ESTIMATION OF CHARACTER STRUCTURE CONVERGENGE (DIVERGENCE) IN PLANT COMMUNITIES: A NESTED HIERARCHICAL MODEL

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Abstract: We examine in this paper the notions of convergence and divergence as applied to the character structure of communities in comparative evolutionary studies. We assume that the character structure is nested hierarchical, as in the natural state, with the same fusion pattern, but with a potentially different complement of character set types in each community being compared. Estimates are derived for character structure convergence and divergence as partial sums of products and related partial correlations, corresponding to levels of the hierarchy and relating the pattern of character set types in pairs of communities. The significance of the estimates is tested based on confidence limits constructed in Monte Carlo simulation. It is shown that the partial correlation coefficients can detect both structural convergence and divergence of any complexity, just as they can identify the specific contribution of any character, simple or complex, to character structure convergence or divergence. The interpretation of the evolutionary significance of partial correlations can follow simple criteria. If the communities have no common species, significant partial correlations are manifesting past episodes of convergent (positive partial correlation) or divergent (negative partial correlation) evolution in similar environments; nonsignificant partial correlations indicate that the evolutionary path of the compared communities has not been convergent. Data from desert and boreal vegetation are analyzed to illustrate the method's application.

Introduction

The characters in which we are interested are adaptive. These characters enable the bearer organisms and indirectly the populations and communities of organisms, to exist in a given environment. Ordinarily, similar adaptations might be expected in similar environments, but it is conceivable that the character structure of plant communities may in fact diverge as a result of specific evolutionary processes (Peet 1978). Clearly, the distinction between convergent and divergent evolution based on the usual criteria, not involving quantitative measures, is ambiguous. This is because three quantitative conditions are involved which have to be evaluated: environmental similarity, character structure convergence or divergence, and overlap of species sets in the compared sites.

Although past work addressed the problem of basing evolutionary studies in our field on quantitative techniques (*e.g.*, Karr and James 1975), to our knowledge no comprehensive methodology has ever been put forward which might be used to objectively measure character structure convergence, divergence, or the lack of either of these, in communities. The lack of a suitable method gave the incentive that lead us to defining the objective of the present work, *i.e.*, to develop methods for application in comparative community studies with an evolutionary objective.

As we develop the topics in this paper, first we define character structure, character set type, and score matrix. Following this, we describe the basic model of the analysis, derive a measure of vergence, and a test criterion. Finally, we present examples involving synthetic and real data. Orlóci's Microsoft BASIC programs for the Macintosh microcomputer are available from him.

Character structure

We define the character structure of a community as a collection of character set types arranged in a logical order (Dale 1968), and a transformation on the collection which quantifies the pattern of the realized character set types within the collection. The character scheme which Dansereau (1957, p. 118) has used in community descriptions may serve as an initial example for such a collection and the transformation which Noy-Meir and Anderson (1971) applied examplifies such a transformation:

LIFE-FORM (TREE, SHRUB, HERB, ...)
 SIZE (TALL, MEDIUM, LOW)
  FUNCTION (DECIDUOUS, SEMIDECIDUOUS, ...)
   LEAF SIZE (LARGE, MEDIUM, SMALL)
    LEAF SHAPE (NEEDLE, SPINE, GRAMINOID, ...)
     LEAF TEXTURE (FILMY, MEMBRANEOUS, SCLEROPHYLL, ...)
      COVERAGE (SPARSE, DISCONTINUOUS, ...)
       ETC.

Many other nested hierarchical schemes are described in the literature, most notably by Ellenberg and Mueller-Dombois (1966, 1974), and Barkman (1979). These schemes serve well the purpose of community descriptions as parallel taxonomies, replacing or complementing a species-based taxonomy.

Character set type

Considering further the Dansereau scheme, we can observe that each character state on one level of the hierarchy is connected to the complete complement of character states on the next lower level. This is because the scheme is hierarchically nested. For example, a tree may be tall, medium or low; a tall tree may be deciduous, semideciduous, etc.; a deciduous tall tree may have large leaves, medium leaves, or small leaves; and so on. This orderly connectedness of the character states allows us to recognize unique pathways throught the hierarchy. For example, a tall three which is deciduous and has large leaves whose shape is oblong with a filmy structure having a discontinuous distribution on the ground is a unique pathway through Dansereau's character hierarchy. Such a path, to be referred to as a *character set type*, represents a nonbrunching chain of connected stems. All possible character set types need not occur in a specific study. If, however, two communities have an identical complement of character set types, real and potential, they are said to have achieved complete *structural convergence.* By the same token, communities having no character set types in common have complete *structural divergence.* Furthermore, communities having an identical character set but unrelated pattern of the character set types, are said to have reached neither structural convergence nor structural divergence. If two structurally convergent communities have no species in common, they may be considered as manifesting *convergent community evolution.*

It is a consequence of the quantitative measure, that convergence or divergence need not be complete to be recognized as such. Furthermore, convergence and divergence are character related properties, therefore both may characterize the same community pair, but with regard to different characters, so that convergence might be the case with some characters and divergence with some others, while still others may exhibit neither convergence nor divergence. As regards to convergent community evolution, the extent to which the species sets overlap should be considered.

