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MEASURING CLIMATIC NICHE WIDTH AND OVERLAP OF VEGETATION TYPES OF CHINA

Chengyong Sun[1,2], Enrico Feoli[1,3] and Mario Lagonegro[3]

1 International Institute for Earth, Environmental and Marine Science and Technology, GGH, via Beirut 7, 34100 Trieste, Italy
2 Permanent address: Department of Ecology, Institute of Botany, Academia Sinica, Beijing 100044, China
3 Permanent address: Dipartimento di Biologia, Università degli Studi di Trieste, via Valerio 32/34, 34127 Trieste, Italy

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Abstract. Two approaches for niche width and overlap are compared based on vegetation types and climatic data from China. One approach applies the trajectory concept and uses a dynamic space, the other applies the hypervolume concept and uses both dynamic and static spaces. The two approaches give similar results when the hypervolume approach is coupled with the dynamical space. Procrustes analysis suggests that the trajectory approach can maintain high levels of information; it should be preferred for ordination purposes. Although the justification of the trajectory approach relies mainly on the fact that a true measure of niche overlap cannot be computed, the two approaches can be used in a complementary way to gain more information concerning the niche position and variability of vegetation types in environmental spaces.

Introduction

Even several decades after Hutchinson's introduction of the concept of niche as a portion of the multidimensional ecological space occupied by a species (Hutchinson 1959), few applications of this geometric concept can be found in niche studies. Recent reviews of niche overlap measures have been given in Neet (1989) and Yu and Orlóci (1990). Ganis (1989) offers a set of computer programs for measuring niche width and overlap based on various criteria. Feoli, Ganis and Zerihun (1988) extend the geometric concept of niche from species to community level. This is useful for a sound conceptual framework to study environmental variability in plant communities and to analyze the spatial relations of vegetation types in the environmental spaces. Sun and Feoli (1991a) has already investigated the climatic niches of vegetation types of China under the trajectory perspective in which, as a new aspect, niche width is measured by trajectory length. The niche overlap concept in conjunction with hypervolumes needs revision. We suggest to complement it with the concept of niche proximity which we estimate by an average Euclidean distance between trajectories. In this paper we compare the approach based on the trajectory concept with the traditional geometric approach based on the hypervolume.

Data

The data contain records from 644 meteorological station of China within the period 1951-1980. The stations are classified according to their location in 23 vegetation types (Table 1), grouped into 8 main phytoclimatic classes (Sun and Feoli 1991b). The data used are monthly averages of average daily temperature, maximum and minimum daily temperature, precipitation, wind speed, and evaporation.

Methods

The hypervolume of the community niche is computed for 2 shapes, an hyperbox and an hyperellipsoid. Two computational reference spaces are defined:

a) Space T (trajectory space) is obtained in principal component analysis (PCA) of climatic data which describe the meteorological station sites over 12 months. This involves 6 climatic variables (rows) and 7728 (644 x 12) monthly descriptions of the meteorological stations. The description is dynamic, based on 12 vectors. This means that in PCA space there are 12 points for each station. The niche includes the trajectories of the stations belonging to the same vegetation type.

b) Space S (static space) is obtained in PCA applied to the matrix describing the stations by 72 variables (6 x 12 as 72 rows and 644 columns) statically. In this, the description of each station is one vector whose elements are the average monthly values of the six climatic variables which define the T space. Each of the six T-space variables gives rise to 12 subvariables, such as average temperature in January, in February, etc. The niche includes all the stations of the same vegetation type with one point for each station. All reference spaces are defined by the PCA axes that account for at

Table 1. List of 23 vegetation types of China. Codes indicate the 8 main phytoclimatic classes described in Sun and Feoli (1991b): C11a - Cold-temperate and temperate coniferous forest and steppe; C11b - Alpine grassland; C12 - Temperate desert and steppe; C13a - Warm temperate deciduous broadleaved forest; C13b - Montane temperate steppe and high mountain subtropical evergreen broadleaved forest; C21 - Subtropical evergreen broadleaved forest; C22a - Tropical rain and monsoon rain forest; C22b - Subtropical montane evergreen broadleaved forest. The first column shows the original sequence of vegetation types according to Chang (1988).

