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Multivariate measure of niche overlap using canonical correspondence analysis[1]

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Abstract: A measure of multidimensional niche overlap based on species scores from canonical correspondence analysis is presented. This measure, N, is the amount of overlap using species scores as approximate weighted averages with respect to multidimensional niche breadth for the community given by $N = 0 - [(u_i - u_j)' V^{-1} (u_i - u_j) g |V|]$. Multidimensional niche overlap was calculated for a representative periphytic community from northern Lake Huron. Classification of species interaction or species similarities was accomplished using cluster analysis of the multidimensional niche overlap values. Two major groups of taxa showing similarities were evident based on niche influence. This influence produced a gradation of species found in clean waters to those found in varying degrees of pollution.
Keywords: niche overlap, canonical correspondence analysis, periphyton, diatoms, multidimensional, cluster analysis.

Résumé: Nous présentons ici une mesure du chevauchement de niches à dimensions multiples reposant sur les coordonnées des points des espèces obtenues d'une analyse canonique des correspondances. Cette mesure, N, est une évaluation du chevauchement à partir du pointage des espèces comme approximation des moyennes pondérées en regard de l'étendue des niches à dimensions multiples pour la communauté. Elle a été obtenue de l'équation suivante : $N = 0 - [(u_i - u_j)' V^{-1} (u_i - u_j) g |V|]$. Le chevauchement de niches à dimensions multiples a été calculé pour une communauté périphytique du nord du lac Huron. La classification de l'action réciproque ou des similitudes entre espèces a été effectuée par le biais d'une analyse de groupement à partir des valeurs de chevauchement de niches à dimensions multiples. Nous avons pu mettre en évidence deux groupes principaux de taxons montrant des similitudes sur la base de l'influence des niches. Cette influence a généré une gamme d'espèces, depuis celles qui sont associées aux eaux propres aux eaux polluées à divers degrés.
Mots-clés: chevauchement de niche, analyse canonique des correspondances, périphyton, diatomées, dimensions multiples, analyse de groupement.

Introduction

Species interactions and community organization are important determinants of how species coexist, survive and thrive. Community structure can be elucidated by examining niche breadth and overlap in terms of niche dimension and shape. Niche dimensionality refers to the number of environmental factors which separate species rather than all the biologically relevant influences in the environment (Levins, 1968). Niche shape refers to the degree of probability that species will interact in an n-dimensional environment; thus, this metric refers to various degrees of species' similarities.

A niche is all the ways an organism needs to adapt to its environment in order to survive (Pianka, 1978). Adaptation is a dynamic process in terms of resource availability, physical and chemical influences and biological interactions, all of which can be assessed spatially and temporally. To analyze niche on a multidimensional basis, ordination techniques such as principal components analysis (Rotenberry & Wiens, 1980) and discriminant analysis (Green, 1971; 1974; Harner & Whitmore, 1977; Dueser & Shugart, 1979; Van Horne & Ford, 1982) have been used. In both of these techniques, environmental gradients are inferred from analysis.

Other ordination techniques which may seem to be useful have restrictions that make them not entirely applicable to multidimensional niche analysis. To use canonical correlation analysis, the number of species cannot be approximately the same as the number of samples (ter Braak, 1990). Redundancy analysis (RA) is sensitive to scaling, being dependent on absolute abundance (ter Braak, 1990), and canonical scores are based on weighted sums (Jongman, ter Braak & van Tongeren, 1987). By using correspondence analysis, there is still the result that environmental gradients are inferred and the problem of the arch effect makes interpretation of all but the first eigenvector difficult (ter Braak & Prentice, 1988), whether or not detrending is used (Greenacre, 1984).