We observe further regarding the Dansereau scheme, that it involves organismal characteristics that range from biological, such as life-form, to purely physical, such as plant cover or size. By no means is the scheme complete, but it has the flexibility to be expanded. How far should we go in expanding a given scheme? We believe that in comparative evolutionary studies, the character set should be broad to cover all aspects of organismal adaptation, including phenological, morphological, histological, and even biochemical characteristics. There is, of course, a limit to the number of characters that a study can possibly use. This limit depends on the user's resources to be spent on scoring and analyzing characters, the level of redundancy in the character set owing to shared variance and entropy (Orlóci 1978, Feoli, Lagonegro and Orlóci 1984, Orlóci and Kenkel 1985), and the level of manageable complexity in nesting characters in a logical and interpretable way. We might note in this regard that the number of character states matters. For example, with seven characters having 3, 3, 2, 3, 3, 3, 2 states respectively, the number of possible character set types is 972 (the product of the number of states). Many of the states might never occur under natural conditions. We plan to discuss the problem of character selection in more detail in a companion paper when character choice becomes critical to achieving the objectives.

Score matrix

Character schemes, such as Dansereau's which replace the species-based systems of vegetation description, may conceivably be applied in two basically different manners: (1) *character states* replace the species, (2) *character set types* replace the species. Under (1) a relevé of the community is a vector of cover/obundance estimates for individuals having been identified with a given character state. Under (2) the relevé is a *score matrix.* A score matrix has as many rows as there are character states in the set, and as many columns as there are character set types in the community. The last row of the score matrix is a cover/abundance vector **X** for the character set types. Having such a construction, the score matrices permit comparisons to be made between communities of different species compositions. Two examples are given in Table 1, one from a saguaro *(Carnegia giganteus)* community and the second from an euphorbia *(Euphorbia caudicifolia)* community. The characters have two states each in each matrix (tall, not tall; green, not green; etc.); only one state is shown for each character in the tables to save space.

Saguaro Desert	CST							Euphorbia Desert	CST						
1. Tall (T)	+	-	-	-	+	-	-		+	-	+	-	-	+	-
2. Green (G)	+	+	+	+	+	-	+		+	-	-	-	+	+	+
3. Spiny (S)	+	-	+	+	+	+	+		+	-	+	+	-	-	-
4. Fleshy (Fl)	-	-	+	-	+	+	+		+	-	-	-	-	-	-
5. Flat (Ft)	-	-	+	-	-	-	-		-	-	-	-	-	-	-
CAE	25	15	7	3	5	1	2		58	5	29	1	1	3	1

Table 1. Score matrices of two communities of stem succulents from Tucson. Arizona (Saguaro Desert) and Karachi, Pakistan (Euphorbia Desert). The matrices were extracted from much larger sets of data. See the description of details in the main text. Legend to symbols: CST - character set type. CAE - cover/abundance estimate.

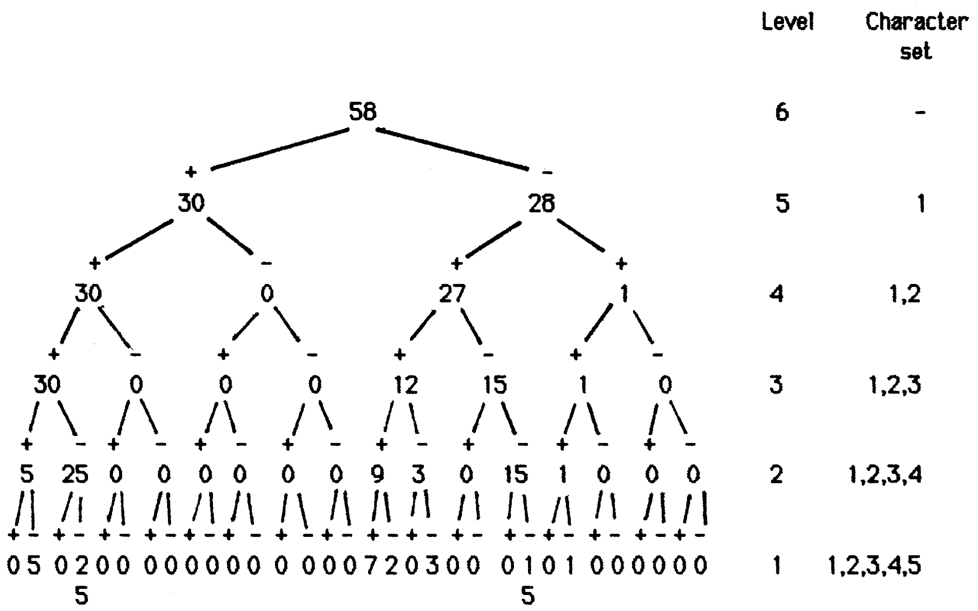

Fig. 1. Hierarchical character structure for the saguaro score matrix (Table 1). The numbers at the base and inside the figure are field estimates of cover abundance.