	Code	Name
1	C11a	Cold Temperate Coniferous Forest
2	C11a	Temperate Coniferous-Broadleaved Mixed Forest, North Part
3	C11a	Temperate Coniferous-Broadleaved Mixed Forest, South Part
14	C11a	Temperate Steppe, North Part
16	C11a	Temperate Steppe, West Part
17	C11a	Temperate Desert, West Part
21	C11b	Tibet Alpine Meadow
22	C11b	Tibet Alpine Steppe
15	C12	Temperate Steppe, Loess Part
18	C12	Temperate Desert, East Part
19	C12	Temperate Desert, South Warm Part
4	C13a	Warm Temperate Deciduous Broadleaved Forest, North Part
5	C13a	Warm Temperate Deciduous Broadleaved Forest, South Part
20	C13b	Subtropical Evergreen Broadleaved Forest Western Mountains
23	C13b	Tibet Temperate Steppe Part
6	C21	Subtropical Evergreen Broadleaved Forest, North Part
7	C21	Subtropical Evergreen Broadleaved Forest, Middle North Part
8	C21	Subtropical Evergreen Broadleaved Forest, Middle South Part
9	C22a	Subtropical Evergreen Broadleaved Forest, South Part
12	C22a	Tropical Monsoon Rain Forest
13	C22a	Tropical Rain Forest West Part
10	C22b	Subtropical Evergreen Broadleaved Forest, Middle of the western part
11	C22b	Subtropical Evergreen Broadleaved Forest, Southwest Part

least 90% of the total variance. There are three axes in the first case and four in the second.

We used the following formulae to measure hypervolumes (H_i) and overlap between box-shaped niches (O_{ij}):

$$H_i = \prod_{k=1}^{n} (x_{ikmax} - x_{ikmin}) \qquad (1)$$

$$O_{ij} = \frac{H_{ij}}{\sqrt{H_i * H_j}} \qquad (2)$$

In these,

$$H_{ij} = [\prod_k (\text{min of max values} - \text{max of min values})_k]_{ij} \qquad (3)$$

n is the dimension of the climatic space, i-max and i-min are the maximum and minimum values of the trajectories of the i-th type. For each hypervolume we also computed the length of diagonal (D_i),

$$D_i = \sqrt{\sum_{k=1}^{n} (x_{ikmax} - x_{ikmin})^2} \qquad (4)$$

and intersections,

$$I_{ij} = \frac{D_{ij}}{\sqrt{D_i * D_j}} \qquad (5)$$

for all i,j where

$$D_{ij} = [\sum_k (\text{min of max values} - \text{max of min values})_k^2]_{ij}^{1/2}.$$

The intersections computed in (5) are transformed according to:

$$I'_{ij} = \max(I_{ij}) - I_{ij} \qquad (6)$$

In the case of niche with an ellipsoidal shape, the hypervolume is,

$$VE_{ij} = (\pi^{n/2}/\Gamma(\frac{n}{2} + 1))\prod_{i=1}^{n} a_i \qquad (7)$$

where

$$\Gamma(x) = \int_0^\infty t^{x-1}e^{-t}dt \qquad (8)$$

The intersection of hypervolumes (IE_{ij}) is:

$$IE_{ij} = (N(i,j) + N(j,i))/(N_i + N_j) \qquad (9)$$

where N(i,j) represents the numbers of objects in the ith group belonging to group j and N_i is the total numbers of objects belonging to group i. In the first case (a) we used the Ganis (1989) program and in the second (b), the program TANTIT (Feoli and Lagonegro 1992). The distances between niches on the basis of trajectories can be computed as in Sun and Feoli (1991a),

$$AD(i,j) = \frac{1}{12}\sum_{k=1}^{12} d_{ijk} \qquad (10)$$

where i and j are the ith and jth trajectories, 12 is the number of months and

$$d_{ijk} = [\sum_{a=1}^{n} (x_{ika} - x_{jka})^2]^{1/2} \qquad (11)$$

The latter is a Euclidean distance between two points corresponding to the kth month of the ith and jth trajectories. Symbol n refers to the number of PCA axes actually used.

