARIABLES ON THE COLUMNS ? (Y/N)
y
INPUT FORMAT (IF BLANK FREE FORMAT)

OVERLAP MATRICES PRINTING ? (Y/N)
y
VARIABLES LABELS (MAX 40 CHARS.) FILE NAME (IF BLANK NOT LABEL)
ie
COMMUNITY OR SPECIES LABELS (MAX 20 CHARS.) FILE NAME
(IF BLANK NOT LABEL)
co
```

```
-----
VARIABLE N. 1 UMIDITY
-----
```

MINIMUM VALUE =	1.760	MAXIMUM VALUE =	2.920	RANGE =	1.160					
	1	2	3	4	5	6	7	8	9	10
INTERVALS BOUNDS	1.760	1.960	2.030	2.070	2.340	2.400	2.450	2.650	2.690	2.920
INTERVALS RANGES	.200	.070	.040	.270	.060	.050	.200	.040	.230	
NUMBER OF OVERLAPS FOR EACH INTERVAL	1	2	3	2	3	2	1	2	1	

GRAPHIC RELATED TO EACH NICHE IN ONE DIMENSION:symbols ' indicate interval bounds



OVERLAP MATRIX

ROW/COL	1	2	3	4	5
1	.310000	.110000	.000000	.000000	.400000E-01
2	.110000	.490000	.110000	.000000	.370000
3	.000000	.110000	.350000	.400000E-01	.600002E-01
4	.000000	.000000	.400000E-01	.270000	.000000
5	.400000E-01	.370000	.600002E-01	.000000	.370000

MUTUAL INFORMATION= 1.68623
 OVERLAP INDEX= .67763

C:\PAOLA\overlap
 MINIMUM VALUES FILE NAME
 min.e
 MAXIMUM VALUES FILE NAME
 max.e
 N. OF ROWS, N. OF COLUMNS
 5,8
 ARE THE ECOLOGICAL VARIABLES ON THE COLUMNS ? (Y/N)
 y
 INPUT FORMAT (IF BLANK FREE FORMAT)
 OVERLAP MATRICES PRINTING ? (Y/N)
 n
 VARIABLES LABELS (MAX 40 CHARS.) FILE NAME (IF BLANK NOT LABEL)
 ie
 COMMUNITY OR SPECIES LABELS (MAX 20 CHARS.) FILE NAME
 (IF BLANK NOT LABEL)
 co