With m characters in the score matrix, a hierarchical character structure of m+1 levels is defined. The mth level is specific to character 1, the m-1st level is specific to the set of characters 1 and 2, the m-2nd level is specific to the set of characters 1, 2 and 3, and so forth. The number of branches on any given level of the hierarchy is determined by the number of character states. With binary characters, such as those in Table 1, the number of branches will be 1, 2, 4, 8, 16, etc. A character hierarchy is shown in Fig. 1. The cover/abundance values of the character set types are those of the saguaro matrix.

Analysis of score matrices

Unlike the methodologies that were described to analyze sets of conventional relevés (see monographs on the topic by Mueller-Dombois and Ellenberg 1974, Orlóci 1978, Feoli, Lagonegro, and Zampar 1982, Gauch 1982, Greig-Smith 1983, Pielou 1984), the analysis of character score matrices does not appear to have a worked methodology. Nevertheless, the nested models of other applications (Greig-Smith 1952, Noy-Meir and Anderson 1971, Orlóci 1971, Feoli, Lagonegro and Orlóci 1984) have direct relevance. The specific model to be examined involves the partition of the sums of squares and products into as many additive components as there are character levels in the hierarchy.

Partitioning sums of squares

The partitioning accords with the simple model

$$Q_A = Q_{1A} + Q_{2A} + \ldots + Q_{mA}$$

In this, 1 to m are labels for hierarchical level and A is a label for community. The Q quantities are sums of squares, such that $Q_{iA} = \sum n_i(X_{ijA}/n_i - \mu_A)^2 - \sum n_{i+1}(X_{(i+1)jA}/n_{i+1} - \mu_A)^2$. Symbol X_{ijA} signifies the cover/abundance of character set type j on level i of the character hierarchy in community A. μ_A symbolizes the mean of all X_{1jA}, and n_i is the number of stems (character states) fused to form a single stem on level i. n_i is the same value for all stems on a given level, irrespective of the community, as long as the same character set is used to describe it, and n_1 is the number of character set types, realized or unrealized in the collection. This number can be calculated as the product of the number of character states (see above). The summations are over k_i stems (j incremented by 1 from 1 to k_i in the first sum) and over k_{i+1} stems (j incremented by 1 from 1 to k_{i+1} in the second sum). In the case of binary characters, $k_{i+1} = k_i/2$. We shall use the symbol $(\mathbf{X}, \mathbf{O})_{iA}$ to designate the k_i cover/abundance values on level i. On level 1 in the saguaro community (Table 1, Fig. 1), $k_1 = 32$ and $(\mathbf{X}, \mathbf{O})_{1A}$ contains 32 elements, seven of which are other than zero. $(\mathbf{X}, \mathbf{O})_{2A}$ has 16 elements of which 6 are non-zero, and so on. Clearly, Q_{iA} is the sum of the sum of squares among the stems (character states) of level i within the stems (character states) of level i+1. In fact, Q_{iA} is the sum of squares specific to level i. The graph $Q_{1A}\ Q_{2A} \ldots Q_{mA}$ for level 1, 2, ..., m is a characteristic profile of the character score matrix, but it is not necessarily unique. The reason is that character score matrices of exact opposites (when such exists) have identical characteristic profiles with regard to sum of squares. Cross products and correlation coefficients form unique profiles. These are considered next.

Partitioning sums of products

That our problem is related to those encountered in pattern analysis should now be obvious. A pattern analytical phenomenon that Pielou (1969) has identified as the *lacunae effect* in Greig-Smith's pattern analysis, directly applies to our case. In the context of our problem, this translates into what we describe as the *score matrix reflection effect*. When two matrices are complete reflections, which can only happen if the character states are binary, the plus scores in the first matrix correspond to minus scores in the second matrix; the character structures are total opposites. To probe the extent to which this effect exists among stands, we examine the character score matrices in pairs. In the course of this examination, we partition the sums of cross poducts into as many additive components each as the number of levels in the character hierarchy. For two communities A and B, this partition yields m components,

$$Q_{AB} = Q_{1AB} + Q_{2AB} + \ldots + Q_{mAB}$$

of which the ith is defined by

$$\begin{aligned} Q_{iAB} &= S_{iAB} - S_{(i+1)AB} \\ &= \sum n_i(X_{ijA}/n_i - \mu_A)(X_{ijB}/n_i - \mu_B) - \\ &\quad \sum n_{i+1}(X_{(i+1)jA}/n_{i+1} - \mu_A)(X_{(i+1)jB}/n_{i+1} - \mu_B) \end{aligned}$$

Q_{iAB} is a sum of products specific to level (character) i. The summation are over all stems (j from 1 to k_i on level i and j from 1 to k_{i+1} on level i+1). The μs are the mean values on level 1 of the hierarchy A or B.

Partitioning the cover/abundance vector

A partition of sums of squares and products, among data types representing the qualitative and quantitative components of the cover/abundance vector, is also defined. To isolate the data types, we use the method of Williams and Dale (1962). Symbolically, $(\mathbf{X}, \mathbf{O}) = (\mathbf{M}, \mathbf{O}) + (\mathbf{X}\text{-}\mathbf{M}, \mathbf{O})$ where **M** is a set of as many replications of the mean of the non-zero values in $(\mathbf{X}, \mathbf{O})$ as the number of elements in **X**. For example, the saguaro hierarchy (A), level 1, has $(\mathbf{X}, \mathbf{O})_{1A} = (0\ 5\ 0\ 25\ \ldots\ 0)$. This vector has a purely qualitative component $(\mathbf{M}, \mathbf{O})_{1A} = (0\ 8.3\ 0\ 8.3\ \ldots\ 0)$ and purely quantitative component $(\mathbf{X}\text{-}\mathbf{M}, \mathbf{O})_{1A} = (0\ -3.3\ 0\ 16.7\ \ldots\ 0)$.