To obtain ordinations of vegetation types on the basis of distances between niches, non metric multidimensional scaling (NMDS) is used as described in Kruskal (1964), Orlóci (1978) and Kenkel and Orlóci (1986). Procrustes analysis (Gower 1975, Digby and Kempton 1987) between the ordinations given by NMDS was computed by SYNTAX IV (Podani 1991).

Table 2. Average values of hypervolumes, diagonals, trajectory lengths and the length of main axis in ellipsoids (MT and MS) in vegetation types (N). Legend: VBT, DBT, and VTT -- hyperbox volume, diagonal of hyperbox and ellipsoid volume, respectively, in space T; VBS, DBS and VTS -- hyperbox volume, diagonal of hyperbox and ellipsoid volume, respectively, in space S; Tl -- trajectory length; MT, MS -- main axis length of ellipsoids in T and S space, respectively.

N	VBT(10^7)	DBT(10^3)	VTT(10^5)	VBS(105)	DBS	VTS(10^8)	Tl	MT	MS
1	106.59	82	336	2	.147	8	167	.213	.042
2	123.50	78	383	28	.302	34	166	.197	.063
3	157.45	74	640	47	.399	89	158	.173	.079
14	273.17	80	508	500	.667	416	170	.245	.124
16	252.65	75	307	13	.360	0	151	.296	.134
17	300.22	77	276	600	.729	719	160	.304	.170
21	27.85	43	156	253	.549	130	103	.109	.089
22	86.26	48	357	204	.494	76	103	.137	.152
15	130.13	61	255	711	.648	449	128	.184	.097
18	238.65	67	125	1661	.861	801	138	.269	.185
19	412.72	73	137	3027	.978	814	147	.302	.154
20	36.16	38	132	395	.562	412	89	.118	.090
23	81.51	43	505	64	.334	175	102	.125	.077
4	164.76	66	691	3229	1.084	415	148	.166	.141
5	84.63	57	435	1478	.890	558	131	.133	.155
6	23.50	51	96	229	.463	86	109	.125	.086
7	57.22	48	166	2965	.983	550	114	.134	.161
8	89.55	46	172	2877	1.000	826	111	.158	.143
9	81.28	42	88	813	.757	267	107	.174	.174
12	110.77	46	59	574	.643	447	114	.228	.129
13	99.15	41	186	1246	.941	1472	98	.218	.196
10	113.01	43	324	5423	.982	928	102	.192	.180
11	111.25	41	268	387	.511	424	102	.196	.132

A correlation analysis was performed between the different values of intersections and average Euclidean distances were computed between the trajectories (Sun and Feoli 1991). Correlations were also computed for trajectory length, hyperboxes diagonal, main axis length of the ellipsoids, and hypervolumes.

Results and conclusions

Table 2 describes the climatic niches of the 23 vegetation types (see Table 1) according to hypervolume, diagonal length, length of the main axis of ellipsoids and trajectory length. The correlations between these is given in Table 3. The minimum spanning tree (MST) for this matrix (Fig. 1) shows that maximal correlations occur within the same type of space (space T or space S) and that trajectory length is maximally correlated with the diagonal of the hyperboxes in space T. The correlations between the parameters computed in the two spaces are very low, however, the correlation between the overlap values in the two spaces are relatively high (Table 4). Also, the MST of this matrix (Fig. 2) indicates maximal correlations within the same space (T or S). The average distance between trajectories is more highly correlated with the overlap when estimated according to formula (6). The length of the longest axis of ellipsoids is highly correlated with the hypervolume and diagonal length of the hyperboxes in the same space.

Table 5 reveals a striking separation of the 23 vegetation types in both climatic spaces (T and S). The frequency distribution of the overlap values shows that in S space the niche separation of vegetation types is better than in T space. The Procrustes results are given in Table 6. It is clear from this that the ordination obtained by different overlap values and different spaces are very similar. The most different ordinations are those based on ellipsoids in T space and hyperboxes in S space. A remarkable conclusion is that ordinations based on overlap are very similar to the ordination obtained by NMDS based on the average Euclidean distance of the trajectories.