```
-----
```

VARIABLE N.	1	UMIDITY

MINIMUM VALUE =	1.760	MAXIMUM VALUE = 2.920
		RANGE = 1.160
	1	2
INTERVALS BOUNDS	1.760	1.960
	2.030	2.070
	2.340	2.400
	2.450	2.650
	2.690	2.920
INTERVALS RANGES	.200	.070
	.040	.270
	.060	.050
	.200	.040
	.230	
NUMBER OF OVERLAPS FOR EACH INTERVAL	1	2
	3	2
	3	2
	1	2
	1	

GRAPHIC RELATED TO EACH NICHE IN ONE DIMENSION:symbols ' indicate interval bounds



MUTUAL INFORMATION= 1.68623
 OVERLAP INDEX= .67763

Program OVNICHE

The program OVNICHE computes the Hurlbert's overlap index (1978) and other indices revised by the same author in which the resource availability are introduced. Furthermore it calculates the indices proposed by Petraitis (1979), Smith (1982) and Feisinger et al. (1981). The first two are testable by the chi-squared distribution and the last by the normal distribution.

The program reads a table (e.g. Tab. 3) in which each individual (species or community) is described by a vector of resource states utilization and optionally reads a vector whose elements are the abundances of each resource state. The measure of resource utilization (n_{ij}) may be direct (quantity of used resource) or indirect. In this case the number of individuals or the biomass of the species using each resource state is considered. If in the field studies it is not possible to obtain the data of resource availability, it is assumed that resources are equally available and consequently all Hurlbert's indices reduce to other indices previously described in the literature.

Program OVNICHE calculates 13 indices, the first seven related to the interspecific encounter (pairwise indices) and the others to the intraspecific encounter. In Tab. 4 the principal characteristics for each index are reported. In order they are:

1. Hurlbert's niche overlap index (symmetric), whose formula is the following:

$$11) L_{12} = (A/N_1N_2) \sum_i (n_{i1} n_{i2}/a_i)$$

$$11a) L_{12} = r \sum_i (n_{i1}/N_1 n_{i2}/N_2)$$

where n_{i1} is the value of the first species associated to the resource state i and n_{i2} is the value of the second species in resource state i , a_i is the availability of resource state i , A is the sum of all resource availability, N_1 and N_2 are respectively the total population of the first and the second species.

By this index Hurlbert formalized his definition of niche overlap as "the degree to which frequency of interspecific

Resource state (i)	Species (j)				Totals	Abundance of resource state (a_i)
	1	2	...	s		
1	n_{11}	n_{12}	.	n_{1s}	t_1	a_1
2	n_{21}	n_{22}	.	n_{2s}	t_2	a_2
.
.
r	n_{1r}	n_{2r}	.	n_{rs}	t_r	a_r
Totals	N_1	N_2	.	N_s	T	A

Tab. 3 - Symbolic notation for a table in which the s species are described by their utilization (n_{ij}) of r resources; for each resource state abundance (a_i) is given, and its total utilization (t_i). The value A represents the total abundances of all resources and T the total utilization by species over all resources. Modified from Hurlbert (1979).

Options	Niche overlap indices	Type	Abundances of resources	Range	Test
1	Hulbert's index	symmetric	*	0 - >1	
2	Competiton coefficient	asymmetric	*	0 - >1	
3	Co-occurrence coefficient	asymmetric	*	not fixed	
4	Petraitis' specific ov.	asymmetric	*	0 - 1	chi-squared
5	Petraitis' general adj. ov.	symmetric	*	0 - 1	
6	Percentage similarity	symmetric	*	0 - 1	z
7	Smith's index	symmetric	*	0 - 1	chi-squared
Niche breadth indices					
8	Patchiness index		*	> 1	
9	Lloyd's mean demand		*	not fixed	
10	Levins' niche breadth		*	1/r - 1	chi-squared
11	Petraitis' niche breadth		*	0 - 1	chi-squared
12	Percentage similarity		*	0 - 1	z
13	Smith's niche breadth		*	0 - 1	chi-squared

Tab. 4 - Characterization of niche overlap and niche breadth indices in program OVNICHE. It can be seen that not the all indices utilize the vector of resources abundances (* if yes) neither all indices are testable by a test statistic (chi-squared or z). Indices 3) and 9) have a not fixed range depending on the scale of the resources abundances.

encounter is higher or lower than it would be if each species utilized each resource state in proportion to its abundance (a_i). If all resource states are equally abundant, equation (11) reduces to Lloyd's (1967) index of "interspecific patchiness" (Eq. 11a). If species don't share the resource states, index L assumes a value of zero; if both utilize each resource state in proportion to its abundance (a_i), index L will have a value of 1, and if the utilization of resource state is preferential by each species in the same way, the value is greater than 1. Petraitis (1979) shows that the index may have the value of 1 also if the utilization of resources is not proportional to their abundance. This is seen as a drawback of the proposed index, however there are no reasons to consider $L=1$ as a reference point.

2. The competition coefficient (asymmetric) as formalized below:

$$12) S_{1(2)} = \Sigma(n_{i1} n_{i2}/a_i) / \Sigma(n_{i1}^2/a_i)$$

$$12a) S_{1(2)} = \Sigma_i(n_{i1}/N_1 n_{i2}/N_2) / \Sigma_i(n_{i1}/N_1)^2$$

where the symbols are the same as in (11). This is very similar to Levins' index (1968)(Eq. 12a) and becomes equal to this when the data consist of relative abundances, such that the totals N_1 and N_2 of the two populations are 100 %.

3. Rathke's (1976) co-occurrence coefficient (asymmetric) given by:

$$13) Z_{1(2)} = \Sigma_i[(n_{i1} n_{i2}) / (N_1 a_i)]$$

$$13a) Z_{1(2)} = \Sigma_i(n_{i1}n_{i2}/N_1)$$