Measuring convergence and divergence

Regarding the properties of the measuring function, our requirements call for one which can detect convergence and also divergence. The partial correlation coefficient which we define as

$$r_{iAB} = Q_{iAB}/(Q_{iA}Q_{iB})^{1/2}, i = 1, \ldots, m$$

using the partial sums of squares and products Q which we defined above, has the desired properties. It has positive and negative values, depending on whether the character structures are divergent or convergent. A zero point signifies an uncorrelated (orthogonal) state of the character structures. We verified these properties in Monte Carlo experiments with artificial score matrices. To create a maximally divergent character structure, we constructed the exact opposite of the saguaro score matrix by changing the original + scores to − scores and the original − scores to + scores.

Correction factor for overlapping species sets

To correct for convergence or divergence, attributable to a shared flora, one may apply the correction factor $C_{AB} = (b+c)/(a+b+c)$ which has a zero value when the two stands are floristically identical. In this: *a* is the number of species shared by the two communities A, B; *b* is the number of species occurring in community A but not in B; and *c* is the number of species being present in community B but not in A. The degree of convergence of character structures, owing to convergent evolution, is the product of r_{iAB} and C_{AB}. It must not be forgotten that all conclusions about convergence or divergence are meaningful only in a comparative sense and with regard to the *a priori* nesting scheme in the character hierarchy.

Testing the significance of the partial correlation coefficient

Our approach to testing significance is by inspecting the confidence limits about the partial correlations for inclusion of zero. The limits are set in Monte Carlo simulation and if a point is enclosed, nonsignificance is declared. First we note that the limits are obtained in an analysis of a large number of artificial score matrices which are generated in a Monte Carlo experiment by computer sampling of imaginary communities at random. Each artificial score matrix is specific to the actual survey site for which it is constructed in as much as it always retains the character set from the original data, the total number of character set types, the total number of + scores, and the total of the cover abundance scores. These totals are apportioned among the cells of the artificial score matrix in a random fashion, without violating the logical structure of the character set in the original score matrix. The score matrix representing the Null Hypothesis in a concrete case is, therefore, the one that would arise if the character set types arose by chance, and if cover/abundance were a consequence of a simple random process. When we construct a dendrogram for the character set types of such a score matrix, chance clumping of the realized character set types is likely to occur. It then follows that the correlations will be distributed about zero with an actual mean correlation approaching zero. How close will an experimental mean fall from the zero line in an actual graph? This depends on the number of artificial score matrices in the experiment. Any observed correlation outside the confidence limits is considered significant.

Computer programs

Programs CSA.RND/1, CSA.RND/2, and CSA.SORT (in MICROSOFT BASIC for the Macintosh microcomputer) compute the partitions of **(X, O)** and Q, determine partial correlations, and set confidence limits. The partial correlations are presented in a vector which is drawn as a profile by one of the programs. The programs must be run in the sequence as listed. One type of characteristic profile (CP) is based on **(X, O)**. Two types are based on the **(M, O)** and **(X-M, O)** components of **(X, O)**. We identify these different types of CPs by symbols such as $r_{*AB(\mathbf{X-M,\ O})}$.

Interpretation of the correlation profiles

Clearly, by distinguishing between data types, the convergence or divergence measured by the correlation coefficient is either qualitative, quantitative, or a mixture of both. The interpretation of correlations will take into account this and also the level in the hierarchy (Fig. 1). Level 1 is the most informative level. On this level, the pattern in the arrangement of the realized and unrealized character set types is under the influence of the entire character set. On each successive level, as fusions occur, the effect of a character is removed. From the pattern on level 2 the effect of character five is removed, from the pattern on level three, the joint effect of characters four and five are removed, and so on. The nominal correlations $r'_{iAB*} = S_{iAB*}/(S_{iAA*}\ S_{iBB*})^{1/2}$ for data type * will thus reflect a combined effect of characters on a level. In contrast, the partial correlations. $r_{iAB*} = Q_{iAB*}/(Q_{iAA*}\ Q_{iBB*})^{1/2}$ will be specific to the single character for which a level is defined.

To reflect on specific aspects of interpreting correlations, let us assume that the sums of products are equal on two levels of the hierarchy, *i.e.* $S_{iAB} = S_{(i+1)AB}$. Such being the case, the specific sum of products Q_{iAB} will be zero, irrespective of the actual magnitude of S_{iAB} and $S_{(i+1)AB}$. What follows from this is that a zero r_{iAB*} on any level i for data type *, irrespective of the r'_{iAB*} and $r'_{(i+1)AB*}$ on levels i and i+1, may be zero, greater than zero, or smaller than zero. We observe further that whereas r'_{iAB*} involves m+1−i characters, r_{iAB*} involves only one, the ith. To this extent, r'_{iAB*} is a canonical correlation of character structures A and B with regard to a set of m+1−i characters on both sides, and r_{iAB*} is a partial correlation of character structures A and B with regard to a single character i. The actual value of the correlation coefficient will be influenced by the order in which the characters are nested. To this extent, the correlations will reflect the the user's choice of the order in which the characters are presented for analysis. To justify the user's choice, the ordering of characters must be well reasoned.

