

# Competitive exclusion, or species aggregation?

## An aid in deciding

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**Summary.** There is a long-standing dispute over whether the analysis of species co-occurrence data, typically on islands in an archipelago, can disclose the forces at work in structuring a community. Here we present and utilise three “scores”  $S$ ,  $C$  and  $T$ .  $S$  gives the mean number of islands shared by a species pair in the presence/absence data under study. The scores  $C$  and  $T$  are based on the way that a pair of species occurs on a pair of islands. When each species occurs on a different island, this adds to the “checkerboard score”  $C$ ; if they occupy the same island, this increases the “togetherness score”  $T$ .

In judging whether observed values of  $S$ ,  $C$  and  $T$  are compatible with a null hypothesis assuming no species interaction, we follow Connor and Simberloff (1979) in generating a “control group” of (constrained) simulated incidence patterns.

Presence/absence matrices can have paradoxical features, in combining a high mutual exclusion by species (checkerboardedness) with a degree of species aggregation that is also high. We show that this is in fact inevitable – that, given the usual constraints,  $C$  and  $T$  can differ only by a constant. This means that extreme checkerboardedness can be produced by forces making for species aggregation, just as well as by those making for avoidance.

If we restrict our attention to a subset of species, the constraints are less rigid and the  $S$ ,  $C$  and  $T$  scores are somewhat freer to vary. We consider the confamilial subsets in the Vanuatu archipelago as likely candidates for revealing any competition forces at work. Calculating the actual  $S$ ,  $C$  and  $T$  scores for these subsets, we compare them with the corresponding scores in a sample of simulated colonization patterns.

The actual species-distributions differ significantly from what we would expect if the colonization choices of different species were uncorrelated (save for some biological constraints). The confamilial species of the real world share more islands, and occur in a pattern less

checkerboarded, and more aggregated, than their simulation counterparts. This suggests that competition pressures, if they exist, are overcome by countervailing factors.

The method used is applicable in other ways, and to a wider class of problems, in analysing the forces behind community structure.

**Key words:** Species co-occurrence – Bird distributions – Community structure – Coexistence principle

Can the data on how species are distributed – over the islands of an archipelago, say – be made to disclose the presence or absence of competitive pressure or of other interactive forces? We present here a method of analysing such data which can lead to useful conclusions in this much-debated field. The parameters used are ones that measure how species shares islands ( $S$ ), and how they tend to avoid each other (the “checkerboardedness”  $C$ ) or tend to aggregate (“togetherness”  $T$ ). It is shown how these measures can be used to indicate the kind of factors at work in producing the observed distribution: whether they are forces making for species avoidance, or ones making for species aggregation.

The  $S$ - and  $C$ -scores have been introduced previously, and provide a test for the comparison of species distribution data (Roberts and Stone 1990; Stone and Roberts 1990). As in our previous work, we apply the biological constraints suggested by Connor and Simberloff (1979). These require that, in the simulated “control group”, a species must be made to settle on the same number of islands, and an island made to hold the same number of species, as in the observed data. (See R&S (1990) for details of the constraints under which the simulated “control group” is assumed to colonise, and the reservations surrounding the term “random” in this context.) Using these scores, we found that both the Vanuatu and Antilles data sets (also analysed by e.g. Connor and Simberloff 1979; Wright and Biehl 1982; Wilson 1987) exhib-

it significantly elevated levels of variation in sharing numbers and of “checkerboardedness” (Stone and Roberts 1990) when compared to the simulation set.

Here the analysis is taken further. We first consider whether checkerboard patterns can be taken as evidence of mutual avoidance and/or competition (see e.g. Diamond 1975). Believing this, we might conclude from the *C*-score test that species avoidance, and possibly competition also, must be seen as significantly at work within these archipelagoes.

However, the *C*-score cannot be used so straightforwardly. In particular, we show that – paradoxical as it may appear – a high *C*-score indicates a high level not only of species avoidance (exclusion), but also of its opposite – species aggregation, as measured by *T*. Thus a process favoring aggregation will generally raise the *C*-score, a result which supports the observation by Connor and Simberloff (1983 page 457) that “many exclusive patterns are expected for non-competitive reasons”.