Alternatively, canonical correspondence analysis (CCA), based on unimodal species response curves, includes the relation between species and their environment in canonical space (ter Braak, 1986). Species scores, as approximate weighted averages, are useful descriptors of favorable habitat and niche space (Prentice & Cramer, 1990). Each constrained axis is a dimension and can be identified as a gradient influenced by an environmental variable represented as a vector in the ordination diagram. Eigenvalues represent measures of species separation or dispersion for each canonical axis (Jongman, ter Braak & van Tongeren, 1987).

The entire ordination is a representation of a sample of a larger population. Constrained eigenvalues represent fractions of the variance. The first constrained eigenvector determines the direction in which the sample from the population has maximum variation. That is, variances are not independent from eigenvector to eigenvector (Van Valen, 1978).

In the CCA ordination, scores of environmental variables influence the gradient of each canonical axis to a greater or lesser

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degree, but not completely. Therefore, each environmental vector is meaningful relative to every other environmental vector. The order of species scores for one environmental variable occurs relative to those for every other environmental variable.

Species axes are sample scores derived from species scores by weighted averaging. Environmental axes are sample scores regressed on environmental variables. In CCA, the weighted correlation matrix of ordination axes shows interdependence between species axes as a positive or negative correlation and independence between environmental axes as a value of 0.000. The result is an interdependence among species such that vectors of species scores over n-axes may be quantitatively compared.

The method presented will provide a multidimensional niche overlap measure of which the result will include quantitative representation of the species-environment relation as well as the degree to which species share tolerances to environmental conditions or interspecies relations. These values may be used in additional quantitative methods to assess species interaction or species similarities with respect to environmental tolerances. Multidimensional niche overlap values will be shown to be a useful way to assess relations between dominant as well as rare species in a community.

Methods

MULTIDIMENSIONAL NICHE OVERLAP

Niche space may be described by closed geometric curves or surfaces in n-dimensional space. That is, with the assumption of normality on a multivariate basis, niche boundaries may be described as probability ellipses for two dimensions, ellipsoids for three dimensions and hyperellipsoids for more than three dimensions. In CCA, the length of a multivariate probability ellipse in a given dimension is proportional to the standard deviation, which represents relative niche breadth on the given canonical function.

Niche overlap is the actual overlap of probability ellipses for two species. The exponent of the multivariate normal density function measures squared distance. The n-dimensional normal density function is:

$$f(x)=\frac{1}{(2\pi)^{n/2}|V|^{1/2}}e^{-(x-\mu)'V^{-1}(x-\mu)} \quad [1]$$

where V is the variance-covariance matrix, x is the canonical score and μ is the mean. Concentration ellipses generated from the estimate of the exponent of this function for two $n \times 1$ vectors (u_1 and u_2) of species scores on several constrained eigenvectors is:

$$(u_1-u_2)'\ V^{-1}(u_1-u_2) \quad [2]$$

Vectors of species scores are vectors of approximate weighted averages. Niche distance is obtained by using the generalized distance (Mahalanobis, 1948) between these vectors of weighted means. This modification is used since the distance measured is between species rather than between a species and the overall mean of the population (or habitat). The distance takes into account covariances between species. Generalization of the two species vector case becomes:

$$D_{ij}^2=(u_i-u_j)'\ V^{-1}(u_i-u_j) \quad [3]$$

where u_i and u_j represent vectors for species i and j, respectively. Overlap of species tolerance ranges is a probability because the generalized distance is distributed as $\chi_n^2(\alpha)$ with n degrees of freedom (Johnson & Wichern, 1992). Probability contours can then be defined as $(1 - \alpha)100$. That is, niche overlap values are probability values with respect to degree of overlap.

