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Dear Clapham,

I have just been looking at Romell's paper in Ecology, and send a few notes along in case you have been thinking of the same problem.

The F% curves of Romell must depend not only on the frequency of species of various abundance, but on the manner in which with increasing sampling unit, the F for any one species passes from a small to a large percentage.

If a species "occupies" exclusively the fraction F_0 of an area, then $F = F_0$ for infinitely small sample areas, whatever the shape of the fraction occupied, and $F > F_0$ for all finite sample areas.

An idea of the manner of increase of F from F_0 to 100, may be obtained from the manner of increase of the percentages of fertile samples from a liquid culture medium as the size of sample is increased

$$F = 1 - e^{-A/\alpha}$$

where A is the sample area and α, a standard area, inverted frequency of plants, clumps, or other natural units. In this formula $F \rightarrow 0$ with A, and would only be correct for small areas if the species were counted as present or absent according as a geometrical point in the clump were within or without the sample area; actually it is counted or not according as the centre of the sample area is within or without an area which may be taken as a square whose side exceeds that of the "quadrat" by a length representing the diameter of the clump. Say:

$$F = 1 - \exp\left\{-\frac{1}{\alpha}\left(\sqrt{A} + \alpha\right)^2\right\} = 1 - e^{-A'/\alpha} \qquad A' > \alpha^2$$

In any case for the great majority of species F must be small, since $\sum F_0$ cannot exceed 100, and F can only lie between 10 and 90 if A'/α lies between .1054 and ".3026, a range of 22 fold in area, or 4.6 fold in the size of the (modified) sample "quadrat" ($\sqrt{A'}$). The U shape of the F curve, stressed by Romell, would necessarily follow if for different species α (or strictly α / A') varied over a range much greater than 20 fold.

This seems to follow merely from sampling, however uniform the environmental conditions of the district may be. Of course for a heterogeneous district the values of F will be averages over different environments, and so might be expected to be more centrally distributed. I am quite attracted in this connection by Romell's suggestion that a sprinkling of rare and exceptional environments will introduce correspondingly rare species with low F values, whose number will be disproportionate to the frequency of the environmental conditions in which they occur. His explanation of the concentration of species at high F values is not so clear, for although varying only a single environmental factor, it is true that the number of species adapted to nearly central conditions will be large owing to the frequency being nearly constant over a considerable range of conditions in the neighbourhood of the centre, yet this is not true if the independent environmental factors are more than one, and in the case of a single factor it should lead, for certain "quadrat" sizes to concentrations not at the extreme near F = 100, but at some other high value such as 60.

Yours sincerely,