It is in examining the behaviour of subsets of species that the *S*, *C*- and *T*-scores can be made to yield useful information. As an example, they are used below to study the occurrence of confamilial species in the Vanuatu archipelago.

**Material and methods**

*The relation between checkerboard and aggregation patterns*

Diamond (1975) maintained that “the 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.” Hence: “Checkerboard distributions are of great interest in demonstrating the existence of competitive exclusion.” In the same spirit, Diamond and Gilpin (1982) asserted: “The simplest and clearest pattern that might be produced by competition is a checkerboard distribution.”

On the other hand, it has been pointed out that checkerboard patterns might result from a variety of factors. Connor and Simberloff (1979) made this clear, when they discussed how checkerboard distributions could arise from allopatric speciation, where formerly conspecific populations geographically speciate without subsequent reinvasion. The checkerboard distributions so created would be independent of any present competition.

To analyse such patterns in species distributions, we use the incidence matrix *A*, which gives the presence/absence data for species in the archipelago under examination. The matrix  $A \equiv (a_{ip})$  has the entries

$$a_{ip} = 1 \text{ if } \mathcal{S}_i \text{ (species } i) \text{ occurs on } \mathcal{I}_p \text{ (island } p), \\ = 0 \text{ otherwise.}$$

The number of islands shared by  $\mathcal{S}_i$  and  $\mathcal{S}_j$  is then the  $(i, j)$ <sup>th</sup> entry  $S_{ij}$  in  $S \equiv AA^T$ , while a typical “checkerboard unit”, formed by  $\mathcal{S}_i, \mathcal{S}_j$  on  $\mathcal{I}_p, \mathcal{I}_q$ , appears as a sub-matrix like *c*, where

$$c = \begin{matrix} & \mathcal{I}_p & \mathcal{I}_q \\ \mathcal{S}_i & \begin{bmatrix} ..1 & \dots & 0.. \\ \dots & \dots & \dots \end{bmatrix} \\ \mathcal{S}_j & \begin{bmatrix} ..0 & \dots & 1.. \end{bmatrix} \end{matrix}$$

With  $\mathcal{S}_i$  present on  $r_i$  islands, the number of these checkerboard units that involve the species pair  $(\mathcal{S}_i, \mathcal{S}_j)$  is  $C_{ij} = (r_i - S_{ij})(r_j - S_{ij})$ . (See Roberts and Stone (1990) and Stone and Roberts (1990) for a fuller discussion of all these properties.)

The *C*-score statistic is defined as the mean number of checkerboard units per species-pair of the community. For  $N_s$  species, there are  $N_s(N_s - 1)/2$  species-pairs, and hence the *C*-score is

$$C = 2 \sum_{i < j} C_{ij} / N_s(N_s - 1).$$

Consider now (after Gilpin and Diamond 1982) a hypothetical archipelago, in which each of twenty islands contains ten bird species, and each of the twenty different bird species inhabits ten islands each. One possible incidence matrix for this archipelago would be *U*, where

$$U = \begin{bmatrix} 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 11111111110000000000 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \\ 00000000011111111111 \end{bmatrix}$$

In the matrix *U*, the number of checkerboard units, and thus the *C*-score, is extraordinarily large (Stone and Roberts 1990) if the species are believed to be making their settlement choices independently of one another. And yet, despite its high checkerboardedness, the incidence matrix *U* has two  $10 - x - 10$  sub-matrices each of which portrays an extreme aggregation of species sharing the same islands.

To examine this apparent contradiction in more depth, it is convenient to introduce a measure of “togetherness”. Consider, then, a situation in which  $\mathcal{S}_i, \mathcal{S}_j$  are found together on  $\mathcal{I}_p$ , but are both absent from  $\mathcal{I}_q$ , as in the sub-matrix *t*, where

$$t = \begin{matrix} & \mathcal{I}_p & \mathcal{I}_q \\ \mathcal{S}_i & \begin{bmatrix} ..1 & \dots & 0.. \\ \dots & \dots & \dots \end{bmatrix} \\ \mathcal{S}_j & \begin{bmatrix} ..1 & \dots & 0.. \end{bmatrix} \end{matrix}$$