Distances calculated between species may not comprise a linear set (Bernstein, 1988). That is, the shortest distance may be factors of ten smaller than the longest distance. To bring the distances into a common scale, a scaling factor, g, is multiplied by the distances. In this way, no one pair of distances will be unduly influential. That is,

$$(u_i-u_j)'\ V^{-1}(u_i-u_j)\,g \quad [4]$$

For n-dimensions there are n-environmental variables affecting the species from a given number of samples. The variance-covariance matrix, V, of species canonical scores as approximate weighted averages per n-dimensions has n-variances and $1/2n(n - 1)$ potentially different covariances. A single numerical value which describes the variation expressed by this matrix is the determinant or generalized variance. The generalized variance is equal to the product of the individual species variances or squared niche breadths. Geometrically, for n-dimensions, the generalized variance is proportional to the square of the volume of the ellipsoid generated by the n-deviation vectors (Johnson & Wichern, 1992). That is,

$$(u_i-u_j)'\ V^{-1}(u_i-u_j)\ \alpha\,|V| \quad [5]$$

Conceptually, the generalized variance is a measure of multidimensional niche breadth (Carnes & Slade, 1982) of the community sampled. If the generalized variance is large, species are spread out or highly dispersed; if it is small, species are close together or not very dispersed.

The effect of multidimensional niche breadth on niche distances and the probability that species' tolerance ranges overlap in the n-dimensional space is:

$$N=0-\left[(u_i-u_j)'\ V^{-1}(u_i-u_j)\,g\,|V|\right] \quad [6]$$

where N is multidimensional niche overlap between species, 0 is the matrix of 1's, and g is a scaling factor. Each multidimensional niche overlap value, when multiplied by 100, represents the percentage of overlap between species affected by n-environmental variables or species interaction as measured at that time.

APPLICATION AND ILLUSTRATION

A small periphytic community from northern Lake Huron is used for illustration. On August 26, 1968, sixteen species of diatoms were identified from a shallow water sample from a locality known locally as Big Tub, Tobermory Lt., Ontario, Canada, 45° 13' N, 82°, 20' W. The abundances of *Cocconeis pediculus* Ehrenb., *Gomphonema olivaceum* var. *calcarea* (Cl.) Cl., other *Gomphonema. spp.*, *Rhoicosphenia curvata* (Kütz.) Grun. ex Rabh., *Diatoma vulgare* Bory., *D. tenue* var. *elongatum* Lyngb., *Cymbella prostrata* var. *auerswaldii* (Rabh.) Reim. in Patr. & Reim., *C. microcephala*

Grun., *Gomphoneis herculeana* (Ehrenb.) Cl., *Achnanthes minutissima* Kütz., other *Achnanthes. spp.*, *Fragilaria vaucheriae* var. *capitellata* (Grun.) Patr. in Patr. & Reim., *F. intermedia* Grun. in V. H., *F. pinnata* Ehrenb., *Cyclotella comta* (Ehrenb.) Kütz., and *Navicula sp.* #44 were used for analysis. At the time, identification of the morphologically variable *Cyclotella comta* was made according to Hustedt (1930). *Gomphonema spp.* and *Achnanthes spp.* represent groups of diatoms not identifiable at the species level. *Navicula sp.* #44 is indigenous to the Great Lakes and has been given a numerical designation by the Center for Great Lakes and Aquatic Sciences. A *Cocconeis pediculus* auxospore was also found. *Cocconeis pediculus* and *Gomphonema olivaceum* var. *calcarea* were the dominant forms accounting for 77.3 and 16.1% of the community, respectively. Abundances of periphytic samples in this location were incorporated into the species used for analysis (Stoermer, unpubl. data).

On July 23, 1969, physical and chemical parameters were measured in surface waters off shore from Tobermory Lt. Of the parameters measured, those used in this analysis were temperature, turbidity, conductivity, pH, alkalinity, total residue, organic nitrogen, ammonia, nitrate, total phosphorus, chloride and iron. During the summer of 1969, other samples at the surface were taken and the data were incorporated in the environmental parameters used for this analysis (unpubl. STORET data, Canada, 1969).

