Williams, C. B. 1951. Intra-generic competition as illustrated by Moreau's records of East African bird communities. *Journal of Animal Ecology.* 20 (2), pp. 246-253.

INTRA-GENERIC COMPETITION AS ILLUSTRATED BY MOREAU'S RECORDS OF EAST AFRICAN BIRD COMMUNITIES

By C. B. WILLIAMS
Rothamsted Experimental Station, Harpenden

In this *Journal* in 1947 (Williams, 1947) I brought forward evidence which seemed to support the idea that, among the factors affecting the survival of species in any animal or plant community, the advantages of close relationship, as indicated by belonging to the same genus, were of greater average importance than any associated drawbacks.

The argument developed was that if the frequency distribution of genera with different numbers of species is known for a larger area enclosing and including the smaller community under consideration, then it is possible to calculate how many genera should be represented in a random* sample of species from the larger area containing the same number of species as that found in the special community. If the species in the community are actually contained in this number of genera, then there is no statistical evidence that generic relationship has been associated with the survival of species in the community. If there are too many genera, then close generic relationship has been a drawback to survival. If, on the contrary, there are too few genera in the natural population, the generic relationship must on an average be advantageous.

Out of sixteen examples from the British Isles, eight for animals and eight for plants, that I gave in the paper quoted, all but one showed too few genera; one showed the same number; and no community showed more genera than would have been expected by chance.

My interpretation of these facts has been criticized chiefly by the statement that the communities or associations considered were too large and were capable of subdivision, so that the congeneric species were not really filling the same 'niche'. There is, however, no limit to which one can divide a habitat into niches or micro-climates, so that by making the niche small enough it is always possible to show that no two species, whether congeneric or not, can co-exist.

What my figures indicated was that as a larger and more complex community is split up into smaller and less complex communities, the number of congeneric species appears to increase above the expected rather than to decrease; or in other words the 'generic diversity' decreases. Once the size of the community has been reduced to a level when one would not, by chance, expect any congeneric species, then their absence cannot be used as an argument either *for* or *against* the idea of intra-generic competition.

In the above paper the measurement of generic diversity was based on the assumption (supported by evidence) that the frequency distribution of the number of genera with different numbers of species was in or close to the Logarithmic Series. Simpson (1949) showed that it is possible to calculate a simple measure of Diversity which is independent of any assumption about the mathematical expression of the frequency distribution.

Simpson argued that in any community consisting of a number of species (N) classified into genera the total number of different ways in which two species can be selected at random from the population is

$$N(N-1)/2;$$

while the number of ways in which 2 species can be selected belonging to the same genus is

$$\Sigma\, n(n-1)/2;$$

where the successive values of n are the number of species in each genus.

Thus the chances that 2 species selected at random should belong to the same genus are

$$\frac{\Sigma\, n(n-1)}{N(N-1)};\ \text{or 1 chance in } \frac{N(N-1)}{\Sigma\, n(n-1)}.$$

This latter figure is a measure of the 'Generic Diversity' of the population.

For example if a population consisted of 10 species with 1, 2, 3, 4 species in each of 4 genera then the number of possible pairs is $10 \times 9/2 = 45$, and the number of possible pairs belonging to the same genus is

$$\frac{(2\times 1)+(3\times 2)+(4\times 3)}{2}=10;$$

therefore the chance that 2 species selected at random would belong to the same genus is 10/45 or 2/9; and the Generic Diversity is 4·5.

In a recent volume of this *Journal*, R. E. Moreau (1948) has discussed the distribution of 172 species

* By 'random', in this connexion, is meant without respect to generic relationship.

of birds, belonging to 9 families of Passerines, in the Usambara Hills of north-east Tanganyika, with special reference to the occurrence of 2 or more species of the same genus co-existing in a single ecological association or community. He shows that there are a number of such cases, but that in many of them the related species have different habits which prevent them competing with each other: they occupy different 'niches' within the community.