where symbols have the same meaning as in equation (11).

This formula expresses the density of the second species encountered, on average, by an individual of the first species. This is the more general expression including the resource state size (a_i) of Lloyd's (1967) interspecific mean crowding (Eq. 13a) of species 1 by species 2, that is a measure of directional overlap.

4. The Petraitis' specific overlap index based on the likelihood that the utilization of resources by one species is identical to the utilization by another species .

$$14) \quad SO_{1(2)} = e^E$$

where e is the neperian number equal to 2.71828.. and $E_{1(2)}$ is given by 15) where symbols are the same as in 11). As Ludwig and Reynolds (1988) already noted, the computation of SO index should require all species to utilize all resources states to avoid the value n_{ij}/N_j becoming undefined in Eq. 15. To overcome this drawback all zeros of the input table are changed arbitrarily with the value 0.000001. SO index varies from 0 to 1.

$$15) \quad E_{1(2)} = \sum_i (n_{i1}/N_1 \ln n_{i2}/N_2) - \sum_i (n_{i1}/N_1 \ln n_{i1}/N_1)$$

Two test statistics are associated to the SO index: the former, test U :

$$16) \quad U_{1(2)} = -2 N_1 \ln SO_{1(2)}$$

for testing the null hypothesis of complete specific overlap of species j onto species k . It has a chi-squared distribution with $r-1$ degrees of freedom (r is the number of resource states). The latter, the log-likelihood ratio W :

$$17) \quad W = N_1 \ln (SO_{1(2)}/SO_{1(j)})$$

for testing the hypothesis that specific overlap by species j onto species k is greater than the overlap of species j onto species m . If $W > 2$ the hypothesis is true.

Also the general overlap (GO) is calculated between species (or communities) as a weighted average of utilization curves (Petraitis, 1979). The formula is:

$$18) \quad GO = e^E$$

where

$$19) \quad E = 1/T \sum_j \sum_i [n_{ij} (\ln t_i/T - \ln n_{ij}/N_1)]$$

where T is the grand-total of the contingency table (Tab. 3) and t_i is the total for each resource state.

The statistic V associated to the GO index, tests the hypothesis of complete overlap between all the species:

$$20) \quad V = -2 T \ln GO$$

It has a chi-squared distribution with $(s-1)(r-1)$ degrees of freedom where s is the number of the species.

According to Smith (1984), index GO is dependent on sample sizes and number of considered species, so he suggests to adjust the GO index after calculating the minimum value of GO (GO_{\min}) for the particular sample under consideration. The formulas are:

$$21) \quad GO_{\min} = e^E$$

where

$$22) \quad E_{\min} = 1/T [\sum_j (N_j \ln N_j) - (T \ln T)]$$

$$23) \quad GO_{\text{adj}} = (GO - GO_{\min}) / (1 - GO_{\min})$$

In this way the range of GO_{adj} is always from 0 to 1, whereas GO changes its range according to s and particularly, in the two-species case, it varies from 0.5 to 1.

Petratis (1985) considers correct the Smith's suggestion for adjusting the GO index by the minimum value, but he remarks that the values of GO and GO_{\min} indices are dependent first of all on the t_i/T terms which are the estimated proportional utilizations if all species use resource i in the same proportion; when GO is equal to GO_{\min} , each species utilizes a different set of resources.

5. The Petratis' general overlap index adjusted according to

Smith (1984) by considering two species at a time. The formula are the ones reported above in Eq. 23 which recalls Eq. 18,19,20,21. In Eq. 19 j goes from 1 to 2. This is a symmetric index and takes values ranging from 0 to 1 (1 = complete overlap).

6. The Proportional Similarity index (PS) or Czekanowsky's Index often used to measure niche overlap (Colwell and Futuyma, 1971). It is a symmetric index and takes on values between 0 and 1. The formula is the following:

$$24) \quad PS = 1 - 0.5 \sum_i |n_{i1}/N_1 - n_{i2}/N_2|$$

the same index can be expressed by

$$25) \quad PS = \sum_i \min(n_{i1}/N_1, n_{i2}/N_2)$$

To test this index Smith (1982) proposed to calculate the variance estimate ($V_{(PS)}$) according to "delta" method (Seber, 1973) and the Z variable to have the confidence intervals. Their formulas are:

$$26) \quad V_{(PS)} = [1 - (\sum_i n_{i1}/N_1 I_i)^2 - \sum_i n_{i1}/N_1 J_i] / N_1$$

$$-1 \quad \text{if} \quad n_{i1}/N_1 > n_{i2}/N_2$$

$$\text{where } I_i = \begin{cases} 0 & n_{i1}/N_1 = n_{i2}/N_2 \\ 1 & n_{i1}/N_1 < n_{i2}/N_2 \end{cases}$$

$$\text{and } J_i = \begin{cases} 1 & \text{if } n_{i1}/N_1 = n_{i2}/N_2 \\ 0 & \text{else} \end{cases}$$

$$27) \quad Z = (PS - .5) / [V(PS)]^{1/2}$$

As it can be seen in the variance formula, the test for PS index is asymmetric even if the PS index is symmetric.

7. The Smith's (1982) overlap index (FT) as a measure of affinity between two distributions; it is a symmetric index and assumes values ranging from 0 to 1.

$$28) \quad FT = \sum_i (n_{i1}/N_1 * n_{i2}/N_2)^{1/2}$$

The chi-square associated to FT index is given by:

$$29) \quad \chi^2_{(FT)} = 8N_j (1 - FT)$$

also this test is asymmetric even if the index is symmetric.

8. The generalized form of Lloyd's (1967) patchiness index given by:

$$30) \quad G = [A/N_1(N_1-r)] \sum_i [n_{i1}(n_{i1}-1)/a_i]$$

According to Hurlbert (1978) this index measures the degree to which the frequency of intraspecific encounter is higher or lower than it would be if each resource state were utilized in proportion to its abundance (a_i).

