

The checkerboard score and species distributions

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Summary. There has been an ongoing controversy over how to decide whether the distribution of species is “random” – i.e., whether it is not greatly different from what it would be if species did not interact. We recently showed (Roberts and Stone (1990)) that in the case of the Vanuatu (formerly New Hebrides) avifauna, the number of islands shared by species pairs was incompatible with a “random” null hypothesis. However, it was difficult to determine the causes or direction of the community’s exceptionality. In this paper, the latter problem is examined further. We use Diamond’s (1975) notion of checkerboard distributions (originally developed as an indicator of competition) and construct a *C*-score statistic which quantifies “checkerboardedness”. This statistic is based on the way two species might colonise a pair of islands; whenever each species colonises a different island this adds 1 to the *C*-score. Following Connor and Simberloff (1979) we generate a “control group” of random colonisation patterns (matrices), and use the *C*-score to determine their checkerboard characteristics. As an alternative mode of enquiry, we make slight alterations to the observed data, repeating this process many times so as to obtain another “control group”. In both cases, when we compare the observed data for the Vanuatu avifauna and the Antillean bat communities with that given by their respective “control group”, we find that these communities have significantly large checkerboard distributions, making implausible the hypothesis that their species distributions are a product of random colonisation.

Key words: Checkerboard pattern – Random colonisation – Species interaction – Community structure – Bird distributions

from species incidence data, something about the forces responsible for population distributions in an archipelago. (For earlier work in this area, see e.g. Connor and Simberloff (1979); Strong et al. (1984); Harvey et al. (1983)). We discussed some of the weaknesses in previous methods of analysis, and introduced a way of detecting non-random effects by the use of an “island-sharing” statistic.

Here we develop and extend this work, using another statistic – the “checkerboard score” – to test actual distributions for non-randomness. The concept of “checkerboardedness” was discussed by Diamond (1975) in a paper which effectively launched the modern controversy over species assembly. Studying the Bismarck Archipelago avifauna, he deduced seven rules of species assembly that asserted the existence of certain patterns and “permissible combinations” of species, arguing: “[T]he simplest distributional pattern that might be sought as possible evidence for competitive exclusion is a checkerboard distribution. In such a pattern, two or more ecologically similar species have mutually exclusive but interdigitating distributions in an archipelago, each island supporting only one species” (pp. 387–388). Further: “Checkerboard distributions are of great interest in demonstrating the existence of competitive exclusion” (p. 392), and in fact the “simplest and clearest pattern that might be produced by competition is a checkerboard distribution” (Diamond and Gilpin, 1982, p. 65).

The new step below lies in quantifying checkerboardedness. A “*C*-score” measure is offered, which proves suitable for examining actual species distributions, and gives conclusions (in the Vanuatu and Antilles cases) that accord well with our previous findings, but disagree with other analyses such as Connor and Simberloff (1979).

Checkerboard patterns

To examine in detail the checkerboard patterns of large communities, it is convenient to describe the data in matrix form, as is customary in many biogeographic analyses. A “presence/absence” or “incidence” matrix is used

In a previous paper (Roberts and Stone 1990) we considered the difficulties arising when one tries to deduce,

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to depict which species are present and where. In the study that follows, each column of the incidence matrix represents a known island, and each row a particular species. A “1” appearing in the (i, p) th entry denotes that species i (\mathcal{S}_i) is on island p (\mathcal{I}_p), while a “0” means it is absent. Thus the incidence matrix $\underline{A}=(a_{ip})$ has the entries

$$a_{ip} = 1 \quad \text{if } \mathcal{S}_i \text{ occurs on } \mathcal{I}_p, \\ = 0 \quad \text{otherwise.}$$

The following “thought experiment” suggests a way to quantify the “checkerboardedness” of an incidence matrix. Suppose two species $\mathcal{S}_i, \mathcal{S}_j$ are released, with each species constrained to settle on one and only one of two particular islands $\mathcal{I}_p, \mathcal{I}_q$. Considering their possible assembly arrangements, note first the basic checkerboard pattern, in which one species occurs on \mathcal{I}_p but not on \mathcal{I}_q , whereas the other is on \mathcal{I}_q but not on \mathcal{I}_p . Such an event will show up thus in the incidence matrix \underline{A} :

$$\begin{array}{c} \mathcal{I}_p \quad \mathcal{I}_q \\ \mathcal{S}_i \left[\begin{array}{cc} \dots & 1 & \dots & 0 & \dots \\ \dots & \dots & \dots & \dots & \dots \end{array} \right] \\ \mathcal{S}_j \left[\begin{array}{cc} \dots & 0 & \dots & 1 & \dots \end{array} \right] \end{array}$$

We will call such an arrangement a basic checkerboard unit; it might be the outcome of some exclusion process. If we are attempting to decide whether there are factors causing a particular species pair to favor checkerboard arrangements, it is of course insufficient to study their occurrence on only two particular islands. For a fuller picture we must examine their checkerboard patterns – or lack of them – over all pairs of islands.