While admitting the probable correctness of these explanations I think that it will be of value to study his data from a statistical point of view, because no attempt was made to show whether or not the number of such cases was larger or smaller than might be expected by chance; and also because Moreau's data, being the results of observations by a field ecologist who is familiar with his terrain and his birds, are likely to be as good as it is possible to get anywhere for such an analysis.

Moreau informs me that these 9 families were selected for particular study because they were the largest families which he considered that he knew adequately. Within these families all species and genera are listed so that there is no selection for generic size. He recognized 172 species of birds in 92 genera, and he subdivided his area into 32 different ecological types. The following are the numbers of genera with different numbers of species in the whole population:

Species/genus ...	1	2	3	4	5	6	7	8	9	10
No. of genera ...	51	24	10	2	—	3	1	—	—	1

The number of genera and species in each of the 9 families and subfamilies recognized by Moreau is shown at the foot of Table 2, where the names of the groups can also be found.

Table 1 shows the classification of Moreau's 32 ecological habitats; Table 2 shows the distribution

Table 1. *Moreau's classification of the ecological habitats*

1. Lowland (0–2500 ft.)	
(*a*) Rain forest	(1) Tree-tops
	(2) Mid-stratum
	(3) Ground-stratum
	(4) Edges
(*b*) Riverine forest	(1) Trees
	(2) Ground-stratum
(*c*) Wooded grassland	(1) Grass
	(2) Trees (deciduous)
	(3) Low semi-evergreen bush
	(4) Tall clumps, semi-green bush
(*d*) Semi-desert thorn country	(1) Trees and bushes
	(2) Ground, including woody herbage
	(3) Riverine strips
(*e*) Induced vegetation	(1) Trees and tall bushes
	(2) Dense low bush
	(3) Herbaceous cover
	(4) Scanty cover
(*f*) Swamp	
2. Intermediate level (2500–4500 ft.)	
(*a*) Rain forest	(1) Tree-tops
	(2) Mid-stratum
	(3) Ground-stratum
	(4) Edges
(*b*) Grassland	
(*c*) Induced vegetation	(1) East Usambara (humid)
	(2) West Usambara (semi-humid)
(*d*) Swamp	
3. Highland (4500–7500 ft.)	
(*a*) Rain forest	(1) Tree-tops
	(2) Mid-stratum
	(3) Ground-stratum
	(4) Edges
(*b*) Moorland	
(*c*) Induced vegetation	

Table 2. *Moreau's data on bird distribution in Usambara Hills, Tanganyika, rearranged to show number of species in different habitats*