During the time period from summer 1968 to summer 1969, little historical data are available on water quality and algal abundances for northern Lake Huron. However, results of a comprehensive water quality study indicated that in the late 1960's to early 1970's, northern Lake Huron was found to be oligotrophic (Dobson, Gilbertson & Sly, 1974). Values reported for alkalinity and total phosphorus (Dobson, Gilbertson & Sly, 1974) are consistent with those used in this analysis. In addition, dissolved oxygen concentrations (Dobson, Gilbertson & Sly, 1974) are characteristic of water conditions reported for summer 1969 environmental data used in this study (unpubl. STORET data, Canada, 1969).

For the late 1960's, few publications exist on algal abundances in northern Lake Huron. However, in 1969, a listing of planktonic and periphytic algae was compiled of species found in the Great Lakes (Michalski, 1969). Qualitatively, for Lake Huron, those species in this 1969 listing (Michalski, 1969) are consistent with most of those species found in the 1968 periphytic composition and abundance used in our study.

The data sets from northern Lake Huron were chosen to illustrate the method of calculating multidimensional niche overlap values since the resultant matrix could be kept to a minimum. Presumably, any species-environmental data set could be used. However, since the number of species squared determines the size of the multidimensional niche overlap matrix, the need for a small species data set as an example of implementing this method should be evident.

To maintain a 16 by 16 multidimensional niche overlap matrix of 256 elements, from the data sets, a simulation was performed to generate species and environmental data for fourteen samples with data values randomly obtained. For each species abundance value, a range was determined based on relative abundance. For each environmental variable measurement, a range was determined based on variation for the season. In the past, simulations have been used in developing ecological methods (see, for example, LaFrance, 1972; Gauch & Whittaker, 1972).

Both RA and CCA were performed on the data. RA was used to determine the general relation between species and environmental variables. From CCA, species scores as approximate weighted averages were used to calculate multidimensional niche overlap. For illustration, to indicate interspecies relation or species similarity with respect to environmental tolerances, cluster analysis was used to classify multidimensional niche overlap values. However, other quantitative methods (such as multidimensional scaling) may be used to further characterize multidimensional niche overlap values.

Results

Since it was known that the assemblage occurred in a narrow range of environmental conditions, RA was performed to assess the relation between species and environmental variables. Constrained eigenvalues were 0.899, 0.040, 0.002 and 0.001 for constrained eigenvectors one, two, three and four, respectively. This represented 95.4, 99.6, 99.8 and 99.9 cumulative percent of the species-environment variation explained for the first four constrained eigenvectors. For RA performed with correction for species error variance, eigenvalues for the first four canonical axes were 0.210, 0.179, 0.138 and 0.116. Cumulative percentage of the species-environment variation explained was 21.0, 39.0, 52.7, and 64.3 for these first four contrained axes. The preliminary analyses indicate an important relation between species and environmental variables.

In CCA, *Cocconeis pediculus* and *Gomphonema olivaceum* var. *calcarea* were analyzed as passive, and therefore downweighted to zero to offset their high degree of influence. These two species were added to the ordination after CCA was performed using transition formulae (ter Braak, 1988). Constrained eigenvalues were 0.078, 0.064, 0.036 and 0.022 for axes 1, 2, 3 and 4, respectively. These eigenvalues represent the variation in the species data explained by the environmental variables and are considered to be informative; with eigenvalues numerically close, those which are less than 0.02 are not reliable (ter Braak, 1988). The cumulative percentage of species-environment variation explained was 32.2, 58.3, 73.1 and 82.0 for the first four canonical axes which was better than the results for RA with correction by the species error variance. Variation not explained by the environmental variables may be spatial since growth habit of these species involves variation of substrate type (Stoermer, 1980).

