



Fig. 2 The relationship between connectance and species number generated with the sampling method of McNaughton from communities with log-series species abundance curves for species distributed independently in space (solid line) for comparison with that reported for African grasslands.

species sampled formed a geometric series, with common ratio $\exp(-1/\alpha)$. Random sampling from such a distribution yields a log-series species abundance curve with diversity index² α . Such curves have frequently been found to provide an adequate description of species abundance data, albeit largely for insects², and have the advantage that they are effectively completely determined by sample size and species number.

Mean values of species number (\hat{s}) and \hat{c} were determined for various values of α . The relations of \hat{s} and \hat{c} to s thus obtained are superimposed on the data of McNaughton in Figs 1 and 2. The curves seem to fit the data points adequately, leaving no residual systematic effect, affirming that the apparent decline in these parameters with increased species number is an artefact of the sampling method used.

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Stability and diversity in grassland communities

IN his analysis of the stability properties of large, randomly constructed model ecosystems, May¹ contradicted the existing ecological dogma—that increased community complexity produces increased stability—by showing that in Lotka-Volterra models, dynamic stability is diminished with increases in: (1) the number of species (S); (2) the average strength of the interactions among species (i); (3) the connectance of the system (c), that is, the proportion of non-zero values for i in the community interaction matrix.

He showed that the system is almost certainly stable if

$$i(Sc)^{1/2} < 1 \quad (1)$$

McNaughton² uses data from a study of the interactions among plant species in 17 grassland stands in the Serengeti National Park to test May's results, and concludes that both average strength of interaction and connectance are negatively correlated with species richness, implying that the structure of these grassland communities is constrained in special ways to meet the requirements for local stability. If this were true, it would be an important conclusion³. Unfortunately, McNaughton's results are an inevitable consequence of varying S , and hence say nothing about whether interactions in these communities are constrained by dynamic interactions between species.

McNaughton measures the strength of interaction among the plant species by applying to nearest-neighbour data⁴ the point correlation coefficient, V (giving limits of +1 if the two species always occur

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together, -1 if they never do, and a value of 0 if the species are distributed independently)⁵, and shows that V is negatively correlated with S . However, he seems to make no allowance for the fact that, as species richness increases, V is bound to decrease. Harris presents the argument in full.

Finally, McNaughton² draws attention to another theoretical possibility, suggested by May¹, which also enhances the probability of stability in ecological systems; namely, that communities are organised into blocks of species. McNaughton suggests that the size of these blocks (or guilds) can be estimated by Sc . Unfortunately, Sc says nothing about whether the connections between species are 'blocked' and cannot measure the size of these blocks, even if they exist. Blocking depends on the arrangement of the interactions between species, and not on how many there are.

However, we agree with McNaughton that it is important to attempt to test stimulating ecological theories in the field, and

we hope that further analysis of data of this kind will now be attempted by others.

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MCNAUGHTON REPLIES—Lawton and Rallison's statement that "as species richness increases, V is bound to decrease" is incorrectly applied to my Letter. As I reported negative values for V , the number of contacts would have increased, not decreased, had my initial report been correct. But it was wrong and Harris accurately identified the flaw.

I am grateful to them for calling attention to my error and hope that other ecologists using 2×2 contingency tests in this type of analysis will not make my mistake, whether using V or other statistics, such as χ^2 . I should have calculated an expected V , based on the species' relative abundance, and then used the t -test based on the z -transformation to determine whether the calculated V departed from the expected value. It is, therefore, of value to other ecologists who use nearest-neighbour analysis, or similar methods based on contingency testing, to have the expected values of the cells.

Using the traditional notation of a, b, c, d , for the cells of the 2×2 table, expected values for all sampling events consisting of two consecutive draws with replacement are, if the individuals are randomly arranged, $a = 2f_x f_y$, $b = f_x^2 + 2f_x h$, $c = f_y^2 + 2f_y h$, and $d = h^2$, where $f_x = n_x/N$, $f_y = n_y/N$, and $h = 1 - f_x - f_y$.

This obviously results in an expected negative value of V that increases in magnitude as f_x and f_y increase. But it also allows a straightforward test of spatial associations comparing observed and expected values of V . If, on the other hand, nearest neighbours of the same species are classified as 'pseudospecies', one traditional method in nearest-neighbour analyses, f_x^2 and f_y^2 are removed from the b and c cells and added to the d cell, resulting in expected positive values of V for randomly distributed individuals.

Another alternative previously used in nearest-neighbour analyses of vegetation is to classify intraspecific nearest neighbours as 'no contacts', eliminating them from the analysis. But then each cell must be corrected by $1 - f_x^2 - f_y^2 = m$, which apparently has not been done, and $a = 2f_x f_y/m$, $b = 2f_x h/m$, $c = 2f_y h/m$, and $d = h^2/m$. Finally, I redrew (selected the next nearest neighbour of another species) when nearest neighbours were members of the same species. To my chagrin, the