Moreau's habitat no.	Capitonidae I	Pycnonotidae II	Muscicapidae III	Turdidae IV	Sylviidae V	Prionopidae and Laniidae VI	Nectariniidae VII	Ploceidae: Plocainae VIII	Ploceidae: Estrelidinae IX
1 a 1	$C_1 C_2 D E_2$	—	$A_2 F$	—	G_5	B_2	F_3	—	—
2	—	B_3	$J_1 L_1$	—	G_2	—	$E F_4$	A_1	—
3	—	$B_4 B_5$	—	$C G_2 M$	—	O	—	—	D
4	—	F G	$B F H M_1$	—	L	$G_1 L$	$F_1 F_6$	—	G H
b 1	A_2	—	—	—	—	—	—	—	—
2	—	$B_1 B_2 B_6$	K	—	—	—	—	—	—
c 1	—	A	—	—	$M_1 M_4 M_5 M_6$	—	—	—	$A_1 P$
2	$A_1 E_1$	—	$G_1 D J_2$	—	K_1	$B_1 K_1$	$A_1 C_1 D_2 D_4$	C	—
3	—	E	—	$K_1 K_2 L_1$	J_1	$F_3 H_2$	—	—	—
4	—	D	$G M_2$	$G_1 L_3$	—	G_1	—	—	—
d 1	B	—	$C_2 J_3$	—	$G_4 J_1 K_2$	$A C D E_2 G_2$	$D_2 F_5$	A_5	—
2	$F_2 F_3$	—	—	$A_2 D L_2$	$F G_6$	$F_1 N$	—	—	$C F M_2 N_2 Q$
3	—	—	—	K_2	—	—	A_2	$A_4 A_6 A_7 A_9$ $A_{10} D_1 D_2 E_1$ $E_2 E_3 F G_1$	M_3
e 1	—	A	$G M_2$	—	—	$G_3 M$	$C_1 D_1 F_1$	$A_6 A_7 A_9$	—
2	—	D	K	$G_1 K_1 K_2 L_3$	—	$F_3 H_2$	—	A_8	—
3	—	—	—	—	$M_1 M_4 N O P$	—	—	$D_1 D_2 G_2 E_1$ $E_2 E_4$	$A_1 P$
4	—	—	—	A_1	—	—	—	—	$K_2 N_1$
f	—	—	—	—	A C D	—	—	B	—
2 a 1	$C_1 C_2 D$	—	—	A_3	—	K_1	—	A_2	—
2	—	$B_3 C_3$	$J_1 L_2$	—	$B G_2$	—	$E F_4$	A_1	—
3	—	$B_4 B_5 B_7$	—	$B C H J_1 M$	$D_2 G_3$	O	—	—	D E
4	—	$C_2 F G$	$A_1 M_1 H$	—	H L	F_3	$F_1 F_2$	—	H
b	—	—	—	F	$C E M_6 O$	—	—	—	—
c 1	—	A	$A_1 E J_2$	G_1	$M_3 P$	$E_1 F_3 H_1 J$	$D_1 F_1$	$A_3 A_8 B$	$A_2 B L M$
2	F_1	—	D	G_1	$M_3 P$	$E_1 F_3$	C_2	$A_3 B$	$L M_1$
d	—	—	—	—	C E	—	—	B	—
3 a 1	$C_1 D$	—	—	A_3	—	K_1	—	A_2	—
2	—	$C_1 C_2$	L_2	—	$B G_2$	—	E	—	—
3	—	$B_4 B_5$	—	$B H J_1 J_2 M$	D_2	F_2	—	—	E
4	—	C_2	A_1	—	$D_1 G_1 H$	F_3	C_3	—	—
b	—	—	—	$F G_3$	D_1	—	$A_1 B$	—	—
c	—	—	E	$F G_3$	—	E_1	$A_1 B C_2$	A_3	$L M_1$
No. of genera	6	6	12	12	15	14	6	7	14
No. of species	11	15	18	20	28	21	17	21	21

Capital letters represent the genera in each family and the subscript numbers the species, if more than one in the genus, according to Moreau's system.

of the species, genera, and families among the habitats; and Table 3 shows the number of species, and the number of genera with 1, 2, 3, etc., species in each of the habitats. One or two misprints in the original tables have been corrected with the co-operation of Mr Moreau.

Table 3. *The number of genera with different numbers of species in each of the 32 habitats*

Habitat group	No. of species	No. of genera with 1 species	2 species	3 species	4 species	5 species	No. of genera
1 *a* 1	9	7	1	—	—	—	8
2	7	7	—	—	—	—	7
3	7	5	1	—	—	—	6
4	13	11	1	—	—	—	12
b 1	1	1	—	—	—	—	1
2	4	1	0	1	—	—	2
c 1	7	3	0	0	1	—	4
2	13	11	1	—	—	—	12
3	7	5	1	—	—	—	6
4	6	6	—	—	—	—	6
d 1	14	14	—	—	—	—	14
2	14	12	1	—	—	—	13
3	15	5	1	1	0	1	8
e 1	11	8	0	1	—	—	9
2	9	7	1	—	—	—	8
3	13	6	2	1	—	—	9
4	3	3	—	—	—	—	3
f	4	4	—	—	—	—	4
2 *a* 1	6	4	1	—	—	—	5
2	9	9	—	—	—	—	9
3	13	10	0	1	—	—	11
4	12	10	1	—	—	—	11
b	5	5	—	—	—	—	5
c 1	20	18	1	—	—	—	19
2	12	12	—	—	—	—	12
d	3	3	—	—	—	—	3
3 *a* 1	5	5	—	—	—	—	5
2	6	4	1	—	—	—	5
3	10	6	2	—	—	—	8
4	7	7	—	—	—	—	7
b	5	5	—	—	—	—	5
c	10	10	—	—	—	—	10
Total	280	224	16	5	1	1	247
Av. per habitat	8·75	7·00	0·50	0·16	0·03	0·03	7·72

Av. no. of species per genus per habitat = 1·132.