Examples

Saguaro, reflected-saguaro, and euphorbia score matrices

The set of raw data has already been given in Table 1. The reflected-saguaro matrix is constructed from the saguaro matrix by exchanging the plus and minus signs. These operations will indeed produce a reflected matrix, since the characters are binary. The basic results of correlation analysis are presented in Table 2. These results are stratified according to data type, hierarchical level (character), and comparison. Explanatory remarks concerning the computation of different quantities are included in the title. We give the partial correlation values in Table 3, and the CPs in Fig. 2. The CP of the saguaro/reflected-saguaro (most contrasting) comparison (A, B in Fig. 2 a, b, c) is negative for each data type (except one point in c), in direct contrast with the saguaro/euphorbia CP (Fig. 2 d, e, f), for which some points of the graphs are on the positive side. We observe that the score matrices represent stands without shared species under similar en-

Data type *	Level in hierarchy i	Character set	Uncentered sums of squares and products SS_{iAA*}	SS_{iAB*}	SS_{iAC*}	SS_{iBC*}	SS_{iCC*}	Degrees of freedom Df
(X,O)	1	5,4,3,2,1	832.8	-105.1	205.3	-177.6	3941.0	31
	2	4,3,2,1	377.8	-105.1	13.87	-165.1	1820.0	15
	3	3,2,1	212.3	-105.1	286.8	-31.37	847.3	7
	4	3,	98.62	-97.62	58.62	-49.62	275.1	3
	5	1	0.1250	-0.1250	5.125	-5.125	210.1	1
(M,O)	1		375.4	-105.1	286.3	-177.6	1071.0	
	2		203.8	-105.1	54.37	-119.6	385.8	
	3		152.3	-70.79	25.37	-32.62	18.37	
	5		19.30	-19.30	10.87	-10.87	6.125	
(X-M,O)	1		457.4	0.0	-347.0	0.0	2870.0	
	2		236.7	0.0	-173.5	14.78	1435.0	
	3		110.9	0.0	154.4	-5.035	475.5	
	4		33.89	-24.45	95.39	-78.50	309.2	
	5		22.54	-22.54	80.57	-80.57	288.0	

Table 2. Intermediate results of the computations. The method is described in the main text. Legend to symbols of score matrices and data types: A - saguaro; B - reflection of saguaro; C - euphorbia; (X, O) - cover/abundance data; (M, O) - qualitative component of (X, O); (X-M, O) - quantitative component of (X, O). Compute uncentered sums of squares and products according to $SS_{iAB} = \sum X_{ijA}X_{ijB}/n_i$, j=1, ...,$n_i$ and $SS_{(i+1)AB} = \sum X_{(i+1)lA}\ (X_{i+1})_{lB}/n_{i+1}$, l = 1, ..., n_{i+1}.

Data type*	Level in hierarchy	Character set	V_{iAA^*}	r_{iAB^*}	r_{iAC^*}	r_{iBC^*}	V_{iCC^*}	90% limits to r_{iAC^*} lower	upper
(X,O)	1	5,4,3,2,1	28.44	0.00	0.19	-0.01	132.56	0.46	-0.50
	2	4,3,2,1	20.69	0.00	-0.68	-0.33	121.69	0.63	-0.54
	3	3,2,1	28.44	-0.06	0.89	-0.07	143.06	0.72	-0.91
	4	2,1	49.25	-0.98	0.67	-0.55	32.50	0.98	-0.99
	5	1	0.12	-1.00	1.00	-1.00	210.12	-	-
(M,O)	1		10.73	0.00	0.68	-0.16	42.88	0.52	-0.38
	2		6.44	0.00	-0.26	-0.25	30.62	0.60	-0.54
	3		19.31	-0.44	0.59	-0.60	30.62	0.77	-0.87
	4		27.89	-0.92	0.55	-0.83	6.12	1.00	-0.92
	5		19.31	-1.00	1.00	-1.00	6.12	-	-
(X-M,O)	1		13.78	0.00	-0.30	-0.02	89.69	0.47	-0.36
	2		15.73	0.00	-0.94	0.57	119.94	0.69	-0.55
	3		19.26	0.31	0.52	0.64	41.56	0.89	-0.83
	4		5.67	-0.16	0.95	0.13	10.62	0.99	-0.96
	5		22.54	-1.00	1.00	-1.00	288.00	-	-