We now show how to calculate C_{ij} , the number of checkerboard units formed by the two species $\mathcal{S}_i, \mathcal{S}_j$, when all island pairs are taken into account. By way of example, suppose the row entries of the incidence matrix \underline{A} for species $\mathcal{S}_i, \mathcal{S}_j$ are as shown in (a) below:

$$\begin{array}{l} \mathcal{S}_i | 1000110101 | 1110000011 | 000011 | \\ \mathcal{S}_j | 1110101110 | 1110111100 | 111100 | \end{array} \begin{array}{l} \text{(a)} \quad \text{(b)} \quad \text{(c)} \end{array}$$

Now re-arrange the pattern, putting the co-occurrences and co-absences at the beginning, so as to obtain (b). Then drop the co-occurrences and co-absences, which contribute nothing to C_{ij} , and obtain (c), which has $2 \times 4 = 8$ checkerboard units. Thus, $C_{ij} = 8$.

In the general case, the number C_{ij} of checkerboard units that involve \mathcal{S}_i and \mathcal{S}_j , can be calculated as follows. Let S_{ij} be the number of co-occurrences of \mathcal{S}_i and \mathcal{S}_j (i.e., the number of islands that the two species share). If r_i is the i th row sum of the incidence matrix,

$$C_{ij} = (r_i - S_{ij})(r_j - S_{ij}).$$

(The first factor on the right here is the number of 1’s in the i th row which have a 0 below them in the j th; the second factor is the number of 1’s in the j th row which have a 0 above them in the i th row.)

We define the checkerboard score for a particular colonisation pattern (matrix) as the mean number of checkerboard units per species-pair of the community.

For M species, there are $P = M(M - 1)/2$ species-pairs, and hence the C -score is:

$$C = \sum_{i < j} C_{ij} / P.$$

Using this statistic, we examine the same field data as Connor and Simberloff (1979), and extract the C -score for each observed data set. Following the method already used with the statistic \bar{S}^2 (see Roberts and Stone 1989), we then determine the significance of this score in two different ways:

First, we compare this value with that given by a “random” sample of matrices, to see if its value is unusual. These matrices will come from an ensemble generated in accordance with a suitable null hypothesis. For a comment on this last glib phrase, on why the appellation “random” needs qualification, and on the doubts attaching to this procedure, see Roberts and Stone (1990) and below.

Second, we alter the data slightly, while still obeying certain constraints, and compare the altered C -score with the original value, to see how unusual the latter value is in the set of closely-similar colonisation patterns.

Imposing the constraints

Connor and Simberloff (1979) randomly generated “possible worlds” of biogeographic patterns to test a null hypothesis of random colonisation. They felt it reasonable to incorporate three constraints. Briefly, these required the number of islands r_i colonised by the i th species \mathcal{S}_i , and the number of species s_p occupying the p th island \mathcal{I}_p , to agree with the actual number; also, a species could not settle on an island, if the number of species accompanying it there lay outside the range of its actual numbers of companion species. (For a more detailed discussion, see Roberts and Stone (1989).)

It was believed that these constraints allowed for factors that could be always present, whether the species interacted or not – factors due, for example, to the island species-area relationships, species colonisation abilities or species incidence functions.

However, these constraints have been accused of making a suitable null hypothesis impossible, by smuggling in species-interaction effects. Evidence presented in Roberts and Stone (1990) indicates that this is a serious objection; nevertheless, these very constraints will now be imposed as part of what might (as in that paper) be called an *a fortiori* strategy.