A preliminary study of the total population of 172 species in 92 genera and 9 family or subfamily divisions gives us the following information:

(1) The total number of ways in which 2 species can be selected from the 172, is $172 \times 171/2 = 14706$.

(2) The number of ways in which 2 species can be selected so as to belong to the same genus is

$$(24 \times 1) + (10 \times 3) + (2 \times 6) + (3 \times 15) + (1 \times 21) + (1 \times 45) = 177.$$

(3) The number of ways in which 2 species can be selected so as to belong to the same group (family or subfamily according to Moreau's grouping) is $\frac{1}{2}(11 \times 10 + 15 \times 14 + 18 \times 17 + 20 \times 19 \ldots) = 1647$: this of course includes the 177 cases where they are in the same genus. Thus of the 14706 ways in which 2 species can be selected at random from the original population:

- in 177 they will be in the same genus;
- in 1470 they will be in the same family but not in the same genus;
- in 1647 they will be in the same family, including the same genus;
- in 13059 they will not be in the same family.

Therefore a random selected pair will be:

- in the same genus once out of 83·1 selections;
- in the same family once out of 8·93 selections;
- not in the same family once out of 1·13 selections.

The numbers 83·1 and 8·93 are Simpson's measure of the Generic and Family Diversity.

It can easily be shown that:

for 3 species the chances that they will be congeneric are 233 out of 833,340 or 1 out of 3577;

for 4 species the chances they will be congeneric are 292 out of 35,208,615 or 1 out of 120,577;

and for 5 species, the chances that they will be congeneric are 1 in just over 3 million.

For an analysis of the frequency of genera with more than 1 species in a single habitat let us take as an example Moreau's habitat 1 *e* 3, which has 13 species in 9 genera, of which 2 genera have 2 species and 1 genus has 3. The 13 species contain $\frac{1}{2}(13 \times 12) = 78$ different pairs. Of these 2 pairs in the 2 genera with 2 species each, and 3 pairs in the genus with 3 species, are congeneric; i.e. a total of 5 out of 78 pairs are congeneric. We have, however, already seen that a random selection from the whole population only gives 1 congeneric pair in 83, so that this particular habitat has about five times as many congeneric pairs as would be expected by chance. For the same habitat the number of possible groups of 3 species is $(13 \times 12 \times 11)/(2 \times 3) = 286$; and the number of congeneric groups of 3 is 1 only, from the single genus containing 3 species. The expected frequency however (see above) is only 1 in 3577.

It is not desirable to argue from single cases, so Table 4 has been prepared to show similar analyses for each of the 32 habitats, for groups of 2, 3, 4 and 5 species, and giving at the bottom the total possible groups and the actual congeneric groups which are found in all the single habitats. The final results for the whole 32 habitats are as follows:

(1) Out of 1372 possible pairs of species selected at random within a habitat, 48 are congeneric. The number expected by random selection is $1372/83{\cdot}1 = 16{\cdot}5$.

(2) Out of 4829 possible groups of 3 species selected at random within a habitat, 19 are congeneric. The expected number by random selection is $4829/3577 = 1{\cdot}35$.

(3) Out of 13,427 possible groups of 4 species selected at random within a habitat, 6 are congeneric. The expected number is $13{,}427/120{,}577 = 0{\cdot}11$.

(4) Out of 30,713 possible groups of five species selected at random within a habitat 1 is a congeneric group. The expected number is 30,713/3 million = 0·01 of a genus.

Thus there are within the single habitat associations:

three times as many congeneric groups of 2 species,

fourteen times as many congeneric groups of 3 species,

fifty times as many congeneric groups of 4 species,

one hundred times as many congeneric groups of 5 species,

as would be expected in a similar set of species groups selected without reference to generic relations.