Table 3. Partial variances and correlations according to comparison and data type. Symbols are identically defined as in Table 2, except V which signifies specific variance. Compute specific sums of squares and products according to $Q_{iUV}(X, O) = S_{iUV}(X, O) - S_{(i+1)UV}(X, O)$ or more directly, $Q_{iUV} = SS_{iUV} - SS_{(i+1)UV} = \sum X_{ijU}X_{ijV}/n_i - \sum X_{(i+1)lU}X_{(i+1)lV}/n_{i+1}, j = 1, ..., n_i$ and $l = 1, ..., n_{i+1}$ which for level $i = 3$ and $U=h=A$ has numerical value 212.3–98.62=113.68. Divide by Df=8–4=7–3=4 to obtain the variance 28.42 specific to character 3. This value differs from the value 28.44 given in Table 3, owing to rounding errors. The value 28.44 is more accurate). Obtain partial correlations based on $r_{iUV}(X, O) = Q_{iUV}(X, O)/\sqrt{[Q_{iUU}(X, O)\,Q_{iVV}(X, O)]}$ and similar basis for other data types. For i=3, U=A and V=C, $r_{3AC}(X, O) = (286.8-58.62)/\sqrt{[(212.3-98.62)\,(847.3-275.1)]} = 0.89$.

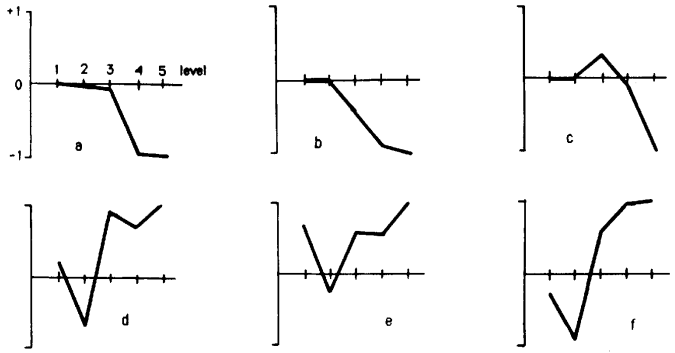

Fig. 2. Profiles of partial correlations of the saguaro (A), reflected-saguaro (B) and euphorbia (C) score matrices (Table 1) according to data type (Table 2). Legend to symbols: a - $r_{iAB}(X, O)$ profile; b - $r_{iAB}(M,0)$ profile; e - $r_{iAB}(X\text{-}M, O)$ profile; d - $r_{iAC}(X,0)$ profile; e - $r_{iAC}(M, O)$ profile; f - $r_{iAC}(X\text{-}M,0)$ profile for all levels i in character hierarchy. The profile for BC was not drawn.

vironmental conditions. The positive partial correlations should therefore be regarded as manifestations that convergent evolution has occurred, and the negative partial correlations should be interpreted as indications of divergent evolution, to an extent indicated by the magnitude of the correlations, and with regard to the characters in the analysis.

Elk Lake, Stewart Lake, and Watson Lake character matrices

The next three communities for which we report results are from three widely separated localities. The easternmost (E) is at the southern limit of the Clay Belt at Elk Lake, Ontario, and the westernmost (W) at Watson Lake in the Yukon. The third locality (S) is just north of Fort St. James at Stewart Lake, west of Prince George in central British Columbia. E and W are in boreal vegetation. S is in a subboreal vegetation (Krajina 1959). Six characters are considered, each with a number of states (20 in total). Table 4 contains the data and Fig. 3 graphs with smoothed upper and lower confidence limits to correlations. Any correlation point that is outside the corresponding limits in the graph is considered significant at the 0.05 probability level (one-sided).

Based on the (**X, O**) data, significant convergence is

Table 4. Score matrices of forest communities from Elk Lake (Ontario), Stewart Lake (British Columbia), and Watson Lake (Yukon Territory).

Character	State	Elk Lake, Ontario													Stewart Lake, British Columbia													Watson Lake, Yukon Territory										
		1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9	10	11
1. Life-form	Tree	+													+	+												+										
	Shrub		+	+	+	+	+					+					+	+	+	+									+	+	+	+						
	Herb									+	+										+	+	+	+									+	+	+			
	Cryptogam							+	+				+	+											+	+	+									+	+	+
2.	Epiphyte											+											+															
	Other	+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3. Size	Tall			+											+	+												+							+			
	Medium	+			+												+	+		+	+	+	+	+	+				+	+				+				
	Low		+			+	+	+	+	+	+		+	+					+							+	+				+	+	+			+	+	+
4. Function	Deciduous			+	+	+	+							+			+	+		+	+	+	+							+				+	+			
	Evergreen	+	+					+	+	+	+	+	+		+	+			+					+	+	+	+	+	+		+	+	+			+	+	+
5. Leaf type	Needle	+	+												+	+												+										
	Graminoid									+													+	+										+				
	Broad			+		+					+	+					+	+	+		+		+						+	+	+				+			
	Compound				+		+													+		+										+	+					
	Thalloid							+	+				+	+											+	+	+									+	+	+
6. Leaf texture	Filmy							+																	+												+	
	Membranous		+	+	+	+	+			+	+	+				+		+	+	+	+	+	+			+			+	+	+	+	+	+	+	+		
	Sclerophyll	+													+		+							+				+										
	Fungoid								+				+	+													+											+
Cover/abundance		60	10	40	10	1	+	10	2	1	2	3	+	1	60	+	20	5	1	5	5	5	1	5	60	20	1	70	10	10	15	10	5	80	15	15	20	5

