

ON THE COVARIANCE OF THE COMMUNITY MATRIX¹

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Abstract. A clarification of the meaning of the covariance of the community matrix is presented along with calculating equations for both the mean species covariance and the covariance of the row and column means. A brief discussion of α selection and its determination of the covariance is given, followed by tables for determining the expected number of species in a community from a knowledge of mean α and cov α .

Much interest in community ecology seems to have been generated by the theoretical constructs surrounding the community matrix (Levins 1968, Vandermeer 1970). Culver (1970), for example, uses the community matrix to investigate the nature of interference and exploitative competition in a community of cave isopods. Culver also points out the fact that the methods formerly used to estimate the covariance of the community matrix lead to the uneasy result that the covariance changes depending upon how the species are ordered.

In the present communication I derive a form for the covariance that is in accord with the original expectation of the expansion of the determinant of the community matrix. The actual computation of this form does not result in a value that changes with a changing ordering of the species, and furthermore, the interpretation of this covariance is much more easily couched in biological language than the former concept was.

The derivation presented by me (Vandermeer 1970) and by Levins (1968) of the expected value of the determinant depended upon the following general relationship,

$$E(\alpha_{ij} \alpha_{ji}) = \bar{\alpha}^2 + \text{cov}(\alpha_{jj} \alpha_{ji}),$$

which is correct given a proper interpretation of $\text{cov}(\alpha_{ij} \alpha_{ji})$. Throughout this paper α_{ij} refers to the effect of species j on i and m refers to the number of species in the community. To see this interpretation, take expectations with respect to one index variable at a time. That is, the expected value of $\alpha_{ij} \alpha_{ji}$ with respect to j is $\bar{\alpha}_i \bar{\alpha}_{.i} + \text{cov} \alpha_i, \alpha_{.i}$. Taking the expectation of that result with respect to i , we obtain

$$E(\alpha_{ij} \alpha_{ji}) = \bar{\alpha}^2 + [\text{cov} \alpha_i, \alpha_{.i} + \text{cov} \bar{\alpha}_i, \bar{\alpha}_{.i}]$$

where the term in the brackets corresponds to what Levins and I have referred to as the covariance of the community matrix [$\text{cov} \alpha$ or $\text{cov}(\alpha_{ij} \alpha_{ji})$].

For purposes of computation the following formulae are useful:

$$\text{cov} \alpha_i, \alpha_{.i} = \sum_{i=1}^m \left\{ \frac{\sum_{j \neq i} \alpha_{ij} \alpha_{ji} - (\sum_{j \neq i} \alpha_{ji} \sum_{j \neq i} \alpha_{ij}) / (m-1)}{m(m-2)} \right\} \quad (1)$$

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$$\text{cov} \bar{\alpha}_i, \bar{\alpha}_{.i} = \frac{\sum_{i=1}^m \bar{\alpha}_i \bar{\alpha}_{.i} - (\sum_{i=1}^m \bar{\alpha}_i \sum_{i=1}^m \bar{\alpha}_{.i}) / m}{m-1} \quad (2)$$

$$\text{where } \bar{\alpha}_i = \sum_{j \neq i} \alpha_{ij} / (m-1)$$

$$\text{and } \bar{\alpha}_{.i} = \sum_{j \neq i} \alpha_{ji} / (m-1).$$

The above equations are written under the assumptions that the community matrix in question is actually a representation of a sample of m species from a larger community. Thus we obtain the usual degrees of freedom ($m-2$) in equation (1) and ($m-1$) in equation (2). If, however, the community matrix in question is a representation of an entire community rather than a sample thereof, the point from which the deviations in the covariance are measured is no longer a sample statistic (mean α) but rather a true parametric value. Thus, if we are concerned with a community matrix that includes all of the species in some community, the term ($m-2$) in equation (1) should be changed to ($m-1$) and the term ($m-1$) in equation (2) should be changed to m .

Considering each term separately we first consider $\text{cov} \bar{\alpha}_i, \bar{\alpha}_{.i}$. Note that $\bar{\alpha}_i$ refers to the mean value of the α 's in the i th column, or the mean interactive effect perpetrated on the community as a whole by the i th species. Call this value the "species effect." A species that exhibits a large effect on most of the other species in the community is said to have a large species effect. On the other hand, $\bar{\alpha}_{.i}$ is the mean value of the α 's in the i th row, or the mean interactive effect perpetrated on the i th species by the community as a whole. Call this value the "community effect." A species that manages more or less to avoid the interactive effects of most of the other species in the community has a low community effect. Thus we have the species effect, which is the mean value of α in a particular column of the community matrix, and the community effect, which is the mean value of α in a particular row of the community matrix.