9. The generalized form of Lloyd's (1967) "mean demand" given by:

$$31) \quad M = \sum_i [n_{i1}^2 / (N_1 a_i)]$$

10. The generalized measure of niche breadth (Levins, 1968) taking into account the variation in abundance (a_i) of resource state given by:

$$32) \quad B = N_1^2 / [A \sum_i (n_{i1}^2 / a_i)]$$

The values of this index range from $1/r$, when only a single resource state is used, to 1 when each resource state is utilized in proportion to its abundance.

The chi-squared associated to B index is given by:

$$33) \quad \chi^2_{(B)} = N_1 (1/B - 1)$$

11. The Petraitis' niche breadth measure based on the likelihood that the species' utilization of resources is the same as the available resources in the environment. Its formula is very similar to the specific overlap index (Eq. 14 and 15):, but E is computed as follows:

$$34) E = \sum_i (n_{i1}/N_1 \ln a_i/A) - \sum_i (n_{i1}/N_1)$$

For each niche breadth measure test U according to Eq. 16) is given.

12. The Percentage Similarity index (PS) as a measure of intersection between the use and availability frequency distributions (Feinsinger et al., 1981). The formula of PS niche breadth index is described in:

$$35) PS = 1 - 0.5 \sum_i |n_{i1}/N_1 - a_i/A|$$

or

$$36) PS = \sum_i \min(n_{i1}/N_1, a_i/A)$$

they are equal to Eq. 24 or 25 but the ratio n_{i2}/N_2 is substituted by the ratio a_i/A . Each PS value is tested by the variable Z as in Eq. 27.

13. The Smith's niche breadth index (FT) as a measure of affinity between two distributions:

$$37) FT = \sum_i (n_{i1}/N_1 * a_i/A)$$

this formula is very similar to the one described in Eq. 28: the ratio n_{i1}/N_2 is substituted by a_i/A . Also this index is tested by the chi-squared calculated to Eq. 29.

INPUT

Program OVNICHE requires as input:

- a) - input file name of the table.
- b) - option concerning the input of resource abundance :
 - 1) all resource abundances are equal
 - 2) resource abundances are read from an external vector
 - 3) abundances are totals of values for each resource
- c) - if in point (b) selected option is 2, the file name of the vector of resource abundances.
- d) - input format of the table; if blank, it is read in free format.
- e) - number of rows and number of columns of the table.
- f) - position of the resource information in the table:
'Y' or blank if on the rows, 'N' if on the columns.
- g) - an index selected from among the following:
 - 1) Hurlbert's index eq. (11)
 - 2) Levins' competition coefficient eq. (12)
 - 3) Rathke's cooccurrence coefficient eq. (13)
 - 4) Petraitis' specific overlap eq. (14)
 - 5) Petraitis' general adjusted overlap eq. (23)
 - 6) Percentage Similarity index eq. (24)
 - 7) Smith's overlap index eq. (28)
 - 8) Lloyd's patchiness index eq. (30)
 - 9) Lloyd's mean demand eq. (31)
 - 10) Hurlbert's niche breadth eq. (32)
 - 11) Petraitis' niche breadth eq. (34)
 - 12) Percentage similarity index eq. (35)
 - 13) Smith's niche breadth eq. (37)
 - 14) to go out
- h) - output file name for the indices tables; if blank, it is not saved. Output format for this table is (10G10.3). If the selected index is a pairwise symmetry index, the high triangular matrix with diagonal is saved, otherwise single vector is saved.

Lake	Lake area (km ²)	Number of birds	
		Phoenicoparrus andinus	Phoenicoparrus jamesi
Laguna Kollpa	1.0	24	343
Laguna Canapa	0.4	125	100
Laguna Khar Kkota	2.0	102	15

Tab. 5 - Abundance of flamingos on lakes. (After Hurlbert, 1978)

Species	corolla length in millimeters			
	1 (0-4 mm)	2 (4-8 mm)	3 (8-12 mm)	4 (> 12 mm)
Bombus appositus	27	47	357	925
Bombus flavifrons	1018	1363	1139	964
Bombus frigidus	333	638	145	13
Bombus occidentalis	155	84	70	51

Tab. 6 - Four species of bumblebees data over four resource classes given by corolla length for flowers visited. (After Ludwig and Reynolds, 1988)

EXAMPLE

An example of input and output of program OVNICHE follows; the majority of the indices are applied to data of Tab. 5 drawn from Hurlbert (1978), describing 2 species of flamingos on 3 lakes: in this case the abundance of the resource is given by the size of each lake.

Petraitis' indices are applied to data of Tab. 6 drawn from Ludwig and Reynold (1988), describing 4 species of bumblebees over 4 resources states given by the corolla length in millimeters for flowers visited.

C:\FAOLA\copy\wziche
 INPUT MATRIX NAME

a3

CHOOSE THE RESOURCE STATE ABUNDANCE PARAMETER

- 1 ALL ABUNDANCES ARE EQUAL
- 2 ABUNDANCES HAVE BE READ FROM AN EXTERNAL VECTOR
- 3 ABUNDANCES ARE TOTALS OF VALUES FOR EACH RESOURCE

2

RESOURCE STATE ABUNDANCES FILE NAME
 (IF BLANK FROM KEYBOARD)

INPUT FORMAT (IF BLANK FREE FORMAT)

N. ROWS, N. COLUMNS

3,2

ARE THE RESOURCES ON THE ROWS ? (Y/N)

y

RESOURCE STATE ABUNDANCES VALUES

1.0 0.4 2.0

ABUNDANCE OF RESOURCES STATES

1	2	3
1.0000	.40000	2.0000

TOTALS OF INDIVIDUALS

1	2
251.00	458.00

TOTAL OF ABUNDANCE RESOURCES = 3.4000

PAIRWISE INDEX

SINGLEWISE INDEX

- | | |
|---------------------------|-----------------------------|
| 1 HURLBERT'S INDEX | 8 LLOYD'S PATCHINESS |
| 2 COMPETITION COEFF. | 9 LLOYD'S MEAN DEMAND |
| 3 COOCCURRENCE COEFF. | 10 HURLBERT'S NICHE BREADTH |
| 4 PETRAITIS' SPEC. OV. | 11 PETRAITIS' NICHE BREADTH |
| 5 PETRAITIS' GEN.ADJ.OV. | 12 PROPORTIONAL SIMILARIT Y |
| 6 PROPORTIONAL SIMILARITY | 13 SMITH'S NICHE BREADTH |
| 7 SMITH'S INDEX | 14 EXIT |

1

OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

OVERLAP HURLBERT'S INDEX

ROW/COL	1	2
1	2.41993	1.19035
2	1.19035	2.31398

PAIRWISE INDEX

SINGLEWISE INDEX

- | | |
|---------------------------|-----------------------------|
| 1 HURLBERT'S INDEX | 8 LLOYD'S PATCHINESS |
| 2 COMPETITION COEFF. | 9 LLOYD'S MEAN DEMAND |
| 3 COOCCURRENCE COEFF. | 10 HURLBERT'S NICHE BREADTH |
| 4 PETRAITIS' SPEC. OV. | 11 PETRAITIS' NICHE BREADTH |
| 5 PETRAITIS' GEN.ADJ.OV. | 12 PROPORTIONAL SIMILARIT Y |
| 6 PROPORTIONAL SIMILARITY | 13 SMITH'S NICHE BREADTH |
| 7 SMITH'S INDEX | 14 EXIT |

2

OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

COMPETITION COEFFICIENT (LEVINS' INDEX)

ROW/COL	1	2
1	1.00000	.897559
2	.281918	1.00000

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

3
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

RATHKE'S COOCCURRENCE COEFFICIENT (INTERSPECIFIC CROWDING)

ROW/COL	1	2
1	178.647	160.347
2	87.8755	311.706

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

6
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

PROPORTIONAL SIMILARITY INDEX (PS)

ROW/COL	1	2
1	1.00000	.346709
2	.346709	1.00000

TEST Z FOR EACH PS INDEX

ROW/COL	1	2
1	50000.0	-4.12932
2	-3.78258	50000.0

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

7
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

SMITH' OVERLAP INDEX (FT)

ROW/COL	1	2
1	1.00000	.712714
2	.712714	1.00000

TEST CHI-SQUARE FOR EACH FT INDEX

ROW/COL	1	2
1	.000000	576.870
2	1052.62	.000000

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

8
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

LLOYD'S PATCHINESS INDEX (INTRASPECIFIC CROWDING)

ROW/COL	2	1
1	2.31398	2.41993

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

9
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

LLOYD'S MEAN DEMAND (INTRASPECIFIC CROWDING)

ROW/COL	1	2
1	178.647	311.706

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

10
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

HURLBERT'S NICHE BREADTH (B')

ROW/COL	1	2
1	.413236	.432156

TEST CHI-SQUARED FOR HURLBERT'S NICHE BREADTH
Degrees of freedom = 2

ROW/COL	1	2
1	356.401	601.802

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

11
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

PETRAITIS' NICHE BREADTH

ROW/COL	2	1
1	.476933	.630746

TEST U FOR PETRAITIS' NICHE BREADTH
Test U has chi-squared distribution. Degrees of freedom = 2

ROW/COL	2	1
1	678.188	231.348

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

12
OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

PROPORTIONAL SIMILARITY (PS) AS NICHE BREADTH

ROW/COL	2	1
1	.444516	.619639

TEST Z FOR PROPORTIONAL SIMILARITY INDEX (PS)

ROW/COL	2	1
1	-1.20880	1.89545

C:\jovniche
 INPUT MATRIX NAME
 bombi
 CHOOSE THE RESOURCE STATE ABUNDANCE PARAMETER

- 1 ALL ABUNDANCES ARE EQUAL
- 2 ABUNDANCES HAVE BE READ FROM AN EXTERNAL VECTOR
- 3 ABUNDANCES ARE TOTALS OF VALUES FOR EACH RESOURCE

1
 INPUT FORMAT (IF BLANK FREE FORMAT)

N.ROWS, N.COLUMNS
 4,4
 ARE THE RESOURCES ON THE ROWS ? (Y/N)
 n

ABUNDANCE OF RESOURCES STATES

	1	2	3	4
	1.0000	1.0000	1.0000	1.0000

TOTALS OF INDIVIDUALS

	1	2	3	4
	1356.0	4484.0	1129.0	360.00

TOTAL OF ABUNDANCE RESOURCES = 4.000

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITIDN COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

13
 OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

SMITH'S NICHE BREADTH (FT)

ROW/COL	2	1
1	.768398	.898672

TEST CHI-SQUARED FOR SMITH'S NICHE BREADTH
 Degrees of freedom = 2

ROW/COL	2	1
1	848.590	203.467

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARIT Y
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

5
 OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

PETRAITIS' GENERAL OVERLAP ADJUSTED ACCORDING TO SMITH (GO-adj)

ROW/COL	1	2	3	4
1	1.00000	.729155	.294891	.565836
2	.729155	1.00000	.872952	.970035
3	.294891	.872952	1.00000	.860491
4	.565836	.970035	.860491	1.00000

14

PAIRWISE INDEX	SINGLEWISE INDEX
1 HURLBERT'S INDEX	8 LLOYD'S PATCHINESS
2 COMPETITION COEFF.	9 LLOYD'S MEAN DEMAND
3 COOCCURRENCE COEFF.	10 HURLBERT'S NICHE BREADTH
4 PETRAITIS' SPEC. OV.	11 PETRAITIS' NICHE BREADTH
5 PETRAITIS' GEN.ADJ.OV.	12 PROPORTIONAL SIMILARITY
6 PROPORTIONAL SIMILARITY	13 SMITH'S NICHE BREADTH
7 SMITH'S INDEX	14 EXIT

4
 OUTPUT INDICES FILE NAME (IF BLANK NOT SAVED)

PETRAITIS' SPECIFIC OVERLAP INDEX (SO)

ROW/COL	1	2	3	4
1	1.00000	.509985	.594360E-01	.358911
2	.384728	1.00000	.574310	.911518
3	.107176	.736156	1.00000	.736300
4	.226102	.902313	.675244	1.00000

Do you wish to have the interactive computation
 of the log-likelihood ratio, W? (Y/N)
 y
 It tests the hypothesis that specific overlap (SO) by
 species I onto sp. K is greater than overlap of sp. I onto sp. M.
 Give I,K and M (all zeros to go out)
 1,2,3
 SO 1 2 compared with SO 1 3 ----> Test W = 2914.7
 Give I,K and M (all zeros to go out)
 0,0,0

TEST U FOR EACH SPECIFIC OVERLAP INDEX

Test U has chi-squared distribution. Degrees of freedom = 3

ROW/COL	1	2	3	4
1	.000000	1826.19	7655.58	2778.94
2	8566.40	.000000	4973.53	830.832
3	5042.75	691.654	.000000	691.213
4	1070.47	74.0114	282.730	.000000

PETRAITIS' GENERAL OVERLAP (GO) = .8443107

TEST V FOR GENERAL OVERLAP INDEX = 2480.6

Test V has chi-squared distribution. Degrees of freedom = 9

MINIMUM VALUE FOR GO (GO-min) = .3503067

ADJUSTED VALUE FOR GO (GO-adj) = .7603649

Program POSTDU

