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ON THE VARIANCE OF EIGENVALUES OF THE COMMUNITY MATRIX: DERIVATION AND APPRAISAL

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Abstract. Eigenvalues, the solutions to the characteristic polynomial, are important measures of community behavior. Their range and practical measurement present difficult challenges in ecology. We therefore present the derivation of variance of eigenvalues of the community matrix, $\text{var}(\lambda) = \text{var}\,(a_{ii}) + (n - 1)a_{ij}a_{ji}$, as well as a novel related formula, namely, the expectancy of pairwise eigenvalues (EPV), $\text{var}(\lambda_{\text{pairwise}}) = \text{var}(a_{ii-\text{pairwise}}) + a_{ij}a_{ji}$. We propose that the two formulae may be useful in evaluating the relative contributions of inter- and intraspecific effects on the behavior of large systems. EPV allows estimating eigenvalue distribution of systems of unknown size.

Key words: community matrix; complex systems; eigenvalues; population dynamics; stability, community; variance.

INTRODUCTION

Measurements of ecosystem stability derived from the so-called "Routh-Hurwitz criteria" use self-effects and interactions among a specific number of community members. The coefficients of the characteristic polynomial of the community matrix are the bases of the criteria, and the eigenvalues (λ), or solutions to the polynomial, can give a valuable index of system behavior (see Vandermeer 1981). Intuitively, it follows that the range of eigenvalues also might be a valuable index of system behavior. Eigenvalues are used to describe the return time, T_r, of a system, where $T_r = 1/[\text{real }(\lambda)]_{\text{max}}$, $\lambda_{\text{max}} < 0$ (Pimm and Lawton 1978). Levins (1975) expressed the variance of eigenvalues as an equation incorporating intra- and interspecific interactions as well as community size. This formula is useful because it allows for general yet robust predictions of system behavior. Levins (1975) thus predicted that an increase in the number of predator–prey relationships could cause instability.

We derive a novel index, the *expectation of the variance of pairwise eigenvalues* (EPV). Although EPV appears similar to the variance of eigenvalues, it may be substantially more practical in its applications. EPV incorporates intra- and interspecific relationships into one descriptor, using information derived only from a subset of pairwise relationships. Levins' formula is a powerful theoretical formula but with limited practical applicability because it requires consideration of the complete system. As an estimate, EPV reflects more realistically the manner in which field ecological data are usually collected and analyzed because it may be calculated without complete system specification.

DERIVATION OF EPV AND VAR(λ)

Levins (1975) described a relationship for the variance of eigenvalues. A derivation of this relationship is not available in the literature. We therefore present below a complete derivation of the expected pairwise-eigenvalue variance, EPV, and of the variance of eigenvalues, var(λ). The joint derivation will demonstrate how closely related the two formulae are to each other. An understanding of the derivation is also important because it presents the manner in which intra- and interspecific relationships pertain to eigenvalues. The

variance of eigenvalues, λ, is expressed in the general form,

$$\text{var}(\lambda) = \overline{\lambda^2} - \bar{\lambda}^2. \tag{1}$$

The derivation is constructed from a collection of determinants of 2×2 sub-matrices. We proceed by deriving both right-hand elements in terms of the community matrix. The following two relationships are given by definition (see Searle 1966):

$$\sum \lambda_i = \sum a_{ii} \tag{2}$$

$$\lambda_1\lambda_2 = \det \begin{vmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{vmatrix} = a_{11}a_{22} - a_{12}a_{21}. \tag{3}$$

These two values are often called the "trace" and the "determinant" of a matrix, respectively. There are $\binom{n}{2}$ possible 2×2 sub-matrices in any community of size n. We begin by determining the square of the sum of the eigenvalues for each 2×2 sub-matrix,

$$\left(\sum_{i=1}^{2} \lambda_i\right)^2 = (\lambda_1 + \lambda_2)^2 = \lambda_1^2 + 2\lambda_1\lambda_2 + \lambda_2^2 \tag{4}$$

or, in terms of the matrix elements,

$$(a_{11} + a_{22})^2 = a_{11}^2 + 2(a_{11}a_{22}) + a_{22}^2 \tag{5}$$

and so on for each sub-matrix. We calculate the sum of the squares of the eigenvalues in similar fashion, using the relationship shown in Eq. 4,