The relabel-equivalence of incidence matrices

Two incidence matrices will be called relabel-equivalent, if they can be derived from each other merely by interchanging (i.e., swapping) pairs of rows and/or columns. For example, matrices \underline{B} and \underline{D} below are not relabel-equivalent, while matrices \underline{B} , \underline{E} and \underline{F} are all relabel-

equivalent, as simple manipulations will confirm. For example, by interchanging columns 2 and 4 in matrix B , one obtains F .

$$B = \begin{vmatrix} 1100 \\ 1100 \\ 0011 \\ 0011 \end{vmatrix} \quad D = \begin{vmatrix} 1100 \\ 1010 \\ 0101 \\ 0011 \end{vmatrix} \quad E = \begin{vmatrix} 1010 \\ 0101 \\ 1010 \\ 0101 \end{vmatrix} \quad F = \begin{vmatrix} 1001 \\ 1001 \\ 0110 \\ 0110 \end{vmatrix}.$$

Swapping rows (columns) describes the relabelling of species (islands). Thus if one examines co-occurrence statistics – such as the number of species-pairs, -trios, etc. that share n islands – all re-label-equivalent matrices must have the same co-occurrence patterns (as Connor and Simberloff (1979) pointed out).

So defined, re-label-equivalence obviously satisfies the mathematical requirements for an equivalence relation (see e.g. Saracino (1980), p. 81), and thus allows us to sort the incidence matrices into equivalence classes. Two matrices from distinct classes will be non-re-label-equivalent, while members of the same class will all be re-label-equivalent.

Members of the same (re-label-) equivalence class all have the same C -score. To see this, let C be the score of a given incidence matrix; if P is the number of species pairs, then

$$C = \sum_{i < j} C_{ij} / P.$$

Suppose now that, after swapping row f with row g , the incidence matrix has the new score C' . Then after the row swap,

$$C'_{ij} = C_{ij}, \quad \text{for } i < f \text{ and } j < g,$$

$$C'_{fj} = C_{gj} \quad \text{and} \quad C'_{gj} = C_{fj} \quad \text{for all } j.$$

Hence

$$C' = \sum_{i < j} C_{ij} / P = C,$$

which proves the invariance of C to row interchanges. A similar argument applies to column interchanges.

As an example, consider all $4-x-4$ presence/absence (incidence) matrices in which each row sum and each column sum is 2. The C -scores of those displayed above are easily found to be

$$C(B) = C(E) = C(F) = 16/6 = 2.67,$$

$$C(D) = 12/6 = 2.00.$$

We see that the three re-label-equivalent matrices B , E and F all have the same C -score.

An important point about sampling procedures now arises. By examining only non-equivalent matrices, Connor and Simberloff (1979) imply that, in the ensemble of allowable matrices, each distinct equivalence class should be given equal weight. As a relevant case study, we generated all the different $4-x-4$ matrices of row and column sum two – 90 in all. These 90 contain only two equivalence classes, represented by B and D respectively. There were 18 distinct matrices re-label-equivalent

to B , with a C -score of 2.67, and 72 distinct matrices re-label-equivalent to D , with a C -score of 2.00.

Even when all members of a set are re-label-equivalent, each matrix stands alone in representing a unique colonisation pattern. Each such pattern is equally likely when the species, while obeying the above constraints, are presumed to colonise independently of each other. Thus the patterns equivalent to D will occur four times as often as the extreme checkerboards equivalent to matrix B . It is therefore incorrect to give the two different matrix classes equal weight as do Connor and Simberloff (1979).

In more general terms, recall that each “randomly colonised” matrix is supposed to represent a particular outcome – a set of (named) species on a set of (named) islands – whereas each re-label-equivalence class represents a whole set of outcomes, even though they happen to have a common value for the statistic C characterising their co-occurrence patterns. In our case, the null hypothesis is that species colonise islands completely independently of any interactions between them. So there is no reason why one matrix or colonisation pattern should be more probable than another. Thus it is distinct matrices, not equivalence classes, which must be given equal probability measure, contrary to the procedure of Connor and Simberloff (1979).