Species axes were interdependent and environmental axes were independent (Table I). Multidimensional niche overlap values were calculated (Table II). Most of the overlap values were high. In general, *Cocconeis pediculus*, *Gomphonema olivaceum* var. *calcarea*, *Cymbella microcephala*, *Achnanthes minutissima* and *Fragilaria intermedia* were found to overlap least with *Rhoicosphenia curvata* and

TABLE I. Weighted correlation matrix of species and environmental axes. Species axis-species axis correlations have small values; therefore, interdependence is indicated. Environmental axis-environmental axis correlations have zero values; therefore, independence is indicated. In addition, species axis-environment axis correlations are given

SPEC AX1	1.0000							
SPEC AX2	-0.0060	1.0000						
SPEC AX3	0.0026	-0.0179	1.0000					
SPEC AX4	-0.0004	0.0028	-0.0012	1.0000				
ENVI AX1	0.9996	0.0000	0.0000	0.0000	1.0000			
ENVI AX2	0.0000	0.9790	0.0000	0.0000	0.0000	1.0000		
ENVI AX3	0.0000	0.0000	0.9962	0.0000	0.0000	0.0000	1.0000	
ENVI AX4	0.0000	0.0000	0.0000	0.9999	0.0000	0.0000	0.0000	1.0000
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4

Gomphoneis herculeana. Cyclotella comta was found to overlap least only with *Rhoicosphenia curvata. Fragilaria vaucheriae* var. *capitellata, Fragilaria pinnata* and *Achnanthes spp.* were found to overlap least only with *Gomphoneis herculeana.* Cluster analyses were performed on multidimensional niche overlap values to classifiy similar species in a hierarchical fashion. Although results were the same using different algorithms, Euclidean distance, complete linkage clustering (farthest neighbor) was chosen for its clarity (Figure 1). Elucidation of niche influence on this classification of species will provide an understanding of the relation between similar species with respect to their tolerance of environmental conditions.

Discussion

From cluster analysis, niche influences based on tolerances to environmental conditions were evident in producing separation of species groups. The first major division assigns *Gomphoneis herculeana* and *Rhoicosphenia curvata* to one group and all other species to another group. Further division indicates that *Gomphoneis herculeana* and *Rhoicosphenia curvata* are joined by *Fragilaria vaucheriae* var. *capitellata, Gomphonema spp.*, and *Diatoma vulgare* as a definable group. Of the other group, *Navicula sp. #44, Fragilaria intermedia, F. pinnata, Gomphonema olivaceum* var. *calcarea, Cocconeis pediculus, Cymbella microcephala, Achnanthes spp.,* and *Diatoma tenue* var. *elongatum* form a subgroup. *Achnanthes minutissima, Cymbella prostrata* var. *auerswaldii,* and *Cyclotella comta* form the other subgroup with *C. comta* as an outlier.

The only centric diatom present, *Cyclotella comta,* is usually planktonic. This taxon, along with most of the pennates, is characteristically tolerant of pH levels greater than 7 and tolerate small amounts of salt (Patrick & Reimer, 1966; Lowe, 1974; Patrick & Reimer, 1975; Beaver, 1981). Only *Achnanthes minutissima* has a pH tolerance of 7 (Lowe, 1974). The presence of *Achnanthes minutissima* may be an indicator of high oxygen content in alkaline waters and is indifferent to calcium and iron (Beaver, 1981).

In addition, *Cocconeis pediculus, Cymbella microcephala* and *Cymbella prostrata* var. *auerswaldii* are found in oxygen rich waters and are calcium indifferent (Beaver, 1981). *Fragilaria pinnata* and *Fragilaria vaucheriae* are found in oxygen rich waters (Beaver, 1981). *Gomphonema olivaceum* var. *calcarea* and *Rhoicosphenia curvata* prefer alkaline waters (Patrick & Reimer, 1966; 1975; Beaver, 1981). *Gomphonema spp.* may be found in waters with low conductivity and low hardness (Patrick & Reimer, 1975). Some species of *Navicula* prefer iron-rich water (Patrick & Reimer, 1966). Alkalinity, pH, conductivity and chloride