Another interesting result to be pointed out is that the correlation between niche width in S space and T space is never significant. Large hypervolume in S space may correspond to small hypervolume in T space and vice versa. The hypervolume computed in S space undergoes high variability and it has very low correlation with the trajectory length. This may be a conse-

Table 3. Pearson's product-moment correlation coefficients between the columns in Table 2 as identified.

	VBT	DPT	VTT	VPG	DPG	VTG	T length	MaxT	MaxS
VBT	1.00								
DPT	.69	1.00							
VTT	.14	.43	1.00						
VPG	.15	-.17	-.02	1.00					
DPG	.19	-.24	-.15	.82	1.00				
VTG	.23	-.25	-.28	.61	.78	1.00			
T length	.65	.98	.48	-.15	-.20	-.24	1.00		
MaxT	.88	.61	-.09	.05	.09	.29	.59	1.00	
MaxS	.29	-.25	-.26	.57	.79	.73	-.23	.33	1.00

Figure 1. Minimum spanning tree based on Table 3.

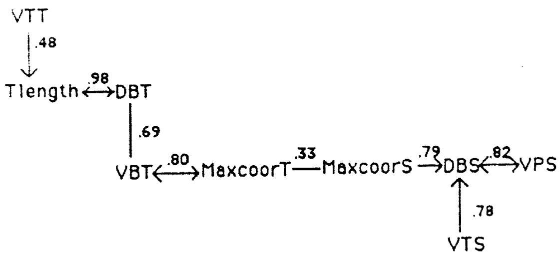

Table 4. Pearson's product-moment correlation coefficients between overlap matrices and the average distance between the trajectories. Legend: TT, BT -- overlaps based on ellipsoids and hyperboxes in space T; TS, BS -- overlaps based on ellipsoids and hyperboxes in space S; TD -- average distance between the trajectories.

	TT	TS	BT	BS	TD
TT	1.00				
TS	.70	1.00			
BT	.81	.80	1.00		
BS	.69	.96	.80	1.00	
TD	-.56	-.52	-.73	-.53	1.00

Figure 2. Minimum spanning tree based on Table 4.

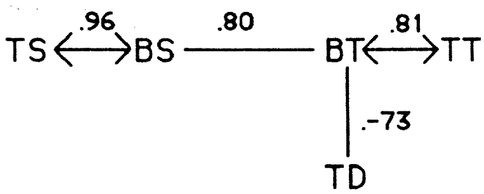

Table 5. Frequency distributions of overlap values in interval class of overlap. Abbreviations as in Table 4.

% Overlap (O)	TT	TS	BT	BS
O = 0	45	201	10	154
0<O< = 30	118	36	155	92
30<O< = 40	25	9	31	4
40<O< = 50	32	4	27	1
50<O< = 60	16	1	16	0
60<O< = 70	11	1	8	2
70<O< = 80	2	1	6	0
80<O< = 90	4	0	0	0
90<O< =100	0	0	0	0

Table 6. Results of Procrustes analysis to compare ordinations obtained by Nonmetric Multidimensional Scaling (NMDS) applied to the matrices of overlap in spaces S and T, and Euclidean distance between the trajectories. The values in the matrix are sum of squares. Abbrevations as in Table 4.

	BS	BT	TS	TT	TD
BS	0				
BT	.42	0			
TS	.42	.45	0		
TT	.76	.49	.63	0	
TD	.38	.33	.22	.37	0

quence of having used 4 dimensions for S space. It actually happens that on the fourth dimension some vegetation type has no variation left. The niche width may be very different if calculated in S or T spaces and if calculated as a hyperbox or hyperellipsoid. Differences, however, are smaller in T spaces than in S spaces. Niches with similar hypervolume may correspond to very different vegetation types, yet, the mutual position of the niches in the climatic space is almost constant irrespective of the type of space, S or T, and the shape assumed to compute the width and overlap. Procrustes analysis suggests that the trajectory approach maintains a high level of information, that is, the ordination based on trajectory distance is the most similar to the other ordinations. For this reason it is tempting to prefer the trajectory approach for ordination purposes. But the trajectory approach has a problem in that the niche overlap cannot be computed. Therefore, the two approaches should be used in a complementary way to maximize the information about the the niche position and variability of vegetation types in environmental spaces.

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