$$\sum_{i=1}^{2} \lambda_i^2 = \lambda_1^2 + \lambda_2^2 = (\lambda_1 + \lambda_2)^2 - 2\lambda_1\lambda_2 \tag{6}$$

or, expressed in terms of matrix elements,

$$a_{11}^2 + 2a_{11}a_{22} + a_{22}^2 - 2a_{11}a_{22} + 2a_{12}a_{21}. \tag{7}$$

Using these equations, we calculate the variance of eigenvalues for each 2×2 sub-matrix using expected values. Thus, we obtain the square of the means,

$$\bar{\lambda}_{i,j} = \frac{1}{2}\sum_{i=1}^{2} \lambda_i = \frac{1}{2}\sum_{i=1}^{2} a_{ii} = \overline{a_{ii}} \tag{8}$$

where $\overline{a_{ii}}$ is the expected value of diagonal elements taken pairwise.

$$\bar{\lambda}_i^2 = \left(\frac{\sum_{i=1}^{2}\lambda_i}{2}\right)^2 = \left(\frac{\sum_{i=1}^{2} a_{ii}}{2}\right)^2 = \overline{a_{ii}}^2 \tag{9}$$

and similarly the mean of the squares,

$$\overline{\lambda_{i,j}^2} = \frac{1}{2}\sum_{i=1}^{2}\lambda_i^2 = \frac{1}{2}\left(\sum_{i=1}^{2} a_{ii}^2 + 2\sum_{i,j=1;i<j}^{2} a_{ij}a_{ji}\right). \tag{10}$$

The expectancy of the variances of a 2×2 sub-matrix is obtained by subtracting Eq. 9 from Eq. 10:

$$\overline{\text{var}}(\lambda_{i,j}) = \frac{1}{2}\left(\sum_{i=1}^{2} a_{ii}^2 + 2\sum_{i,j=1;i<j}^{2} a_{ij}a_{ji}\right) - \overline{a_{ii}}^2 \tag{11}$$

$$= \overline{a_{ii}^2} - \overline{a_{ii}}^2 + \sum_{i,j=1;i<j}^{2} a_{ij}a_{ji} \tag{12}$$

$$= \text{var}(a_{ii}) + \sum_{i,j=1;i<j}^{2} a_{ij}a_{ji}. \tag{13}$$

For a community matrix of size n, we take the expected value of the variances computed from all possible 2×2 sub-matrices that can be derived from it. Since there are $\binom{n}{2} = n(n-1)/2$ different pairings, then

$$\overline{a_{ij}a_{ji}} = \frac{2}{n(n-1)}\sum_{i,j=1;i<j}^{2} a_{ij}a_{ji} \tag{14}$$

and similarly the denominator used to compute the expected values of the pairwise $\text{var}(a_{ii})$ and of $\text{var}(\lambda)$ is also $n(n-1)/2$. The expected variance of pairwise eigenvalues, or EPV, is therefore

$$\overline{\text{var}}(\lambda_{a_{ii}-\text{pairwise}}) = \text{EPV} = \overline{\text{var}}(a_{ii-\text{pairwise}}) + \overline{a_{ij}a_{ji}}. \tag{15}$$

In order to derive the actual variance of the eigenvalues (i.e., non-pairwise) for a community matrix of size n, we generalize from Eqs. 9 and 10 and consider the n diagonal elements simultaneously; thus,

$$\bar{\lambda}_i^2 = \left(\frac{\sum_{i=1}^{n}\lambda_i}{n}\right)^2 = \left(\frac{\sum_{i=1}^{n} a_{ii}}{n}\right)^2 = \overline{a_{ii}}^2 \tag{16}$$

where $\overline{a_{ii}}$ is henceforth the expected value of the diagonal elements of the entire matrix (i.e., not pairwise). Similarly for the mean of the squares,

$$\overline{\lambda_{i,j}^2} = \frac{1}{n}\sum_{i=1}^{2}\lambda_i^2 = \frac{1}{n}\left(\sum_{i=1}^{n} a_{ii}^2 + 2\sum_{i,j=1;i<j}^{n} a_{ij}a_{ji}\right). \tag{17}$$