Data type*	Level hierarchy	Character	Correlation			90% confidence limits for correlations					
			r_{iES*}	r_{iEW*}	r_{iSW*}	lower	upper	lower	upper	lower	upper
(X,O)	1	6,5,4,3,2,1	−0.01	0.02	0.43	0.15	−0.05	0.22	−0.52	0.06	−0.07
	2	5,4,3,2,1	0.04	0.05	0.48	0.16	−0.11	0.30	−0.12	0.19	−0.16
	3	4,3,2,1	0.04	−0.03	0.50	0.28	−0.51	0.49	−0.37	0.55	−0.52
	4	3,2,1	−0.41	−0.12	0.54	0.53	−0.50	0.72	−0.54	0.55	−0.43
	5	2,1	0.70	0.65	0.70	0.86	−0.77	0.95	−0.93	0.80	−0.94
	6	1	0.05	−0.40	−0.63	-	-	-	-	-	-
(M,O)	1		0.14	0.25	0.30	0.08	−0.05	0.17	−0.03	0.06	−0.08
	2		0.42	0.42	0.58	0.18	−0.12	0.26	−0.09	0.24	−0.16
	3		0.36	0.40	0.58	0.37	−0.53	0.50	−0.42	0.47	−0.58
	4		−0.04	0.62	0.57	0.56	−0.44	0.61	−0.55	0.61	−0.42
	5		0.93	0.93	0.97	0.92	−0.47	0.94	−0.91	0.98	−0.88
	6		0.58	0.86	0.89	-	-	-	-	-	-
(X-M,O)	1		0.07	0.06	0.44	0.18	−0.08	0.20	−0.06	0.02	−0.06
	2		0.05	0.06	0.39	0.24	−0.12	0.19	−0.23	0.12	−0.11
	3		0.13	0.18	0.28	0.31	−0.60	0.39	−0.46	0.56	−0.31
	4		−0.11	0.05	0.11	0.37	−0.53	0.31	−0.42	0.36	−0.61
	5		0.48	0.48	0.26	0.96	−0.84	0.68	−0.90	0.87	−0.81
	6		0.29	0.54	0.07	-	-	-	-	-	-

Table 5. Partial correlations computed for the score matrices in Table 4. The symbols have identical meanings as in the previous tables.

found in character structures between communities S and W on hierarchical levels 1, 2, 3 and 4 (Fig. 3c). In other cases of this data type, only one correlation value (Fig. 3 a, level 5) appears to reach significance. Based on the (**M, O**) data, many comparisons indicate significant convergence, except levels 4, 6 for E, S (Fig. 3 d), level 6 for E, W (Fig. 3 e), and level 6 for S, W (Fig. 3 f). In the case of the (**X-M, O**) data (Fig. 3 ghi), the significant correlation is limited to level 1 and 2 for comparison S, W (Fig. 3 i). To interpret a measured convergence, one must consider the number of shared species in the communities. We estimated the C values as $C_{ES} = 0.77$, $C_{EW} = 0.72$, $C_{SW} = 0.25$. Clearly, the perception of the type of community evolution has to be modified accordingly, and significant correlations would have to be interpreted as largely a consequence of convergent evolution (high C values, low numbers of com-

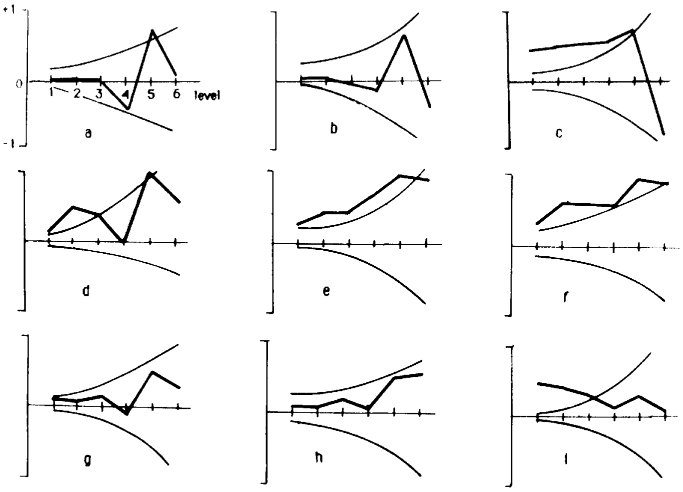

Fig. 3. Profiles of partial correlations and the 90% confidence limits for the Elk Lake (E), Stewart Lake (S) and Watson Lake (W) score matrices (Table 4), according to data type. The hypothesis tested stipulates a zero partial population correlation. The limits are smoothed by interpolation. Data type designations are explained in the main text. Legend to symbols: a - $r_{*ES}(X, O)$ profile, b - $r_{*EW}(X, O)$ profile, c - $r_{*SW}(X, O)$ profile, d - $r_{*ES}(M, O)$ profile, e - $r_{*EW}(M, O)$, f - $r_{*SW}(M, O)$, g - $r_{*ES}(X\text{-}M, O)$ profile, h - $r_{*EW}(X\text{-}M, O)$ profile, i - $r_{*SW}(X\text{-}M, O)$ profile.