Let  $T_{ij}$  be the number of such submatrices, when we take into account all those pairs of islands in which  $\mathcal{S}_i, \mathcal{S}_j$  are together on one island but both absent from the other. Further, let *T* be the mean number of such submatrices per species-pair. Given that there are  $N_s(N_s - 1)$  species-pairs, then

$$T = 2 \sum_{i < j} T_{ij} / N_s(N_s - 1).$$

Since *C* and *T* apparently reflect quite opposite behaviours of the species-pairs, it might seem plausible that a colonization pattern with a *T* higher than usual would have a *C* lower than usual. But this, however plausible, is flatly untrue, and the real relation between these quantities must be appreciated if they are to serve as analytical aids. In fact, in all matrices with the same row and

column constraints, the *C*-score and the *T*-score differ only by a fixed constant – i.e.,

$$C = T + \text{constant.}$$

This explains, for example, why the matrix *U* above, which has an excess of checkerboard patterns when compared to those expected on a null hypothesis of uncorrelated colonization choices, also has an excess of aggregation patterns, in which species share the same islands.

The identity itself is easy to prove:

First we need an expression for  $\sum S_{ij}$ , the total number of islands shared. A derivation originally given in Roberts and Stone 1990 is repeated here for convenience:

$$\begin{aligned} \sum_{i \neq j} S_{ij} &= \sum_{i,j} S_{ij} - \sum_i S_{ii} \\ &= \sum_{i,j} \sum_k a_{ik} a_{jk} - \sum_i r_i \\ &= \sum_k (\sum_i a_{ik}) (\sum_j a_{jk}) - N_T \\ &= \sum_k c_k^2 - N_T \end{aligned}$$

where island  $\mathcal{I}_k$  holds  $c_k$  out of the  $N_S$  species, species  $\mathcal{I}_i$  occurs on  $r_i$  islands, and  $\sum c_k = \sum r_k = N_T$  is the species-occurrence count totalled over all  $N_I$  islands.

To find  $C_{ij}$  and  $T_{ij}$ , we have to count the number of submatrices of the form, respectively,

$$\begin{matrix} \mathcal{I}_p & & \mathcal{I}_q \\ \mathcal{I}_i & \begin{bmatrix} 0 & \dots & 1 \dots \\ \dots & \dots & \dots \\ \dots & \dots & \dots \end{bmatrix} & \text{and} & \mathcal{I}_i & \begin{bmatrix} 1 & \dots & 0 \dots \\ \dots & \dots & \dots \\ \dots & \dots & \dots \end{bmatrix} \\ \mathcal{I}_j & \begin{bmatrix} 1 & \dots & 0 \dots \\ \dots & \dots & \dots \end{bmatrix} & & & \mathcal{I}_j & \begin{bmatrix} 1 & \dots & 0 \dots \\ \dots & \dots & \dots \end{bmatrix} \end{matrix}$$

and their partners with  $i, j$  exchanged, for all islands  $\mathcal{I}_p, \mathcal{I}_q$ . Now, the number of (11) columns is just  $S_{ij}$ , while the number with (10) is  $(r_i - S_{ij})$  and those with (01) is  $(r_j - S_{ij})$ ; this leaves  $(N_I + S_{ij} - r_i - r_j)$  as the number with (00). Thus

$$\begin{aligned} C_{ij} &= (r_i - S_{ij})(r_j - S_{ij}), \\ T_{ij} &= S_{ij}(N_I + S_{ij} - r_i - r_j). \end{aligned}$$

Subtracting:

$$C_{ij} - T_{ij} = r_i r_j - N_I S_{ij},$$

so that

$$\begin{aligned} N_S(N_S - 1)(C - T) &= \sum_{i \neq j} r_i r_j - N_I \sum_{i \neq j} S_{ij} \\ &= \sum_{i \neq j} r_i r_j - N_I \sum_k c_k^2 + N_I N_T. \end{aligned}$$