Given that there are n individual diagonal elements and therefore n eigenvalues, the variance of eigenvalues is therefore

$$\text{var}(\lambda_n) = \frac{1}{n}\left(\sum_{i=1}^{n} a_{ii}^2 + 2\sum_{i,j=1;i<j}^{n} a_{ij}a_{ji}\right) - \overline{a_{ii}}^2 \tag{18}$$

$$= \overline{a_{ii}^2} - \overline{a_{ii}}^2 + \frac{2}{n}\sum_{i,j=1;i<j}^{n} a_{ij}a_{ji} \tag{19}$$

$$= \text{var}(a_{ii}) + \frac{2}{n}\sum_{i,j=1;i<j}^{n} a_{ij}a_{ji}. \tag{20}$$

Since there are $\binom{n}{2} = n(n-1)/2$ different off-diagonal pairings, then

$$\overline{a_{ij}a_{ji}} = \frac{2}{n(n-1)}\sum_{i,j=1;i<j}^{n} a_{ij}a_{ji} \tag{21}$$

$$\frac{n(n-1)}{2}\overline{a_{ij}a_{ji}} = \sum_{i,j=1;i<j}^{n} a_{ij}a_{ji} \tag{22}$$

and, following substitution of Eq. 22 into Eq. 20, we obtain Levins' (1975) variance of the eigenvalues for the entire community matrix taken simultaneously:

$$\text{var}(\lambda) = \text{var}(a_{ii}) + (n - 1)\overline{a_{ij}a_{ji}}. \qquad (23)$$

A Numerical Example

We demonstrate the calculations of EPV and var(λ) with a numerical example. The matrix shown has not been selected for any particular resemblance to systems occurring in nature. Given the matrix,

$$\begin{bmatrix} 2 & -2 & \sqrt{6} \\ -2 & 5 & 3 \\ \sqrt{6} & -1 & 1 \end{bmatrix}$$

there are $n(n - 1)/2 = 3$ possible 2×2 matrices that may be constructed:

$$\begin{bmatrix} 2 & -2 \\ -2 & 5 \end{bmatrix} \qquad (24)$$

with eigenvalues = 1, 6 and var(λ) = 6.25;

$$\begin{bmatrix} 2 & \sqrt{6} \\ \sqrt{6} & 1 \end{bmatrix} \qquad (25)$$

with eigenvalues = -1, 4 and var(λ) = 6.25; and

$$\begin{bmatrix} 5 & 3 \\ -1 & 1 \end{bmatrix} \qquad (26)$$

with eigenvalues = 2, 4 and var(λ) = 1.00.

The expected value of these three variances (Eqs. 24–26) is, $\overline{\text{var}}(a_{ii-\text{pairwise},3\times3}) = 4.5$. From the diagonal elements of the three matrices, we have three sets of a_{ii}, (2, 5), (2, 1), and (5, 1), with variances of 2.25, 0.25, and 4.00, respectively. The expected value of the variances of these pairs of a_{ii}, $\overline{\text{var}}(a_{ii-\text{pairwise},3\times3})$, is 6.5/3 $\sim$ 2.2. The off-diagonals of the three base matrices yield the following $a_{ij}a_{ji}$ terms: $(-2)(-2) = 4$; $(6)(6) = 6$, and $(-1)(3) = -3$, respectively. The expected value of the $a_{ij}a_{ji}$ terms is 7/3 or $\sim$2.33. To demonstrate equality, we note that $\overline{\text{var}}(\lambda_{\text{pairwise},3\times3}) = 4.5$ and is equal to $\overline{\text{var}}(a_{ii-\text{pairwise},3\times3}) + E(a_{ij}a_{ji}) = 6.5/3 + 7/3 = 13.5/3 = 4.5$. Eq. 15 is satisfied.

In the case of the equation for var(λ), we note that, for the eigenvalues of the 3×3 matrix, which are $(-1.27, 4.64 + 0.56i, 4.64 - 0.56i)$, var($\lambda$) = 7.56 (some standard statistical packages will yield a different answer since the domain of their input is the real number field; we carried out hand calculations), while var(a_{ii}) = 2.89, so that var(a_{ii}) + $(n - 1)E(a_{ij}a_{ji}) = 2.89 + (3 - 1)(7/3) = 7.56$, and Eq. 23 is also satisfied.