The same form of argument used above for species belonging to the same genus can be applied also to the relative frequency of species belonging to the same family. Out of the 14,706 ways of selecting 2 species at random there are 1647 pairs belonging to the same family. One would thus expect 1 random pair out of 8·93 to belong to the same family.

The total number of possible pairs within single habitats is 817 and the actual number of these pairs within the same family is 277. The expected number on random selection is 91·5. There are thus three times as many pairs of species of the same family within single habitats as would be expected by random selection from the total population of the whole area. Therefore not only has generic relationship some advantageous effect in determining the simultaneous survival of 2 species in a less complex animal association; but, in this particular set of data, the same also appears to be true of family relationship.

I have submitted the above analysis to Mr Moreau for his comments, and he replies that habitat 1 *d* 3 (lowland; semi-desert; riverine strips) was 'occupied during only that part of the year when food appears to be superabundant'. It is thus not so clear-cut as the others, and species may move in for feeding purposes only.

A high proportion of the congeneric species are found in this habitat. I am not sure that Moreau's statement makes it desirable to remove this habitat from consideration, as competition for food is one of the more definite types of interspecific competition. However, I have recalculated all the above figures relating to congeneric species, leaving out habitat 1 *d* 3.

In this habitat 7 species occur which are not mentioned in any other habitat. This reduces the total number of species in the area to 165 and reduces the size of several genera.

The following are the results:

I. *For pairs of species*

Whole fauna:

Total possible pairs 13,530

Congeneric pairs 153

Chance of a random pair being congeneric is 1 in 88·4

Single habitats:

Total possible pairs 1267

Congeneric pairs 33

or 1 congeneric pair in 38

This is 2·3 times as many as expected.

Table 4. *The number of species of birds in each of Moreau's 32 habitats—together with the number of different groups of 2, 3, 4 and 5 species which it is possible to select within each habitat, and the actual number of these groups that would be congeneric*

Habitat	No. of species	Pair of species		Three species		Four species		Five species	
		Possible	Congeneric	Possible	Congeneric	Possible	Congeneric	Possible	Congeneric
1 *a* 1	9	36	1	84	0	126	0	126	0
2	7	21	0	35	0	35	0	21	0
3	7	21	1	35	0	35	0	21	0
4	13	78	1	286	0	715	0	1,287	0
b 1	1	0	0	0	0	0	0	0	0
2	4	6	3	4	1	1	0	0	0
c 1	7	21	6	35	4	35	1	21	0
2	13	78	1	286	0	715	0	1,287	0
3	7	21	1	35	0	35	0	21	0
4	6	15	0	20	0	15	0	6	0
d 1	14	91	0	364	0	1,001	0	2,002	0
2	14	91	1	364	0	1,001	0	2,002	0
3	15	105	15	455	11	1,356	5	3,003	1
e 1	11	55	3	165	1	330	0	462	0
2	9	36	1	84	0	126	0	126	0
3	13	78	5	286	1	715	0	1,287	0
4	3	3	0	1	0	0	0	0	0
f	4	6	0	4	0	1	0	0	0
2 *a* 1	6	15	1	20	0	15	0	6	0
2	9	36	0	84	0	126	0	126	0
3	13	78	3	286	1	715	0	1,287	0
4	12	66	1	220	0	495	0	792	0
b	5	10	0	10	0	5	0	1	0
c 1	20	190	1	1,140	0	4,845	0	15,504	0
2	12	66	0	220	0	495	0	792	0
d	3	3	0	1	0	0	0	0	0
3 *a* 1	5	10	0	10	0	5	0	1	0
2	6	15	1	20	0	15	0	6	0
3	10	45	2	120	0	210	0	252	0
4	7	21	0	35	0	35	0	21	0
b	5	10	0	10	0	5	0	1	0
c	10	45	0	120	0	210	0	252	0
Total		1,372	48	4,829	19	13,427	6	30,713	1

II. *For groups of* 3 *species*

Whole fauna:
Total possible threes 735,130
Congeneric threes 165
or 1 in 4460
Single habitats:
Possible threes 4374
Congeneric threes 8
or 1 in 547
This is eight times the expected frequency.