This program was extracted from Anderberg's library (1973) and rearranged for new aims . Original data are ordered according to any sequence, for instance the one obtained in a dendrogram. Clusters are identified by simply stating the number of data units in each cluster, say N1, N2 and so on. Thus the first N1 units in the sequence list are in the first cluster, the next N2 units in the second cluster and so on. In the output each cluster is described by its data units, their scores on all variables and, for each variable, some statistics such as average, standard deviations and other useful values such as total, frequency, minimum value and maximum value. All these values are saved if requested. The tables of minimum and maximum values are needed as input of programs HYPERV and OVERLAP to compute community niches.

INPUT

The program POSTDU requires as input:

- a) - the name of the input table.
- b) - the name of the sequence file of the data units (relevés or other community samples); if blank, the sequence is unchanged, if equal to 'K' the sequence enters from keyboard.
- c) - the file name of the labels of the columns ; if blank, the program gives numeric labels.
- d) - the file name of the labels of the rows; if blank, the program gives numeric labels.
The length of labels is 20 characters for data units and 8 characters for variables.
- e) - number of rows, number of columns and number of clusters.
- f) - indication if the elaboration is to be done according to the sequence of rows (R) or of columns (C).
- g) - input format of the table; if blank, the table is read in free format.
- h) - the new sequence of data units if the input in point (b) is 'K'.

- i) - the number of data units for each cluster if the number of clusters is greater than 1.
- 1) Now, the program requires some output table names for the various values and statistics computed for each cluster. If the given name is blank, the new table for that statistic is not saved. The required file names are:
 - 1) - file name for the average values table; this table is saved with format (10G10.3).
 - 2) - file name for the frequency table; this table is saved with format (20I4)
 - 3) - file name for the standard deviations values; this table is saved with format (10G10.3)
 - 4) - file name for total values tables; this table is saved with format (10G10.3)
 - 5) - file name for minimum values table; this table is saved with format (10F10.3). This output will be needed for HYPERV and OVERLAP programs.
 - 6) - file name for maximum values table; this table is saved with format (10F10.3). This output will be needed for HYPERV and OVERLAP programs.

In all the output tables the community or species niches are described on the rows and the variables on the columns, independently of the input arrangement.

EXAMPLES

An example of input and output is reported below: the input table (Tab. 7) is taken from Lagonegro and Feoli (1985); in it 20 vegetation types (individuated by Poldini, 1982) are described on the basis of the Landolt's ecological indicators (mean values for each type). The cluster analysis allowed to individuate 5 groups of vegetation types (Feoli, Ganis and Poldini, 1988). Program POSTDU calculates the minimum and the maximum values for each ecological indicator value for each group.

GROUPS	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Unidity	1.76	2.07	1.90	2.30	1.96	2.45	2.44	2.34	2.47	2.61	2.69	2.64	2.77	2.82	2.92	2.65	2.68	2.40	2.13	2.03
Ph	3.84	3.72	3.91	3.57	3.68	3.42	3.20	3.60	3.52	3.33	3.38	3.10	3.43	3.32	3.37	3.50	3.41	3.64	3.56	3.68
Nutrients	2.28	2.55	2.22	2.46	2.32	2.54	2.45	2.45	2.54	2.62	2.69	2.62	2.87	2.91	3.01	2.64	2.73	2.53	2.27	2.19
Humus	2.90	3.10	2.94	3.10	3.07	3.27	3.28	3.28	3.26	3.37	3.38	3.39	3.44	3.46	3.46	3.32	3.40	3.21	3.05	2.99
Dispersion	3.12	2.95	2.81	3.37	3.17	3.49	3.54	3.32	3.53	3.58	3.61	3.63	3.68	3.66	3.57	3.45	3.49	3.25	3.04	2.83
Light	3.06	2.98	3.16	2.96	3.05	2.82	2.89	2.83	2.80	2.66	2.65	2.66	2.46	2.41	2.35	2.72	2.53	2.86	3.06	3.17
Temperature	4.71	4.46	4.02	4.16	4.29	3.89	3.77	3.84	3.78	3.73	3.87	3.77	3.80	3.64	3.54	3.51	3.50	3.58	3.71	3.62
Continentalty	2.60	2.70	3.25	2.85	2.95	2.84	2.83	3.04	2.90	2.84	2.67	2.65	2.60	2.68	2.70	2.94	2.87	3.09	3.19	3.24

Tab. 7 - Vegetation types described on the basis of the Landolt's indicators.

GROUPS	I	I	I	II	II	II	II	III	III	III	III	III	IV	IV	IV	IV	IV	V	V	V
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
PHANER. CESP.	37	34	33	39	44	42	28	53	60	51	55	22	43	47	40	46	33	27	40	36
PHANER. SCAP.	10	5	5	13	11	20	22	12	26	26	20	22	24	29	28	13	23	10	18	18
PHANER. LIAN.	11	6	3	11	10	6	6	5	8	8	7	7	9	10	7	4	8	4	3	0
CHAMAEPH. REPT.	0	0	0	0	0	0	0	1	2	1	1	3	5	2	3	0	1	0	1	0
CHAMAEPH. SUPP.	0	1	7	7	13	5	8	7	7	3	0	4	2	0	0	2	1	2	20	20
CHAMAEPH. FRUT.	0	0	0	0	0	1	4	0	0	1	0	1	0	0	0	4	1	2	5	5
THEROPHYTE SCAP.	0	3	0	2	2	3	5	0	2	2	3	5	0	0	0	0	0	0	3	1
GEOPHYTE RAD.	0	0	0	3	1	1	0	3	4	3	5	2	3	2	1	0	0	3	0	0
GEOPHYTE BULB.	2	4	3	0	1	5	1	9	8	5	13	7	15	13	8	4	6	7	6	8
GEOPHYTE RHIZ.	6	7	16	17	25	42	23	47	36	32	43	37	44	57	62	35	61	11	20	21
HEMICR. CESP.	4	7	15	17	16	16	32	24	25	25	24	21	18	15	12	17	19	20	22	26
HEMICR. REPT.	0	0	0	1	0	3	2	2	2	5	3	4	6	6	3	1	4	0	1	2
HEMICR. SCAP.	3	1	42	37	25	60	74	55	58	58	45	60	51	67	57	65	77	41	48	48
HEMICR. ROS.	1	0	6	10	6	15	15	10	8	8	11	9	15	12	15	2	11	1	5	5
MANOPHANEROPHYTE	16	15	10	14	16	9	4	14	18	11	11	7	15	8	8	14	10	10	15	14

Tab. 8 - Vegetation types described on the basis of the life-growth forms.