A great deal of information about the structure of the community is available from a direct examination of the row and column means, but for this paper

we are interested in the covariance between them. Intuitively, if one can easily predict the value of the community effect from a knowledge of the species effect, the absolute value of $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ will be high. Specifically, if a large species effect implies a large community effect and a small species effect implies a small community effect, $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ will be large and positive. On the other hand, if a large species effect implies a small community effect, $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ will be large and negative. If it is impossible to say anything about the species effect from a knowledge of the community effect, $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ is near zero.

Next consider the term $\text{cov } \alpha_i, \alpha_i$. Each species has a particular value of $\text{cov } \alpha_i, \alpha_i$, i.e., the "species covariance" for the i th species. If a large α_{ij} implies a large α_{ji} for all values of j , the species covariance for the i th species is large and positive. If a large α_{ij} implies a small α_{ji} for all values of j , the species covariance is large and negative. If it is not possible to predict the value of α_{ji} from a knowledge of α_{ij} , the species covariance is near zero. The quantity $\text{cov } \alpha_i, \alpha_i$ is obviously the mean value of all the species covariances.

The computation of $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ and $\text{cov } \alpha_i, \alpha_i$ is illustrated in the following example. Consider the community matrix presented by Culver (1970), where his negative values have been replaced by zeros and all α 's have been rounded to one decimal place. Thus we have the following community matrix:

$$\begin{vmatrix} 1 & 0 & .1 & 0 \\ 0 & 1 & 1.1 & .6 \\ .1 & .8 & 1 & .4 \\ .1 & .8 & .8 & 1 \end{vmatrix}$$

The species effects (row means, deleting principal diagonal) are .03, .57, .43, .57, and the community effects (column means, deleting principal diagonal) are .07, .53, .67, .33. The sum of the species effects is 1.60, the sum of the community effects is 1.60, and the sum of the cross products is .78. Thus the final marginal covariance ($\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$) is

$$[.78 - (1.60)(1.60)/4]/3 = .047.$$

It is next necessary to compute a species covariance for each species and take the average of the species covariances. Consider, for example, species number 2 in the above community matrix. We are concerned with the second row and second column of the matrix, namely 0, 1, 1.1, .6, and 0, 1, .8, .8. Because of the original derivation of the expected value of the determinant we must ignore the 1's in the principle diagonal, making the row and column of concern 0, 1.1, .6 and 0, .8, .8. The row sum is 1.7, the column sum is 1.6, and the sum of products is 1.36. Thus the species covariance for the second

species is $[1.36 - (1.7)(1.6)/3]/2 = .225$. Performing this operation for all four species in the community, we obtain $\text{cov } \alpha_1, \alpha_1 = .047$, $\text{cov } \alpha_2, \alpha_2 = .225$, $\text{cov } \alpha_3, \alpha_3 = .170$, and $\text{cov } \alpha_4, \alpha_4 = .116$, which gives a mean species covariance of .149.

The creation of methods to measure the actual interaction coefficients in any natural situation is the most difficult problem facing community matrix theory. I will not discuss that problem in this paper, but it is important to emphasize that the estimation of α 's is distinct from the various other features of the theory. In this paper we assume that α 's have been estimated and that they are correct. Given that assumption we can compute $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$, $\text{cov } \alpha_i, \alpha_i$, and $\bar{\alpha}$ and determine from tabulated values what the number of species in a saturated community is expected to be. For details of how such tables are derived see Levins (1968) or Vandermeer (1970).

The table presented in Levins (1968) shows expected values for only positive covariances. It is not difficult to imagine communities with negative covariances, e.g., a large species effect implies a small community effect. To see how such a relationship could come about, consider briefly the evolution of interspecific competitive ability. Analogous to r and K selection (MacArthur and Wilson 1967) we now consider the processes of α selection. Creating an artificial dichotomy, and supposing interference competition to be negligible, a species might evolve a high competitive ability either by becoming good at escaping the effects of potential competitors, or by becoming more efficient at utilizing a limiting resource. That is, a species could become a good competitor either by decreasing its community effect or increasing its species effect. Evolution might proceed in such a way that competition is either maximized or ignored, meaning that a large species effect implies a small community effect and $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ is large and negative. On the other hand it might be argued that in maximizing competitive ability a species must concentrate on either the species effect or the community effect. Naturally this set of circumstances results in $\text{cov } \bar{\alpha}_i, \bar{\alpha}_i$ being large and positive.

