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The Colwell – Futuyma method for measuring niche breadth and overlap: a critique

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The paper by Colwell and Futuyma (1971), "On the measurement of niche breadth and overlap", has become a classic in the ecological literature (Colwell 1982). Not only was it the first clear statement of the fact that niche overlap does not necessarily measure the intensity of competition between species, it was also the first clear exposition of the weaknesses inherent in the simple niche metrics commonly used in community ecology. Besides making these indisputable contributions, Colwell and Futuyma developed a relatively complex method to solve the problems involved in the definition of the resource categories on which niche measures are based. When applied in practice, this method has been received diversely (Sabath and Jones 1973, Inger and Colwell 1977, Clarke 1977, Hanski and Koskela 1977, Hanski 1978). But, despite several partial criticisms, the soundness of its theoretical principle has remained unquestioned. Although niche studies are much less fashionable today than 15 years ago, they still are a powerful basic tool for descriptive and heuristic purposes. Thus a clear view of the validity of niche metrics is important. I shall here argue that the very foundations of the Colwell-Futuyma method are incorrect.

The method comprises three steps: (1) an "eco-assay" of the resource states by a census of the plant and animal species in each quadrat; (2) the calculation of weighting factors for the resource states according to their "distinctness"; and (3) the expansion of the resource matrix by representing each resource state in proportion to its weighting factor. The second step is critical. Colwell and Futuyma make two claims to derive their weighting factors. First, that a "standardized measure of resource state heterogeneity" is given by the information function

$$M(X) = \frac{m(X)}{H(X)} = \frac{H(X) + H(Y) - H(XY)}{H(X)} \qquad (1)$$

where $H(X)$ is the Shannon-Wiener function of uncertainty with respect to resource state;
$H(Y)$ is the uncertainty with respect to species; and
$H(XY)$ is the total uncertainty with respect to both species and resource state.

And second, that partitioning heterogeneity by resource states provides the "distinctness" $M_j(X)$ of resource state j, which can then be used as a weighting factor in the expansion of the matrix. Neither of these claims appears to me justified.

The function $m(X)$ in Eq. (1) is a standard measure of "relatedness" between two classifications, i.e. it measures the reduction in the amount of information required to locate an element in one classification, if it has been located in the other. Accordingly, $M(X)$ is a measure of relative relatedness. In order to demonstrate its relevance as a measure of resource state heterogeneity, Colwell and Futuyma explored only two borderline cases. They showed that $M(X)$ is maximum (equal to 1) when each resource state is associated with different species, and $M(X)$ is minimum (equal to 0) when all species are equally distributed over resource states. Unfortunately, between those two extremes there is no clear relationship between $M(X)$ and resource state heterogeneity, because $M(X)$, being a measure of relative interdependence, depends as much on the distribution of the relative abundances of the species as on the distribution of the proportions of resource-state utilization by the species, and in a way that is not biologically definable.

Table 1. Hypothetical example of resource matrices with calculation of the Colwell-Futuyma weighting factors.

	case 1				case 2			
	resource states				resource states			
	1	2	3	total	1	2	3	total
species 1	50	30	10	90	500	300	100	900
species 2	10	30	50	90	10	30	50	90
total	60	60	60	180	510	330	150	990
$M_j(X)$	0.074	0	0.074	0.146	0.023	0	0.035	0.058

This is illustrated in the hypothetical example of Table 1. In this example, only two species are considered for the sake of clarity, and the problem of circularity of niche metrics as stressed by Colwell and Futuyma is ignored intentionally to concentrate on the intrinsic problems of the measures of resource state heterogeneity and "distinctness". One may consider, for instance, that the species in this example are not the species for which niche metrics are to be computed. The comparison between the two cases considered clearly shows the dependence of M(X) on species relative abundances (recall that M(X) is equal to the sum of the $M_j(X)$). Yet there is no reason to consider that resource heterogeneity is different in the two cases, since the species discriminate between resource states exactly in the same way in both cases. Niche breadth and overlap both are parameters related to the spreading of species population responses along a niche axis, and should therefore not be intrinsically dependent on population abundance (Hanski 1978). Note that the M-function is also used by some authors to measure niche breadth and overlap themselves. Indeed the standardized measures proposed by Pielou (1972) can be shown to reduce to the complement of M(X) for niche breadth and to the complement of M(Y) for niche overlap (except that Brillouin's information measure is used instead of Shannon-Wiener's). Horn's (1966) index of overlap is also equal to the complement of M(Y). Thus the above criticism applies to these measures too.

The dependence of M(X) on species relative abundances could, however, be eliminated by reducing absolute numbers to proportions. But the next operation of Colwell and Futuyma is much more problematic. It is conceptually difficult to understand how partitioning a measure of heterogeneity results in so many measures of "distinctness".