```

poptdu
INPUT TABLE FILE NAME
ecol
INPUT SEQUENCE FILE NAME (IF BLANK, NO CHANGE)
      (IF 'K' FROM KEYBOARD)

COLUMNS LABELS FILE NAME (IF BLANK, NO LABELS)
lab.e
ROWS LABELS FILE NAME (IF BLANK, NO LABELS)
ie
ROWS,COLUMNS, NUMBER OF CLUSTERS (MAX 50)
0,20,5
ELAB. ACCORDING TO NEW ROWS SEQUENCE(R) OR COLUMNS(C)
c
INPUT FORMAT (IF BLANK, FREE FORMAT)

N.OF ENTITIES FOR EACH CLUSTER
3,4,5,5,3
FILES NAMES FOR THE FOLLOWING VALUES COMPUTED FOR
EACH CLUSTER - IF BLANK THE VALUES ARE NOT SAVED

1 FILE NAME FOR THE AVERAGE VALUE (10G10.3)

2 FILE NAME FOR THE FREQUENCIES (20I4)

3 FILE NAME FOR STANDARD DEV. VALUES (10G10.3)

4 FILE NAME FOR THE TOTAL VALUES (10G10.3)

5 FILE NAME FOR THE MINIMUM VALUES (10F10.3)
min.e
6 FILE NAME FOR THE MAXIMUM VALUES (10F10.3)
max.e

```

CLUSTER 1 CONTAINING 3 DATA UNITS.

DATA UNITS	ID	SCORES ON VARIABLES							
		UMIDITY	pH	NUTRIENT	HUMUS	DISPERSI	LIGHT	TEMPERAT	CONTINEN
Releve 1	1	1.76	3.84	2.28	2.90	3.12	3.06	4.71	2.60
Releve 2	2	2.07	3.72	2.55	3.10	2.95	2.98	4.46	2.70
Releve 3	3	1.90	3.91	2.22	2.94	2.81	3.16	4.02	3.25
MINIMUM VALUE		1.76	3.72	2.22	2.90	2.81	2.98	4.02	2.60
MAXIMUM VALUE		2.07	3.91	2.55	3.10	3.12	3.16	4.71	3.25
MEANS		1.91	3.82	2.35	2.98	2.96	3.07	4.40	2.85
STANDARD DEVIATIONS		.127	.785E-01	.144	.864E-01	.127	.736E-01	.285	.286
FREQUENCIES		3	3	3	3	3	3	3	3
TOTALS		5.73	11.5	7.05	8.94	8.88	9.20	13.2	8.55

Program SPRANG

Program SPRANG prepares the minimum and the maximum environmental matrices for each species or for each character state of species. It reads two or three matrices, the first describing the relevés by the ecological variables, the second describing the relevés by species and the third describing the species by character states, e.g. morphological ones.

For each species, present at least 3 times in the data table, the minimum and maximum values of all ecological factors are extracted; the same procedure is used for the construction of the minimum and maximum environmental data matrices related to the character states. Also in this case only the states present at least 3 times are considered.

The two output matrices of SPRANG can be read by HYPERV and OVERLAP programs.

Program SPRANG optionally prepares output that can be read by any program for discriminant analysis in order to test and visualize the intersection between the species or the characters on the basis of the ecological data of the relevés in which they are present.

INPUT

Program SPRANG requires as input:

- a) - option for choosing:
 - 1) input preparation for HYPERV and/or OVERLAP programs
 - 2) input preparation for DISCRIMINANT ANALYSIS
- b) - option indicating the matrices in input:
 - 1) environmental and species matrices
 - 2) environmental, species and character states matrices
- c) - input file name of the table of relevés described by species; species must be in the rows and relevés in the columns.
- d) - number of rows (species) and number of columns (relevés) in the matrix in (c).
- e) - the input file name of the table of the species described

by some characters (species must be in the rows and characters in the columns) if in point (b) the chosen option is 2.

- f) - number of rows (species) and number of columns (characters) in the table in (e).
- g) - input file name of the table of the releves described by the environmental data; environmental variables must be in the rows and releves in the columns.
- h) - number of rows (environmental data) and number of columns (releves) of the table in (g).
- i) - the input file name of the species characters labels (length of 20 chars. maximum; if blank the labels are not read) if in point (b) the chosen option is 2.
- l) - input file name of the environmental variables labels; these labels can have a length of 8 chars. maximum. If blank, the labels are not read.
- m) - input format of the table read in (c); if blank, it is read in free format.
- n) - input format of the table read in (e); if blank, it is read in free format.
- o) - input format of the table read in (g); if blank, it is read in free format.
- p) - the output file name for the minimum environmental values; output format for this table is (10F10.3) (the species or species characters are written in the rows and the environmental variables in the columns) if in point (a) the chosen option is 1.
- q) - the output file name for maximum ecological values; the output format of this table is (10F10.3) if in point (a) the chosen option is 1. This table and the one in point (15) are read by HYPERV and OVERLAP programs.
- r) - the output file name for the data set to be submitted to discriminant analysis if in point (a) the chosen option is 2. The output format of this table is (10F10.3). Only if in point (b) the chosen option is 1, the value of each species is printed as the last value in each row of the output table.

EXAMPLE

An example of input and output is reported below; the program reads Tab. 7 already described in the explanation of program POSTDU and Tab. 8 in which 20 vegetation types are described by the life-growth forms. For each life-growth form the minimum and maximum value for each ecological variable are found.

```
C:\PAOLA>type minsp
      CHOOSE OPTION:
1 INPUT PREPARATION FOR Hyperv OR Overlap PROGRAMS
2 INPUT PREPARATION FOR Discriminant Analysis
1
      HAVE YOU:
1 ENVIRONMENTAL AND SPECIES MATRICES?
2 ENVIRONMENTAL, SPECIES AND SPECIES CHARACTERS MATRICES
1
SPECIES TABLE NAME
biol
N. OF ROWS (=SPECIES), N. OF COLUMNS OF biol

15,20
ENVIRONMENTAL DATA TABLE NAME
ecol
N. ROWS (=ENVIR. VARIABLES), N. COLUMNS OF ecol

8,20
SPECIES LABELS (MAX 20 CHARS.) FILE NAME
      (IF BLANK, NO LABELS)

fb
ECOLOGICAL VARIABLES LABELS FILE NAME (MAX 3 CHARS.)
      (IF BLANK, NO LABELS)

ie
INPUT FORMAT OF biol          ( IF BLANK, FREE FORMAT)

INPUT FORMAT OF ecol         ( IF BLANK, FREE FORMAT)