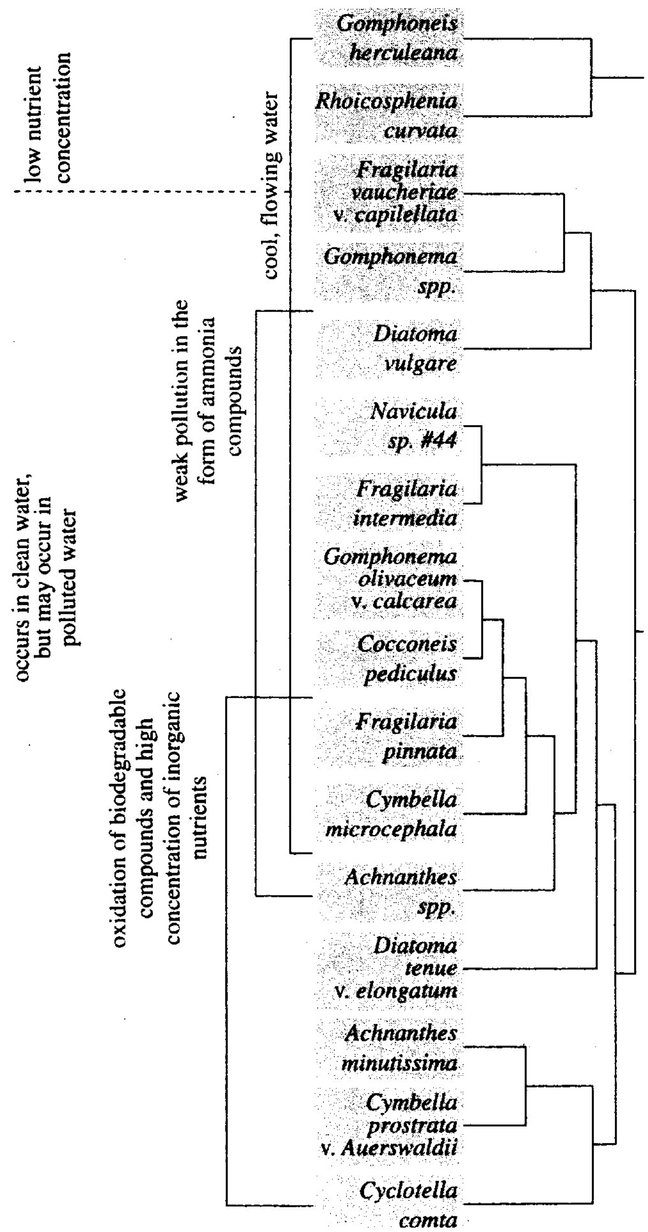

FIGURE 1. Complete linkage clustering of multidimensional niche overlap values for species. Largest group divisions indicate niche influences as tolerance of environmental conditions.