Inger and Colwell (1977) made explicit the notion of "distinctness" that was implicit in Colwell and Futuyma (1971). They defined the distinctness of a resource state as the degree to which the biota of that resource state deviates proportionally from the biota of the matrix as a whole. This is indeed what the $M_j(X)$ measure when species abundances are equal (Table 1, case 1). Thus $M_2(X)$ is zero because the two species use resource state 2 in the same proportions. However, note again that

when species abundances are different (case 2), this interpretation of the $M_j(X)$ is no longer possible (how to interpret the difference between $M_1(X)$ and $M_3(X)$?).

But the very concept of "distinctness" as defined above is inconsistent with the original formulation of the fundamental problems related to the measurement of the niche in the beginning of the paper of Colwell and Futuyma. The problem that was posed was to restore the shape of the niche along a gradient when we only measured population responses at some points (quadrats) along that gradient and do not know how these points are spaced: "resource states should be equally distinct, or equally spaced, not in relation to some physical or chemical variable measured in ordinary units, but in relation to an ecological variable, ideally measured in units of "subjective" effect on the organisms in question" (p. 570). But spacing points equally can only be done if we know the *distance* between successive points. Distinctness of resource states, like distance between points, is in essence a relative notion, which applies to comparisons between resource states, not to resource states individually. The "distance" of an individual point has no meaning, nor does the "distinctness" of an individual resource state: it is always a distance from another point, a "distinctness" from another resource state. What has been derived is a measure of how distinct the proportional uses of a resource state by different species are, but not a measure of how distinct resource states are. In other words, the method compares species for each resource state instead of comparing resource states.

Thus, in the example of Table 1, it seems reasonable to consider that all three resource states are equally distinct in both cases, in view of the regular utilization gradient of both species, while the Colwell-Futuyma method would allot a zero distinctness value to state 2 and, consequently, make the latter disappear in the expanded matrix. On the other hand, two wholly redundant resource states (i.e. two identical columns) may have high $M_j(X)$, provided that they are used in heterogeneous proportions by the various species.

One should not confuse a niche axis along which all population responses are identical – such an axis has no information content with respect to niche overlap and can be discarded in the estimation of the latter – and a

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particular resource state, which represents a point along a niche axis, for which population responses are identical proportionally. In the latter case, it is important to keep the information contained in all resource states in order to describe the population responses along the axis as a whole. Otherwise one simply excludes the possibility that species may be very similar and biases the interpretation of niche relationships in an evolutionary context.

What then would be a correct way of measuring distinctness? I do not believe there can be a universal solution to that problem, but one of the many measures of ecological distance between resource states (between pairs of columns in the matrix) would certainly be more appropriate. This is basically what Vandermeer (1972) suggested. We would then have to deal with a matrix of distance measures between pairs of resource states instead of a vector of individual measures for each resource state. In any case, the method must be such that two redundant resource states (two identical columns) are considered as not distinct from one another, since they represent samples at the same point along the gradient – this at least provides an adequate criterion for defining zero distinctness.

Lastly, even if it proved possible this way to associate some weighting factor to each resource state, it is worth recalling that the third step in the Colwell-Futuyma method, viz. matrix expansion, cannot be used without qualification. Matrix expansion can restore an ecologically realistic description of the niche only when samples (resource states) are "small" enough compared with niche breadth (Hanski 1978), so that they can be regarded as points along a gradient, and when population responses are expressed in the form of a density of resource utilization. These are the conditions implicitly considered by Colwell and Futuyma. When they are not met, matrix expansion is inadequate. Such is often the case with food resources. When data are available only on the respective use of food categories, and not on the selectivity in food choice, matrix expansion will clearly be of no help to restore the shape of the niche, since (1) the problem lies in the form of the population response, not only in the spacing of the niche axis; (2) in most cases, food categories are heterogeneous (including e.g. different species); then it is not a matter of reproducing categories, but above all of dividing and grouping them so that they can correspond to real ecological distinctions from the point of view of the species

considered. The alternative method of matrix expansion proposed by Sale (1974), who splits the proportion of resource use made up of each category into a number of parts that is proportional to the abundance of the category, does not do any better in this respect. Not only does it fail to restore the true shape of the niche, but it also introduces confusion between distinctness and abundance and fails accordingly to tackle the problems raised by Colwell and Futuyma.

Given the multitude of possible aspects to be considered in the niche, there is likely no universal recipe for solving the difficulties inherent in its measurement. The best recommendations that can be made about it are, first, to choose carefully the population response and definition of categories that are relevant to each particular situation while collecting data, and second, to use simple measures such as Levins's (1968) with constant awareness of their limitations and of the need to interpret them while analyzing data.

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