Since all the quantities in this equation save *C* and *T* are constant, we see that

$$C = T + \text{const.}$$

**Discussion**

*Alternative explanations for checkerboards*

It remains possible, of course, for a pattern of disjoint aggregations like those of *U* to be created by a competition process. As pointed out by Diamond and Marshall 1976, p. 722, some patterns of aggregation could be the result of a “well-matched set of related species, and possibly co-evolved local populations, that competitively exclude invaders for long times.” But we cannot ignore

the possibility that other processes are at work, involving no species interaction whatsoever – ones which, for example, directly force a high level of aggregation, so that an extreme checkerboardedness is created as a by-product, so to speak. For example:

a) Suppose there are two different colonization routes, so that species 1–10 colonise islands 1–10 while species 11–20 colonise islands 11–20. If we assume that each island has habitats suitable to its prospective colonists, and that inter-island dispersion can be neglected, then the incidence matrix *U* will result. In these circumstances, without the species having to compete or indeed interact in any way at all, the aggregation-score *T* is extremely high – and so too is the checkerboard score *C*.

This is no mere academic possibility. In the Vanuatu case, for example, Diamond and Marshall (1976) note that the avifauna are likely to have five different colonization routes. They also report that some species indeed lose their inter-island dispersal ability after invading an island.

b) Suppose islands 1–10 have suitable habitats only for species 1–10, while the remaining species, because of their habitat requirements, can survive only on islands 11–20. Again, in the complete absence of competitive processes, the incidence matrix *U*, with its extreme *C*-score, will result. Relevant here is the note by Diamond and Marshall (1976), that “certain specialised habitats are absent or scarce on many Vanuatu islands and occur extensively only on certain islands, generally larger islands...” (p. 712). This factor alone could well bring about unusual aggregation of species, and would arise independently of the species/area relationship or of competition.

*Exclusion or co-existence? – the Vanuatu avifauna*

All of this forms part of an old problem: will ecologically similar species competitively exclude one another, or tend rather to coexist and aggregate together? Directly relevant is the study by Williams (1951 p. 253) of East African bird communities. He concluded:

“(1) That biological competition between closely related species is probably on average greater than that between those less closely related.

(2) That closely related species are probably more suited to similar physical environments, and to similar extra-generic competition.

(3) That the balance of these two major factors, physical and biological, which determine the survival of species in different habitats, as shown by actual proportional survival in Nature, appears to indicate that the advantages of close relationship are on average greater than the drawbacks.”

den Boer (1980) drew on Williams’ work when he framed the coexistence principle: “Taxonomically closely related species are also ecologically closely related, and will thus be found coexisting in the same sites more frequently than could be expected by a random distribution of species...” (p. 300).

Table 1.

Species number	Family
1	Podicipedae
2 3	Ardeidae
4 5 6	Anatidae
7 8	Accipitridae
9	Falconidae
10	Megapodiidae
11 to 14	Rallidae
15 to 22	Columbidae
23 24	Psittacidae
25 26	Cuculidae
27	Tytonidae
28 29 30	Apodidae
31 32	Alcedinidae
33	Hirundinidae
34 35 36	Campiphagidae
37	Turdidae
38 39	Sylviidae
40 to 45	Muscicapidae
46	Pachycephalidae
47	Artamidae
48 49	Sturnidae
50 51 52	Meliphagidae
53 54	Zosteropidae
55 56	Ploceidae

To test this coexistence principle, we examined species-pairs amongst the Vanuatu avifauna that are ecologically similar. This would be best done by sorting them into ecological guilds, but since these have not as yet been delineated in Vanuatu, we examined all the sets of confamilial species. Now, as Gilpin and Diamond (1982) have pointed out, bird families do not necessarily coincide with ecological guilds, but it is difficult to classify these complex avifaunas in any more accurate way than that given by families (Graves and Gotelli 1983). We have taken the view of Graves and Gotelli who "do not believe families represent units of interspecific competition. However, species within a family are usually ecologically and morphologically similar; therefore non-randomness of island avifaunas may be detected at the family level" (page 331).

We took the 56 bird species listed in Diamond and Marshall (1976) and assigned them to families; the detailed assignments are given in Table 1.

On these assignments, 48 species had confamilial partners, these 48 being distributed over 16 different families. Out of the 1540 pairs of species, there are just 70 in which both members of the pair belong to the same family.