Discussion

The two indices are related in their applicability but, broadly speaking, differ in that var(λ), the variance of

eigenvalues, is a theoretical tool for explanation while EPV, the expected pairwise-eigenvalue variance, is a practical implementation of var(λ). Var(λ) is a system parameter, derived from a completely specified community matrix; it is an attribute. In contrast, EPV does not require a completely specified matrix; it is an estimate. Indeed, the theoretical power of var(λ) is its practical limitation; the system must be completely specified. Since one can never be certain of specifying a system completely, any value of var(λ) may be inadequate. EPV however circumvents this practical consideration by not requiring a completely specified system. EPV may therefore be a practical tool that incorporates the relative contributions of two major components of system behavior, namely, inter- and intraspecific effects.

The value of either index can be used as a static estimate. More useful, we suggest, is the potential use of EPV as a comparative index of dynamic change. For example, as a monitoring tool for disturbed ecosystems, EPV may reflect ongoing trade-offs between intra-and interspecific effects as invasive species displace native species and form new interrelationships. Opportunistic species often exhibit rapid growth, high reproductive rate, and tolerance to a broad variety of environmental conditions. Diversity may be lost as systems adapt and incorporate these new species (Li et al. 1999). We hypothesize that as diversity is lost, the eigenvalues will become more homogeneous and EPV will decrease as the more fragile specialists and slower-to-reproduce species are overpowered and driven to extinction. EPV provides a real-time method for monitoring such trends.

Because the domains of var(λ) and EPV include both real and complex numbers, eigenvalues and pairwise eigenvalues are not typical random variables, and var(λ) and EPV are not "statistics." We use the standard calculation of variance to generate the values of var(λ) and EPV, but we make no assumptions regarding their distributional properties. Accordingly, as Levins (1975) pointed out, it is possible for var(λ) < 0 to occur. This situation will occur under realistic conditions. Thus, from Eq. 23 it can be seen that when inter-specific relationships are overwhelmingly predator–prey, in strength and/or in number, that is when $a_{ij}a_{ji}$ is negative, then their mean value can overwhelm the always-positive var(a_{ii}), and var(λ) will therefore be negative. Mathematically speaking, and as demonstrated by the calculations in the previous section, negative values of the variance of eigenvalues can only arise when imaginary components, common in eigenvalues (Vandermeer 1981), are present in their solutions. A negative value therefore indicates cyclic and therefore potentially less stable behavior.

We suggest the following specific interpretations to values of var(λ) and EPV, keeping in mind that we

have presented only the theory. When values are negative, they are indicative both of intense and/or numerous predator–prey interactions. Interestingly, a negative value can only arise in this way. When near zero, the indices indicate that each variable of the system has nearly uniform recovery time (since recovery time is inversely related to λ). This may occur through a balance between the positive variance of self-effects and a negative mean of (mostly) predator–prey relationships. A near-zero value therefore may be a very useful diagnostic tool for identifying "true" communities or sub-communities whose components respond at a similar rate. Positive values may be indicative of a community that is weakly linked and where self-effects dominate, possibly an assemblage more than a community. Alternatively, a positive value may indicate a preponderance of positive feedback through mutualism or interference, also suggesting an assemblage or transition more than a community.

The index EPV thus differs from var(λ) in that it is an equation for the mean of the variance of pairwise eigenvalues of a system rather than of the system eigenvalues themselves. In addition, the variable n, for community size, is absent from the formula for EPV. The hypothesis—that an increase in the number, alone, of predator–prey relationships, with a constant negative mean, can lead to destabilization—was put forward from the equation for var(λ) (Levins 1975). As a corollary, it may also be that an increase in positive interactions (interference and mutualism) in the presence of predator–prey relationships could counter the tendency towards a negative variance. Were the mean of $a_{ij}a_{ji}$ to be small because of that reason or because of the cumulative (high n) effect of pervasive weak relationships, as suggested in a recent study (McCann et al. 1998), a community could still exhibit a small variance and therefore recover from input at a near-uniform rate. The debate over the relationships of community size, strength, and type of interactions with stability is still ongoing.

The formula for var(λ) may provide a powerful conceptual formula for understanding and predicting general system behavior, as Levins (1975) has already suggested. Its derivation from the community matrix clarifies its biological basis. EPV provides a specific practical index for evaluation of the common underlying community model. As previous work has suggested (Harte 1979, Haydon 1994), the theory of eigenvalue distribution can yield valuable insights. The variances of eigenvalues and EPV may add useful and novel tools to assess the theory and practical considerations associated with eigenvalue distribution, and may thus provide additional insights into complex systems.

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