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NOTE

Detection of species sequences across environmental gradients*

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ABSTRACT: A computationally simple method is described for the detection of species sequences across environmental gradients in situations where patterns may be confused or obscure. The technique was tested using data on the occurrence of 5 mangrove species in 4 transects from the estuary of the Norman River, Northern Australia.

In ecology it is frequently necessary to discover whether a presumed environmental gradient is accompanied by a progressive change in species-composition. Sharply-defined sequences of this type are often clearly detectable but there also many situations where underlying patterns, if present, are confused or obscure. Indeed, circumstances may exist where the sequence of species, whether flora or fauna, exhibits so many reversals or inconsistencies from site to site that it appears overall to be near-random. However, prolonged observation in the field not uncommonly suggests that there may well be an underlying sequence, if only in that a given species appears more likely to occur at one end of the gradient than at the other. This is, in fact, a typical 'signal-to-noise' problem. The difficulty is to find a means of defining objectively the most probable signal structure, and of comparing the strength of this with that of the accompanying noise. In this Note we describe a computationally simple method of doing so which appears to be effective. Our particular interest is in estuarine mangroves, for which the ubiquity of circumscribed sequences has been questioned (Bunt & Williams 1981). The general question of zonal patterning has been addressed by Pielou (1977).

We suppose an estuary which contains a total of *s* mangrove species whose sequential tendency it is desired to study. We lay out a series of transects, each beginning at the water's edge and continuing progressively further inland to the mangrove limit. The number of sites in each transect is immaterial, but at each site the presence of any of the species of interest is recorded. For the analysis we first set up an all-zero matrix $\underset{\sim}{A}$ of dimensions $s \times s$. Consider a single transect of *n* sites, and suppose for simplicity that it contains only 4 species *x, y, z* and *w*. Start at the first site, at the water's edge, and suppose this contains Species *x* and *z*. Consider first Species *x*. Scan through Sites 2 to *n* and note whether any species other than *x* occurs in one of the higher-numbered sites. It is immaterial *how many* times there is such an occurrence; the question is, Does it occur anywhere? We are considering Species *x*; suppose Species *y, z* and *w* all occur somewhere further along the transect. We then increment A *(x, y)*, A *(x, z)* and A *(x, w)* by 1. Now repeat the process with Species *z*, also in the first site; perhaps *x, y* and *z* will all occur in later sites. If so, A *(z, x)*, A *(z, y)* and A *(z, w)* are all incremented by 1.

Now pass to Site 2 and repeat the process. Continue in this way until Site (*n*-1), the last site for which the procedure is possible, is reached. Now take the next transect and repeat the procedure, incrementing the elements of $\underset{\sim}{A}$ as before. When all transects have been so treated, the Matrix $\underset{\sim}{A}$ will be a transition matrix for the whole estuary, using the convention 'from rows to columns', in that every element represents the number of times the species defined by the column occurs higher in the sequence than the species defined by the row.

$\underset{\sim}{A}$ will usually be an asymmetric matrix, since in general $a_{ij} \neq a_{ji}$. Such a matrix can always be decomposed into the sum of a symmetric and a skew-symmetric matrix. We therefore first define a symmetric Matrix $\underset{\sim}{B}$, such that $b_{ij} = b_{ji} = \frac{1}{2}\ (a_{ij} + a_{ji})$. We then define a skew-symmetric Matrix $\underset{\sim}{C}$ such that $\underset{\sim}{C} = \underset{\sim}{A} - \underset{\sim}{B}$. Matrix $\underset{\sim}{C}$ summarizes the magnitude and sign of the species-

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species asymmetries. Consider now the column sums of $\underset{\sim}{C}$. A species whose column-elements are predominantly positive must be a species which, more often than not, follows others. As a mangrove, it must be high in the inland sequence and its column sum will be a high positive. At the other extreme, a species commonly near the water's edge will tend to precede others, will have many of its column-elements negative, and its column-sum will be a high negative. The ordering of the column sums thus provides the underlying sequence required.

We can compare the between-column variance with the combined within-column variance by a conventional single-factor analysis of variance. However, since the principal diagonal is by definition everywhere zero, there are only $s\,(s-1)$ degrees of freedom in all; and since the grand mean is also by definition zero, no degree of freedom is lost for the calculation of the mean. As a result there are $(s-1)$ degrees of freedom for between columns, and $(s-1)^2$ for within. In our present state of knowledge we cannot assign a significance level to the resulting variance ratio, since we do not consider that the elements of a skew-symmetric matrix can be regarded as normally distributed. The statistical status of this variance ratio is under investigation elsewhere. Meanwhile, we treat it as a comparative measure of sequential strength.

We conclude with a small-scale concrete sample. The estuary is that of the Norman River, in northern Australia, in which 4 transects were laid down and examined. Of the 10 species in whose sequential properties we were particularly interested, only 5 were encountered in this exercise; these were (1) *Avicennia* sp.; (2) *Ceriops tagal*; (3) *Excoecaria agallocha*; (4) *Lumnitzera racemosa*; and (5) *Rhizophora stylosa*. The resulting $\underset{\sim}{A}$, $\underset{\sim}{B}$ and $\underset{\sim}{C}$ matrices are set out in Table 1, in which have also been included the $\underset{\sim}{C}$ column sums and the analysis of variance. It will be observed that the suggested sequence from water's edge to inland is *Avicennia* – *Rhizophora* – *Lumnitzera* – *Ceriops* – *Excoecaria*; this, from the personal experience of the senior author, is entirely plausible and accords basically with zonal patterns described by Macnae (1968) under Australian conditions. To establish such a sequence purely by inspection of the field data for the estuary of the Norman River, however, would have been quite fortuitous and heavily subject to individual judgement and bias. From our admittedly limited experience, a variance ratio of 3.679 suggests a fairly strong sequential pattern.

Other ecologists, we believe, might find it worthwhile exploring the efficacy of such an analysis under analogous circumstances in communities of a similar or different kind.

Table 1. $\underset{\sim}{A}$, $\underset{\sim}{B}$ and $\underset{\sim}{C}$ matrices for the Norman River

		Species				
		1	*2*	*3*	*4*	*5*
Matrix $\underset{\sim}{A}$	*1*	–	12	24	6	8
	2	4	–	4	0	1
	3	15	2	–	6	0
	4	6	0	5	–	0
	5	8	8	8	0	–
Matrix $\underset{\sim}{B}$	*1*	–	8.0	19.5	6.0	0.0
	2	8.0	–	3.0	0.0	4.5
	3	19.5	3.0	–	5.5	4.0
	4	6.0	0.0	5.5	–	0.0
	5	8.0	4.5	4.0	0.0	–
Matrix $\underset{\sim}{C}$	*1*	0.0	4.0	4.5	0.0	0.0
	2	−4.0	0.0	1.0	0.0	−3.5
	3	−4.5	−1.0	0.0	0.5	−4.5
	4	0.0	0.0	−0.5	0.0	0.0
	5	0.0	3.5	4.0	0.0	0.0
Column sums of $\underset{\sim}{C}$		−8.5	+6.5	+9.0	+0.5	−7.5

Analysis of variance

Source of variance	Sum of squares	Degrees of freedom	Mean square	Variance ratio
Total	131.5			
Between columns	63.0	4	15.750	3.679
Within columns	68.5	16	4.281	

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