TABLE II. Multidimensional niche overlap values

	Cocconeis pediculus	*Gomphonema olivaceum v. calcarea*	*Rhoicosphenia curvata*	*Diatoma vulgare*	*Cymbella prostrata v. auerswaldii*	*Gomphoneis herculeana*	*Cymbella microcephala*	*Achnanthes spp.*	*Gomphonema spp.*	*Fragilaria vaucheriae v. capitellata*	*Achnanthes minutissima*	*Cyclotella comta*	*Diatoma tenue v. elongatum*	*Fragilaria intermedia*	*Fragilaria pinnata*	*Navicula sp. #44*
Cocconeis pediculus	1.0000	0.9866	0.7344	0.8950	0.7972	0.6967	0.9555	0.8977	0.7826	0.8577	0.8733	0.8385	0.8825	0.9802	0.9730	0.9495
Gomphonema olivaceum v. calcarea	0.9866	1.0000	0.6991	0.8424	0.8521	0.6116	0.9777	0.9177	0.8090	0.8706	0.9050	0.7931	0.8460	0.9368	0.9812	0.9414
Rhoicosphenia curvata	0.7344	0.6991	1.0000	0.5743	0.6481	0.6553	0.7355	0.8896	0.5817	0.4256	0.6789	0.4865	0.9125	0.7594	0.7835	0.7255
Diatoma vulgare	0.8950	0.8424	0.5743	1.0000	0.4173	0.4980	0.8046	0.6793	0.6279	0.6669	0.5635	0.6133	0.7336	0.9294	0.8415	0.7309
Cymbella prostrata v. auerswaldii	0.7972	0.8521	0.6481	0.4173	1.0000	0.6020	0.8722	0.8848	0.7706	0.8088	0.9181	0.6991	0.7804	0.6844	0.8165	0.8568
Gomphoneis herculeana	0.6967	0.6116	0.6553	0.4980	0.6020	1.0000	0.6242	0.5954	0.6058	0.6913	0.5462	0.7727	0.8627	0.7213	0.5668	0.7048
Cymbella microcephala	0.9555	0.9777	0.7355	0.8046	0.8722	0.6242	1.0000	0.9270	0.9085	0.8891	0.8506	0.6929	0.8846	0.8901	0.9519	0.8782
Achnanthes spp.	0.8977	0.9177	0.8896	0.6793	0.8848	0.5954	0.9270	1.0000	0.7469	0.6922	0.9142	0.6623	0.8949	0.8539	0.9543	0.9002
Gomphonema spp.	0.7826	0.8090	0.5817	0.6279	0.7706	0.6058	0.9085	0.7469	1.0000	0.8915	0.5897	0.4580	0.8225	0.6870	0.7328	0.6315
Fragilaria vaucheriae v. capitellata	0.8577	0.8706	0.4256	0.6669	0.8088	0.6913	0.8891	0.6922	0.8915	1.0000	0.7131	0.7493	0.7587	0.7683	0.7601	0.7817
Achnanthes minutissima	0.8733	0.9050	0.6789	0.5635	0.9181	0.5462	0.8506	0.9142	0.5897	0.7131	1.0000	0.8196	0.7479	0.8093	0.9126	0.9629
Cyclotella comta	0.8385	0.7931	0.4865	0.6133	0.6991	0.7727	0.6929	0.6623	0.4580	0.7493	0.8196	1.0000	0.7037	0.8375	0.7506	0.9203
Diatoma tenue v. elongatum	0.8825	0.8460	0.9125	0.7336	0.7804	0.8627	0.8846	0.8949	0.8225	0.7587	0.7479	0.7037	1.0000	0.8808	0.8517	0.8346
Fragilaria intermedia	0.9802	0.9368	0.7594	0.9294	0.6844	0.7213	0.8901	0.8539	0.6870	0.7683	0.8093	0.8375	0.8808	1.0000	0.9431	0.9260
Fragilaria pinnata	0.9730	0.9812	0.7835	0.8415	0.8165	0.5668	0.9519	0.9543	0.7328	0.7601	0.9126	0.7506	0.8517	0.9431	1.0000	0.9411
Navicula sp. #44	0.9495	0.9414	0.7255	0.7309	0.8568	0.7048	0.8782	0.9002	0.6315	0.7817	0.9629	0.9203	0.8346	0.9260	0.9411	1.0000

have approximately the same niche influence for all species and were not instrumental in defining niche differences.