We then calculated the values of the statistics  $S$ ,  $T$ ,  $C$  described above, for these 70 pairs. For example, the  $S$ -score was calculated as

$$S_{fam} = \sum S_{ij} / 70,$$

the summation being taken over all 70 confamilial species pairs. The results were:

$$S_{fam}(\text{actual}) = 11.70, \quad C_{fam}(\text{actual}) = 5.64, \quad T_{fam}(\text{actual}) = 25.36.$$

Table 2.

Param.	Actual	Simuld	$\sigma(\text{simuld})$	$\Delta/\sigma$	Estimated probability
$S$	11.70	11.54	0.07	2.3	<0.001
$C$	5.64	7.29	0.82	2.0	0.001
$T$	25.36	21.96	1.32	2.6	0.004

Are these values of a size that we would expect even if the colonizing choices of two species were completely uncorrelated? To answer this question, we generated colonization patterns (incidence matrices) that were, overtly at least, free from any such correlations. For details of the generation method (interchanges) and the constraints it was made to obey, see Roberts and Stone 1990. This latter paper also discusses the controversy over whether the constraints incorporate competition effects, and the reason why it is irrelevant there (the *a fortiori* strategy).

For the 70 confamilial pairs only, in each pattern so generated we evaluated  $S$ ,  $C$  and  $T$  and then their arithmetic means for 1000 such patterns. The results are displayed in Table 2. The column headed  $\Delta/\sigma$  gives the number of S.D.'s in the difference  $\Delta = |\text{actual} - \text{simulated}|$ . As the sampling distribution of these quantities is unknown, a more transparent measure of significance is given by the column headed "Estimated probability", which simply states the rarity in the sample of 1000 of values as extreme as the actual value.

Since the randomness of this sampling has not been (and quite possibly cannot be) proved, it is desirable to check the exceptionality of the actual distributions by a different method. We therefore generated another sample by carrying out only a small number of swaps, but returning to the actual pattern as a starting point for each member of the sample. (For a fuller discussion of this check and its interpretation, see Roberts and Stone (1990).)

In a sample of 1000 thus obtained from the actual pattern by a sequence of 40 random swaps, the fractions of the simulation patterns having values of the statistics at least as extreme as the actual pattern were as follows:

$$S(\text{simulated}) \geq S(\text{actual}): 0.100$$

$$C(\text{simulated}) \leq C(\text{actual}): 0.092$$

$$T(\text{simulated}) \geq T(\text{actual}): 0.068.$$

The procedure used obtains the values of these statistics in a distribution very close to that actually observed, and repeats this for 1000 different directions in the space of matrices with the same row and column totals. The results indicate that the observed pattern occurs in a relatively small and highly exceptional volume of this phase space.

## Results

### *Interpretation of the Vanuatu results*

Before analysing these results, some explanatory remarks may be useful:

In a complete species assembly, subject to the three constraints on density and incidence, the mean value of  $S$  cannot vary from one pattern to another (in the present case, it remains fixed at 9.57, as proved in Roberts and Stone (1990). Moreover, as mentioned above,  $C$  and  $T$  can differ only by a constant. Thus a complete colonization pattern cannot show increased avoidance by some pairs (high “checkerboardedness”  $C$ ) unless it also shows increased aggregation by others (high “togetherness”  $T$ ).

But here we are not dealing with the whole species assembly and all the pair-relationships it contains, but only a subset of these pairs. Now the mean value of  $S$  can vary; moreover, there is no requirement on  $C$  and  $T$  to preserve a constant difference. (Both these effects stem from the same cause: in the simulations, an island has to accept a fixed number of species, but not a fixed number of *confamilial* species, so that the “column constraints” are absent when attention is confined to families.) We cannot conclude, for instance, that an exceptionally low observed  $C_{fam}$  implies an observed  $T_{fam}$  that is likewise exceptionally low. We must independently determine whether  $T_{fam}$ , measuring aggregations and sharing by confamilial species-pairs, is greater or less than that expected from random colonization.