Generating random matrices

To generate the full ensemble as we did above, or even to calculate its size, is not practicable for constrained matrices much larger than $4-x-4$. Accordingly, we used a computer to generate a representative random sample. (We had to be on guard against the flaws contained in some procedures extant for generating allegedly random numbers – see the discussion in e.g. Park and Miller (1988).) Two methods were employed, the same conclusion following from each:

a) The method of random interchanges

Take a pair of islands, and select any species which occurs on the first of them but not on the second. Then find, if possible, a species which occurs on the second but not on the first. Then, if we interchange the species between islands, each still occurs on the same total number of islands, and each island still contains the same number of species; that is, such an interchange leaves the island-total and species-total constraints still obeyed. But, by performing an arbitrary number of such interchanges, we generally obtain a different species distribution over the islands – with different checkerboard scores. (For a fuller description, see Roberts and Stone (1990).)

b) The Milne method

Connor and Simberloff (1979) attempted to generate a random sample of allowable matrices, in a manner that

in some respects resembled a colonising process (guided by the null hypothesis of random colonisation). Thus species were (randomly) picked one at a time, and placed on a randomly chosen available island (subject to the three constraints). This continued until either the presence/absence matrix was filled, or a “hang-up” situation arose.

“Hang-ups” occur when, after inserting a number of 1’s within the matrix, it becomes impossible to fill the matrix any further without breaking the given constraints. For example, the partially-filled matrix \underline{G} below (with row and column totals adjoined) can never be completed and has thus “hung up”. On the other hand, \underline{H} is an allowable matrix subject to the same constraints.

$$\underline{G} = \begin{array}{c|c|c} 0111 & 3 & \\ \hline 0110 & 2 & \\ \hline ?000 & 2, & \\ \hline 1000 & 1 & \\ \hline 3221 & & \end{array}, \quad \underline{H} = \begin{array}{c|c|c} 1110 & 3 & \\ \hline 1100 & 2 & \\ \hline 1010 & 2, & \\ \hline 0001 & 1 & \\ \hline 3221 & & \end{array}.$$

Connor and Simberloff found that “hang-up” situations occurred with great frequency, when they attempted to generate large and tightly structured matrices by this matrix “filling” method. The problem leads to a large amount of computer time being required to produce a single allowable member of the ensemble. However, B. Milne (private communication) has recently developed a technique for randomly filling a constrained matrix, so that a large number of allowable matrices can be generated rapidly. The computer program makes use of a look-ahead technique, whereby a “1” is inserted in the matrix only if it will not produce a “hang-up” situation. Using this program, a sample of 1000 matrices was quickly generated for each data set examined.

Analysing an ensemble

To help explain the procedure employed, we analyse (after Gilpin and Diamond (1982)) a simple case: $20 - x - 20$ matrices with all row and column sums equal to ten. (This would describe an archipelago in which each of the twenty islands contained ten bird species, and each of the twenty bird species inhabited ten islands.) 1000 such matrices were generated randomly by the Milne method, the sample yielding the estimates:

$$\langle C \rangle = 29.009, \quad \sigma(C) = 0.136. \quad (\text{Sample size } 1000)$$

Random interchanging (for details see Roberts and Stone (1990)) produced a similar histogram with

$$\langle C \rangle = 29.026, \quad \sigma(C) = 0.147. \quad (\text{Sample size } 1000)$$

Note that the two methods give very similar statistics. Of interest are the two matrices \underline{U} and \underline{V} below, with C -scores of 52.6 and 30.3 respectively. In the whole ensemble, the most exclusive matrix possible would be equivalent to the matrix \underline{U} .

$$\underline{U} = \begin{array}{c|c} 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 11111111110000000000 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline 00000000001111111111 & \\ \hline C(\underline{U}) = 52.6, & \\ \hline 00101011110100001110 & \\ \hline 11010100001011110001 & \\ \hline 00101111001001001110 & \\ \hline 11010000110110110001 & \\ \hline 10110000000011111011 & \\ \hline 01001111111100000100 & \\ \hline 10011101011001001100 & \\ \hline 01100010100110110011 & \\ \hline 00101011100100110110 & \\ \hline 11010100011011001001 & \\ \hline 11010111100001011000 & \\ \hline 00101000011110100111 & \\ \hline 10000111100011001110 & \\ \hline 01111000011100110001 & \\ \hline 11001100100111000110 & \\ \hline 00110011011000111001 & \\ \hline 00010101101011101010 & \\ \hline 11101010010100010101 & \\ \hline 01101101010001010101 & \\ \hline 10010010101110101010 & \\ \hline C(\underline{V}) = 30.3. & \end{array}$$

Matrix \underline{U} 's C -score of 52.6 exceeds the estimated mean by almost 200 times the estimated standard deviation. Not one of the 1000 randomly generated matrices had a C -score so extreme; the largest was less than four times the estimated s.d. Thus the C -test easily picks high levels of exclusiveness.