The species in this assemblage were found in shallow water and subjected to some wave action. Those species which prefer cool, flowing waters are *Gomphonema olivaceum* and *Gomphoneis herculeana* (Patrick & Reimer, 1975) as well as *Rhoicosphenia curvata*, *Diatoma vulgare* and *Fragilaria vaucheriae* (Patrick & Reimer, 1966). *Fragilaria vaucheriae* var. *capitellata* (Patrick & Reimer, 1966) and *Gomphonema olivaceum* var. *calcarea* (Patrick & Reimer, 1975; Beaver, 1981) have been found in both standing and flowing waters. *Fragilaria intermedia* has been found in the plankton of river assemblages and is therefore tolerant of both standing and flowing waters (Krieger, 1927). From cluster analysis, these species form a group in which temperature and turbidity (as a proxy for flowing water) are the major niche influences. Alternatively, many of these species may be classified as shallow, littoral, wave-zone taxa (Kingston *et al.*, 1983). All of these species occur in temperatures from 0 to 15°C (Lowe, 1974). *Diatoma vulgare* does occur as a winter dominant (Beaver, 1981). Although *Cymbella prostrata* var. *auerswaldii* is found in streams (Lowe, 1974), cluster analysis reveals that this is not its primary niche influence on a multidimensional basis in this analysis (Figure 1).

Total phosphorus, ammonia, organic nitrogen and nitrate have varying degrees of niche influence on *Diatoma vulgare, Navicula sp. #44, Fragilaria intermedia, Gomphonema olivaceum* var. *calcarea, Cocconeis pediculus, Fragilaria pinnata, Cymbella microcephala, Achnanthes spp., Diatoma tenue* var. *elongatum, Achnanthes minutissima, Cymbella prostrata* var. *auerswaldii,* and *Cyclotella comta* (Figure 1). Various *Navicula* species, *Fragilaria intermedia, F. pinnata, Gomphonema olivaceum* var. *calcarea, Cocconeis pediculus, Diatoma vulgare,* and *Cymbella microcephala* (Lowe, 1974; Beaver, 1981) are influenced by weak pollution in the form of ammonia compounds. *Cocconeis pediculus* does occur in oligotrophic habitats (Stoermer, 1980).

Fragilaria pinnata, Cymbella microcephala, Achnanthes spp., Diatoma tenue var. *elongatum, Achnanthes minutissima, Cymbella prostrata* var. *auerswaldii,* and *Cyclotella comta* are influenced by complete oxidation of biodegradable compounds and found in habitats with high concentrations of inorganic nutrients (Lowe, 1974). *Achnanthes minutissma* is tolerant of nutrient enrichment, but found in oligotrophic habitats as well (Stoermer, 1980). Many of these taxa may be found in deep, cold, dark, more stable areas (Kingston *et al.*, 1983).

Fragilaria vaucheriae var. *capitellata* may be found in oligotrophic waters, and *Gomphoneis herculeana* may be found in undisturbed areas (Stoermer, 1980). *Cocconeis pediculus, Cyclotella comta, Diatoma tenue* var. *elongatum,* various *Navicula* species (Lowe, 1974), and *Diatoma vulgare* (Beaver, 1981) are found in both clean and polluted waters. Species tolerant of eutrophy are *Cymbella prostrata* (Stoermer, 1980), *Rhoicosphenia curvata, Diatoma vulgare, Fragilaria vaucheriae, Gomphomena olivaceum, Fragilaria pinnata,* and various *Navicula* species (Lowe, 1974; Beaver, 1981). *Diatoma tenue* var. *elongatum* is tolerant of heavy nutrient and chloride loadings (Stoermer, 1980). Given the environmental conditions, all the species have broad tolerance to pollution. However, there is a general gradation of species found in clean waters to those tolerant of varying degrees of pollution as indicated in cluster analysis (Figure 1).

The species in the assemblage analyzed are more similar than different since they were found in a narrow range of environmental conditions. From species scores in CCA, multidimensional niche overlap values were calculated. Cluster analysis of those values were useful in determining species similarities and exploring the fine differences among the interspecies relation with respect to environmental tolerances in this community. This multivariate method provides a way to include both dominant and rare species in analyses and determines species similarities with to respect to the environmental conditions that are influential. Essentially, by using species scores as "data", calculating covaried distance between these scores and rescaling of this to result in a probability value, this multidimensional niche overlap method is a useful means for analyzing interspecies relations.

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