With these points in mind, we return to the results given by the simulations. The most striking thing, probably, is what it tells us about the number of islands shared, on the average, by a confamilial pair, as given by the parameter  $S$ : in the first method used, not even one simulation pattern in the whole sample of 1000 showed as large a value of  $S$  as actually occurs. In other words, the occurrence of a species on an island is strongly and *positively* correlated with the presence of a confamilial species.

This finding is confirmed by the value found within families for the checkerboard score  $C$ , often and plausibly associated with competition (see Diamond (1975), Gilpin and Diamond (1982). We see from Table 2 that  $C$  is significantly less than what would be expected if settlements were uncorrelated. On the other hand, the  $T$ -score for “togetherness” within families is large, and exceeded by only four out of the 1000 simulation patterns.

These results, when taken together, make the Vanuatu data tend not to support the hypothesis of competitive exclusion, but to agree rather with the coexistence principle.

### Conclusion

In interpreting the results presented here, the imposed incidence constraints must be borne in mind. These constraints are controversial (Diamond and Gilpin 1982), and we have previously adopted them as part of an *a fortiori* strategy, accepting Connor and Simberloff's challenge to test for competition “in shaping co-occurrence patterns, over and above whatever role competition may play in determining how many species an island has or how many island an island occupies” (see Connor and Simberloff 1984).

However, the aim of this paper is somewhat different. Here we have presented a set of statistical tools which allow one to probe matrices more finely perhaps than other techniques allow. The  $S$ ,  $C$  and  $T$ -tests are in fact quite general and not necessarily confined to the study of column- and row-constrained incidence matrices. When applied to the Vanuatu avifauna, this approach has brought to light a number of complicating factors that might otherwise have gone unnoticed. In particular, any unusual degree of “checkerboardedness” within an incidence matrix was found to require careful analysis, and not to be taken too quickly as the signature of competition.

If we accept the null hypothesis put forward by Connor and Simberloff, the Vanuatu and Antilles data sets, when each is taken in its entirety, indicate significant levels of checkerboard patterns when analysed by the  $C$ -score test (Stone and Roberts 1990). If it were competition that was responsible for this, one would expect such patterns to be most easily observed amongst the confamilial species. However, in the Vanuatu avifauna, these ecologically similar species share more islands, show a significantly lower checkerboard score  $C$  and have a higher togetherness score  $T$ , than do their simulation counterparts. Thus the Vanuatu avifauna do not appear to display patterns associated with competition. More plausibly, the presence/absence matrix suggests the aggregation associated with the coexistence principle.

The information so disclosed may or may not be regarded as conclusive; but it is certainly relevant, suggestive and difficult to ignore. This seems to justify a methodological claim for the quantities  $S$ ,  $C$  and  $T$ : despite the fact that, over an entire colonization matrix,  $S$  and  $(C - T)$  must be constant, they can still provide useful information about the processes behind species distributions.

The crucial point here is that the scores can vary independently when attention is restricted to a subset of species, since then the row and column constraints built into the simulation process no longer apply. Above, the subsets examined were of confamilial species; this is only one type of application for these tools, and others are easily envisaged. For example, attraction towards similar habitats, a tendency for confamilial species to have followed the same colonization route, or have similar colonization abilities, may all be factors that come into play. Diamond and Marshall (1976, 1977) have demonstrated the importance of these processes for the Vanuatu avifauna.

Do the results obtained hinge critically upon the Connor and Simberloff null hypothesis and the constraints it imposes? We have since examined this important issue by using the  $S$ ,  $C$  and  $T$  scores in a way which is independent of these and indeed of any other constraints. The values of these statistics given by a set of confamilial species have been compared with those given by a set of nonfamilial species, the latter set being chosen as one with the same settlement pattern. (We say that two sets of species have the same settlement pattern if their arrays of island-settlement numbers are in one-to-one correspondence.) Such a test requires information from the

observed presence/absence matrix only and thus eliminates the need to construct a random ensemble of control matrices.

While the results obtained agree in their general drift with those reported here, they are less unambiguous and call for a more complicated analysis. There are interesting indications, for example, of a phenomenon also suggested by the findings of Schoener and Adler (1991) in examining the distribution of birds and lizards on the Bahamas: mutual avoidance becoming more manifest when higher-order interactions are examined. This work will be reported later.

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