Diamond and Gilpin (1982) examined the matrix \underline{V} above (their Fig. 4), where ten out of the possible 190 pairs are in a “perfect checkerboard” arrangement. They reported that although “the inference of exclusion was very strong” in this matrix, the Connor-Simberloff test found nothing unusual. (But note Simberloff and Connor (1984) who state that, after classes are lumped together, their χ^2 test finds the matrix \underline{V} is indeed exceptional.)

The C -score test for this matrix, on the other hand, gives $C(\underline{V}) = 30.3$. Using the Monte Carlo estimates for the distribution parameters (see above), this value exceeds the mean by more than ten times the estimated

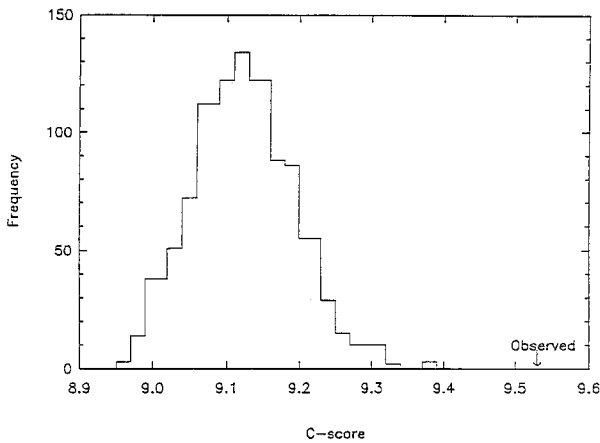


Fig. 1. Histogram of the frequency distribution of values of the checkerboard score C , in a sample of 1000 random colonisation patterns for avifauna of the Vanuatu archipelago. The sample was generated by the Milne method. The actual value of C , indicated on the figure (“Observed”), exceeds any found in the sample

s.d. Confirming the rarity thus suggested, not one of the 1000 randomly-generated allowable matrices was so highly exclusive. Thus the C -test finds the checkerboardedness of V to be highly significant.

These tests give us some confidence in the procedure’s ability to detect extreme patterns.

Analysis of field-data – the Vanuatu avifauna

The field-data on the Vanuatu (formerly New Hebrides) avifauna (56 bird species on 28 islands), gathered by Diamond and Marshall (1976) and examined by Connor and Simberloff (1979), will now be re-analysed using the C -test. Upon randomly filling 1000 matrices by the Milne method, subject to the constraints derived from the actual field-data (i.e., fixed row and column sums as well as incidence ranges), the histogram of Fig. 1 was obtained, giving the estimates

$$\langle C \rangle = 9.128, \quad \sigma(C) = 0.072. \quad (\text{Sample size } 1000)$$

The same test was performed again, on a sample generated by the method of random interchanges. The statistics found were altogether similar to those obtained by the Milne method. The method of interchanges gave the estimates

$$\langle C \rangle = 9.112, \quad \sigma(C) = 0.067. \quad (\text{Sample size} = 1000)$$

Yet the observed matrix had the score $C(\text{Vanuatu}) = 9.53$, distant from the mean by almost 6 times the (estimated) standard deviation. More transparently, the largest C -score in the sample of 1000 matrices was only 9.409 by the Milne method (9.347 by the method of interchanges) giving a Monte Carlo estimate for the probability P that the null hypothesis was true:

$$P < 0.001.$$

These results conflict sharply with those obtained by Connor and Simberloff, whose R -mode analysis pro-

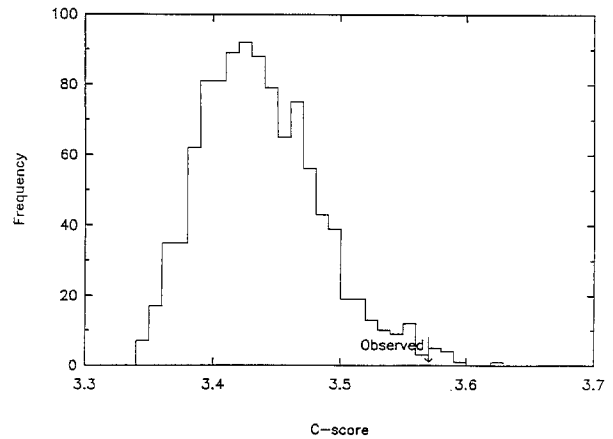


Fig. 2. As Fig. 1, but for Antillean bats. The actual (“Observed”) value of C was exceeded by only 20 patterns in the sample

duced a very close matching between the observed and expected matrix, with $\chi^2 = 16.34$ (27 df) giving $0.95 > P > 0.90$. We have already shown (Roberts and Stone (1990)) the reasons for this discrepancy. Briefly: the chi-square test is inappropriate for this R -mode analysis because the cell-numbers are far from independent; and even if the chi-square test were valid, the number of degrees of freedom (27) used by Connor and Simberloff is more than twice the value estimated by fitting the first moment of the empirical data given by the random sample.