OUTPUT FILE NAME FOR MINIMUM VALUES (IOF10.S)
minsp.e
OUTPUT FILE NAME FOR MAXIMUM VALUES (IOF10.S)
maxsp.e
```

MINIMUM AND MAXIMUM VALUES OF ECOLOGICAL VARIABLES FOR EACH SPECIES

			1	2	3	4	5	6	7	8
			UMIDITY	pH	NUTRIENT	HUMUS	DISPERSI	LIGHT	TEMPERAT	CONTINEN
1	1 PHANER. CESP.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
2	2 PHANER. SCAP.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
3	3 PHANER. LIAN.	MIN	1.760	3.100	2.220	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.160	4.710	3.250
4	4 CHAMAEPH. REPT.	MIN	2.130	3.100	2.270	3.050	3.040	2.350	3.500	2.600
		MAX	2.920	3.600	3.010	3.460	3.680	3.060	3.870	3.190
5	5 CHAMAEPH. SUFF.	MIN	1.900	3.100	2.190	2.940	2.810	2.460	3.500	2.600
		MAX	2.770	3.910	2.870	3.460	3.680	3.170	4.460	3.250
6	6 CHAMAEPH. FRUT.	MIN	2.030	3.100	2.190	2.990	2.830	2.530	3.500	2.650
		MAX	2.680	3.680	2.730	3.400	3.630	3.170	3.890	3.240
7	7 THEROPHYTE SCAP.	MIN	1.960	3.100	2.190	2.990	2.830	2.650	3.620	2.650
		MAX	2.690	3.720	2.690	3.390	3.630	3.170	4.460	3.240
8	8 GEOPHYTE. RAD.	MIN	1.960	3.100	2.320	3.070	3.170	2.350	3.540	2.600
		MAX	2.920	3.680	3.010	3.460	3.680	3.050	4.290	3.090
9	9 GEOPHYTE. BULB.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
10	10 GEOPHYTE. RHIZ.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
11	11 HEMICR. CESP.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
12	12 HEMICR. REPT.	MIN	2.030	3.100	2.190	2.990	2.830	2.350	3.500	2.600
		MAX	2.920	3.680	3.010	3.460	3.680	3.170	4.160	3.240
13	13 HEMICR. SCAP.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
14	14 HEMICR. ROS.	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250
15	15 NANOPHANEROPHYTE	MIN	1.760	3.100	2.190	2.900	2.810	2.350	3.500	2.600
		MAX	2.920	3.910	3.010	3.460	3.680	3.170	4.710	3.250

Minimum values table is on file mins0.e

Maximum values table is on file maxs0.e

Number of considered species = 15

References

- Abrams, P. 1980. Some comments on measuring niche overlap. *Ecology* 61(1) : 44-49.
- Anderberg, M.R. 1973. *Cluster Analysis for Application*. Academic Press, New York.
- Burgman, M.A. 1988. The habitat volumes of scarce and ubiquitous plants: a test of the model of environmental control. *American Naturalist*, 133.
- Cody, M.L. 1974. *Competition and the structure of bird communities*. Princeton University Press, Princeton, NJ.
- Colwell, R.K. and Futuyma D.J. 1971. On the measurement of niche breadth and overlap. *Ecology* 52:567-576.
- Feinsinger P., Spears E.E. and Poole R.W. 1981. A simple measure of niche breadth. *Ecology* 62(1):27-32.
- Feoli, E. 1984. Some aspects of classification and ordination of vegetation data in perspective. *Studia Geobotanica* 4:23-24.
- Feoli, E., Ganis P. and Poldini L. 1988. Relazioni tra corologia e descrizioni tassonomiche e morfologiche della vegetazione dei boschi ad *Ostrya Carpinifolia* Scop. del Friuli Venezia-Giulia. (in press)
- Feoli, E., Ganis P. and Woldu Z. 1988. Community niche, an effective concept to measure diversity of gradients and hyperspaces. *Coenoses* 3(2) : 79-82.
- Giller, P.S. 1984. *Community Structure and the Niche*. Chapman and hall. London. New York.
- Holt, R.D. 1987. On the relation between niche overlap and competition: the effect of incommensurable niche dimensions. *oikos* 48:110-114.

- Horn, H. 1966. Measurement of "overlap" in comparative ecological studies. *American Naturalist* 100:419-424.
- Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. *Ecology* 59 (1): 67-77.
- Hurlbert, S.H. 1981. Ecological consequences of foraging mode. *Ecology* 62:991-999.
- Hurlbert, S.H. 1982. Notes on the measurement of overlap. *Ecology* 63(1): 252-253.
- Hutchinson, G.E. 1957. Concluding remarks. *Cold Spring Harbor Symp. Quant. Biol.* 22: 415-27.
- Hutchinson, G.E. 1978. *An Introduction to Population Ecology*. New Haven, Yale University Press.
- Lagonegro, M., Feoli E. 1985. *Analisi multivariata di dati. Manuale d'uso di programmi BASIC per personal computers*. Libreria Goliardica. Trieste.
- Levins, R. 1968. *Evolution in changing environments: some theoretical explorations*. Princeton Univ. Press, Princeton, New Jersey. 120 p.
- Lloyd, M. 1967. Mean crowding. *Journal of Animal Ecology* 36:1-30.
- Ludwig J.A., Reynolds J.F. 1988. *Statistical Ecology. A primer on methods and computing*. J. Wiley & Sons. New York.
- May, R.M. 1975a. *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton.
- May, R.M. 1975b. Some notes of estimating the competition matrix. *Ecology* 56: 737-741.
- Maurer, B.A. 1982. Statistical inference for Mac Arthur-Levins niche overlap. *Ecology* 63(6):1712-1719.

Petraitis, P.S. 1979. Likelihood measures of niche breadth and overlap. *Ecology* 60:703-710.

Petraitis, P.S. 1985. The relationship between likelihood niche measure and replicated tests for goodness-of-fit. *Ecology* 66(6):1983-1985.

Pianka, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53-74.

Pianka, E.R. 1981. Competition and niche theory. In: May, R.M. (ed.), *Theoretical ecology*. Second Ed., Sinauer Associates, Sunderland, MA, pp. 167-196.

Poldini, L. 1982. *Ostrya carpinifolia* rich woods and bushes of Friuli-Venezia Giulia (NE-Italy) and neighbouring territories. *Studia Geobotanica* 2:69-122.

Rathke, B.J. 1976. Competition and coexistence within a guild of herbivorous insects. *Ecology* 57:76-87.

Seber, G.A.F. 1973. *The estimation of animal abundance and related parameters*. C. Griffin, London, England.

Smith, E.P. 1982. Niche breadth, resources availability, and inference. *Ecology* 63(6): 1675-1681.

Smith, E.P. 1984. A note on the general likelihood measure of overlap. *Ecology* 65(1): 323-324.

Sugihara, G. 1986. Shuffled stichs: on calculating nonrandom niche overlaps. *The American Naturalist* 127:554-560.

INDEX

Introduction.....	3
Programs.....	4
Program HYPERV.....	5
Program OVERLAP.....	13
Program OVNICHE.....	16
Program POSTDU.....	31
Program SPRANG.....	35
References.....	39

GEAD-EQ reports already published:

- 1) M. Lagonegro - SBAFT : software per banche dati di flore territoriali (con listings in Fortran77 per OLIVETTI M 20 ed M 24 operanti sotto MS-DOS) - (1985) 101 pp.
- 2) P. Ganis - FUSAF : manuale per l'uso di programmi ad integrazione della banca dati SBAFT - (1985) 93 pp.
- 3) M. Lagonegro - Alcuni programmi in BASIC associati a semplici modelli per l'ecologia - (1986) 65 pp.
- 4) M. Lagonegro - Performances of a proximity index defined on a dendrogram table or a minimum spanning tree graph - (1986) 63 pp.
- 5) M. Scimone, P. Ganis & E. Feoli - Programmi BASIC per il calcolo di misure di diversita' in comunita' ecologiche - (1987) 34 pp.
- 6) M. Lagonegro & V. Hull - Models for simple aquatic system - Equations and programs - (1987) 93 pp.
- 7) D.W. Goodall, P. Ganis & E. Feoli - Probabilistic methods in classification: a manual for seven computer programs - (1987) 52 pp.
- 8) M. Lagonegro & V. Hull - Simulazione dei processi trofici degli ambienti acquatici - Manuale d'uso di un modello numerico con programmi in FORTRAN - (1989) 86 pp.

Stampa
Tito/Lito Astra
Via Cosulich, 9 — Trieste