The above is not meant to be an exhaustive treatment of α selection but merely to show that the covariance is expected to be either positive or negative. In fact, examples computed from nature include both positive and negative covariances.

In light of the above, Tables 1 and 2 are presented as potentially useful extensions of the original table presented by Levins. The row headings of Tables 1 and 2 are the various values of $\text{cov } \alpha$ where $\text{cov } \alpha = \text{cov } \bar{\alpha}_i, \bar{\alpha}_i + \text{cov } \alpha_i, \alpha_i$, and the column headings are the values of $\bar{\alpha}$. In computing Tables 1 and 2, a great deal of round-off error frequently led to expected numbers of species clearly too large or too small to

TABLE 1. The expected number of species in a community as a function of $\bar{\alpha}$ (columns) and cov α (rows), for positive covariances

cov α	$\bar{\alpha}$.0125	.025	.0375	.0625	.0875	.0925	.0975	.105	.120	.140	.160	.20	.40	.60	.80
.003		67	65	58	44	35	34	32	30	28	27	24	22	15	11	6
.006		44	43	42	40	34	32	32	28	27	24	22	20	15	11	5
.009		33	32	32	30	30	28	27	28	26	24	22	21	13	8	4
.012		26	26	25	24	23	23	23	23	22	21	20	19	13	7	4
.015		22	21	21	20	19	19	19	19	18	18	17	16	10	6	3
.018		19	18	18	18	17	17	17	16	16	15	15	14	9	6	3
.021		16	16	16	16	15	15	15	15	14	14	13	12	8	5	3
.024		15	15	14	14	13	13	13	13	13	12	12	11	8	5	3
.030		12	12	12	12	11	11	11	11	11	11	10	10	7	4	3
.036		11	11	11	10	10	10	10	10	10	9	9	8	6	4	2
.048		9	9	9	8	8	8	8	8	8	8	7	7	5	4	2
.084		6	6	6	6	6	6	5	5	5	5	5	5	4	3	2
.120		5	5	5	4	4	4	4	4	4	4	4	4	3	2	2

TABLE 2. The expected number of species in a community as a function of $\bar{\alpha}$ (columns) and cov α (rows), for negative covariances

cov α	$\bar{\alpha}$.15	.20	.25	.30	.35	.40	.45	.50	.55	.60	.65	.70	.75	.80	.90	1.0	1.025	1.05	1.075	1.10	
-.475		79	60	48	40	35	30	29	26	24	23	22	21	19	19	18	17	16	9	7	5	5
-.450		76	58	47	39	35	30	28	26	24	22	21	20	18	19	17	16	15	9	6	5	5
-.425		76	57	46	38	34	30	28	26	23	20	20	20	18	18	16	16	15	9	5	5	5
-.400		73	57	45	38	32	30	28	25	22	20	20	20	18	18	16	16	14	8	5	4	4
-.375		72	51	44	37	32	29	27	25	22	20	19	19	17	17	15	15	14	7	5	3	3
-.350		68	50	42	35	31	28	25	24	21	20	19	18	17	17	15	15	14	7	5	3	3
-.325		68	49	41	35	31	28	24	23	20	20	19	18	17	16	15	14	14	7	5	3	3
-.300		63	48	38	34	31	27	24	23	20	20	18	18	16	16	15	14	14	6	3	3	3
-.275		61	47	38	33	28	26	24	23	20	20	17	17	16	16	14	14	14	5	3	3	3
-.250		61	44	36	31	28	26	23	22	20	19	17	17	16	15	14	14	14	5	3	3	3
-.225		56	44	34	30	27	25	23	21	20	19	17	16	16	15	14	13	9	5	3	2	2
-.200		56	43	34	30	26	24	23	20	19	18	16	16	15	14	14	12	7	4	3	2	2
-.175		52	42	33	29	24	22	22	20	18	18	16	15	14	14	13	12	7	3	2	1	1
-.150		48	39	32	27	24	22	21	19	18	17	16	14	14	14	12	12	5	3	1	1	1
-.125		47	38	31	26	23	21	20	19	17	16	15	14	13	13	12	12	5	3	1	1	1
-.100		43	35	29	25	22	20	18	18	16	16	14	14	12	12	12	11	5	3	1	1	1
-.050		36	30	24	22	20	18	16	16	14	14	12	12	12	10	10	10	4	2	1	1	1

fit into the mode of the table. In such cases, $\bar{\alpha}$ and cov α were changed very slightly and a new expected number of species computed. This "round-off" procedure results in a monotonically decreasing number of species in each row and column of Tables 1 and 2.

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