Analysis of field data – the Antillean bats

The above analysis was repeated for the data on the Antillean bat community (59 species on 25 islands) given in Baker and Genoways (1978). The sample histogram (see Fig. 2) as found by the Milne method gave the estimates:

$$\langle C \rangle = 3.441, \quad \sigma(C) = 0.051. \quad (\text{Sample size } 1000)$$

The method of random interchanges gave:

$$\langle C \rangle = 3.451, \quad \sigma(C) = 0.055. \quad (\text{Sample size } 1000)$$

The observed matrix had the score $C(\text{Antilles}) = 3.57$, which exceeded the (estimated) mean by 2.6 times the (estimated) standard deviation (Milne method), or 2.2 times (method of random interchanges). To confirm the rarity of the observed matrix, of the 1000 allowable matrices randomly generated by the Milne method, only 20 (2.0%) were found to be so highly exclusive. By the “method of interchanges”, 37 (3.7%) of a sample of 1000 allowable random matrices were as exclusive.

A complementary test

Although the tests above give evidence of some weight, the work shares a defect with all the previous studies on this topic using allegedly random samples: they have never been *proved* random. As discussed in Roberts and

Table 1

<i>n</i> (Number of interchanges)					
(0)	10	20	100	200	400
<i>N</i> (Number in the sample)					
(1)	1000	1000	1000	1000	1000
$\langle C \rangle$					
(9.53)	9.40	9.32	9.12	9.11	9.11
Number with $C \geq$ observed					
(1)	9	0	0	0	0

Stone (1990), the possibility is left open – small though it may appear – that the selection method does not yield a sample having (at least asymptotically) the distribution in the ensemble.

We therefore repeat here, for the Vanuatu case, the complementary test described in the previous paper: we carry out n random interchanges on the observed incidence pattern, where n is only a small fraction of the total number of checkerboard units ($=M(M-1) \times C/2 = 14676$), and study the properties of the resulting matrix. Repeating this process N times (starting each time with the observed pattern), we have a sample of N matrices to compare with the observed pattern.

The results for the Vanuatu data are shown in Table 1.

Again, as in the previous paper, the implication of these results can be shaped into a challenge for anyone wishing to claim that the observed Vanuatu distribution is not exceptional: if this claim is true, then it should not be difficult to construct other colonisation patterns obeying the constraints (independently of the observed data, and not having some manifestly special design like that of the matrix \underline{U} above), which have a “local maximum” comparable in strength to that of the observed pattern. This means: patterns which can stand comparison with one that, when a mere 0.14% of its checkerboard units are altered, yields a pattern of lesser checkerboardedness, and does this for every such (random) alteration in a sample of 1000.

Conclusion

The statistic C used above suggests itself as a handy tool in the analysis of species distributions. Its use has exposed the Vanuatu and Antilles data sets as resulting from unusual colonisation patterns, with significantly high checkerboardedness. The null hypothesis – that the data differs little from what one would expect had the islands been randomly colonised – is to be doubted, at the (empirical) significance levels of $P < 0.001$ (Vanuatu) and $P < 0.04$ (Antilles).

Although others have reached similar conclusions (e.g. Gilpin and Diamond (1982), Wright and Biehl

(1982)), it should be noted that their work did not incorporate the constraints assumed by Connor and Simberloff which are fully included above (and in our previous paper – Roberts and Stone (1990)).

The constraints may well incorporate, as has been suggested, built-in hidden structures arising from competition. But the above results show that, if so, they are far from including the full impact of the processes at work, as revealed in the significantly higher C -scores of the field data.

Can we therefore conclude that evidence has been found here, for biological factors which tend to keep species apart? After examining this question, and probing more deeply with the C -score technique, we believe that the truth is somewhat more complicated than this; a report is in preparation.

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