Level	Character set	Number of states	Number of stems	Degrees of freedom specific to level
1	6,5,4,3,2,1	4	960	(4-1) 240 = 960-240 = 720
2	5,4,3,2,1	5	240	(5-1)48 = 240-48 = 192
3	4,3,2,1	2	48	(2-1)24 = 48-24 = 24
4	3,2,1	3	24	(3-1)8 = 24-8 = 16
5	2,1	5	8	(2-1)4 = 8-4 = 4
6	1	4	4	4-1 = 3
7	-	1	1	-

Table 6. The relationship of hierarchical level, characters, number of stems, and degrees of freedom in the score matrices of Table 4.

mon species) in the Elk Lake/Stewart Lake and Elk Lake/Watson Lake comparisons, and to parallel evolution in the Stewart Lake/Watson Lake comparison.

We note that the character hierarchy has 960 stems on level 1 (character 6) and 4 stems on level 6 (character 1). The large size would make the actual drawing of the dendrogram impractical. This required us to formulate a counting function to label the position of any realized character set type in the imaginary string of stems on any level of the hierarchy. Based on the labels, and knowing that the unrealized character set types correspond to zero cover/abundance, the computation of matrices **Q** (and **r**) can be performed without actually drawing a dendrogram. Regarding the rational for determining the degrees of freedom that we give in Table 5, the relationship of characters, hierarchical level, number of stems, and degrees of freedom should be examined in Table 6. On the most elaborate level (level 1, variable 6) there are 960 zero and nonzero cover/abundance values which leaves 959 degrees of freedom. On the next level, after fusions, there are 240 zero and nonzero values; these leave 239 degrees of freedom. The degrees of freedom specific to level 1 is 720; these are the degrees of freedom among the stems of level 1 within the stems of level 2, *i.e.* 240×3. On level 3, there are 48 zero and non-zero values and degrees of freedom 47. The degrees of freedom specific to level 2 are 239—47 = 48×4 = 192; this is the same as k_2—k_3. In general, the degrees of freedom specific to a given hierarchical level i is equal to the number of stems k_i on that level minus the number of stems on the next higher level k_{i+1}, *i.e.* $df_i = k_i - k_{i+1}$, regardless of the number of character states actually fused to form a particular stem.

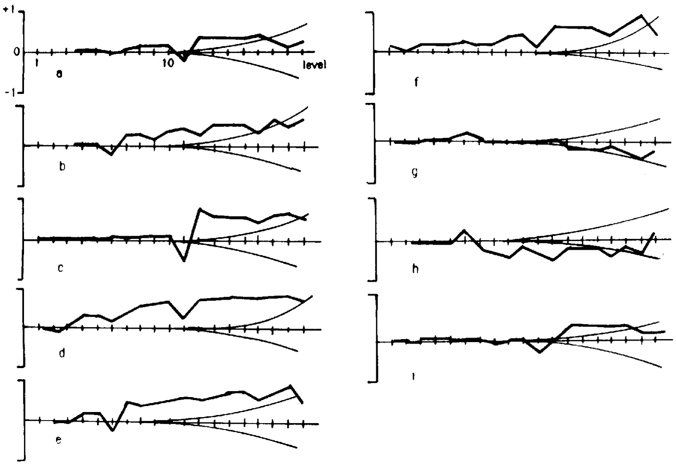

Fig. 4. Profiles of partial correlation and 90% confidence limits. Coastal euphorbia (A, Tenerife), highaltitude (B, Tenerife) and saguaro (C, Tucson) deserts are compared. The character set is as follows: 1 - stem present (two states), 2 - stem succulent (two states), 3 - stem erect (two states), 4 - stem caespitose (two states), 5 - life-form (10 states), 6 - stem with branches (two states), 7 - stem cylindrical (two states), 8 - stem green (two states), 9 - pulvinate form (two states), 10 - stem laticiferous (two states), 11 - stem thorny (two states), 12 - leaf size (four states), 13 - leaf compound (two states), 14 - leaf linear (two states), 15 - leaf evergreen (two states), 16 - poikilohydric (two states), 17 - leaf density (four states), 18 - leaf hairy (two states), 19 - leaf glutinose (two states). This sequence of characters corresponds to hierarchical levels from high (level 19) to low (level 1). Symbols have identical meaning for data types as in Fig. 3. Symbols a to i identify the comparison AB, AC, BC for data types (X, O), (X-M) and (X-M, O).

Tenerife, Canary Islands and Tucson, Arizona score matrices

The character set is listed in the title of Fig. 4 and the partial correlation profiles are given in the same figure. The profiles indicate no real contribution of the characters to convergence or divergence on the lower levels of the hierarchy. Considering that no species are shared, portions of the profiles above the zero line indicate convergent evolution. The character structures tend to be more convergent in qualitative terms and more divergent in quantitative terms, except the high-altitude and saguaro communities (profile i). Considering individual characters, the general pattern of relationships varies. For example, the high altitude desert differs substantially from the other two with respect to pulvinate forms (character 9, level 11), but the relationships are reserved when the stands are compared based on linear leaf form (character 14, level 6). The confidence limits indicate generally significant departures from zero expected partial correlation.

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