III. *For groups for* 4 *species*

Whole fauna:
Possible fours 29,772,765
Congeneric fours 151
or 1 in 197,171
Single habitats:
Possible fours 12,071
Congeneric fours 1
This is fifteen times the expected frequency.

Thus the effect of eliminating habitat 1 *d* 3 is to reduce the extent of the steady increase of observed over expected groups of congeneric species; but the same direction of increase remains, with no suggestion of any effect in the opposite direction.

DISCUSSION

It would appear from the above that when the bird populations of different ecological habitats, as defined by a competent field ornithologist, are studied, and when these habitats are sufficiently restricted so as to contain from 1 to 20 species with an average of less than 9, the statistical analysis of the relative numbers of species in different genera shows a definite excess of congeneric groups with 2 or more species above what would be expected by selection without reference to generic relations; and further that this excess seems to increase as the number of congeneric species increases.

When I brought forward somewhat similar evidence in 1947 for populations of insects and plants in the British Isles, the evidence was criticized by saying that the areas taken were too large and too complex, and within each there were many different habitats. While this is true of some of the areas previously considered, e.g. Wicken Fen or Windsor Forest—it is not true of some others—e.g. single plots on Park Grass Experimental Field at Rothamsted. But in any case the object was not to select absolutely simple environments (if, indeed, such things exist) but to select in pairs a more simple and a less simple area, the latter including the former, and to show that decreased ecological complexity was associated with decreased, and not with increased, generic diversity.

It appears to be established from the British evidence already discussed, and the above new evidence from East African birds, that within the limits of the evidence there are more congeneric groups in the simpler association than would be expected by random sampling from the larger fauna and flora of the surrounding area.

The average number of species in these bird associations is less than 9, and the number of expected pairs of congeneric species is only 1 in 83 pairs; so that it is not usually possible to demonstrate a difference from the expected in a single habitat. When, however, the results of all the 32 habitats are put together the result is overwhelmingly in support of less generic diversity in the simpler habitats.

If one accepts the usual view that closely related (congeneric) species compete so seriously with each other that it is not possible, or at least difficult, for them to co-exist in a single habitat, it is obvious that such habitats must be still smaller or simpler than those we have discussed, and with still fewer species,—in fact probably what are often called 'niches'.

It is also obvious, however, that the fewer the species there are in an association, the less chance there is of finding two congeneric species, even by chance and not by biological causes. How, then, is it possible to demonstrate that such competition is taking place. If a habitat contained say 4 species each in its own genus, and if (as is very probable) it could be shown that without any biological competition one would have expected such a result, how is it possible to demonstrate that there are more genera than would be expected? Only, it would seem, by having the 4 species in 5 genera!

The position at present is that down to the limits of about 9 species per habitat it is still possible to show that there is on an average an excess of congeneric species; that is to say too few genera—or a lower generic diversity than would be expected by random sampling. The upholders of the intra-generic competition theory believe that beyond this point there is a sudden reversal. But much beyond this point it does not appear to be possible to use the data of number of species and numbers of genera in small habitats to prove or disprove any continuation or reversal of the process of decreasing generic diversity.

What data then can be brought forward for analysis? Since up to the limits of present analysis there is no evidence of reversal it is surely the business of the supporters of the theory of intra-generic competition to produce evidence which supports it and shows statistically significant departures from the expected. I see at present no reason to alter my provisional explanation given in 1947, namely:

(1) That biological competition between closely related species is probably on an 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.

REFERENCES

Moreau, R. E. (1948). 'Ecological isolation in a rich tropical avifauna.' J. Anim. Ecol. 17: 113–26.

Simpson, E. H. (1949). 'Measurement of Diversity.' Nature, Lond., 163: 688.

Williams, C. B. (1947). 'The generic relations of species in small ecological communities.' J. Anim. Ecol. 16: 11–18.